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Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*)

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Atlantic bluefin tuna are a symbol of both the conflict between preservationist and utilitarian views of top ocean predators, and the struggle to reach international consensus on the management of migratory species. Currently, Atlantic bluefin tuna are managed as an early-maturing eastern stock, which spawns in the Mediterranean Sea, and a late-maturing western stock, which spawns in the Gulf of Mexico. However, electronic tagging studies show that many bluefin tuna, assumed to be of a mature size, do not visit either spawning ground during the spawning season. Whether these fish are spawning in an alternate location, skip-spawning, or not spawning until an older age affects how vulnerable this species is to anthropogenic stressors including exploitation. We use larval collections to demonstrate a bluefin tuna spawning ground in the Slope Sea, between the Gulf Stream and northeast United States continental shelf. We contend that western Atlantic bluefin tuna have a differential spawning migration, with larger individuals spawning in the Gulf of Mexico, and smaller individuals spawning in the Slope Sea. The current life history model, which assumes only Gulf of Mexico spawning, overestimates age at maturity for the western stock. Furthermore, individual tuna occupy both the Slope Sea and Mediterranean Sea in separate years, contrary to the prevailing view that individuals exhibit complete spawning-site fidelity. Overall, this complexity of spawning migrations questions whether there is complete independence in the dynamics of eastern and western Atlantic bluefin tuna and leads to lower estimates of the vulnerability of this species to exploitation and other anthropogenic stressors.

ichthyoplankton | Scombridae | large pelagic fish | pop-up satellite archival tag | population structure

Long-distance migrations pose a unique challenge to fisheries management, as conservation actions taken on a regional scale can be undermined if less stringent measures are implemented across other parts of the migratory pathway. Few species exemplify this problem better than Atlantic bluefin tuna (*Thunnus thynnus*). This species is harvested by the fisheries of over 20 nations, from the tropics to subarctic and coastal to international waters. Contentious international disputes have persisted for decades over how many bluefin tuna to harvest and how to allocate catch among nations. By the start of the 21st century, intense fishing pressure had driven this species to historically low population levels, a decline that has since reversed as fishing mortality has decreased under stricter management (1). However, despite this recent positive trend, many challenges remain in developing an ecologically sustainable fishery for bluefin tuna that also provides economic and social benefits to the fishing communities throughout its range. Among the most prominent of these challenges is the need for stock assessment models and management regulations that better account for the complex movements of this species.

The movements of Atlantic bluefin tuna are among the best documented of any highly migratory species, but how to interpret these migrations within the broader context of life history and population structure remains controversial. Currently, Atlantic bluefin tuna are assessed by the International Commission for the Conservation of Atlantic Tunas as an eastern stock, which spawns in the Mediterranean Sea, and a western stock, which spawns in the Gulf of Mexico. Based on sampling on these two spawning grounds, the eastern bluefin tuna stock assessment uses an age at 50% maturity of 4 y and the western bluefin tuna stock assessment uses a "knife-edge" age at maturity (i.e., all fish reach maturity at the same age) of 9 y. Electronic tagging shows that many bluefin tuna much older than these estimated ages at maturity do not occupy either known spawning ground during the spawning season (2–5). This contradiction has been attributed to fish not maturing until an older age than assumed in the assessment (age at 50% maturity: eastern fish, 6–10 y; western fish, 14–16 y) or not spawning every year (6–8). Alternatively, energetic and life history modeling (9), reproductive studies (10–12), and analyses of tag data (3, 4) provide evidence for undocumented spawning grounds, and an age at 50% maturity of 4–5 y throughout the Atlantic. These two depictions of bluefin tuna life history have vastly different implications for management. The documentation

Significance

We present unequivocal evidence that Atlantic bluefin tuna spawn in the Slope Sea, counter to the current assumption that the Gulf of Mexico and Mediterranean Sea are the exclusive spawning grounds. We also demonstrate that age at maturity of western bluefin tuna is currently overestimated, that this stock exhibits size-structured spawning migrations, and that migratory connections exist between western and eastern Atlantic spawning grounds. Atlantic bluefin tuna support a highly contentious international fishery, and our results present an alternate life history model to inform the management of this species. The implications of our work are most pronounced for western Atlantic bluefin tuna, which have a life history less vulnerable to overexploitation and extinction than is currently estimated.

ECOLOGY

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of an additional spawning ground would require that bluefin tuna population structure be reevaluated, possibly leading to different conclusions concerning the suitability of proposed and implemented spatial management strategies. Additionally, populations that mature late and spawn in restricted areas are considered more vulnerable to overexploitation and environmental change than earlier maturing populations with broader spawning distributions (13, 14).

Over 40 y ago, an area named the Slope Sea, north of the Gulf Stream and south of the northeast US continental shelf (15), was suggested to be an Atlantic bluefin tuna spawning ground (10, 16). The primary support for this hypothesis came from an exploratory longline cruise in this area from June to July 1957 that found bluefin tuna in spawning condition (10, 17). Recent reproductive studies on adjacent foraging grounds in the Gulf of Maine (11, 12), electronic tagging data analyses (2, 4), and energetic modeling studies (9) provided further circumstantial evidence for spawning in this area. However, targeted surveys for bluefin tuna larvae in the Slope Sea were never performed, and most research over the past few decades has dismissed the idea that substantial levels of spawning occur in the western Atlantic outside of the Gulf of Mexico. Here, we use opportunistic ichthyoplankton sampling to present unequivocal evidence that the Slope Sea is an important bluefin tuna spawning ground. We then use this information, coupled with electronic tagging, to reinterpret the life history, migration pathways, and population structure of Atlantic bluefin tuna.

Results and Discussion

We found larval bluefin tuna in the Slope Sea demonstrating an additional western Atlantic spawning ground (Fig. 1*A*). A total of 67 bluefin tuna larvae was collected during sampling from June 23 to August 9, 2013, across a broad area of the western Slope Sea (Fig. 1*B* and Tables S1 and S2). Diagnostic morphological characters were used to identify each of these larvae to species, with the identity of 18 larvae, including 10 fixed in formalin, verified using genetic sequencing (Fig. 1 *C* and *D*, and Figs. S1 and S2; details are given in *SI Text*). Sequence from one additional larva, identified morphologically as a bluefin tuna, was consistent with albacore (*Thunnus alalunga*). This larva was not necessarily misidentified, as ~3% of bluefin tuna from the Mediterranean Sea contain introgressed albacore mitochondrial DNA (7).

Nearly all larvae collected in the Slope Sea were unequivocally spawned in the Slope Sea, rather than being transported into the area from the Gulf of Mexico. Larval sizes and published growth rates (18) indicate that about 40% of the larvae were spawned in July when adult bluefin tuna are not present in the Gulf of Mexico (6). Additionally, >60% of the larvae were ≤3.0-mm standard length (SL), and were thus spawned within 6 d of collection (18). Based on an analysis of satellite-tracked drifters (details are given in *SI Text*), the minimum transport time from the easternmost point in the Gulf of Mexico to the southernmost latitude of the Slope Sea is 10.5 d, with less than 25% of drifters covering this distance in fewer than 20 d (Fig. S3).

Our results indicate that the length and age at maturity for western Atlantic bluefin tuna has long been overestimated due to an incomplete understanding of the full distribution of spawning. Currently, a knife-edge maturity of 190-cm fork length (FL) (age, 9) is used in the assessment based on the smallest mature individual found in the Gulf of Mexico. Electronic tagging data shows that larger fish undertake extensive annual migrations between the Gulf of Mexico in the winter and spring and Atlantic Canada in the summer and fall, whereas smaller fish undertake shorter migrations between the North Sargasso Sea and the northeast United States continental shelf (Fig. 2 *A*–*C*). Only the largest individuals migrate into the Gulf of Mexico, with just 50% doing so by 240-cm FL (age, 15) (Fig. 2*D*). Potential Slope Sea spawners were classified as those fish that spent ≥20 d in the Slope Sea from June 1 to August 15; 20 d was chosen based on estimates of bluefin tuna spawning duration (8, 19). Over 75% of individuals 133- to 212-cm FL (age, 5–11) were classified as potential Slope Sea spawners (Fig. 2*D*). The difference in tuna size structure on the two spawning grounds during the spawning season is also evident in longline catch data (Fig. S4).

Our assertion of a younger age at maturity for western Atlantic bluefin tuna is supported by three additional lines of evidence. First, endocrine measurements indicated that all >131-cm FL (age, 5) fish caught in the Gulf of Maine, an area adjacent to the Slope Sea, were mature (11). Second, microscopic examination of gonads sampled in the Gulf of Maine found that females 185- to 235-cm FL (age, 9–14) had atretic follicles in June and July, indicative of recent and proximate spawning, whereas fish >235-cm FL (age, 15+) had primary-stage oocytes indicative of earlier and

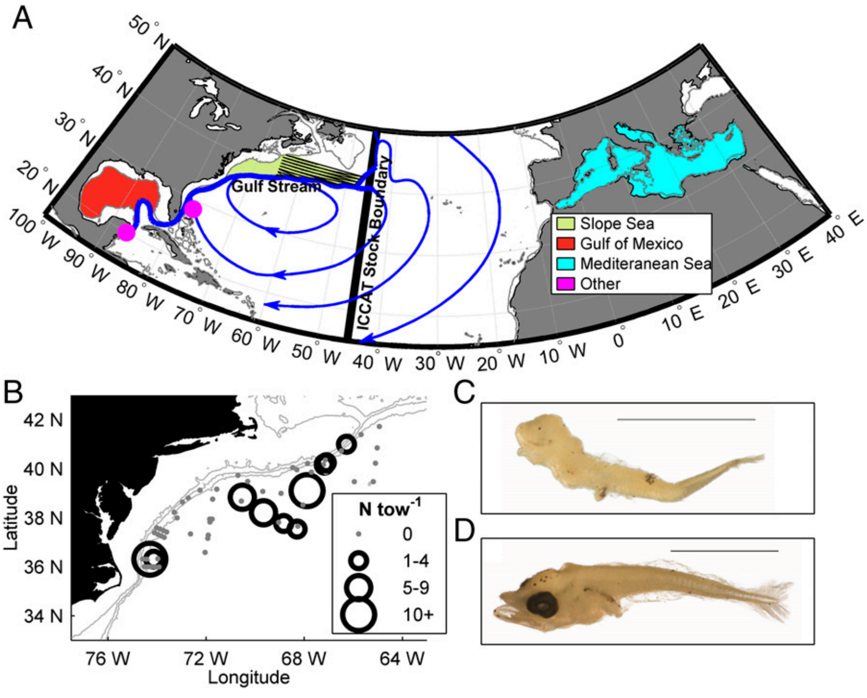

Fig. 1. Distribution of Atlantic bluefin tuna spawning and larvae. (*A*) Known spawning regions in the Gulf of Mexico, Mediterranean Sea, and Slope Sea. Hatched area of the Slope Sea was not sampled. A few larvae have also been collected in the Yucatan Channel and Blake Plateau (22, 23). Blue arrows indicate general circulation patterns. (*B*) Collection locations of larvae in 2013. (*C* and *D*) Genetically identified formalin-fixed bluefin tuna larvae collected in the Slope Sea. (*C*) GU1302-Station 141-Fish 3; 2.3-mm SL; GenBank accession no. KT285186. (*D*) HB1303-Station 084-Fish 2; 3.9-mm SL; GenBank accession no. KT285188. (Scale bars: *C* and *D*, 1 mm.) Background debris has been digitally removed from images.

more distant spawning; fish <185-cm FL were not sampled (12). Third, a June to July 1957 exploratory longline survey in the Slope Sea found that bluefin tuna 95- to 123-cm FL (age, 3–4) were immature, 121- to 220-cm FL (age, 4–12) had developing to running-ripe gonads, and >220-cm FL were mostly spent (10, 17). Although updated reproductive studies directly on the Slope Sea spawning ground are clearly needed, the available evidence indicates that the western stock matures around 120- to 140-cm FL (age, 4–5), and exhibits size-structured spawning migrations, consistent with the maturity schedule for eastern Atlantic bluefin tuna and evidence for size-structured spawning grounds in Pacific bluefin tuna (*Thunnus orientalis*) (20).

Our findings indicate that the majority of western Atlantic bluefin tuna spawning occurs outside of the Gulf of Mexico, rather than being restricted exclusively to the Gulf of Mexico. Spawning biomass per recruit was calculated at different ages at maturity and rates of fishing mortality and was then partitioned into Gulf of Mexico and non-Gulf of Mexico spawners using estimates of the proportion of Gulf of Mexico migration at age (Fig. 2*D*). Only 32% [95% confidence interval (CI): 22–41%] of spawning is estimated to occur in the Gulf of Mexico, assuming recent fishing mortality (1) and maturity at age 5 (Fig. 3*A*). Higher fishing mortality causes age truncation and a lower proportion of spawning in the Gulf of Mexico. For most combinations of fishing mortality and maturity, <50% of egg production is estimated to occur in the Gulf of Mexico (Fig. 3*B*), a conclusion that generally holds even if larger individuals spawn proportionately more eggs by weight than smaller individuals (Table S3). Larval data further support the conclusion that a majority of spawning occurs outside of the Gulf of Mexico. The sampled number of bluefin tuna larvae in 2013 in the western Slope Sea (0.74 tow^{-1} over a 275,000-km^2 area) is 20% higher than the decadal average from the Gulf of Mexico (0.48 tow^{-1} over a 350,000-km^2 area) (18, 21), and a factor of 7 and a factor of 20 higher than the numbers collected north of the Bahamas (22) and in the Yucatan Channel, respectively (23) (Fig. 3*C*). Notably, the opportunistic nature of our Slope Sea sampling likely leads to conservative estimates of larval bluefin tuna abundance, as the sampling area was constrained to west of 65° W, and a disproportionate number of stations occurred along the continental shelf edge where larval abundance was low. These limitations, along with inherent uncertainty in evaluating just a single year of data, can be overcome by a directed larval sampling effort in the Slope Sea.

Both the Gulf of Mexico and Slope Sea spawning grounds occur in similar oceanographic regimes. Both areas are on the northern side of the north Atlantic western boundary current, termed the Loop Current and Gulf Stream in the two respective regions (Fig. S5). Anticyclonic warm core rings and other mesoscale and submesoscale oceanographic features are common to both areas (15,

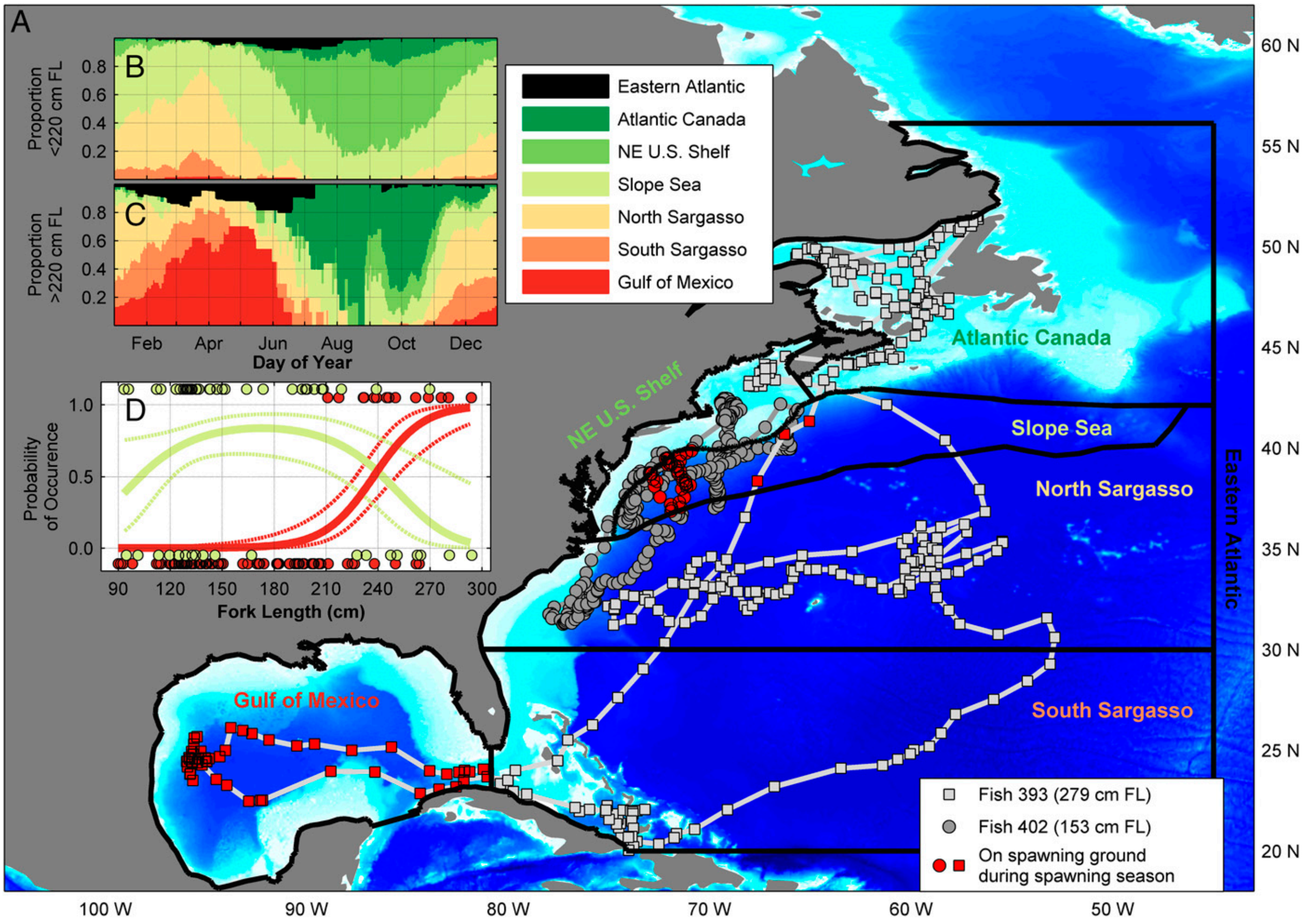

Fig. 2. Size-structured spawning and feeding migrations of bluefin tuna in the western Atlantic Ocean. (*A*) Representative 1-y tracks of one giant (279-cm FL) and one medium (153-cm FL) bluefin tuna. (*B* and *C*) Proportion of track position by day of year in seven regions of the North Atlantic for all tagged fish within a size class. (*B*) Bluefin tuna <220-cm FL (n = 212). (*C*) Bluefin tuna >220-cm FL (n = 104). (*D*) Probability of occurrence, by length, of electronically tagged bluefin tuna in the Gulf of Mexico (red) and Slope Sea (green) spawning grounds during the respective spawning seasons. The classification of individual fish as potential Gulf of Mexico and Slope Sea spawners are presented on the upper (yes) and lower (no) axes. First-degree and second-degree polynomial logistic functions (±95% CI) were fit for the Gulf of Mexico ($P = 1/[1+\exp[-[b_0+b_1L]]]$; $b_0 = -15.6$, $b_1 = 0.0652$) and Slope Sea ($P = 1/[1+\exp[-[b_0+b_1L+b_2L^2]]]$; $b_0 = -8.29$, $b_1 = 0.115$, $b_2 = -3.32*10^{-4}$), respectively.

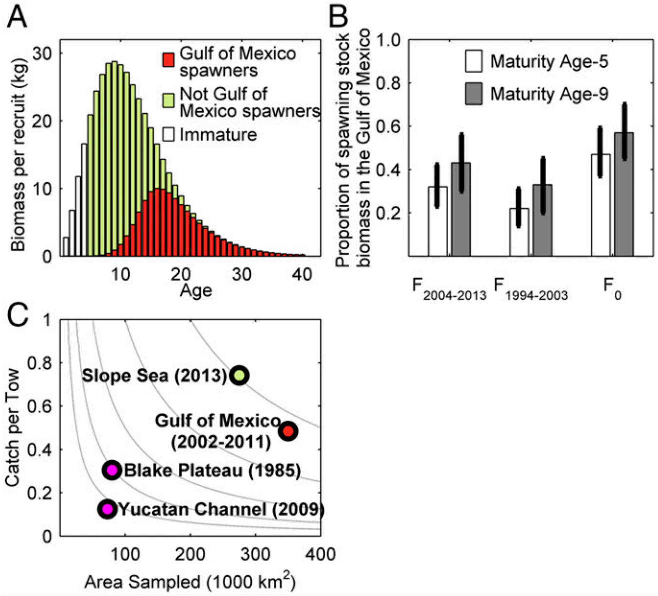

Fig. 3. Estimated proportion of western Atlantic spawning that occurs in the Gulf of Mexico. (*A*) Relative biomass of Gulf of Mexico spawners using the 2004–2013 average estimated fishing mortality rate and the age pattern of Gulf of Mexico migration (Fig. 2*D*). (*B*) Sensitivity of the proportion of Gulf of Mexico spawning to different ages at maturity and levels of fishing mortality (medium: 2004–2013; high: 1994–2003; F_0: no fishing). CIs (95%) are based on the uncertainty in the proportion at age migrating to the Gulf of Mexico. (*C*) Relative total larval abundance (a product of N tow^{-1} and area sampled), in the Gulf of Mexico (2002–2011) (21), the western Slope Sea (2013), the Yucatan Channel (2009) (23), and the Blake Plateau (1985) (22). Each contour line represents a doubling of total larval abundance. All sampling used the same protocol.

24), and these features are hypothesized to enhance larval survival (25). The optimal 23–28 °C temperature for bluefin tuna spawning (24) occurs about 2 mo later in the Slope Sea versus the Gulf of Mexico, and the differences in timing of spawning are consistent with the difference in timing of optimal temperature (Fig. 4).

Size-structured migrations, a type of differential migration, are common in the animal kingdom (13), but the partitioning of both spawning and feeding areas is comparatively rare and less well explored. The ability of larger fish to swim faster and at less relative energetic cost than smaller fish (9, 13), provides larger fish more flexibility in spawning location choice, but on its own does not explain if and how these fish benefit from spawning in the Gulf of Mexico rather than the Slope Sea. One possibility is that large fish are able to arrive at northern feeding grounds earlier in the summer (10) by taking advantage of their fast swimming speed and the 2-mo difference in the timing of optimal spawning temperatures between regions (Fig. 4). Alternatively, the Gulf of Mexico may provide better feeding or reduced predation for larvae, or the earlier spawning time may allow juveniles to achieve a larger size at the end of the first year, factors that may increase survival through the early life stages.

The discovery of the Slope Sea spawning ground requires a reevaluation of the nature and levels of mixing between the eastern and western Atlantic stocks. Otolith stable isotopes have indicated that bluefin tuna exhibit high levels of natal homing to eastern or western Atlantic spawning grounds (26), a conclusion generally supported by genetic analyses of fish from the Mediterranean Sea and Gulf of Mexico (7). The absence of tagged fish moving between the Gulf of Mexico and Mediterranean Sea has also previously been used to support the hypothesis of complete reproductive isolation between the two stocks (5, 7). However, some ~200-cm FL fish have migrated to the Mediterranean Sea after an extended period of western Atlantic residency. These fish exhibited the same seasonal migration as similar-size fish in our study (Fig. 2*B*), including the occupation of the Slope Sea during the spawning season (2, 5, 27). These migratory tracks suggest that reproductive mixing between the eastern and western stocks may occur in the Slope Sea and that the population structure of bluefin tuna may be more complex than is currently depicted (4, 28). To fully evaluate bluefin tuna population structure, biological samples from spawning fish and larvae collected in the Slope Sea need to be included in future analyses.

Our results have four important implications for the assessment and management of Atlantic bluefin tuna. First, the western Atlantic bluefin tuna stock assessment should use a younger age at maturity (11). Lowering the age at maturity will increase estimates of spawning stock biomass and will likely lead to higher estimates of sustainable fishing mortality rates (14, 29, 30). Second, analyses of the vulnerability of Atlantic bluefin tuna to climate change (31), the *Deepwater Horizon* oil spill (32), as well as the location of fishery closures to protect spawning fish, assume that the Gulf of Mexico and Mediterranean Sea are the only spawning grounds. These quantitative analyses and decisions need to be revisited. On a conceptual level, a diversity of migration strategies exposes a population to a variety of environmental conditions, and should confer added long-term stability in the face of climate and ecosystem variability (13). Third, the level and size selectivity of fishing mortality drives the ratio of spawning in the Gulf of Mexico versus the Slope Sea. Determining the relative quality of these two regions as nursery habitat is important for understanding long-term recruitment variability. Fourth, estimates of the nature and extent of mixing from tagging data need to be reevaluated to account for Slope Sea spawning. Spatially explicit population models show that changes in the distribution of catch can help achieve management goals, assuming levels of mixing in different areas of the ocean are known (33).

Overall, the discovery of a bluefin tuna spawning ground highlights the need to further integrate traditional shipboard sampling with electronic tagging studies in testing many of the long-held assumptions that underlie the management of this iconic species. Two priorities for field studies on the Slope Sea spawning ground are to evaluate how consistent the 2013 distribution and abundance of larvae is in additional years, and to refine information on the reproductive status of different size classes of fish. More broadly, this work reveals how limited plankton sampling has been in the open ocean, and of this sampling, how little has been analyzed with the taxonomic expertise necessary to resolve spawning by economically valuable fishes. The possibility that there are additional undocumented bluefin tuna spawning grounds should continue to be evaluated.

Methods

Ichthyoplankton Sampling. Two National Oceanic and Atmospheric Administration (NOAA) Northeast Fisheries Science Center (NEFSC) cruises sampled ichthyoplankton in the Slope Sea in 2013. From June 9 to June 24, 2013, an

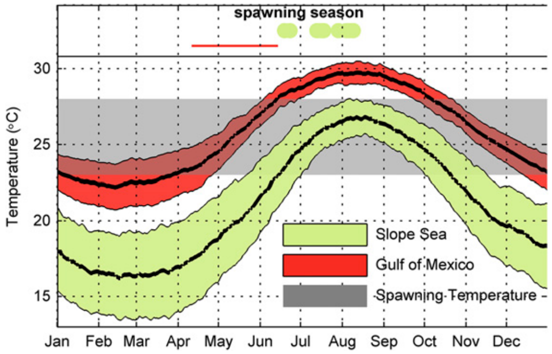

Fig. 4. Mean (±SD) SST cycles across the bluefin tuna spawning grounds in the northern Gulf of Mexico and southwestern Slope Sea. Spawning temperatures (23–28 °C) for bluefin tuna are denoted in gray. The reported timing of spawning is based on available larval collections in the Gulf of Mexico (24) and Slope Sea.

Ecosystem Monitoring (ECOMON) cruise on the NOAA Ship *Gordon Gunter* (GU1302) sampled the northeast US continental shelf using a random stratified design (34). Four offshore transects into the Slope Sea from June 21 to June 23, 2013, were added to this cruise. The second cruise occurred from July 1 to August 18, 2013, on the NOAA Ship Henry B. Bigelow (HB1303). This cruise was part of the Atlantic Marine Assessment Program for Protected Species (AMAPPS), which evaluates the abundance and distribution of marine mammals, seabirds, and sea turtles. Plankton sampling on HB1303 was scheduled around the visual surveys for protected species. For our study, we only considered stations offshore of the 1,000-m isobaths on both cruises; these stations occur outside of the area on the continental shelf and shelf break that is typically sampled by the NEFSC.

Plankton was sampled at most stations with a double-oblique tow of a 61-cm-diameter bongo net equipped with 333-μm mesh nets on each side of the frame (34). The net was deployed to 200-m depth at stations off the continental shelf. The ship's speed through the water during the plankton tows was ∼1.5 kn (2.8 km/h), and 300–400 m^3 of water was filtered for tows to 200 m. A 1-m^2 multiple opening/closing net and environmental sampling system (MOCNESS) was deployed at additional stations during the HB1303 cruise. Details of ichthyoplankton sample processing, morphological and molecular approaches to larval bluefin tuna identification, and full station data and larval bluefin tuna counts and measurements (Tables S1 and S2) are available in *SI Text*.

Oceanographic Data. In situ oceanographic data were collected with a Seabird Electronics SBE Model 19+ V2 profiling CTD (conductivity, temperature, depth) attached above the bongo net, or directly by the MOCNESS sensors (Table S1). All data collected by the CTD have been uploaded to the National Oceanographic Data Center (https://www.nodc.noaa.gov/) and can also be accessed at the NEFSC ftp site (ftp://ftp.nefsc.noaa.gov/pub/hydro/). Seasonal cycles of sea surface temperature (SST) for the Slope Sea and Gulf of Mexico spawning grounds were developed using the NOAA 1/4° daily optimal interpolation SST (OISST) data (https://www.ncdc.noaa.gov/oisst) (35) from 1982 to 2014 in the areas of high larval abundance in the southwestern Slope Sea (south of 38.5°N and west of 65°W; north of the mean Gulf Stream position) and the northern Gulf of Mexico (26–28°N, 95–85°W).

Electronic Tag Deployment and Data Processing. Electronic tagging of Atlantic bluefin tuna was conducted from 2002 to 2014, with >90% of tags deployed during the months of July to November. Full details of different tagging campaigns, tagging protocols, and tag functionality are described elsewhere (3, 4, 36, 37). The majority of the deployed tags were pop-up satellite archival tags (PSATs), which are designed to release from fish after a predetermined length of time and transmit data via satellite [Microwave Telemetry, Inc., models PTT-100 (n = 348) and X-Tag (n = 219); and Wildlife Computers models Mk10 (n = 10) and MiniPAT (n = 19)]. Most PSATs were programmed for 1-y deployments. Additionally, 132 implanted archival tags were deployed [Wildlife Computers MK-9 (n = 20); Lotek LTD 2310 (n = 82) and LTD 2350 (n = 30)]. This tagging approach requires the recapture of the fish and the return of the tag. Four archival tags were recovered.

Position estimates from electronic tags use light-based geolocation that require measurements of day length and time of sunrise and sunset. Position estimates were refined using a state-space Kalman filter that also incorporates SST and depth (4, 38–40). Geolocation analysis was carried out using the R statistical software, except for tagging years 2002–2006, which were completed by Collecte Localization Satellites (CLS) using proprietary software.

Electronic Tagging Analysis. We characterized the annual migrations patterns of two size classes (>220- and ≤220-cm FL) of bluefin tuna using electronic tagging data. Tag locations were assigned to one of six regions in the western Atlantic or a seventh region encompassing the eastern Atlantic (Fig. 2). Boundaries among regions followed meridians of longitude, parallels of latitude, or bathymetric contours, with the exception of the Slope Sea, which was defined as a polygon with (*i*) the southern boundary formed by the mean location of the Gulf Stream to the bifurcation point at 47°W (41); (*ii*) the northwestern boundary formed by the 500-m isobath from Cape Hatteras, NC, to 62°W; and (*iii*) the northeastern boundary separating Slope Sea water from Labrador Sea water formed by a line between 43°N 62°W and 42°N 46°W (15). The first 30 d of locations were excluded from the analyses to limit the influence of tag deployment location. The proportion of locations within each region was calculated for each day of year. A total of 212 fish <220-cm FL and 104 fish >220-cm FL were included in the analysis, although the number of fish with active tags varied by day of year. The most tag locations were available for December and the least for September.

Electronic tagging data were used to characterize the size structure of bluefin tuna that were potential Slope Sea and Gulf of Mexico spawners. Our focus was on western Atlantic spawning, and thus we did not consider tagged bluefin tuna that were resident in the eastern Atlantic (east of 45°W) for the entirety of both the Gulf of Mexico and Slope Sea spawning seasons (April to August). Fish with tags attached through at least April 30 were classified as potential Gulf of Mexico spawners if they visited waters west of 81°W during any time from March to June. For Slope Sea spawners, we only included fish in the analysis if the tag remained attached through at least July 15. Most (>95%) of the tagged fish occupied the Slope Sea at some point during the spawning season, including many that rapidly passed through the area during their migration north from the Gulf of Mexico to the United States or Canadian continental shelf. We considered a bluefin tuna a potential Slope Sea spawner if it occupied the Slope Sea for ≥20 d from June 1 to August 15. The 20-d duration was based on published reports that bluefin tuna have a spawning period of 18 d (7 d SD) in the Gulf of Mexico (8) and 23.9 d (range, 19–31 d) in the Mediterranean Sea (19).

We fit polynomial logistic functions to characterize the proportion of fish at length classified as potential Slope Sea spawners and potential Gulf of Mexico spawners. The Akaike information criterion was used to select between a first-order ($P = 1/[1 + \exp[-[b_0 + b_1 L]]]$) and second-order ($P = 1/[1 + \exp[-[b_0 + b_1 L + b_2 L^2]]]$) polynomial logistic function for each spawning ground. Lengths used in this model were projected forward from the length at tagging to May 1 for the Gulf of Mexico analysis and July 1 for the Slope Sea analysis using the established growth equation (42).

Proportion of Spawning in the Gulf of Mexico. We used the following equation to estimate the proportion of western Atlantic bluefin tuna spawning that occurs in the Gulf of Mexico (P_{GOMEX}) under different scenarios of fishing mortality and age at maturity:

$$P_{GOMEX} = \sum_{t=1}^{40} N_t W_t m_t P_{t,GOMEX} \Bigg/ \sum_{t=1}^{40} N_t W_t m_t, \tag{1}$$

where N_t is the relative number of fish at age t, W_t is the weight at age t, m_t is the maturity at age t for the population as a whole, and $P_{t,GOMEX}$ is the proportion of fish at age t that migrate to the Gulf of Mexico. Weight at age (W_t) was calculated using a two-step process. First, the Von Bertalanffy growth function was used to calculate length at age (42):

$$L_t = L_\infty * [1 - \exp[-k[t - t_0]]], \tag{2}$$

with $L_\infty = 314.9$, $k = 0.089$, and $t_0 = -1.13$. Second, weights were calculated from lengths:

$$W_t = aL_t^b, \tag{3}$$

with $a = 1.59*10^{-5}$ and $b = 3.02$ (1). For simplicity, maturity at age (m_t) was assumed to be knife edge at age 5 or age 9, the latter consistent with the current stock assessment. The logistic function characterizing the length structure of fish that migrate to the Gulf of Mexico, provided an estimate of $P_{t,GOMEX}$, with lengths converted to ages. CIs for the proportion of spawning in the Gulf of Mexico were developed by bootstrapping the fish used in developing the logistic function.

The relative age structure of a population averaged across years can be calculated using an age-specific total mortality rate (Z_t) with the number at age 1 (recruitment) set to 1:

$$N_{t+1} = N_t * e^{-Zt}. \tag{4}$$

Total mortality (Z_t) is the sum of natural mortality (M_t) and fishing mortality (F_t). We used M = 0.14 for all ages to remain consistent with the stock assessment, and evaluated three scenarios for age-specific fishing mortality. The first scenario was no fishing mortality on any age class (i.e., F = 0). The second scenario was the average estimated fishing mortality rate (0.04–0.06 for ages 3–14, and 0.076 for ages ≥15) from the stock assessment for the most recent decade (2004–2013) when fishing mortality rates are thought to have reached 40-y lows. The third fishing mortality scenario corresponded to 1994–2003 when fishing mortality was higher (0.05 at age 3–0.16 at ages ≥15). Estimates of both natural and fishing mortality rates in bluefin tuna are uncertain (1, 28, 43). The proportion of spawning in the Gulf of Mexico will be underestimated if total mortality is overestimated. Notably, <5% of bluefin tuna caught in the fishery from 1996 to 2007 were >20 y in age (44), suggesting that a substantial overestimate of total mortality is unlikely, unless the fishery is selective against older fish.

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