ICES Journal of Marine Science, 2023, **80**, 861–877
DOI: 10.1093/icesjms/fsad015
Advance access publication date: 16 February 2023
Original Article

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Evidence of bluefin tuna (*Thunnus thynnus*) spawning in the Slope Sea region of the Northwest Atlantic from electronic tags

Emilius A. Aalto[1,*], Simon Dedman[1], Michael J.W. Stokesbury[2], Robert J. Schallert[1], Michael Castleton[1], and Barbara A. Block[1]

[1]Hopkins Marine Station, Stanford University, 120 Oceanview Blvd, Pacific Grove, CA 93950, USA
[2]Biology Department, Acadia University, 15 University Ave, Wolfville, NS B4P 2R6, Canada

[*] *Corresponding author:tel: (203) 809-6376;* e-mail: aalto@cs.stanford.edu.

Atlantic bluefin tuna (ABT) are large, wide-ranging pelagic predators, which typically migrate between foraging regions in the North Atlantic and two principal spawning regions, the Gulf of Mexico and the Mediterranean Sea. A new spawning area has been described in the Slope Sea (SS) region off New England; however, the relationship between ABT that spawn in the SS and ABT using the principal spawning regions remains poorly understood. We used electronic tags to examine the location, temperature, and diving behaviour of ABT in the SS, and identified 24 individuals that were present during the spawning season (June–August) with tag data showing temperatures and behaviour consistent with spawning ABT. In general, the SS spawners had similar spatial ranges to Mediterranean-spawning ABT; however, some individuals displayed distinct behaviours that were identified first in the Gulf of Mexico spawners. Using monthly spatial distributions, we estimated that the SS spawners have high exposure to fishing pressure relative to other ABT and may represent a disproportionate share of the West Atlantic catch. This analysis provides the first description of the behaviour of ABT frequenting this spawning ground, creating a foundation for integrating this region into multi-stock management and, potentially, conserving an important source of genetic diversity.

Keywords: Atlantic bluefin tuna, electronic tagging, Slope Sea, spawning.

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*; ABT) are wide-ranging pelagic predators that reach over 680 kg (Magnuson *et al.*, 1994; Mather *et al.*, 1995). They have unique physiology and biomechanics that includes endothermy, centralization of their powerful oxidative swimming musculature, and specializations that increase efficiency when swimming (Neill *et al.*, 1974; Stevens *et al.*, 2000; Blank *et al.*, 2004). Their unique biology enables a wide spatial distribution occupying diverse habitats from subtropical to subpolar seas (Mather *et al.*, 1995). ABT are capable of moving rapidly between diverse ecosystems from coastlines to open ocean, and electronic tagging has demonstrated their ability to range widely at trans-oceanic scales. They consume a diverse range of prey, from small caloric-rich epipelagic fish such as anchovies, herring, and menhaden to crustaceans such as krill (Goñi and Arrizabalaga, 2010; Logan *et al.*, 2011). Additionally, adult ABT are able to forage on larger prey such as halibut, as well as deeper mesopelagic neckton such as squid and myctophids (Chase, 2002; Butler, 2007; Pleizier *et al.*, 2012; Madigan *et al.*, 2015). Mature ABT have been shown to follow annual migrations between their spawning grounds (typically in warm temperate or sub-tropical waters) and the colder, more productive foraging grounds in the North Atlantic (Stokesbury *et al.*, 2004; Block *et al.*, 2005; Teo *et al.*, 2007a; Fromentin *et al.*, 2014; Wilson *et al.*, 2015; Druon *et al.*, 2016; Hazen *et al.*, 2016).

ABT are one of the world's most commercially important marine species, with annual reported catch of ~30 000 metric tons with a value well over $1 billion USD (Macfadyen *et al.*, 2021). The fishery is currently managed by The International Commission for the Conservation of Atlantic Tunas (ICCAT) as two independent stocks, each affiliated with a different primary spawning ground. ICCAT uses the 45°W longitudinal meridian as a dividing line (ICCAT, 2018), though the two stocks intermix across much of their West Atlantic range (e.g. Lutcavage *et al.*, 1999; Block *et al.*, 2001, 2005; Rooker *et al.*, 2008b, 2019; Galuardi *et al.*, 2010; Arregui *et al.*, 2018; Puncher *et al.*, 2018). The western stock spawns primarily in the Gulf of Mexico (GOM) during spring months (April through June) and travels to the northwestern Atlantic to feed during the summer and early fall (July through October; Block *et al.*, 2005; Teo *et al.*, 2007a; Walli *et al.*, 2009; Wilson *et al.*, 2015). The principal spawning ground for the eastern Atlantic stock is the western and central Mediterranean Sea (Med; Cermeño *et al.*, 2015; Abascal *et al.*, 2016). The eastern stock is estimated to have ~10 times the biomass of the western stock (Rouyer *et al.*, 2018), and accounts for ~90% of recent catch (ICCAT, 2017). Both stocks are considered to be in recovery from prior depletion (ICCAT, 2020, 2021).

Over two decades, electronic tagging, otolith microchemistry, and genetics analyses have rapidly improved our understanding of ABT, but many questions still remain about population structure in the Atlantic ocean (Block *et al.*, 2005; Rooker *et al.* 2008b; Schloesser *et al.*, 2010; Puncher *et al.*, 2018). Although it is hypothesized that many eastern-stock fish remain in the East Atlantic their entire lives, electronic

Received: 25 June 2022; **Revised:** 12 January 2023; **Accepted:** 13 January 2023

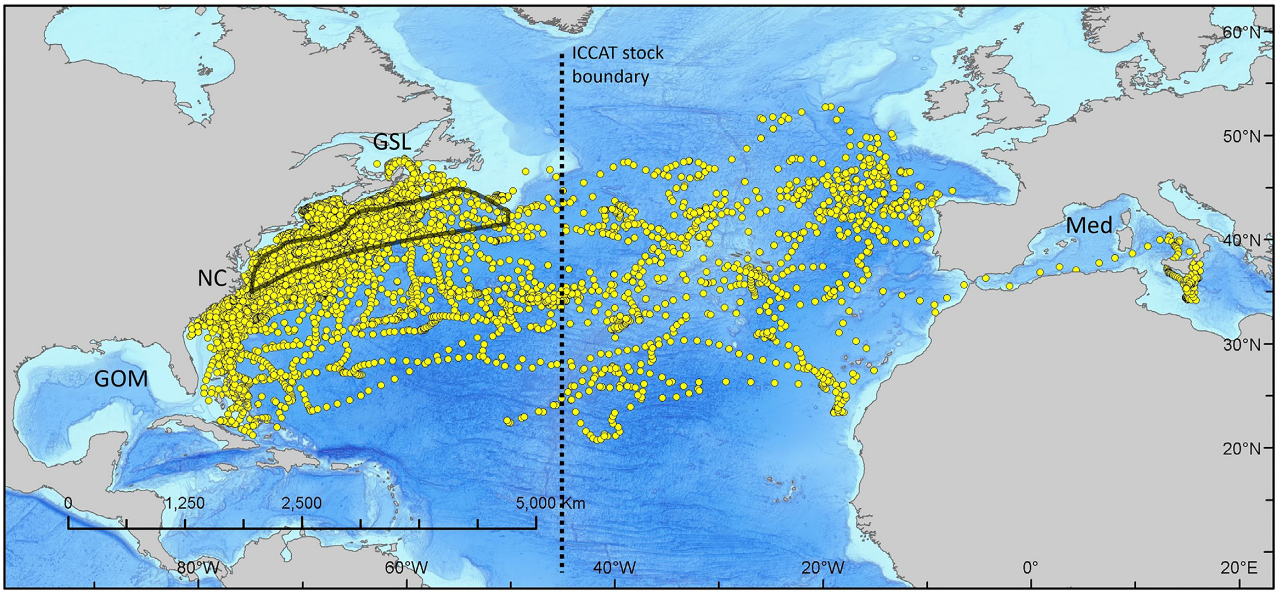

Figure 1. Combined tracks for the 24 SS spawning ABT (*T. thynnus*). The SS is outlined in black. The labels indicate tagging locations [Gulf of St. Lawrence, Canada (GSL) and North Carolina, United States (NC)] and the two primary spawning grounds [Gulf of Mexico (GOM) and the Mediterranean (Med)].

tagging and microconstituent analyses demonstrate that some individual ABT migrate to the north-western Atlantic by age one, comprising up to 40% of the ABT off the coast of North America (Block *et al.*, 2005; Rooker *et al.*, 2008a, b; Dickhut *et al.*, 2009; Teo and Boustany, 2016; Arregui *et al.*, 2018). Tagging and otolith data suggest that, after several years of growth, they travel back to the Med around age nine to spawn, with most of those fish thought not to return to the West Atlantic (Rooker *et al.*, 2008a; Teo and Boustany, 2016). Genetic analyses indicate that the western and eastern stocks are at least partially distinct yet no genetic markers have enabled full separation of the populations (Carlsson *et al.*, 2007; Boustany *et al.*, 2008; Puncher *et al.*, 2018). The western stock, that primarily breeds in the GOM, has been proposed to have a larger body size (Mather *et al.*, 1995) and later onset of maturity (Corriero *et al.*, 2005; Diaz and Turner, 2007) yet tagging studies indicate entry from bluefin that utilize the Atlantic ocean for a foraging ground into the Med remains similar to the GOM (Block *et al.*, 2005). While sharing the northwestern Atlantic, however, the two stocks' movement patterns are largely similar, with mature individuals leaving the northern portion of their range by late December and migrating to their respective spawning grounds or mid-latitude foraging regions during winter and spring, then returning to the north in the early summer (Block *et al.*, 2005; Walli *et al.*, 2009; Galuardi and Lutcavage, 2012; Teo and Boustany, 2016).

Although this two-stock paradigm has long been the foundation of ABT research and management, it is becoming increasingly evident that the true stock structure is more complex than "GOM or Med." Population subdivision of European ABT has also been proposed to exist within the Med, with the migratory stock from the Western Med distinct from the resident population in the Central and Eastern Med (Carlsson *et al.*, 2004, 2007; Boustany *et al.*, 2008) and evidence of spawning in the Eastern Med (Karakulak *et al.*, 2004) and the Bay of Biscay (Rodriguez *et al.*, 2021). Although only the western stock is currently recognized to spawn in the GOM (Fromentin and Powers, 2005; Teo and Boustany, 2016), genetic evidence suggests limited interbreeding with the eastern stock may be occurring, complicating the two stock hypothesis (Johnstone *et al.*, 2021). Additionally, there is potential support for more complex population structure within the western stock and genetics should address whether introgression is occurring between the populations (Muhling *et al.*, 2011a; Brophy *et al.*, 2020).

In the Atlantic ocean, the slope waters off the North American continental slope near New England (the "Slope Sea," SS; see Figure 1) have long been considered a potential spawning ground following historical observations of "ripe" adults (i.e. ready to spawn; Baglin, 1976; Mather *et al.*, 1995). Oceanographic analyses (Rypina *et al.*, 2019, 2021) have indicated that the Gulf Stream running close to the large slope escarpment produces warmer ocean temperatures with cyclonic and anticyclonic eddies, conducive for spawning. Recent spawning by ABT has been confirmed by larval surveys (Richardson *et al.*, 2016a; Hernández *et al.*, 2022). Back tracking of the larvae has suggested the vast majority originated in the SS (Hernández *et al.*, 2022), though in a few cases Cape Hatteras and other regions such as the Bahamas have been indicated as possible spawning areas (Mather *et al.*, 1995; Hernández *et al.*, 2022). Thus, an expansive potential spawning ground exists in the western Atlantic from south of Cape Hatteras to the slope off the Gulf of Maine.

Characterizing the individuals spawning in the SS has been difficult as it is a corridor along which adult ABT from the GOM and Caribbean waters travel, as well as an area of high mixing between the western and eastern stocks, including both juveniles and adults (Block *et al.*, 2001, 2005; Teo and Boustany, 2016). Richardson *et al.* (2016a) assert that the larvae sampled in the region indicate it is a major breeding ground for the western stock, and potentially shows they spawn at a younger age than those in the GOM. This view is contested

(Richardson *et al*., 2016b; Safina, 2016; Walter *et al*., 2016), with Safina (2016) suggesting that the larvae could be of eastern stock, or possibly originating further south (e.g. from off the Carolinas as seen by Lamkin *et al*., 2014). Whether the SS represents a secondary spawning ground for one or both of the primary stocks, or a third independent stock altogether, could have significant implications for ABT conservation and management, but genetic analyses of SS larvae have so far been inconclusive (Rodríguez-Ezpeleta *et al*., 2019).

Here, we present electronic tagging data with geolocation positions ($n = 10\ 068$ d) from individual ABT ($n = 24$) that occupy waters conducive for spawning and simultaneously show diving, internal and external temperatures that are consistent with spawning bluefin tuna within the SS, as assessed using electronic tagging data we have collected over the past two decades from deployments off North Carolina (NC), United States, and in the Gulf of St. Lawrence, Canada (GSL). We analysed dive behaviour, ambient and body temperatures when available, spatial distribution, and migratory movements for the adult ABT presumed to be SS spawners to examine their biology and behaviours in these waters. We also assessed their exposure to fishing pressure in the West Atlantic relative to assigned-stock individuals, using the assignations *eastern* and *western* to refer to Med-identified and GOM-identified fish, respectively. Finally, we discuss which SS spawning scenarios are most supported by these tracks, and the potential management implications of identifying a third spawning ground.

Methods

Tagging methodology

Archival and pop-up satellite archival tag data sets were compiled from the Stanford University TAG A Giant program data base using tags deployed from 1996 to 2020. Electronic tags were primarily deployed at two locations during these years, the GSL [$n = 290$, mean Curved Fork Length (CFL) 263 cm, *SD* 21, range 187–313] and the coastal waters of NC off Cape Lookout or Cape Hatteras ($n = 968$, mean CFL 195 cm, *SD* 26, range 95–272), using methods previously described for these deployments and data (Block *et al*., 1998, 2001; Stokesbury *et al*., 2004; Wilson *et al*., 2015). Procedures were conducted under protocols approved by the Stanford University Administrative Panel on Laboratory Care in accordance with the Institutional Animal Care and Use Committee's proper guidelines and the University Animal Care Committee protocol #18–11, and all procedures approved under annual permits issued either by NOAA in US waters or by Fisheries and Oceans Canada license # SG-RHQ-18–159A when in Canadian waters. The archival tags were models MK7 from Wildlife Computers (pre-2002) and LTD2310/2350 from Lotek, Inc (post-2002), and recorded pressure (depth), light intensity, ambient and internal temperature data, at 1 s to 2 min intervals. The tags were surgically implanted into the tunas and were recaptured from 1 to 8 years post-release. The satellite tags were PAT2 and miniPAT models (247A, 348F, 348 K, and 390B) from Wildlife Computers, with the same sensors excepting internal temperature, and were programmed to release and transmit data after ~1 year. Post processing of data sets for sensor drift and corrections, daily position geolocation using threshold light models (Teo *et al*., 2004; Block *et al*., 2011; Wilson *et al*., 2011, 2015) followed the prior procedures including fish length estimations from on deck measurements and products created from processed positions into state-space models (Block *et al*., 2005, 2011). Age was estimated from length using the von Bertalanffy growth curves used by ICCAT, parameterized separately for the eastern stock (Cort *et al*., 2014) and the western stock and unknown individuals (Restrepo *et al*., 2010).

Western and eastern stock assignment

In the absence of genetic identification, we spatially assigned tagged ABT individuals to the western or eastern stock if their tracks entered the GOM or Med, respectively. In addition, a fish which was eventually harvested (post-tag detachment) in one of the two spawning grounds was similarly assigned. Using this methodology and focusing on fish tagged in the West Atlantic, our TAG database provided tracks for 94 western stock, 47 eastern stock, and 309 unassigned individuals (i.e. did not enter either region). We used these tracks to search for possible SS spawning candidates, as well as for eventual comparison between the assigned-stock individuals and the SS spawners.

Definition of SS

We defined the SS as the slope waters of the North American Shelf bathymetrically 200–3000 m constrained to its north and west by the North American continental shelf (MERCINA *et al*., 2001) and to its south and east by Cape Hatteras, the north wall of the Gulf Stream, and the southernmost extent of the Grand Banks (~983 000 km^2; Figures 1 and 2). Warm-core eddies propagating north from the Gulf Stream heat the SS region (Auer, 1987) so that by the early summer areas in the centre of the SS west of ~63°W satisfy both spawning (22–29°C; Teo *et al*., 2007b; Hazen *et al*., 2016) and larval (20.5–26°C; Gordoa and Carreras, 2014) temperature criteria, as well as larval retention criteria (Rypina *et al*., 2019). Because many of our tracks were from the early 2000s, we defined the Gulf Stream using a wide region corresponding to its median historical position; note that recent oceanographic trends have moved this boundary northward, potentially narrowing the SS region but allowing warm water to intrude into the Gulf of Maine (Meyer-Gutbrod *et al*., 2021).

Identification of spawning

We first considered any individual a potential SS spawner if it spent at least 10 d in the SS during the spawning season (broadly defined as May through August). For each candidate individual, we visually analysed horizontal movement patterns, ambient temperatures, dive behaviour and, when available with archival tags, internal temperatures to aid in identifying spawning behaviours as previously described in Block *et al*. (2001, 2005), Teo *et al*. (2007a), and Aranda *et al*. (2013), spawning ABT have a variety of unique behaviours. From these prior analyses, it has been recognized that when bluefin are in warm waters conducive for spawning they often take on oscillatory diving behaviours with unique periodicity. Fish from the GOM, for example, perform shallow, distinct night and day dives (diel behaviour) for multiple days [a mean breeding phase of 18 d in Teo *et al*. (2007a) and 24 d in Aranda *et al*. (2013)], with increased oscillatory dives at night departing from the surface waters. This increase of activity is accompanied by a rise in internal temperature, which often peaks at dawn. Spawning occurs exclusively in very warm

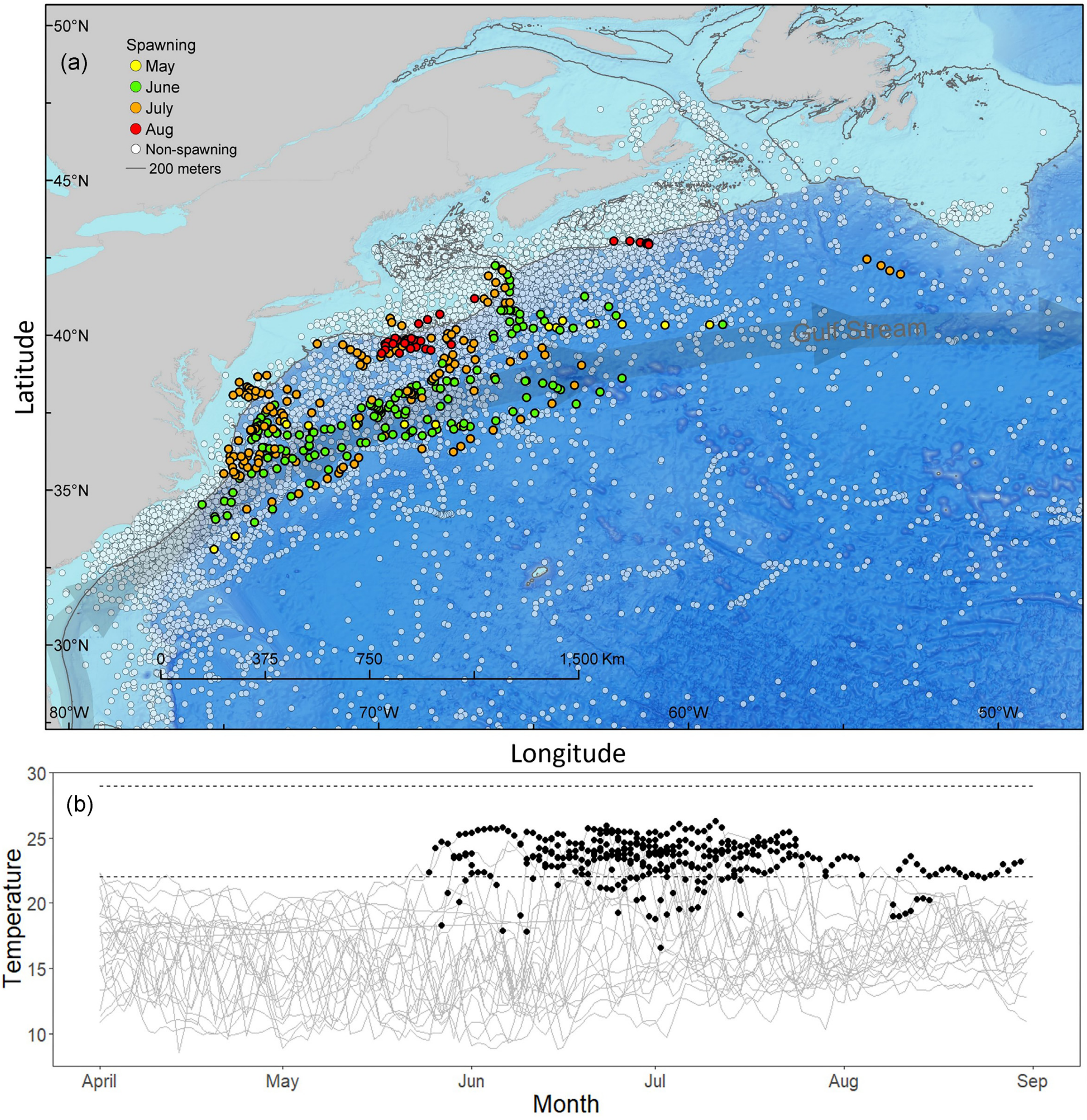

Figure 2. Spawning in the SS. (a) Daily positions for the 24 spawning ABT (*T. thynnus*) in and around the SS. Points are coloured by month on the days when spawning was observed, with white indicating no spawning. (b) Mean daily external temperature during the observed spawning period (smoothed in 3-d intervals). Spawning days are indicated with black circles. Suitable spawning temperatures are between the two horizontal lines.

water (>22°C), and internal temperatures remain consistently higher than ambient without the cooling/heating cycle seen during foraging (i.e. from dives in colder water followed by internal heat from digestion). Residency in the SS was used to identify candidate spawners; however, for each candidate we examined the entire track within the spawning season and did not limit identification of spawning to only days within the designated SS boundary. Putative spawning events were included if at least one of the spawning days was within the boundary (either directly or within the range of geolocation error).

Spatial analyses

We calculated mean monthly latitudinal and longitudinal position for each fish and compared ranges for each stock by month. We used two-sided Student's *t*-tests (Student, 1908) to compare mean values for latitude and longitude, applying a Bonferroni correction (Weisstein, 2004) for the monthly comparisons, as well as mean daily depth, distance to shore, and sea surface temperature (SST), which do not require normal data as long as the sample size is sufficient (Lumley *et al.*, 2002). For differences in distributions of values by stock, we used Wilcoxon–Mann–Whitney signed-rank tests for comparison (Mann and Whitney, 1947; Wilcoxon, 1992) and assessed distributional similarities between stocks via overlap analysis using the distribution-free $\hat{\eta}$ index (Pastore and Calcagnì, 2019).

Exposure to fishing pressure

As part of managing the ABT stocks, ICCAT collects extensive catch and effort data including fleet, location, and gear type under the Task 2 designation (https://www.iccat.int/en/t2ce.asp). These data can be combined with estimates of stock distribution to determine the exposure of a stock to fishing pressure across space and time, as described in Aalto *et al.* (2021). Here, we apply the same methodology to the identified SS spawners: we used the tag location data to generate monthly spatial distribution maps for each stock (western, eastern, and SS, aggregating to 1° × 1° boxes across all years; Supplementary Figure S19), then combined these with the spatial fishing effort data for each month to determine fishing exposure as

$$Exposure_{m,s,g} = \sum_{i} \sum_{j} Rel.density_{m,s,i,j} * Effort_{m,g,i,j},$$

where m is the month, s is the stock, g is the gear type, and i and j represent the latitudinal and longitudinal grid cells. Relative density was calculated as proportion of total tag-days (days of tag data across all fish in a specific stock) in a specific grid cell during that month. Effort was quantified as number of hooks (for longline data) or hours fished (for rod and reel data). Exposure was then standardized across stocks (with the highest monthly exposure set = 1.0), allowing comparison of relative exposure to different gears between stocks. Although the lack of systematic survey data and genetic identification makes it impossible to precisely estimate SS spawner abundance relative to the two primary stocks, we were able to estimate the proportion of Task 2 catch coming from the SS "stock" under different relative abundance scenarios derived from the proportion of SS spawners seen in the total dataset.

Results

Identification of spawning

To identify bluefin tuna that utilize the SS waters, we first reduced the full tag-track dataset examined for this study ($n = 450$, mean tag duration 215 d, range 9–1936; mean CFL = 229 cm, *SD* 35, range 95–313) down to a pool of "potential spawners" (i.e. those with tracks extending into June: $n = 250$, mean duration 302 d, range 44–1936; mean CFL = 224 cm, *SD* 35, range 95–298). This was then filtered to include only those with 10 + days in the SS during the potential spawning season (June, July, and August), when temperatures are consistent with potential spawning. This reduced the dataset of the potential ABTSS spawners ($n = 170$, mean duration 321 d, range 72–1936; mean CFL = 214 cm, *SD* 34, range 95–289). Within this subset, we identified 24 individuals that demonstrate evidence of behaviours consistent with previously identified tag-based spawning behaviours within the SS (mean duration 420 d, range 192–994; mean CFL = 219 cm, *SD* 28, range 165–284; Table 1, Figures 1 and 2). The putative spawning events recorded by the tagged bluefin tuna spanned years 1999–2021 (Table 1). They occurred primarily in the portion of the SS west of Nova Scotia (i.e. between 65°W and 75°W), most commonly in late June and early July but four times in late May and twice in mid-August (Figures 2a and 3c and d), and were almost exclusively in water temperatures considered suitable for spawning (22–29°C; Figure 2b). Mean duration of the identified breeding phases was 11 d with an *SD* of 6 d, shorter than those seen in Teo *et al.* (2007a) and Aranda *et al.* (2013). Distributions for size, estimated age, and spawning days are given in Figure 3. Archival data recorded in 1–2 s high resolution intervals from four channels on the tags were used to examine the diving patterns, physiological (body temperature), and behavioural data used to identify spawning (Figure 4 and Supplementary Figure S5).

Most of the ABT identified as SS spawners were electronically tagged in NC as young adults ($n = 19$; mean CFL = 207 cm, *SD* 16, range 165–229; mean est. age = 10.2, range 6.4–12.6), and the remaining individuals were tagged in Canadian waters in the GSL and were much larger fish at release($n = 5$; mean CFL = 264 cm, *SD* 13, range 254–284; mean est. age = 17.9, range 15.9–22.0). The range, while tagged, of the 24 spawners tags indicate they utilized foraging areas primarily along the West Atlantic seaboard; importantly, though, nine individuals crossed the 45° meridian into the East Atlantic (including one, which entered the Mediterranean). A total of four example SS tracks are shown in Figure 5, with other individual tracks shown in Supplementary Figures S1–S3. A total of 20 of the 24 spawning individuals had no prior assigned stock (i.e. were not observed to enter one of the two primary spawning grounds). The remaining four were initially assigned spatially to the eastern stock: #5103508 entered the Med (Supplementary Figure S2), and the other three (#s 5100132, 5103489, and 5109003) were assigned to the Med stock based on eventual harvest location (i.e. where the fish was caught). Of the three fish with tracks encompassing two or more spawning seasons, two, #5103509 (CFL = 209 cm at tagging) and #5105049 (216 cm) spawned in the SS multiple years in a row (2003–04 and 2005–07, respectively; Figure 6 and Supplementary Figure S5), demonstrating site fidelity for the SS spawning ground during the spring and early summer.

Two individuals (#5100117 and #5118008) spawned slightly outside the SS boundaries but were included because movement of the Gulf Stream or geolocation error could place the spawning events within the SS. Two individuals (#5112032 and # 5121039) spawned south of the SS and were, thus excluded from this analysis but are described in the supplemental information (Supplementary Figure S4).

Spatial analysis

Total geographic spatial range identified from geolocation data for the SS spawners was more similar to the ABT identified previously from the eastern (i.e. Med-identified) stock (e.g. Stokesbury *et al.*, 2004; Block *et al.*, 2005) than the western (i.e. GOM-identified) stock (Figure 7, Supplementary Table S1). Although all differences in mean and distribution at the annual scale were significant, we did not consider a statistical comparison across the entire year to be informative given the complex migratory patterns. When compared to the eastern stock (annual mean lat 39.5°N ± 5.85 *SD*, lon 50.2°W ± 25.7), the SS spawners had similar latitudinal (37.9°N ± 4.70) and longitudinal ranges (63.8°W ± 16.8) with one fish entering the Med (roughly, longitude 0°; Supplementary Figure S18b) and travelling to the waters around Sicily (in particular, the Malta Trough). Many eastern-stock fish travelled further north, especially in the East Atlantic

Table 1. Individual bluefin tuna (*T. thynnus*) identified as spawning in the SS region.

TOPP id	Assigned stock	Tagging date	Tagging location[a]	Length at tagging (cm CFL)	Est. age at tagging	Track length (days)	Tag model	Tag type	Spawning period(s)
5100107	Unk	1999–01–01	34.58°N, 76.37°W	219	11.2	460	MK7	Archival	1999–05–30–1999–06–06
5100108	Unk	1999–01–06	34.39°N, 76.28°W	229	12.2	375	MK7	Archival	1999–06–09–1999–06–16
5100117	Unk	1999–01–14	34.63°N, 76.30°W	214	10.7	204	MK7	Archival	1999–07–29–1999–08–04
5100127	Unk	1999–01–16	34.51°N, 76.64°W	217	11.0	192	MK7	Archival	1999–06–28–1999–07–12
5100132	Eastern[b]	1999–01–17	34.54°N, 76.65°W	199	8.8	449	MK7	Archival	1999–06–10–1999–06–15
5101289	Unk	2001–01–07	34.64°N, 76.35°W	227	12.0	207	PAT2	Satellite	2001–06–20–2001–06–25
5103481	Unk	2003–01–13	34.28°N, 76.59°W	209	10.2	375	LTD2310	Archival	2003–07–12–2003–07–25
5103485	Unk	2003–01–14	34.41°N, 76.53°W	213	10.6	213	LTD2310	Archival	2003–06–25–2003–07–03
5103489	Eastern[b]	2003–01–16	34.54°N, 76.30°W	185	7.8	445	LTD2310	Archival	2003–06–28–2003–07–05
5103508	Eastern[b]	2003–01–18	34.49°N, 76.27°W	209	9.7	655	LTD2310	Archival	2003–06–21–2003–07–03
5103509	Unk	2003–01–18	34.47°N, 76.26°W	209	10.2	746	LTD2310	Archival	2003–07–15–2003–07–23, 2004–06–21–2004–07–14
5103517	Unk	2003–01–18	34.58°N, 76.32°W	207	10.0	384	LTD2310	Archival	2003–08–09–2003–08–30
5103524	Unk	2003–01–21	34.39°N, 76.35°W	199	9.3	371	LTD2310	Archival	2003–06–09–2003–07–03
5103547	Unk	2003–01–26	34.66°N, 76.28°W	190	8.6	287	LTD2310	Archival	2003–06–22–2003–07–02
5104484	Unk	2004–01–09	34.51°N, 76.25°W	222	11.5	345	LTD2310	Archival	2004–06–24–2004–07–13
5104497	Unk	2004–01–14	34.52°N, 76.21°W	219	11.2	788	LTD2310	Archival	2005–06–24–2005–07–18
5105049	Unk	2005–01–08	34.47°N, 76.52°W	216	10.9	994	LTD2310	Archival	2005–06–29–2005–07–10, 2006–06–13–2006–06–28, 2007–07–08–2007–07–24
5107027	Unk	2007–03–24	35.05°N, 75.26°W	165	6.4	440	LTD2310	Archival	2007–07–14–2007–07–29
5109003	Eastern[b]	2009–01–03	34.45°N, 76.63°W	188	8.0	398	LTD2350	Archival	2009–06–15–2009–06–25
5114024	Unk	2014–10–22	46.15°N, 61.49°W	270	18.1	307	miniPAT	Satellite	2015–05–25–2015–06–01, 2015–06–10–2015–06–24
5118008	Unk	2018–09–28	46.02°N, 61.59°W	254	15.4	362	miniPAT	Satellite	2019–05–30–2019–06–09
5120021	Unk	2020–09–26	45.99°N, 61.61°W	256	15.7	357	miniPAT	Satellite	2021–07–02–2021–07–05, 2021–08–09–2021–08–15
5120032	Unk	2020–10–04	45.98°N, 61.71°W	284	21.0	347	miniPAT	Satellite	2021–06–19–2021–06–25
5120035	Unk	2020–10–06	46.20°N, 61.44°W	258	16.0	367	miniPAT	Satellite	2021–05–27–2021–06–01

a. First 19 locations near NC, United States; remaining five in the GSL, Canada.
b. 5103508 was assigned to the eastern stock based on satellite track; the remaining fish were assigned based on post-tracking harvest location.

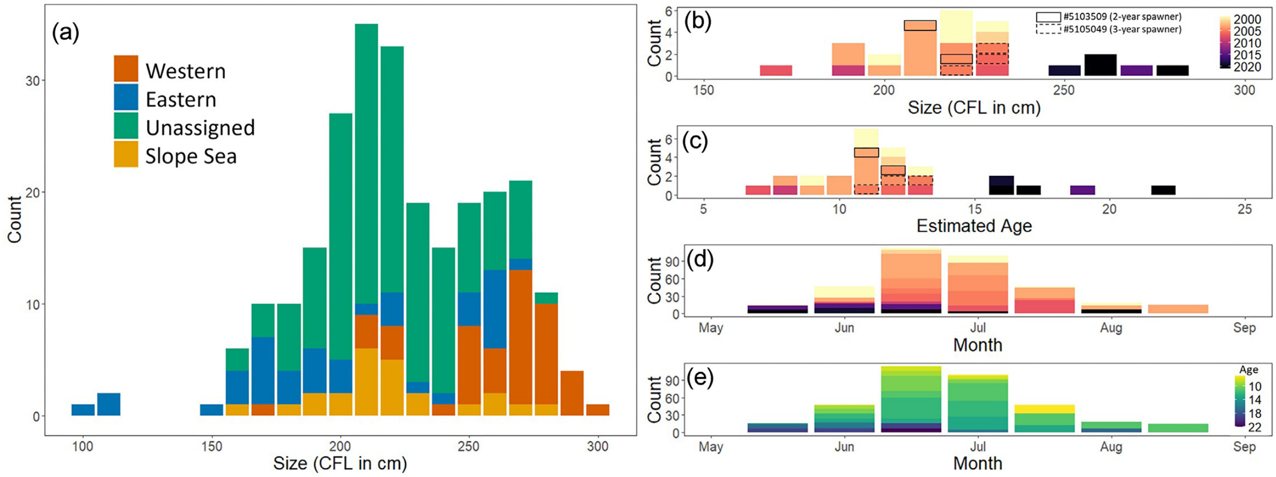

Figure 3. Distributions of SS spawning ABT (*T. thynnus*). (a) Length at tagging for all individuals with tracks, which extended into June ($n = 250$; western = 45, eastern = 40, unassigned = 141, SS = 24). (b) Size distribution of SS spawners during spawning events. The colour indicates the year of the spawning event. Size is projected using von Bertalanffy growth curves from CFL at time of tagging. The linked entries for the two multi-year spawners are indicated with the solid and dashed boxes. (c) Estimated age distribution during spawning events. Age at tagging was estimated from CFL using the growth curves. Same details as for (b). (d) Distribution of spawning days, grouped into half-months and aggregated across all spawning events. The colour indicates the spawning year. (e) Distribution of spawning days coloured by age of spawner. Details otherwise the same as for (d).

(though only nine SS tracks are available for comparison in that region) and in the winter (Figure 7a). The latter difference could be the result of tagging bias, however, as most of the SS spawners were tagged early in the year off NC and thus were unlikely to move to higher latitudes in that period. The SS spawners were more dissimilar from the western stock (annual mean lat 33.5°N ± 8.03, lon 75.8°W ± 12.3), with less travel to the south, an earlier return north (Figure 7a), and a much wider longitudinal range (Figure 7b), though several did go farther south than most eastern-stock fish (Supplementary Figure S18a). Note that the majority of the oldest fish stayed entirely in the West Atlantic (orange and white lines, Supplementary Figure S18) despite their maturity.

Comparing the stocks on a monthly timescale (Figure 7), the SS spawners were significantly different (Supplementary Table S1) from the western stock in both latitudinal mean and distribution in all months except July, August, and November (Figure 7a), and differed longitudinally January through June (Figure 7b). The SS spawners differed mainly in distribution from the eastern stock, latitudinally in November through February and longitudinally October through February and May through August. Collectively, SS spawners had statistically similar ranges (9 lat months, 9 lon) and distributions (8 lat months, 3 lon) to the eastern stock in more months than for the western stock (range 3 lat, 6 lon; distribution 2 lat, 4 lon). In addition, they were more similar to the eastern stock in mean depth, distance to shore, and mean daily SST (Supplementary Figures S20 and S21).

During the spawning months (May through August), we found that the SS spawners generally remained to the south and west of the GOM- and MED-identified stocks when in the SS and nearby regions (Supplementary Figures S9–S12). In May and June (Supplementary Figures S9 and 10), the eastern stock is concentrated further north. The western stock is still moving up the coast from the spawning areas in the GOM during those months, but the individuals that have reached the SS in June are concentrated further to the east and north (Supplementary Figure S11). In July (Supplementary Figure S12), the SS fish appear to be further south than both primary stocks, though that effect may be partly tautological due to the spawning observation dates and was not significant. In August (Supplementary Figure S13), the SS spawners mingled with the other stocks, but remained south of the main western-stock regions such as the Scotian shelf and the GSL. These differences were statistically significant for the western stock in May and June and both stocks in August (Supplementary Table S1). During the rest of the year, the SS spawners followed a similar pattern to many eastern-stock fish (and, potentially, juvenile western fish) and overwintered off NC (see Supplementary Figures S6–S17 for all months).

Exposure to fishing pressure

We used stock-specific spatial distributions to determine relative stock exposure to fishing pressure by comparing stock location to ICCAT effort data using the methodology described in Aalto *et al.* (2021) (see Supplementary Figure S19 for the monthly distribution contours). The SS spawners had similar exposure to that of the eastern stock, though their more coastal distribution meant slightly higher exposure to longline fleets in the late summer (Figure 8a and b) and rod and reel fishing during June and July, key spawning months (Figure 8c and d).

The SS spawners identified represent 19 tracks out of 166 total tagged in the fall near NC with tracks that extend into the spawning season (i.e. at least through June; Table 2), suggesting that ~12% of the fish in the region at that time may be SS spawners (and 5 out of 80 for the GSL, or ~6%), at least across the age range tagged. Taken across the full dataset the proportion of SS spawners is consistently 6–13% across age groups (<10 yo, 10–15 yo, 15+; Table 2). Note that the SS spawners have a size distribution similar to that of the overall dataset, except the smallest eastern stock fish (Figure 3a).

Using the fishing exposure data, we estimated relative proportion of Task 2 catch in the West Atlantic under four different relative abundance scenarios (Figure 9): 3.1%, a conservative scenario set to half of the smallest regional propor-

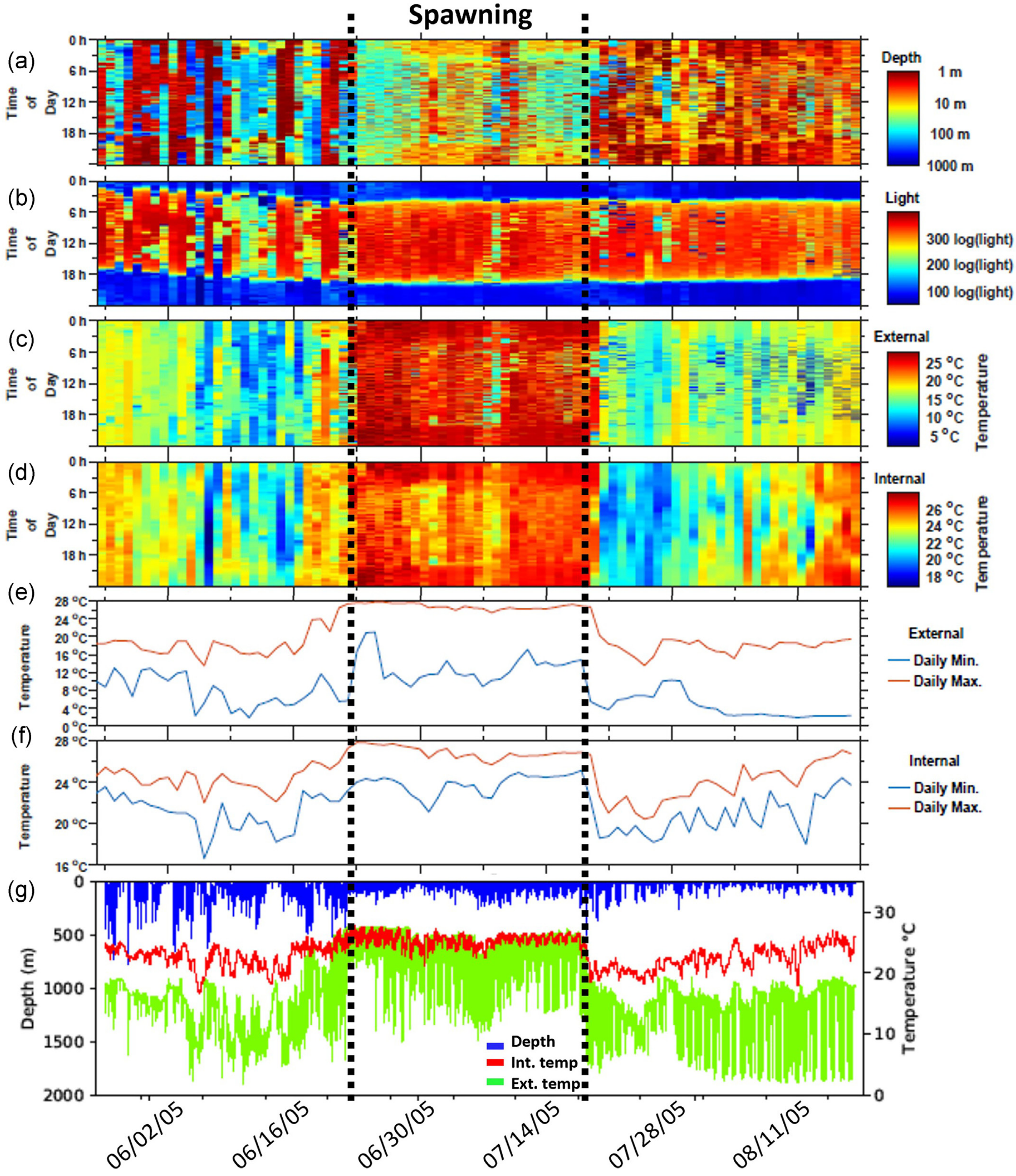

Figure 4. Spawning proxies for ABT (*T. thynnus*) #5104497 for spawning period 6/24/05 through 7/18/05. Examples of behaviours associated with spawning as described in Teo *et al.* (2007a). (a) Depth. Note shift in dive pattern to shallower waters at night and deeper (but not very deep) waters during the day. (b) Light. Note steady sunrise/sunset timing, indicating little longitudinal travel. (c) External temperature. Note consistently >23°C. (d) Internal temperature. *Y*-axis values differ from external temperature. Note heightened value, especially at night. (e) External temperature range. Note relative stability of maximum and minimum temperatures. (f) Internal temperature range. Note both minimum and maximum are elevated, and stable with regard to external temperature. (g) Depth and temperature patterns during spawning. *Y*-axis indicates depth on the left (blue) and temperature on the right (red internal and green external). Note cyclic up-down diving pattern during spawning period, and heightened temperatures with low internal temperature range.

tion; 6.3%, the smallest regional proportion (Canada); 9.6%, the overall proportion across both regions; and 11.5%, the highest regional proportion (NC). Although relative abundance ranged from 3.1 to 11.5%, estimated catch proportion ranged from 6.4 to 21.4%, depending on gear type (Supplementary Table S2). High relative catch of SS stock was focused in March and April pre-2008 and November post-2008 for longline (Figure 10a), and June pre-2008 for rod and reel (Figure 10b), driven by the heightened relative exposure during those months (Figure 8b and d).

Discussion

The 24 archival and satellite tag derived tracks identified here provide significant records of adult ABT spawning in the slope waters of the Northwest Atlantic, confirming what

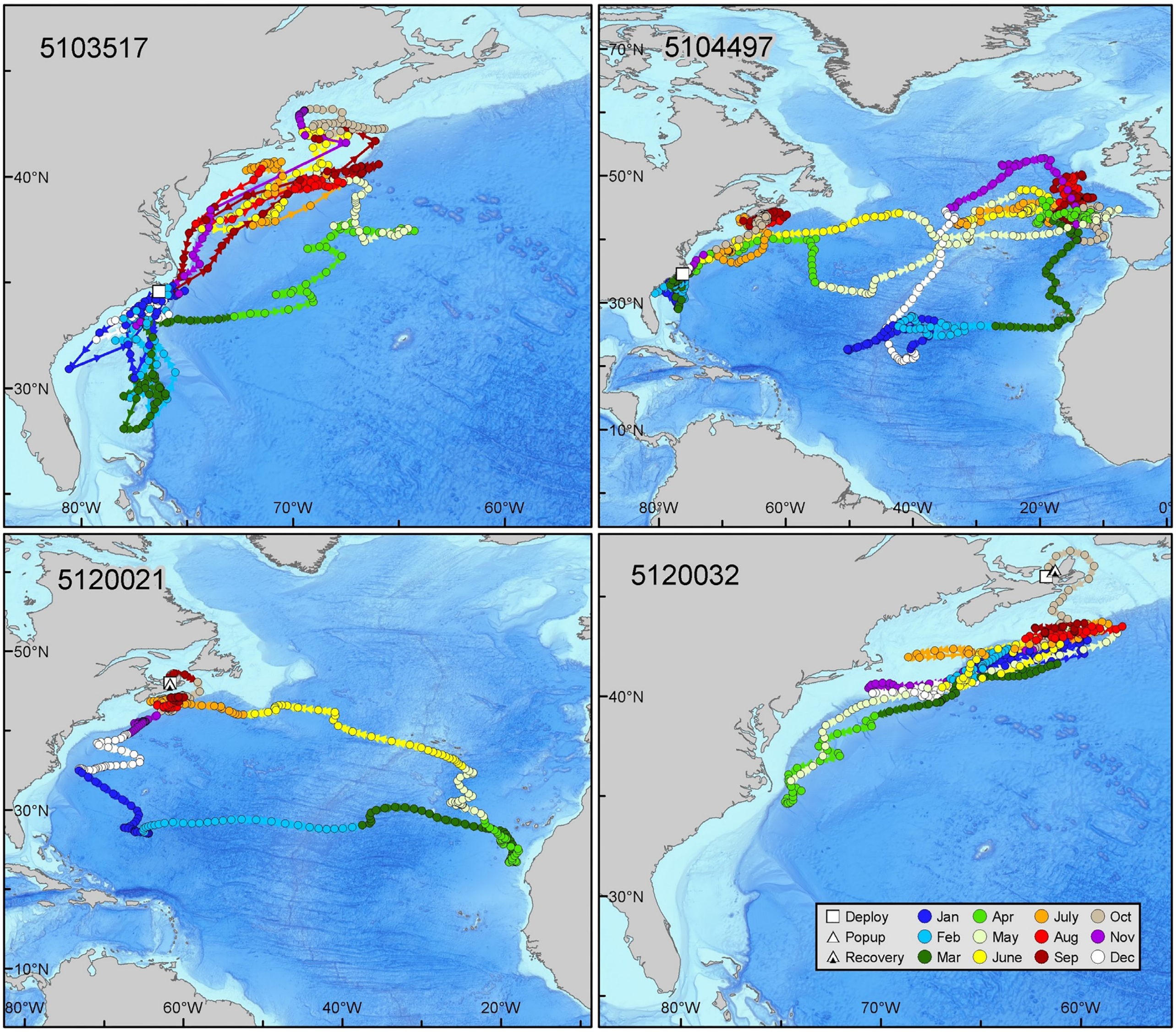

Figure 5. Representative tracks for individual ABT (*T. thynnus*). The top two (#5103517 and #5104497) were tagged in NC, United States, in 2003 and 2004, respectively. The bottom two (#5120021 and #5120032) were tagged in the GSL, Canada, in 2020.

larval studies have reported (e.g. Mather *et al.*, 1995; Richardson *et al.*, 2016a; Rodríguez-Ezpeleta *et al.*, 2019; Hernández *et al.* 2022): the presence of a third spawning ground in the western North Atlantic. Our analyses shows that these ABT spawners have movement and behaviours most similar to that of eastern-stock individuals, with wide longitudinal ranges (Figure 7)—including travelling into the Mediterranean in one case—and spatial aggregation in the Gulf of Maine and the western portion of the SS, areas with higher eastern-stock presence (Supplementary Figures S9–S12). Importantly, some of the SS fish do have spawning diving behaviours similar to the previously reported GOM fish (Teo *et al.*, 2007a), potentially indicating an extension of the GOM fish into these waters periodically to spawn as they return to their northern foraging grounds. Because most of the track durations were <1 year, the degree of spawning site fidelity is unclear; however, two archival-tagged fish were observed to spawn in the SS two and three years in a row. Spawning across a wide range of age classes (10–18 years), including repeat spawning by two individuals up to ages 12 and 13, supports the hypothesis of a true third spawning stock, rather than an early breeding site for eastern- and/or western-stock fish. The behaviours described here have been observed during the entire electronic tagging campaign spanning over 26 years of direct observations that began in 1996. Importantly, the differing types of spatial tracks and inital tagging locations (see *Limitations* below) suggest that the SS could also be potentially a zone of inter-breeding between the two primary stocks, consistent with the results of genetic analyses indicative of potential introgression (Rodríguez-Ezpeleta *et al.*, 2019). This will require more efforts in genomics to resolve, and finclips from these spawning fish may be of value in these analyses.

Our findings complement the larval analyses of Richardson *et al.* (2016a) and Hernández *et al.* (2021), providing detailed behavioural data for the adult spawners that these and other authors (e.g. Mather *et al.*, 1995) inferred were present. However, most of the spawners we identified were >10 years old (16 of 24, or 67%, compared to 177 out of 250, or 71%, in the full potential spawner dataset) and, therefore, these results

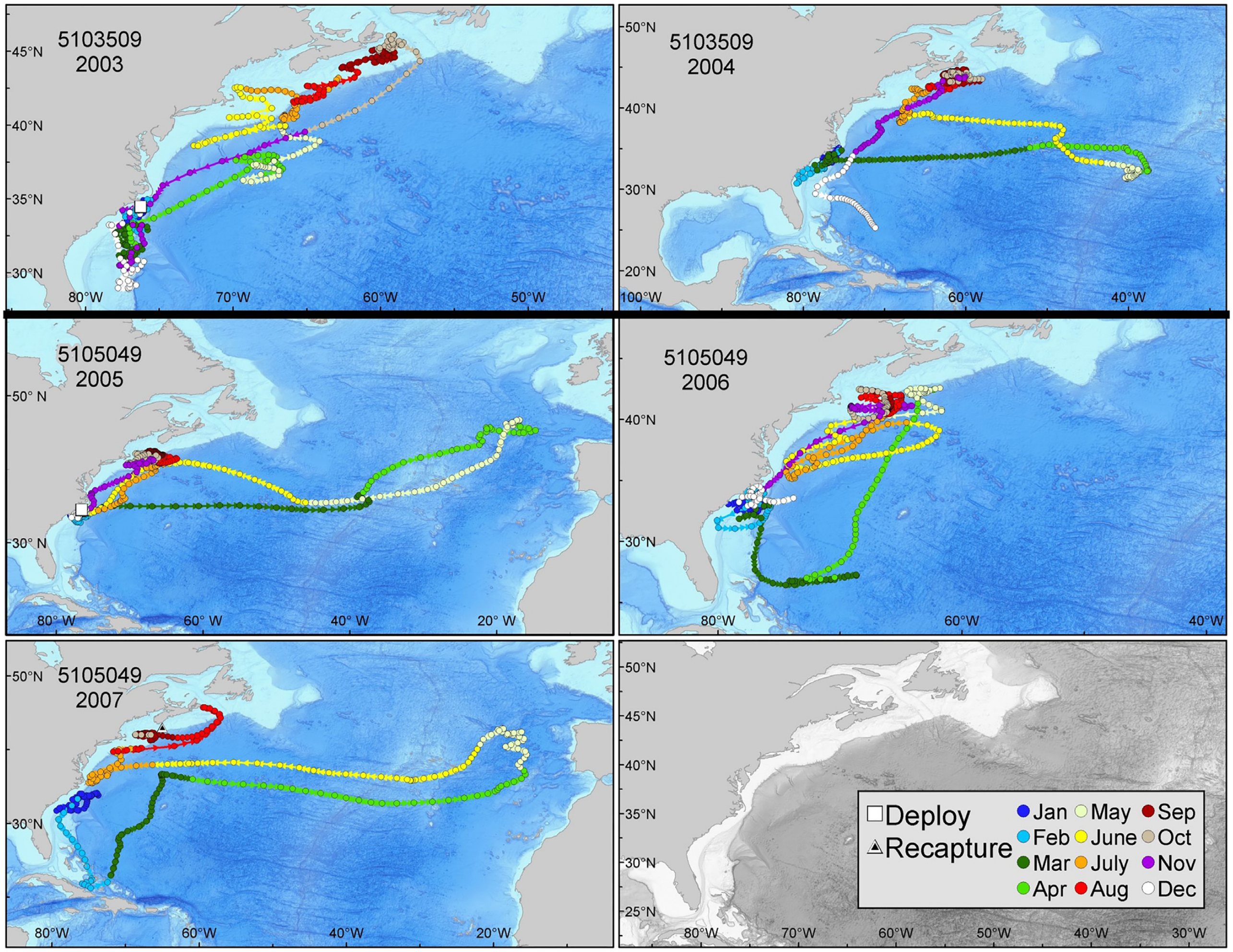

Figure 6. Tracks for two ABT (*T. thynnus*) spawning in the Slope Sea multiple years in a row. Spawning was observed in the SS in each year for #5103509 (July in 2003, June–July in 2004; top two panels) and #5105049 (June in 2006, July in 2005, and 2007; remaining panels).

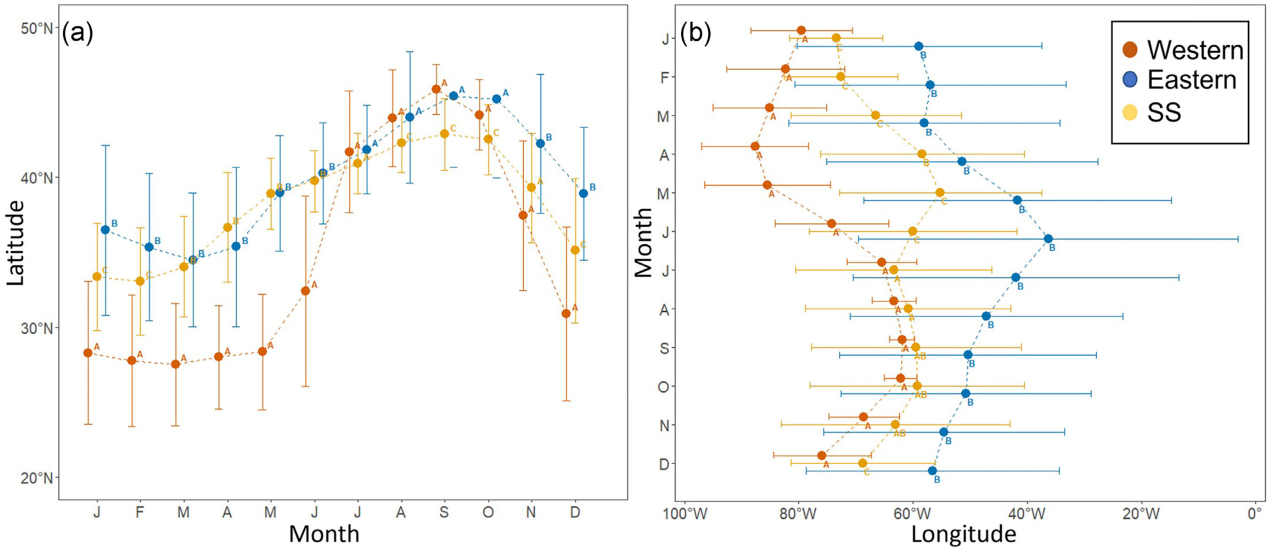

Figure 7. Spatial range comparisons between the SS spawning ABT (*T. thynnus*) and the two primary stocks. (a) Statistical comparisons of latitude. Points indicate mean monthly value aggregated for each fish, then across the entire stock, with slight offsets for visual clarity. Error bars show 1 *SD*. Labels indicate groupings with statistically significant difference in means (Student's *t*-test), with the western stock ($n = 92$) always defined as group A, eastern stock ($n = 43$) as B if different from the western, and the SS spawners ($n = 24$) either A, B, AB, or C depending on how they differ from the other two. (b) Statistical comparisons of longitude. Details per (a).

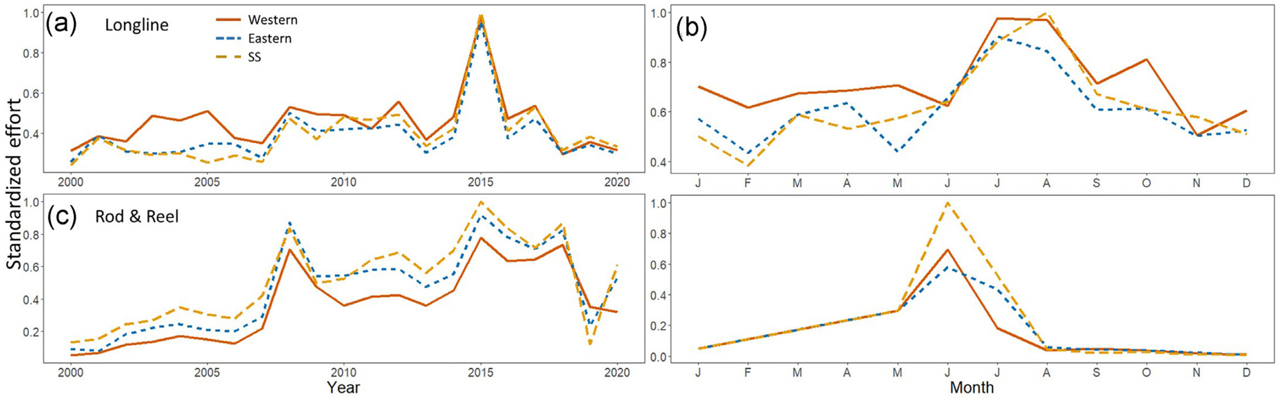

Figure 8. Relative exposure to fishing pressure between the ABT (*T. thynnus*) stocks. The *y*-axis indicates relative exposure to fishing effort (for a specific gear type) since the year 2000, standardized to the maximum across the time period. (a) and (b) Exposure to longline effort by (a) year and (b) month. (c) and (d) Exposure to rod and reel effort by (c) year and (d) month. Note that the effort metrics are not comparable across gear types, only the relative exposure between stocks within each sub-graph.

Table 2. Proportion tagged bluefin tuna (*T. thynnus*) spawning in the SS by age and location.

	SS spawners	Total tagged with tracks[a]	SS proportion
Overall	24	250	0.096
<10 yo	7	73	0.096
10–15 yo	12	109	0.110
15 + yo	5	68	0.074
NC	19	166	0.115
<10 yo	7	72	0.097
10–15 yo	12	92	0.130
15 + yo	0	2	0.000
Canada	5	80	0.063
<10 yo	0	1	0.000
10–15 yo	0	14	0.000
15 + yo	5	65	0.077

a. Total includes all western-tagged fish with tracks that extend into the spawning season (June and beyond). Note that "overall" includes four fish tagged outside of NC and Canada.

do not support Richardson *et al.*'s hypothesis that the SS is *primarily* a spawning ground for smaller individuals, nor do they support the argument for a lower age of maturity. The size distribution of the SS spawners ($n = 24$, 219 cm +/− 28 cm at tagging) is closer to that seen for GOM spawners ($n = 147$, 236 cm +/− 20) than for Mediterranean spawners ($n = 40$, 198 cm +/− 28) in Knapp *et al.* (2014), though the differences are not significant. Although our tagging is biased towards larger individuals, (see "Limitations" below), between 1996 and 2020 we added tracks from 123 fish tagged in the west at <10 years old, of which 73 extended into June the following year (55 into July). A total of seven of the 73 were classified as SS spawners, the same as the proportion across the entire dataset. Furthermore, with the identified SS spawners comprising only ∼12% of NC-tagged fish (and ∼6% of those tagged in the GSL), we do not find support for the contention that the SS spawning ground may be responsible for a more significant portion of western spawning than the GOM. We agree, however, that there must be a more thorough evaluation of the abundance of SS spawners before their role in ABT population structure can be assessed.

Although our spawners were generally eastern in spatial behaviour, there were a variety of migratory patterns observed in adult ABT utilizing these waters. For example, some individuals remained entirely in the West Atlantic while others had much greater longitudinal range, crossing to the coasts of Europe and Africa (Figures 6; Supplementary Figures S1–S3). This may be an indication that more than one population of ABT is spawning in this large region that spans much of the continental slope waters of North America with warm eddy-rich Gulf Stream associations. The presence of GSL-tagged SS spawners starting in 2014 primarily reflects a change in our location for deployment of electronic tags; however, given that tagging in the GSL began before 2014 (31 tracks extending to June, 13 to July from 2008 to 2013 without any evidence of SS spawning; Wilson *et al.*, 2015), it may also reflect a range shift, or a change in behaviour for the current SS population. Alternatively, climate warming of the SS waters may cause individuals from both primary stocks to shift their spawning locations northward, i.e. treating the SS as an alternate spawning ground (ASG). We find that of the five scenarios put forward in Rodriguez-Ezpeleta *et al.* (2019)—ASG for eastern fish, ASG for western fish, ASG for both stocks, inter-breeding ground for both stocks, or independent stock—our results are most consistent with the latter three, as the differing longitudinal ranges observed suggest more than a single source of SS stock genetics. GOM fish continued to spawn in the GOM during the same years we identify SS spawning, indicating there was significant spawning habitat in the GOM and suggesting that the SS activity is distinct and persistent.

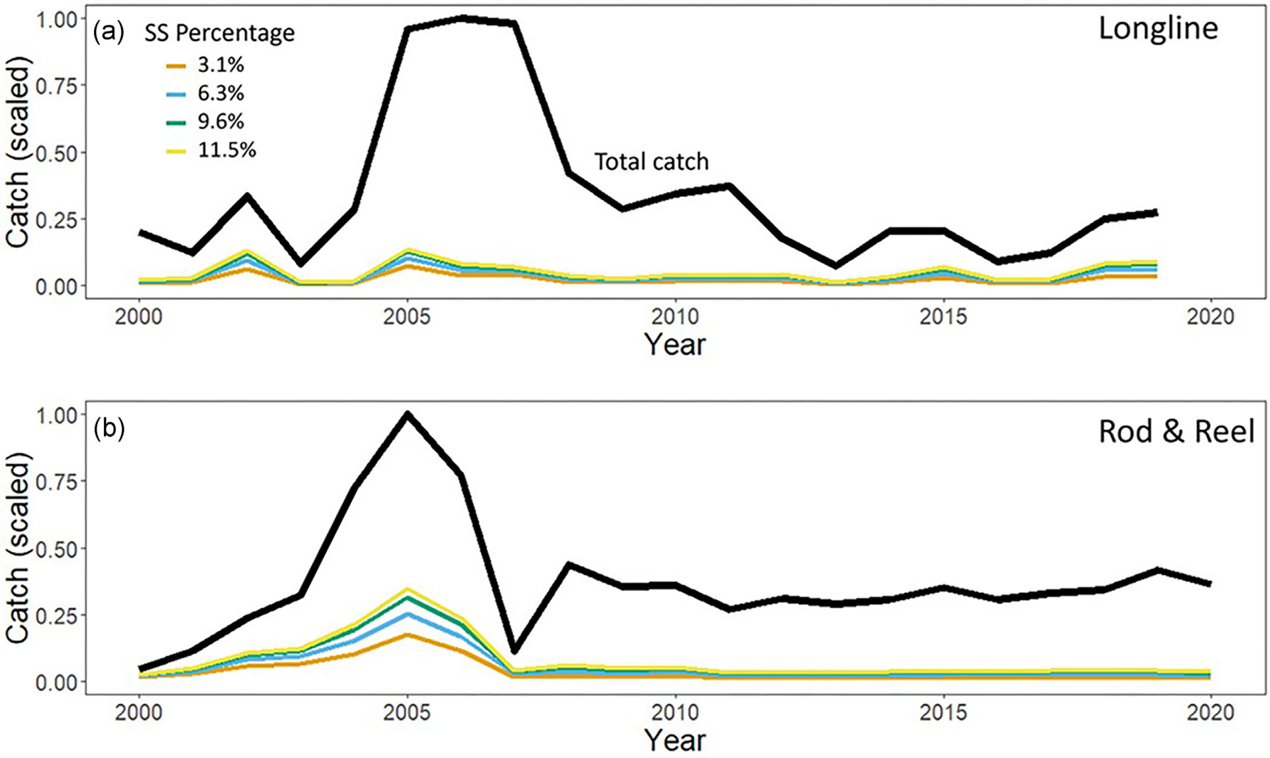

Figure 9. Estimated proportion of Task 2 catch from SS stock ABT (*T. thynnus*) during the tagging period for different SS stock abundance estimates. Black line indicates total catch of all stocks, scaled so maximum annual catch = 1, and coloured lines indicate estimated proportion of catch from SS stock for different estimated levels of SS relative abundance. (a) Longline catch. Note that the correct 2020 values were not available. (b) Rod and reel catch.

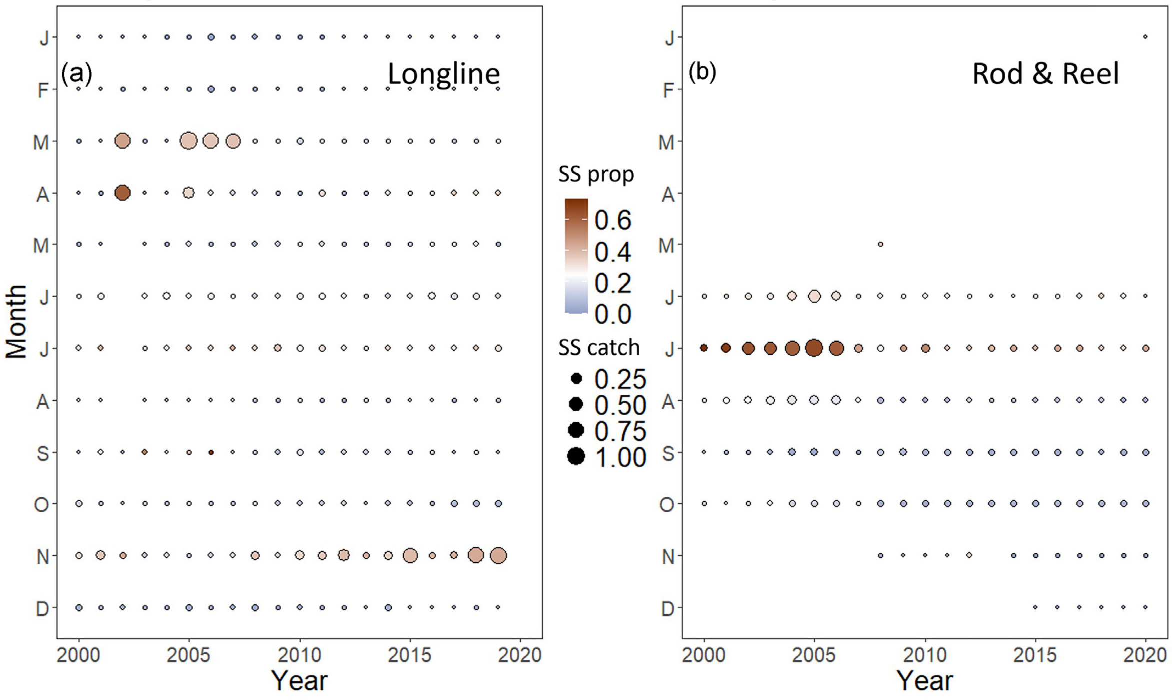

Figure 10. Estimated proportion of Task 2 ABT (*T. thynnus*) catch by month and year for estimated SS stock of 9.6%. Size indicates catch scaled so the maximum monthly catch observed = 1, and colour indicates proportion of total catch. Patterns of relative exposure are the same under different abundance scenarios. (a) Longline catch. Note that the correct 2020 values were not available. (b) Rod and reel catch.

Management implications

The existence of a third spawning ground will increase the complexity of ABT management modelling, especially given the tagging data indicating that these regions are also used by both the GOM- and Med-identified stocks. Current fishery models, whether single stock (e.g. VPA and stock synthesis) or multi-stock (e.g. M3), assume that the two primary stocks inter-mingle mainly when foraging and not on their respective spawning grounds. Spawning outside of the GOM and Western Med is occasionally reported (e.g. Karakulak *et al*., 2004; Rodriguez *et al*., 2021) but assumed to be inconsequential and not factored into management models. Thus, larval surveys in the GOM and Western Med are taken to be representative of stock status, genetic analyses assume no inter-breeding is presently occuring, and fishing restrictions meant to promote spawning—such as the closure of the GOM ABT fishery—do not include seasonal protection in the SS. The identification of the SS as a significant mixed-stock spawning ground would challenge these assumptions and necessitate the integration of its effects into management models. Additionally, the supply of these SS fish close to North America will provide new challenges for quota allocations to already well-mixed western fisheries.

The importance of the SS spawning ground depends on what proportion of the western and eastern stocks are spawning there and whether the two stocks are inter-breeding or, potentially, whether the SS spawners represent an independent stock. An unaccounted-for spawning ground representing, e.g. <10% of total Northwest Atlantic spawning is unlikely to affect management model outputs, given the high variance inherent in fish recruitment projections (e.g. Fromentin and Ravier, 2005; Harford *et al*., 2017) and the mobility of ABT. However, if SS spawning is 10–30% of total Northwest Atlantic spawning, as argued by Richardson *et al*. (2016a), then its effects on population dynamics could be substantial. Given the heightened exposure of SS spawners to West Atlantic fishing pressure during their spawning period (Figure 9b and d), seasonal protections in the region could increase recovery in the West Atlantic if a high proportion of potential SS spawners are currently caught before reproducing. Although the estimated proportion of SS spawners (based on proportion of tagged individuals) ranged from 6 to 12% (Table 2), the corresponding share of West Atlantic catch in the Task 2 effort simulation was 27–208% higher than would be proportionally expected, due to high fishing exposure (Figure 10 and Supplementary Table S2). Note that only West Atlantic catch is considered here; total fishing exposure of the eastern stock is much higher due to high fishing pressure in the Mediterranean. In addition, the ICCAT Task 2 spatial catch/effort data is not necessarily representative of the total distribution of fishing catch and effort. However, assessment of this spawning ground and its interaction with fisheries is currently absent from ICCAT's management. Understanding the behaviour of these spawners and estimating their abundance relative to both primary stocks is essential for clarifying their importance to ABT's population structure, estimating their share of total ABT catch, and potentially managing them as an independent stock.

Because both western- and eastern-stock individuals can be found in the SS during the spawning months, it may create an opportunity for inter-breeding between the stocks. Although western-assigned fish (i.e. fish which entered the GOM during the spawning season) occasionally swim across the Atlantic, none have been known to enter the Med; however, there is some genetic evidence that a small proportion have done so (e.g. Block *et al*., 2005; Boustany *et al*., 2008; Rooker *et al*., 2014). The presence of GOM fish in the Med requires corroboration with more recent techniques as this genetic signal could also be a potential result of introgression at the SS. Similarly, in recent years, genetic studies have also shown that eastern-stock individuals do sometimes enter the eastern GOM and spawn, leading to the appearance of eastern genetic signatures in GOM larvae (Johnstone *et al*., 2021, Reeb *et al*. pers. comm.), but the SS has the potential to be a greater source of introgression. Even if inter-breeding is occurring, it is unclear how individuals born as SS larvae behave as adults. Although we observed multi-year site fidelity in two of the SS spawners, SS larvae may nonetheless revert to the spawning ground most affiliated with their western- or eastern-stock genetics. If they do maintain fidelity to the SS, there is the potential for the emergence (or identification, if already extant) of an independent stock. Further genetic analyses of larvae and adult spawners may be able to discriminate between SS individuals and the western and eastern stocks, allowing managers to begin estimating biomass and catch proportion. Given that it is most likely a small population compared to the western and eastern stocks, such data would necessitate a decision about whether the SS stock should be considered a conservation priority, with all the spawning ground protections and catch reductions this entails. Protecting the SS may become more critical to the health of the western stock if climate change renders the GOM inhospitable to ABT spawning (Muhling *et al*., 2011b).

Limitations and next steps

We identified spawning in this study via visual inspection of dive behaviour, together with light and external temperature data (and internal, if available) and using previously described criteria for proxies of spawning. The easiest way to find putative spawning is to examine external temperature data and look for the warmest and most prolonged event of warming. We can then go into the record and look at diving periodicity, diel behaviours, internal temperature, and movement behaviour (e.g. Teo *et al*., 2007a; Aranda *et al*., 2013). This is an indirect observation, as direct validation of spawning in the field for a tagged fish is near impossible. Consequently, it is possible that some of the spawning events shown here were misidentified and the conclusions regarding SS spawning frequency or other characteristics of the SS spawners are overstated or inaccurate. However, Aranda *et al*. (2013) established via video evidence that high-frequency shallow dives were directly associated with spawning, and estimated that actual spawning events occurred in ∼83% of the days in the inferred spawning period.

Identified SS spawners in this study were considered by spatial use of the ocean to be more similar to eastern-stock fish in their behaviour; however, this may partially result from electronic tagging bias (i.e. the location at which we tag). Western-stock individuals in our database were, on average, larger than eastern-stock individuals. We preferentially in our early years tagged larger fish in the GSL (>250 cm CFL), an area with historically high western-stock presence, potentially limiting the number of small western-stock individuals tracked. Conversely, the NC location, the site for the younger year classes of fish we tagged, has a much higher eastern-stock presence due to high mixing at this location. Consequently, if spawning in the SS is related to size, our data may be biased towards the tagging of eastern-stock individuals. However, the distribution of SS spawners is similar to the distribution of the total "potential spawner" dataset (i.e. those with tracks extending into June; Figure 3a), suggesting that the 24 individuals identified here are representative of the larger population, at least for individuals greater than 150 cm.

Getting an accurate estimate of the size of the SS spawning population will be difficult and time-consuming and will likely require additional efforts for tagging and fishery surveys specific to the SS, pooling of data among working groups, and further developments in genetics-based stock assignment using whole genome sequencing techniques. Recent resurgence of bluefin tuna fishing from NC to the mid-Atlantic may enable increased electronic tagging in this location and directly in the SS fishing areas to the north. We, and others, are working on a more accurate analysis of western and eastern stock introgression and will apply these methods to the genetic samples from all the SS spawners to determine how they relate to the two primary stocks. To explore the implications of a third spawning ground, we plan to use ABT spatial population simulations to study changes in dynamics for different SS biomass levels under the five SS spawning scenarios. We will also integrate these scenarios into the M3 mixing model (Carruthers, 2017) and explore how they affect management decisions aimed at balancing utilization of the rapidly recovering eastern stock with protection of the weaker western stock, especially if preserving the SS spawners as an independent stock were to become a management priority. If these models prove sensitive to the presence of the SS spawning ground, the results may motivate managing bodies such as ICCAT to pursue the research necessary to formally assess the role the SS plays in ABT population structure.

Conclusion

The TAG data sets spanning from 1996 to present enabled a retrospective analyses and identified 24 putative SS spawners. The ABT identified in this study represent the first characterization of spawning adults in the SS, with ages ranging from 6 to 21 years old and multi-year site fidelity for at least two individuals. Their movement and behaviour suggest that they are primarily, though likely not exclusively, of eastern-stock origin. These data support the hypothesis that the SS is a mixed-stock spawning ground, increasing the potential for inter-breeding between the western and eastern stocks and, given the ages and repeat spawning, possibly representing an independently breeding stock. The spawners have high exposure to the rod and reel fishery during their spawning period, suggesting that seasonal protections could increase overall ABT breeding success in the West Atlantic. Because of the implications for both western stock recovery and ABT genetics, we strongly urge further research to better assess the size of the SS spawning population and determine its significance to ABT stock dynamics and sustainable management.

Acknowledgements

This research was funded by the NOAA Bluefin Tuna Research Program, TAG-A-Giant Fund of The Ocean Foundation, Stanford University, and an NSERC Discovery Grant to MJWS. MJWS was supported by the Canada Research Chairs Program. GSL bluefin were tagged under a Fisheries and Ocean Scientific License to Fish #SG-RHQ-19–120 and Acadia Animal Care Protocol # 12–16R#3. The authors thank the fishers of Morehead City and Cape Hatteras North Carolina, for supporting the TAG A Giant Campaign, particularly Captains Dale Britt, Gary Stuve, the late Captain John Jenkins and in Port Hood Canada, Captain Dennis Cameron, Lloyd McInnis, the late Captain Steve McInnis, and Captain Bernie and Kenny Chisolm for their dedication and fishing effort on behalf of the research program. The authors also thank sponsors of tags and postdocs, students, and technicians who helped electronically tag Atlantic bluefin tuna the past 25 years.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

Data availability

All analyses were conducted in R version 4.0.2 (R Core Team, 2021), with code for figures and analyses available in Stanford Digital Repository, at https://doi.org/10.25740/qm788vt3986. The data underlying this article will be shared on reasonable request to the corresponding author.

Authors' contributions

EA identified spawning candidates, performed spatial and harvest analyses, composed figures, and wrote the manuscript.

SD performed environmental analyses and produced figures.

MS carried out tagging activities.

RS carried out tagging activities.

MC processed tag data and produced figures.

BB tagged fish, identified spawning behaviour, and revised the manuscript.

References

Aalto, E. A., Ferretti, F., Lauretta, M. V, Walter, J. F., Stokesbury, M. J. W., Schallert, R. J., and Block, B. A. 2021. Stock-of-origin catch estimation of Atlantic bluefin tuna (*Thunnus thynnus*) based on observed spatial distributions. Canadian Journal of Fisheries and Aquatic Sciences, 78: 1193–1204.

Abascal, F. J., Medina, A., De La Serna, J. M., Godoy, D., and Aranda, G. 2016. Tracking bluefin tuna reproductive migration into the Mediterranean Sea with electronic pop-up satellite archival tags using two tagging procedures. Fisheries Oceanography, 25: 54–66.

Aranda, G., Abascal, F. J., Varela, J. L., and Medina, A. 2013. Spawning behaviour and post-spawning migration patterns of Atlantic bluefin tuna (*Thunnus thynnus*) ascertained from satellite archival tags. PLoS ONE, 8: e76445.

Arregui, I., Galuardi, B., Goñi, N., Lam, C. H., Fraile, I., Santiago, J., Lutcavage, M. *et al.* 2018. Movements and geographic distribution of juvenile bluefin tuna in the Northeast Atlantic, described through internal and satellite archival tags. ICES Journal of Marine Science, 75: 1560–1572.

Auer, S. J. 1987. Five-year climatological survey of the Gulf Stream system and its associated rings. Journal of Geophysical Research, 92: 11709–11726.

Baglin, R. E. 1976. A preliminary study of the gonadal development and fecundity of the western Atlantic bluefin tuna. ICCAT Collected Volume of Scientific Papers, 5: 279–289.

Blank, J. M., Morrissette, J. M., Landeira-Fernandez, A. M., Blackwell, S. B., Williams, T. D., and Block, B. A. 2004. In situ cardiac performance of Pacific bluefin tuna hearts in response to acute temperature change. Journal of Experimental Biology, 207: 881–890.

Block, B. A., Dewar, H., Williams, T., and Prince, E. D. 1998. Archival tagging of Atlantic bluefin tuna (*Thunnus thynnus thynnus*). Marine Technology Society Journal, 32: 37.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A. *et al.* 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science, 293: 1310–1314.

Block, B. A., Teo, S. L. H., Walli, A., Boustany, A., Stokesbury, M. J. W., Farwell, C. J., Weng, K. C. *et al.* 2005. Electronic tagging and population structure of Atlantic bluefin tuna. Nature, 434: 1121.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L. *et al.* 2011. Tracking apex marine predator movements in a dynamic ocean. Nature, 475: 86–90.

Boustany, A. M., Reeb, C. A., and Block, B. A. 2008. Mitochondrial DNA and electronic tracking reveal population structure of Atlantic bluefin tuna (*Thunnus thynnus*). Marine Biology, 156: 13–24.

Brophy, D., Rodríguez-Ezpeleta, N., Fraile, I., and Arrizabalaga, H. 2020. Combining genetic markers with stable isotopes in otoliths reveals complexity in the stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). Scientific Reports, 10: 1–17.

Butler, C. M. 2007. Atlantic bluefin tuna (*Thunnus thynnus*) feeding ecology and potential ecosystem effects during winter in North Carolina. MSc thesis, NC State University Libraries, Raleigh.

Carlsson, J., McDowell, J. A. N. R., Díaz-Jaimes, P., Carlsson, J. E. L., Boles, S. B., Gold, J. R., and Graves, J. E. 2004. Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (*Thunnus thynnus thynnus*) population structure in the Mediterranean Sea. Molecular Ecology, 13: 3345–3356.

Carlsson, J., McDowell, J. R., Carlsson, J. E. L., and Graves, J. E. 2007. Genetic identity of YOY bluefin tuna from the eastern and western Atlantic spawning areas. Journal of Heredity. 98: 23–28.

Carruthers, T. 2017. Modifiable Multistock Model (M3): A User's Guide. https://www.iccat.int/GBYP/Docs/Modelling_Phase_6_M3_Software_User_Guide.pdf. [Last accessed date 14 March 2021].

Cermeño, P., Quílez-Badia, G., Ospina-Alvarez, A., Sainz-Trápaga, S., Boustany, A. M., Seitz, A. C., Tudela, S. *et al.* 2015. Electronic tagging of Atlantic bluefin tuna (*Thunnus thynnus*, L.) reveals habitat use and behaviors in the Mediterranean Sea. PLoS ONE. 10: e0116638.

Chase, B. C. 2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. Fishery Bulletin, 100: 168–180.

Corriero, A., Karakulak, S., Santamaria, N., Deflorio, M., Spedicato, D., Addis, P., Desantis, S. *et al.* 2005. Size and age at sexual maturity of female bluefin tuna (*Thunnus thynnus* L. 1758) from the Mediterranean Sea. Journal of Applied Ichthyology. 21: 483–486.

Cort, J. L., Arregui, I., Estruch, V. D., and Deguara, S. 2014. Validation of the growth equation applicable to the eastern Atlantic bluefin tuna, *Thunnus thynnus* (L.), using L max, tag-recapture, and first dorsal spine analysis. Reviews in Fisheries Science and Aquaculture, 22: 239–255.

Diaz, G. A., and Turner, S. C. 2007. Size frequency distribution analysis, age composition, and maturity of western bluefin tuna in the Gulf of Mexico from the US (1981-2005) and Japanese (1975-1981) longline fleets. ICCAT Collective Volume of Scientific Papers, 60: 1160–1170.

Dickhut, R. M., Deshpande, A. D., Cincinelli, A., Cochran, M. A., Corsolini, S., Brill, R. W., Secor, D. H. *et al.* 2009. Atlantic bluefin tuna (*Thunnus thynnus*) population dynamics delineated by organochlorine tracers. Environmental Science and Technology, 43: 8522–8527.

Druon, J.-N., Fromentin, J.-M., Hanke, A. R., Arrizabalaga, H., Damalas, D., Tičina, V., Quílez-Badia, G. *et al.* 2016. Habitat suitability of the Atlantic bluefin tuna by size class: an ecological niche approach. Progress in Oceanography, 142: 30–46.

Fromentin, J.-M., and Ravier, C. 2005. The East Atlantic and Mediterranean bluefin tuna stock: looking for sustainability in a context of large uncertainties and strong political pressures. Bulletin of Marine Science, 76: 353–362.

Fromentin, J., and Powers, J. E. 2005. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish and Fisheries, 6: 281–306.

Fromentin, J., Reygondeau, G., Bonhommeau, S., and Beaugrand, G. 2014. Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish and Fisheries, 23: 147–156.

Galuardi, B., Royer, F., Golet, W., Logan, J., Neilson, J., and Lutcavage, M. 2010. Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. Canadian Journal of Fisheries and Aquatic Sciences, 67: 966–976.

Galuardi, B., and Lutcavage, M. 2012. Dispersal routes and habitat utilization of juvenile Atlantic bluefin tuna, *Thunnus thynnus*, tracked with mini PSAT and archival tags. PLoS ONE, 7: e37829.

Goñi, N., and Arrizabalaga, H. 2010. Seasonal and interannual variability of fat content of juvenile albacore (*Thunnus alalunga*) and bluefin (*Thunnus thynnus*) tunas during their feeding migration to the Bay of Biscay. Progress in Oceanography, 86: 115–123.

Gordoa, A., and Carreras, G. 2014. Determination of temporal spawning patterns and hatching time in response to temperature of Atlantic bluefin tuna (*Thunnus thynnus*) in the Western Mediterranean. PLoS ONE, 9: e90691.

Harford, W. J., Karnauskas, M., Walter, J. F., and Liu, H. 2017. Nonparametric modeling reveals environmental effects on bluefin tuna recruitment in Atlantic, Pacific, and Southern Oceans. Fisheries Oceanography, 26: 396–412.

Hazen, E. L., Carlisle, A. B., Wilson, S. G., Ganong, J. E., Castleton, M. R., Schallert, R. J., Stokesbury, M. J. W. *et al.* 2016. Quantifying overlap between the Deepwater Horizon oil spill and predicted bluefin tuna spawning habitat in the Gulf of Mexico. Scientific Reports, 6: 33824.

Hernández, C. M., Richardson, D. E., Rypina, I. I., Chen, K., Marancik, K. E., Shulzitski, K., and Llopiz, J. K. 2022. Support for the Slope Sea as a major spawning ground for Atlantic bluefin tuna: evidence from larval abundance, growth rates, and particle-tracking simulations. Canadian Journal of Fisheries and Aquatic Sciences, 79: 814–824.

ICCAT. 2017. Report of the 2017 ICCAT bluefin stock assessment meeting. International Commission for the Conservation of Atlantic Tuna, Madrid.

ICCAT. 2018. Executive summary of Atlantic bluefin tuna. International Commission for the Conservation of Atlantic Tuna, Madrid.

ICCAT. 2020. 2020 advice to the Commission. International Commission for the Conservation of Atlantic Tuna, Madrid.

ICCAT. 2021. Report of the 2021 western bluefin stock assessment meeting. International Commission for the Conservation of Atlantic Tuna, Madrid.

Johnstone, C., Pérez, M., Malca, E., Quintanilla, J. M., Gerard, T., Lozano-Peral, D., Alemany, F. *et al.* 2021. Genetic connectivity between Atlantic bluefin tuna larvae spawned in the Gulf of Mexico and in the Mediterranean Sea. PeerJ, 9: e11568.

Karakulak, S., Oray, I., Corriero, A., Deflorio, M., Santamaria, N., Desantis, S., and De Metrio, G. 2004. Evidence of a spawning area for the bluefin tuna (*Thunnus thynnus* L.) in the eastern Mediterranean. Journal of Applied Ichthyology, 20: 318–320.

Knapp, J. M., Aranda, G., Medina, A., and Lutcavage, M. 2014. Comparative assessment of the reproductive status of female Atlantic bluefin tuna from the Gulf of Mexico and the Mediterranean Sea. PLoS ONE, 9: e98233.

Lamkin, J. T., Muhling, B. A., Malca, E., Laiz-Carrión, R., Gerard, T., Privoznik, S., Liu, Y. *et al.* 2014. Do western Atlantic bluefin tuna spawn outside of the Gulf of Mexico? Results from a larval survey in the Atlantic Ocean in 2013. Collective Volume of Scientific Papers ICCAT, 71: 1736–1745.

Logan, J. M., Rodríguez-Marín, E., Goñi, N., Barreiro, S., Arrizabalaga, H., Golet, W., and Lutcavage, M. 2011. Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. Marine Biology, 158: 73–85.

Lumley, T., Diehr, P., Emerson, S., and Chen, L. 2002. The importance of the normality assumption in large public health data sets. Annual Review of Public Health, 23: 151–169.

Lutcavage, M. E., Brill, R. W., Skomal, G. B., Chase, B. C., and Howey, P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic?. Canadian Journal of Fisheries and Aquatic Sciences, 56: 173–177.

Macfadyen, G., Huntington, T., Defaux, V., Llewellin, P., and James, P. 2021. Netting Billions: A Global Valuation of Tuna (An Update). Poseidon Aquatic Resources Management Ltd, Lymington.

Madigan, D. J., Carlisle, A. B., Gardner, L. D., Jayasundara, N., Micheli, F., Schaefer, K. M., Fuller, D. W. *et al.* 2015. Assessing niche width of endothermic fish from genes to ecosystem. Proceedings of the National Academy of Sciences, 112: 8350–8355.

Magnuson, J. J., Block, B. A., Deriso, R., Gold, J., Grant, W., Quinn, T. I., Saila, S. *et al.* 1994. An Assessment of Atlantic Bluefin Tuna. National Academy Press, Washington, DC.

Mann, H. B., and Whitney, D. R. 1947. On a test of whether one of two random variables is stochastically larger than the other. The Annals of Mathematical Statistics, 18: 50–60.

Mather, F. J., Mason, J. M., and Jones, a C. 1995. Historical document: life history and fisheries of Atlantic bluefin tuna. NOAA Technical Memorandum, NMFS-SEFSC: 165. National Oceanic and Atmospheric Administration, Washington, DC. http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Historical+Document+:+Life+History+and+Fisheries+of+Atlantic+Bluefin+Tuna#0. [Last accessed date 20 June 2021].

, MERCINA Pershing, A. J., Greene, C. H., Hannah, C., Sameoto, D., Head, E., Mountain, D. G. *et al.* 2001. Oceanographic responses to climate in the northwest Atlantic. Oceanography, 14: 76–82.

Meyer-Gutbrod, E. L., Greene, C. H., Davies, K. T. A., and Johns, D. G. 2021. Ocean regime shift is driving collapse of the North Atlantic right whale population. Oceanography, 34: 22–31.

Muhling, B. A., Lamkin, J. T., Quattro, J. M., Smith, R. H., Roberts, M. A., Roffer, M. A., and Ramírez, K. 2011a. Collection of larval bluefin tuna (*Thunnus thynnus*) outside documented western Atlantic spawning grounds. Bulletin of Marine Science, 87: 687–694.

Muhling, B. A., Lee, S.-K., Lamkin, J. T., and Liu, Y. 2011b. Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico. ICES Journal of Marine Science, 68: 1051–1062.

Neill, W. H., Stevens, E. D., Carey, F. G., Lawson, K. D., Mrosovsky, N., and Frair, W. 1974. Thermal inertia versus thermoregulation in "warm" turtles and tunas. Science, 184: 1008–1010.

Pastore, M., and Calcagnì, A. 2019. Measuring distribution similarities between samples: a distribution-free overlapping index. Frontiers in Psychology, 10: 1089. [Last accessed date 31 October 2022].

Pleizier, N. K., Campana, S. E., Schaller, R. J., Wilson, S. G., and Block, B. A. 2012. Atlantic bluefin tuna (*Thunnus thynnus*) diet in the Gulf of St. Lawrence and on the eastern Scotian Shelf. Journal of Northwest Atlantic Fishery Science, 44: 67–76,

Puncher, G. N., Cariani, A., Maes, G. E., Van Houdt, J., Herten, K., Cannas, R., Rodriguez-Ezpeleta, N. *et al.* 2018. Spatial dynamics and mixing of bluefin tuna in the Atlantic Ocean and Mediterranean Sea revealed using next-generation sequencing. Molecular Ecology Resources, 18: 620–638.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org.

Restrepo, V. R., Diaz, G. A., Walter, J. F., Neilson, J. D., Campana, S. E., Secor, D., and Wingate, R. L. 2010. Updated estimate of the growth curve of western Atlantic bluefin tuna. Aquatic Living Resources, 23: 335–342.

Richardson, D. E., Marancik, K. E., Guyon, J. R., Lutcavage, M. E., Galuardi, B., Lam, C. H., Walsh, H. J. *et al.* 2016a. Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). Proceedings of the National Academy of Sciences, 113: 3299–3304.

Richardson, D. E., Marancik, K. E., Guyon, J. R., Lutcavage, M. E., Galuardi, B., Lam, C. H., Walsh, H. J. *et al.* 2016b. Reply to Safina and Walter et al.: multiple lines of evidence for size-structured spawning migrations in western Atlantic bluefin tuna. Proceedings of the National Academy of Sciences, 113: E4262–E4263.

Rodríguez-Ezpeleta, N., Díaz-Arce, N., Walter, J. F., Richardson, D. E., Rooker, J. R., Nøttestad, L., Hanke, A. R. *et al.* 2019. Determining natal origin for improved management of Atlantic bluefin tuna. Frontiers in Ecology and the Environment, 17: 439–444.

Rodriguez, J. M., Johnstone, C., and Lozano-Peral, D. 2021. Evidence of Atlantic bluefin tuna spawning in the Bay of Biscay, NE Atlantic. Journal of Fish Biology, 99: 964–969.

Rooker, J. R., Secor, D. H., De Metrio, G., Schloesser, R., Block, B. A., and Neilson, J. D. 2008a. Natal homing and connectivity in Atlantic bluefin tuna populations. Science, 322: 742–744.

Rooker, J. R., Secor, D. H., DeMetrio, G., Kaufman, A. J., Ríos, A. B., and Ticina, V. 2008b. Evidence of trans-Atlantic movement and natal homing of bluefin tuna from stable isotopes in otoliths. Marine Ecology Progress Series, 368: 231–239.

Rooker, J. R., Arrizabalaga, H., Fraile, I., Secor, D. H., Dettman, D. L., Abid, N., Addis, P. *et al.* 2014. Crossing the line: migratory and homing behaviors of Atlantic bluefin tuna. Marine Ecology Progress Series, 504: 265–276.

Rooker, J. R., Fraile, I., Liu, H., Abid, N., Dance, M. A., Itoh, T., Kimoto, A. *et al.* 2019. Wide-ranging temporal variation in transoceanic movement and population mixing of bluefin tuna in the North Atlantic Ocean. Frontiers in Marine Science, 6: 398.

Rouyer, T., Kimoto, A., Kell, L., Walter, J. F., Lauretta, M., Zarrad, R., Ortiz, M. *et al.* 2018. Preliminary 2017 stock assessment results for the Eastern and Mediterranean Atlantic bluefin tuna stock. ICCAT Collective Volume of Scientific Papers, 74: 3234–3275.

Rypina, I. I., Chen, K., Hernández, C. M., Pratt, L. J., and Llopiz, J. K. 2019. Investigating the suitability of the Slope Sea for Atlantic bluefin tuna spawning using a high-resolution ocean circulation model. ICES Journal of Marine Science, 76: 1666–1677.

Rypina, I. I., Dotzel, M. M., Pratt, L. J., Hernandez, C. M., and Llopiz, J. K. 2021. Exploring interannual variability in potential spawning habitat for Atlantic bluefin tuna in the Slope Sea. Progress in Oceanography, 192: 102514.

Safina, C. 2016. Data do not support new claims about bluefin tuna spawning or abundance. Proceedings of the National Academy of Sciences, 113: E4261–E4261.

Schloesser, R. W., Neilson, J. D., Secor, D. H., and Rooker, J. R. 2010. Natal origin of Atlantic bluefin tuna (*Thunnus thynnus*) from Canadian waters based on otolith δ 13C and δ 18O. Canadian Journal of Fisheries and Aquatic Sciences, 67: 563–569.

Stevens, E. D., Kanwisher, J. W., and Carey, F. G. 2000. Muscle temperature in free-swimming giant Atlantic bluefin tuna (*Thunnus thynnus* L.). Journal of Thermal Biology, 25: 419–423.

Stokesbury, M. J. W., Teo, S. L. H., Seitz, A., O'Dor, R. K., and Block, B. A. 2004. Movement of Atlantic bluefin tuna (*Thunnus thynnus*) as determined by satellite tagging experiments initiated off New England. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1976–1987.

Student. 1908. The probable error of a mean. Biometrika. 6: 1–25.

Teo, S. H. L., and Boustany, A. 2016. Movements and habitat use of Atlantic bluefin tuna. *In* Biology and Ecology of Bluefin Tuna, pp. 137–188. CRC Press, Boca Raton, FL.

Teo, S. L. H., Boustany, A., Blackwell, S., Walli, A., Weng, K. C., and Block, B. A. 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Marine Ecology Progress Series, 283: 81–98.

Teo, S. L. H., Boustany, A., Dewar, H., Stokesbury, M. J. W., Weng, K. C., Beemer, S., Seitz, A. C. *et al*. 2007a. Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. Marine Biology, 151: 1–18.

Teo, S. L. H., Boustany, A. M., and Block, B. A. 2007b. Oceanographic preferences of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. Marine Biology, 152: 1105–1119.

Walli, A., Teo, S. L. H., Boustany, A., Farwell, C. J., Williams, T., Dewar, H., Prince, E. *et al*. 2009. Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. PLoS ONE, 4: e6151.

Walter, J. F., Porch, C. E., Lauretta, M. V, Cass-Calay, S. L., and Brown, C. A. 2016. Implications of alternative spawning for bluefin tuna remain unclear. Proceedings of the National Academy of Sciences, 113: E4259–E4260.

Weisstein, E. W. 2004. Bonferroni correction. Wolfram Research, Inc, Champaign, IL.

Wilcoxon, F. 1992. Individual comparisons by ranking methods. *In* Breakthroughs in Statistics, pp. 196–202. Springer, Berlin.

Wilson, S. G., Lawson, G. L., Stokesbury, M. J. W., Spares, A., Boustany, A. M., Neilson, J. D., and Block, B. A. 2011. Movements of Atlantic bluefin tuna from the Gulf of St. Lawrence to their spawning grounds. Collective Volume of Scientific Papers ICCAT, 66: 1247–1256.

Wilson, S. G., Jonsen, I. D., Schallert, R. J., Ganong, J. E., Castleton, M. R., Spares, A. D., Boustany, A. M. *et al*. 2015. Tracking the fidelity of Atlantic bluefin tuna released in Canadian waters to the Gulf of Mexico spawning grounds. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1700–1717.

Handling Editor: Howard Browman