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ARTICLE

Tracking the fidelity of Atlantic bluefin tuna released in Canadian waters to the Gulf of Mexico spawning grounds

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Abstract: The objective of this study was to advance the use of pop-up satellite archival tags to track the migrations of Atlantic bluefin tuna (*Thunnus thynnus*) to their spawning grounds. Deployment of tags occurred in the Gulf of St. Lawrence, Canada, during fall months from 2007 to 2013. Pop-up satellite archival tags ($n = 135$) were attached to 125 Atlantic bluefin tuna (curved fork length (CFL) = 268 ± 20 cm (mean ± SD)) with the objective of keeping tags on until visitation to a spawning area or longer. A dataset of 18 800 days was acquired, which included 5800 days of time-series data from 19 recovered satellite tags. Many Atlantic bluefin tuna visited the Gulf of Mexico spawning grounds (74%), the mean size of which was 275 ± 14 cm (CFL ± SD, $n = 49$), with a measured CFL of 243 to 302 cm. These fish had a mean entry date into the Gulf of Mexico of 14 January ± 42 days (SD). The mean residency period for fish that had tracks with entrance and exit from the Gulf of Mexico was 123 ± 49 days (SD) ($n = 22$). Atlantic bluefin tuna that moved into the Gulf of Mexico during the spawning season remained west of the 45°W meridian for the duration of the track. Electronic tagging datasets from two fish were obtained before, during, and after the Deepwater Horizon oil spill. Both fish utilized habitat in the vicinity of the Macondo Well on 20 April 2010 when the Deepwater Horizon oil drilling rig accident occurred. Spawning hotspots are identified in the Gulf of Mexico using kernel density analyses and compared with the newly established closed areas.

Résumé : L'étude a pour but de favoriser l'utilisation d'étiquettes satellites autodétachables pour suivre la migration des thons rouges de l'Atlantique (*Thunnus thynnus*) vers leurs lieux de frai. Un déploiement d'étiquettes a eu lieu dans le golfe du Saint-Laurent (Canada) durant les mois d'automne de 2007 à 2013. Les étiquettes satellites autodétachables ($n = 135$) ont été fixées à 125 thons rouges de l'Atlantique (longueur courbée à la fourche moyenne : 268 ± 20 cm, ET) en prévision qu'elles restent fixées jusqu'à la visite d'un lieu de frai ou plus longtemps. Un ensemble de données couvrant 18 800 jours a été obtenu, dont 5800 jours de données en séries chronologiques obtenues de 19 étiquettes satellites récupérées. De nombreux thons rouges de l'Atlantique ont visité la zone de frai du golfe du Mexique (74 %) et avaient une taille moyenne de 275 ± 14 cm (LCF ± ET, $n = 49$), les LCF mesurées allant de 243 cm à 302 cm. La date d'entrée moyenne dans le golfe du Mexique de ces poissons était le 14 janvier ± 42 jours (ET). La période de résidence moyenne pour les poissons dont les parcours comprenaient l'entrée et la sortie du golfe du Mexique était de 123 ± 49 jours (ET) ($n = 22$). Les thons rouges qui entraient dans le golfe du Mexique durant la période de frai sont demeurés à l'ouest du méridien 45°O pour la durée de la période de suivi. Des données électroniques de marquage de deux poissons ont été obtenues avant, durant et après le déversement de pétrole de Deepwater Horizon. Ces deux poissons utilisaient des habitats à proximité du puits Macondo, le 20 avril 2010, quand l'accident de la plateforme de forage Deepwater Horizon s'est produit. Des points chauds de frai ont été cernés dans le golfe du Mexique à l'aide d'analyses de la densité des noyaux et ont été comparés aux zones fermées à la pêche nouvellement établies. [Traduit par la Rédaction]

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) is a large (>650 kg) and long-lived *Thunnus* species that has a range that extends throughout the North Atlantic, from North America to coastal Greenland seas (MacKenzie et al. 2014) to Ireland (Stokesbury et al. 2007) and Norway and into the South Atlantic as far south as Argentina (Di Natale et al. 2013; Mather et al. 1995). Known spawning areas include the Gulf of Mexico (GOM) and adjacent waters and the Mediterranean Sea (Mather et al. 1995). This bluefin is one of three species of bluefin tunas; the other two species are the Pacific bluefin tuna (*Thunnus orientalis*), which occupies the Pacific Ocean, and the Southern bluefin tuna (*Thunnus maccoyyi*), which occupies the Southern and Indian oceans.

Electronic tagging of Atlantic bluefin tuna has emerged as a powerful tool to reduce the uncertainty in scientific knowledge on this species and inform fisheries management (Block et al. 1998, 2001, 2005; Galuardi and Lutcavage 2012; Lawson et al. 2010; Lutcavage et al. 1999; Teo et al. 2007*a*, 2007*b*; Stokesbury et al. 2004, 2011; Walli et al. 2009; Wilson et al. 2005) and stock assessment models (Taylor et al. 2011). Atlantic bluefin tuna are currently managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as two fisheries management units separated by the 45°W meridian in the North Atlantic: a western management unit that spawns in the GOM, Caribbean, and Bahamas and an eastern management unit that spawns in the Mediterranean Sea (National Research Council (NRC) 1994). In the Mediterranean

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Sea, two populations that may have varied life histories have been proposed from recent electronic tagging data and genetics (Cermeño et al. 2015; Fromentin and Lopuszanski 2013; Carlsson et al. 2004; Riccioni et al. 2010, 2013). Although Mediterranean Sea and GOM populations are much reduced from historical biomass levels, the western spawning population is known to be significantly smaller and more severely depleted than the eastern spawning populations (ICCAT 2014).

Tagging, genetics, organochlorine content, and microconstituent analyses of otoliths indicate that the two Atlantic bluefin tuna management units extensively mix when foraging in waters along the eastern seaboard of North America (Block et al. 2005; Boustany et al. 2008; Dickhut et al. 2009; Rooker et al. 2008, 2013, 2014; Schloesser et al. 2010). A significant portion of the Atlantic bluefin tuna in coastal waters off North Carolina and the mid-Atlantic states are now known to be of eastern origin (Rooker et al. 2008; Secor et al. 2013). In northern waters, Atlantic bluefin tuna inhabiting Canada's Gulf of St. Lawrence (GSL) have been shown by microconstituent analyses to be primarily of western origin (Rooker et al. 2008; Schloesser et al. 2010), although more recent measurements suggest some mixing in the GSL (Hanke et al. 2015). To date, mixing between populations is not known to occur on the Atlantic bluefin tuna's GOM and Mediterranean Sea spawning grounds. Natal homing is hypothesized to maintain the structure of Atlantic bluefin tuna populations within management units (Block et al. 2005; Teo et al. 2007*a*; Rooker et al. 2008, 2014). Implanted archival tags provide multiyear tracks and have demonstrated that spawning site fidelity in Atlantic bluefin tuna occurs, with individuals returning to the GOM spawning ground for up to three consecutive years (Teo et al. 2007*a*) and to the Mediterranean Sea for four consecutive years (Block et al. 2005).

The GOM is the presumed spawning ground of Canadian giants. The Deepwater Horizon oil spill, which occurred in April of 2010, encompassed a portion of this bluefin's spawning ground in the eastern GOM. This spill was the largest offshore oil spill in the history of the United States (US) (Crone and Tolstoy 2010) and occurred during the Atlantic bluefin tuna's known spawning period in continental shelf waters (Muhling et al. 2010; Teo et al. 2007*a*). In a recent ruling for purposes of calculating the maximum civil penalty under the U.S. Clean Water Act, the court determined that 3.19 million barrels of oil were discharged into waters of the GOM. The oil is known to impact cardiac tissues of larval and juvenile Atlantic bluefin and yellowfin tunas (Brette et al. 2014; Incardona et al. 2014). How the spillage of oil impacted mature Atlantic bluefin tuna remains unknown.

In this study, we use electronic tagging techniques to better understand the GSL assemblage of Atlantic bluefin tuna, to discern their routes of migration to the spawning grounds and their use of habitat near the Deepwater Horizon oil spill, and to improve our understanding of their use of the GOM waters as a spawning ground. Additional information on fidelity between spawning and foraging grounds was obtained by increasing the track duration and physically recovering pop-up satellite archival tags following detachment.

Methods

Study area

All electronic tagging was conducted in the GSL out of Port Hood on Cape Breton Island, Nova Scotia. Atlantic bluefin tuna move into high-latitude locations to forage on energy rich fish. They aggregate in southern GSL waters from early summer (June) through late fall to feed on Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) (Pleizier et al. 2012; Stokesbury et al. 2011). Atlantic bluefin tuna have been caught in these waters by commercial and recreational fishers since the 1960s, with large fluctuations in abundance. They are targeted by a commercial rod and reel fishery that caught 207 t in 2011, representing 44% of the Canadian quota (Lester et al. 2013). Most of these fish are of presumed western Atlantic bluefin tuna spawning size (>age 8 to age 10), with GSL Atlantic bluefin tuna (commercially captured) averaging 301 kg in 2011.

Electronic tag deployments occurred in the months of September and October in consecutive years from 2007 to 2013 (Table 1). The region selected for the electronic tagging experiments was the Northumberland Strait in the southern GSL, a semi-enclosed sea connected to the North Atlantic Ocean via the Cabot Strait and the Strait of Belle Isle (Koutitonsky and Bugden 1991).

Electronic tagging

Atlantic bluefin tuna were tagged with two generations of pop-up satellite archival tags (PAT tags, Wildlife Computers Inc.): the MK10 PAT (77 g) and the newer miniPAT (57 g) tag, which represents a significant size reduction in the instrument. Some fish were double-tagged during the introduction of the miniPAT tag to compare retention and geolocation performance estimates, with the longest dataset from each fish being selected for analysis. To maximize tagging opportunities, one or more commercial fishing vessels were often utilized to catch Atlantic bluefin tuna in addition to the designated tagging vessel, which was outfitted with a large transom door. The fish were caught on rod and reel with live or freshly caught dead mackerel or herring baits.

Once the Atlantic bluefin tuna were caught on hook and line, the fish was leadered close to the vessel and brought onboard the tagging vessel using a specially designed titanium lip-hook that enabled pulling the fish through the transom door onto a vinyl mat that was slick and wet (Supplementary Fig. S1).[1] The mat permits the fish to slide easily without much friction or damage to the body. A saltwater hose was inserted immediately into the fish's mouth to oxygenate the gills. A soft cloth soaked in a fish protectant solution (PolyAqua) was placed over the eyes to keep the fish calm. Fish were measured for curved fork length (CFL), sampled for genetics, tagged, and released within 1 to 2 min of capture. When possible, pictures of tag position were obtained upon release (Supplementary Fig. S2).[1] The tags were secured externally using a two-point attachment technique (Lawson et al. 2010). Tag attachment leaders improved during the study, and most were built with a single layer of 180 kg monofilament (Momoi, Kobe, Japan), a cover layer of aramide braided cord that provided increased abrasion resistance over the monofilament, and up to two layers of heat shrink wrap, attached at one end to the tag and then to each titanium dart.

The tags were programmed to record ambient water temperatures, depth, and light intensity at 15- to 60-s intervals. A constant depth (±2.5 m) for 4 days triggered tag release and data transmission in the event that the tag prematurely detached and was on the surface or the fish had died and was on the seafloor. On the preprogrammed date and time, the tags released from the fish, floated to the surface, and transmitted data summaries to Earth-orbiting Argos satellites. The satellite tags needed to be physically recovered to acquire full archival records from their memory. To obtain complete tracks to the spawning grounds and back, the tags were programmed to detach from the fish during their predicted months of return to the GSL foraging ground during the following summer. Once a satellite tag was at the surface and transmitting and if it was close to shore, a team of researchers and the recovery vessel were directed to the coordinates obtained from the tag in near real time via the Argos satellite system. A handheld Argos AL-1 PTT locator (North Star Science and Technology,

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0110.

Table 1. Deployment and pop-up satellite tag metadata for 94 tags attached to Atlantic bluefin tuna in Canada's southern Gulf of St. Lawrence from 2007 to 2013.

			Deployment			Pop-Up			
ID	CFL	Tag type	Date	Latitude	Longitude	Date	Latitude	Longitude	Fidelity
5107036	244	MK10	10/19/2007	46.17	−61.52	4/9/2008	29.78	−59.96	Neutral
5107037	302	MK10	10/19/2007	46.18	−61.52	3/21/2008	19.66	−94.70	GOM
5107038	255	MK10	10/19/2007	46.20	−61.50	5/4/2008	35.62	−70.57	Neutral
5107042	244	MK10	10/24/2007	46.17	−61.59	6/1/2008	38.88	−66.21	Neutral
5107043	272	MK10	10/24/2007	46.17	−61.59	4/1/2008	26.51	−86.18	GOM
5107046	261	MK10	10/25/2007	46.13	−61.53	4/24/2008	26.57	−91.92	GOM
5107047	275	MK10	10/25/2007	46.16	−61.51	12/9/2007	24.54	−73.76	Neutral
5107048	246	MK10	10/26/2007	46.15	−61.52	2/7/2008	38.82	−58.47	Neutral
5108017	288	MK10	10/20/2008	46.20	−61.54	6/9/2009	26.14	−77.77	GOM
5108020	292	MK10	10/25/2008	46.29	−61.49	5/28/2009	27.69	−79.28	GOM
5108021	269	MK10	10/25/2008	46.27	−61.47	6/15/2009	26.16	−78.83	GOM
5108022	267	MK10	10/25/2008	46.26	−61.46	6/14/2009	38.68	11.30	Med.
5108023	270	MK10	10/25/2008	46.29	−61.40	1/29/2009	26.22	−79.94	GOM
5108024	265	MK10	10/25/2008	46.21	−61.49	5/29/2009	27.70	−79.14	GOM
5109023	250	MK10	10/18/2009	46.11	−61.74	5/28/2010	34.86	−73.29	Neutral
5109024	273	MK10	10/18/2009	46.14	−61.63	6/15/2010	47.07	−60.40	Neutral
5109026	269	MK10	10/22/2009	46.21	−61.55	6/19/2010	44.78	−62.65	GOM
5109027	293	MK10	10/22/2009	46.18	−61.56	3/28/2010	25.10	−93.11	GOM
5109029	277	MK10	10/24/2009	46.21	−61.61	6/30/2010	47.60	−64.65	GOM
5109030	261	MK10	10/24/2009	46.24	−61.61	3/2/2010	32.15	−75.62	Neutral
5110056	266	MK10	9/18/2010	46.01	−62.14	4/22/2011	47.18	−23.79	Neutral
5110058	271	MK10	9/19/2010	46.02	−62.20	4/3/2011	36.88	−65.08	Neutral
5110059	278	MK10	9/19/2010	46.03	−62.21	3/9/2011	24.45	−75.49	Neutral
5110060	250	MK10	9/19/2010	46.05	−62.19	3/17/2011	26.20	−79.95	Neutral
5110061	231	MK10	9/19/2010	46.03	−62.19	6/7/2011	43.40	−64.99	Neutral
5110062	261	MK10	9/19/2010	46.03	−62.19	3/6/2011	21.20	−94.96	GOM
5110063	289	MK10	9/19/2010	46.02	−62.20	5/6/2011	26.43	−90.85	GOM
5110064	262	MK10	9/19/2010	46.01	−62.20	5/3/2011	39.05	−69.16	Neutral
5110065	257	MK10	9/20/2010	46.04	−62.21	4/15/2011	26.31	−92.16	GOM
5110067	293	MK10	9/24/2010	46.05	−62.10	3/26/2011	27.69	−94.43	GOM
5110068	273	MK10	9/24/2010	46.06	−62.08	2/5/2011	27.23	−56.64	Neutral
5110070	288	MK10	9/24/2010	46.06	−62.10	2/3/2011	22.22	−94.09	GOM
5110072	298	MK10	9/24/2010	46.08	−62.09	1/1/2011	32.87	−70.34	Neutral
5110073	302	MK10	9/24/2010	46.08	−62.09	2/4/2011	24.93	−85.28	GOM
5110074	284	MK10	9/24/2010	46.08	−62.09	5/26/2011	28.86	−86.89	GOM
5110075	276	MK10	9/25/2010	46.06	−62.09	7/1/2011	29.50	−86.77	GOM
5110076	289	MK10	9/25/2010	46.05	−62.10	1/5/2011	23.86	−93.96	GOM
5110077	284	MK10	9/25/2010	46.06	−62.10	3/10/2011	25.06	−77.97	Neutral
5110078	282	MK10	9/25/2010	46.06	−62.10	3/1/2011	27.18	−89.23	GOM
5110079	275	MK10	9/25/2010	46.07	−62.09	3/29/2011	28.03	−94.71	GOM
5110080	234	MK10	10/13/2010	46.22	−61.67	3/30/2011	36.91	−69.37	Neutral
5110081	266	MK10	10/13/2010	46.22	−61.66	3/29/2011	36.78	−36.89	Neutral
5110083	240	MK10	10/14/2010	46.21	−61.82	4/29/2011	39.59	−68.98	Neutral
5110085	187	MK10	10/14/2010	46.20	−61.62	5/27/2011	40.46	−66.15	Neutral
5110087	272	miniPAT	10/14/2010	46.13	−61.61	4/12/2011	48.00	−40.00	Neutral
5110088	228	MK10	10/16/2010	46.25	−61.36	4/29/2011	37.18	−55.84	Neutral
5110089	190	MK10	10/16/2010	46.25	−61.37	11/25/2010	40.00	−68.06	Neutral
5111015	270	miniPAT	9/24/2011	46.05	−61.60	6/1/2012	41.09	−19.85	Neutral
5111016	280	miniPAT	9/24/2011	46.05	−61.61	6/10/2012	40.01	−70.96	GOM
5111017	261	miniPAT	9/24/2011	46.04	−61.63	6/20/2012	38.30	8.12	Med.
5111022	288	miniPAT	9/26/2011	46.03	−61.60	4/4/2012	27.07	−92.99	GOM
5111023	256	miniPAT	9/26/2011	46.03	−61.61	6/1/2012	41.39	−63.12	Neutral
5111024	253	miniPAT	9/26/2011	46.03	−61.59	6/10/2012	40.80	−66.55	GOM
5111025	250	miniPAT	9/26/2011	46.03	−61.59	6/20/2012	47.99	−65.05	GOM
5111026	252	miniPAT	9/26/2011	46.04	−61.60	6/30/2012	46.35	−61.96	GOM
5111027	266	miniPAT	9/28/2011	46.04	−61.61	6/11/2012	42.62	−70.66	GOM
5111028	266	miniPAT	9/28/2011	46.03	−61.60	7/20/2012	45.75	−61.58	Neutral
5111031	285	miniPAT	10/1/2011	46.00	−61.73	4/1/2012	21.91	−77.54	Neutral
5111032	250	miniPAT	10/3/2011	46.08	−61.67	5/7/2012	33.88	−10.06	Neutral
5111033	270	miniPAT	10/3/2011	46.07	−61.74	7/10/2012	46.61	−63.48	GOM
5111034	276	miniPAT	10/3/2011	46.08	−61.65	6/27/2012	47.70	−64.38	GOM
5111041	281	MK10	10/13/2011	46.18	−61.46	1/20/2012	22.83	−70.91	Neutral
5111045	277	miniPAT	10/19/2011	46.09	−61.56	7/12/2012	47.48	−60.99	GOM
5111046	243	MK10	10/19/2011	46.09	−61.58	3/26/2012	23.70	−96.36	GOM

Table 1 (*concluded*).

			Deployment			Pop-Up			
ID	CFL	Tag type	Date	Latitude	Longitude	Date	Latitude	Longitude	Fidelity
5111050	273	MK10	10/21/2011	46.11	−61.56	2/7/2012	23.29	−80.88	GOM
5111051	278	miniPAT	10/22/2011	46.09	−61.56	4/16/2012	30.18	−72.85	Neutral
5111052	285	miniPAT	10/23/2011	46.01	−61.71	5/8/2012	27.19	−95.93	GOM
5111055	240	MK10	10/25/2011	46.03	−61.76	11/19/2011	39.69	−69.48	Neutral
5111056	243	MK10	10/25/2011	46.01	−61.73	3/15/2012	25.76	−78.86	Neutral
5112028	270	miniPAT	9/23/2012	46.02	−62.20	7/1/2013	40.44	−70.78	Neutral
5112030	283	miniPAT	9/24/2012	46.01	−62.23	7/1/2013	46.76	−60.94	GOM
5112032	260	miniPAT	9/24/2012	46.01	−62.31	7/10/2013	46.99	−60.82	Neutral
5112033[a]	278	miniPAT	9/24/2012	46.01	−62.31				GOM
5112034	270	miniPAT	9/29/2012	46.00	−62.33	7/11/2013	46.28	−44.24	Neutral
5112035	259	miniPAT	9/29/2012	46.00	−62.33	7/20/2013	24.05	−94.48	GOM
5112036	261	miniPAT	9/29/2012	46.00	−62.33	4/23/2013	37.62	−37.05	Neutral
5112037	268	miniPAT	9/29/2012	46.04	−62.31	6/10/2013	23.98	−80.81	GOM
5112038	277	miniPAT	10/5/2012	46.00	−62.31	5/1/2013	27.30	−89.81	GOM
5112039	273	miniPAT	10/5/2012	45.98	−62.35	8/1/2013	46.24	−62.15	GOM
5112041	284	miniPAT	10/5/2012	46.00	−62.34	8/2/2013	45.67	−61.43	GOM
5112044	265	MK10	10/9/2012	46.11	−61.98	1/9/2013	31.42	−76.58	Neutral
5112046	250	MK10	10/9/2012	46.09	−62.01	2/8/2013	25.47	−71.20	Neutral
5113015	284	miniPAT	9/28/2013	45.99	−61.61	5/15/2014	27.22	−95.35	GOM
5113016	251	miniPAT	9/28/2013	45.99	−61.61	7/15/2014	43.13	−70.43	GOM
5113017	282	MK10	9/29/2013	45.99	−61.61	2/15/2014	26.20	−85.90	GOM
5113019	262	miniPAT	9/29/2013	45.97	−61.61	7/15/2014	47.30	−64.87	Neutral
5113021	265	miniPAT	9/29/2013	45.98	−61.61	1/27/2014	35.31	−75.35	Neutral
5113022	271	miniPAT	9/29/2013	45.97	−61.62	4/29/2014	26.12	−94.26	GOM
5113024	274	miniPAT	9/30/2013	45.98	−61.62	4/16/2014	24.16	−86.73	GOM
5113025	269	MK10	9/30/2013	45.97	−61.62	11/7/2013	30.69	−64.05	Neutral
5113029	277	miniPAT	9/30/2013	45.97	−61.62	5/20/2014	24.47	−80.63	GOM
5113031	269	miniPAT	10/1/2013	45.97	−61.63	7/25/2014	44.43	−66.96	GOM
5113032	313	MK10	10/1/2013	45.97	−61.62	2/15/2014	35.45	−68.64	Neutral
5113033	298	miniPAT	10/1/2013	45.96	−61.63	6/13/2014	25.66	−79.32	GOM

Note: Deployment and pop-up dates are expressed as month/day/year. CFL, curved fork length; GOM, Gulf of Mexico; Med., Mediterranean Sea; neutral, neither GOM nor Mediterranean Sea waters visited, obscuring origin of fish.

[a] 5112033: this tag did not pop-up and report but was recovered on St. Joseph Island, Texas.

King George, Virginia) provided signal strength and direction, allowing the recovery team to home in on the tag for recovery.

Improvements in external tag attachments

The objectives of this study were to advance the use of externally attached PAT tags to obtain location data from the spawning ground visitation and behavioral data from adult Atlantic bluefin tuna before, during, and after entry and exit to a spawning ground. To achieve this end, we focused on working in the GSL fishery to increase the probability of attaching tags to mature GOM breeders to obtain round-trip tracks between foraging and spawning grounds. Prior archival and satellite electronic tagging of Atlantic bluefin tuna by the same scientific research team in coastal waters off North Carolina and Massachusetts had led to a relatively small number of GOM tracks and a larger proportion of Mediterranean Sea or adolescent tracks (Block et al. 2005; Walli et al. 2009). We hypothesized that by tagging the largest Atlantic bluefin tuna accessible on day trips, on their southern GSL foraging ground late in the fall, we could maximize the probability of getting a western spawner and tag retention to achieve our overall goal of obtaining a GOM track. In addition, we focused on this time of year to minimize the duration that a tag had to be attached to the fish to increase the chance of obtaining GOM tracks.

To achieve the desired outcome (round-trip tracks between the GSL and the GOM), required three key advancements: (*i*) the handling of large Atlantic bluefin tuna on the deck of commercial fishing boats to attach the tags with a desired placement; (*ii*) the development of secure attachments that would retain external tags on large Atlantic bluefin tuna to enable enough retention time; and (*iii*) reduction in size of the Wildlife Computers pop-up satellite archival tags. Together the advancement in satellite tag technology and tagging techniques enabled acquisition of tracks of sufficient length to record entrance and exit dates of GSL-tagged giant Atlantic bluefin tuna to their spawning ground, as well as the return trip to the GSL foraging ground in many cases. In addition, all tag deployments were conducted late in the foraging season following the commercial fishing season to reduce the time required for the external tags to be carried by the fish and reduce the chance of early recapture by the commercial fishery.

Data processing

Raw PAT tag data were processed in a three-step process. First, the light-level data were processed using an algorithm provided by the tag manufacturer (Wildlife Computers Global Position Estimator Version 2) to calculate longitude estimates based on the time of local noon or midnight. Then latitude estimates were calculated by matching sea surface temperatures (SSTs) recorded by the tag with remotely sensed SSTs (Teo et al. 2004). A state–space modeling (SSM) approach, described below, was then used to refine daily position estimates into the most probable track and enabled quantifying the uncertainty associated with each daily position (Jonsen et al. 2005).

We fitted a Bayesian SSM to the geolocation data to regularize the location estimates in time, interpolate through small gaps due to missing observed locations, and account for errors in the light level derived estimates of longitude and the SST-derived estimates of latitude (Teo et al. 2004). The model was adapted from Block et al. (2011) to account for bathymetric information that further improved the resulting location estimates by constraining locations to occur in water at least as deep as the observed maximum dive depth recorded by the PAT tags. A 6-h time step was used to fit the model to the geolocation data as this minimized move steps across land. The resulting location estimates were then subsampled back to a 24-h time step for all subsequent analyses. The model was validated with endpoint data from tagged Atlantic bluefin tuna ($n = 72$).

The SSM is comprised of a process model (from Jonsen et al. 2005) that assumes that the first differences in locations are a correlated random walk with mean turn angle θ and move autocorrelation γ:

$$\text{(1)} \qquad \boldsymbol{d}_t = \gamma \mathbf{T}(\theta)\boldsymbol{d}_{t-1} + \boldsymbol{\eta}_t$$

where $\boldsymbol{d}_t$ is the first difference in the true but unobserved locations $\boldsymbol{x}_t$ and $\boldsymbol{x}_{t-1}$ and $\mathbf{T}(\theta)$ is a matrix describing the rotation between $\boldsymbol{d}_t$ and $\boldsymbol{d}_{t-1}$,

$$\text{(2)} \qquad \mathbf{T}(\theta) = \begin{pmatrix} \cos\theta & -\sin\theta \\ \sin\theta & \cos\theta \end{pmatrix}$$

and $\boldsymbol{\eta}_t$ is the stochastic deviation in movement between times t and $t - 1$, which is assumed to be normally distributed with mean 0 and variance–covariance $\boldsymbol{\Sigma}$:

$$\text{(3)} \qquad \boldsymbol{\Sigma} = \begin{pmatrix} \sigma_1^2 & \rho\sigma_1\sigma_2 \\ \rho\sigma_1\sigma_2 & \sigma_2^2 \end{pmatrix}$$

where σ_1 and σ_2 are the standard deviations (SDs) in longitude and latitude, respectively.

The process model (eq. 1) was fitted to tuna geolocation data using an observation model that allowed irregularly timed observations (due to seasonal and latitudinal shifts in twilight times) with constant and normally distributed errors (Block et al. 2011):

$$\text{(4)} \qquad \boldsymbol{y}_{t,i} = (1 - j_i)\boldsymbol{x}_{t-1} + j_i\boldsymbol{x}_t + \boldsymbol{\varepsilon}_{t,i}$$

where $\boldsymbol{y}_{t,i}$ is the pair i of longitude and latitude data observed within regular time step t, j_i is the proportion of this time step elapsed prior to observation i, and $\boldsymbol{\varepsilon}_{t,i}$ are random, serially independent observation errors due to the geolocation process.

Geolocation errors were assumed to be normally distributed so that $\boldsymbol{\varepsilon}_{t,i,1} \sim \mathrm{N}(0, \psi\tau_1)$ for longitude and similarly for latitude, where τ_1 and τ_2 are the fixed precision parameters and ψ is an estimated parameter that allows for variability in the scale of errors arising from variability among tags. The values of τ_1 and τ_2 (0.24 ± 0.008° and 0.735 ± 0.026° (±SE), respectively) were fixed at estimates obtained from an analysis of geolocations and Argos locations derived from 72 PAT tags drifting at the ocean surface after tag pop-off (Winship et al. 2012).

A bathymetry mask was applied as a prior on location estimates so that locations were not on land or in water shallower than that implied by the tag-recorded depth data. To construct the mask, we used the 30 arc-second resolution (approximately 1 km) Global Predicted Bathymetry gridded dataset (v15.1; Smith and Sandwell 1997). Due to computational constraints, we resampled this dataset to a 0.28° resolution grid. The bathymetry values were inverted so that grid cells containing land had large negative values and those containing water had positive values. The constraint was incorporated into the SSM as follows:

$$\text{(5)} \qquad o_t = \text{Bernoulli}\,(p_t)$$

where o_t is a dummy variable of 1s (termed the "Ones Trick" in WinBUGS; Lunn et al. 2000) of the same length as the number of location states $\boldsymbol{x}_t$ to be estimated and p_t are the associated probabilities from a lognormal likelihood:

$$\text{(6)} \qquad p_t = \mathrm{LN}\left(z_t; \mu_t + \sigma^2, \sigma^2\right)$$

where z_t is the bathymetric maximum from the 0.28° grid cell containing location state $\boldsymbol{x}_t$, μ_t is the log of maximum of tag-recorded depths during time step t (6 h), and σ^2 is fixed at 0.25. Adding σ^2 to μ_t ensures that the peak probability density occurs when z_t equals the maximum tag-recorded depth. This approach constrains the estimation of the location states $\boldsymbol{x}_t$ so that they have zero probability of occurring on land and a low probability of occurring in water where the bathymetry is shallower than the tag-recorded depth, thus constraining the estimated track to more plausible regions with respect to depth. In the course of testing, we found that this constraint at times too strongly constrained location estimates to very deep water. We therefore scaled $p_t = p_t^{0.05}$ to flatten the overall probability density.

To implement this approach, initial values (required for the Markov Chain Monte Carlo (MCMC) estimation approach used to fit the SSM to data) for the location estimates must be chosen so that they are not placed in an area with much shallower bathymetry than the observed daily maximum dive depths. Failure to choose sensible initial location values in this manner would cause the MCMC sampler to fail to converge. We therefore used the R package "gdistance" (van Etten 2012) to calculate sensible initial values in suitably deep water, given the observed daily maximum dive depths.

We used JAGS to fit the SSM to individual tuna tracks via MCMC. For each track, two MCMC chains were run, each 120 000 iterations long. A sample of 10 000 iterations from the joint posterior probability distribution was obtained by discarding the first 20 000 iterations and retaining every 10th of the remaining iterations. Combining the samples from both chains yielded 20 000 posterior samples for each longitude and latitude estimate. We used Geweke's convergence diagnostic (Geweke 1992) and other standard diagnostic plots (R package "coda"; Plummer et al. 2006) to assess convergence of the MCMC samples. All plots of tracks and subsequent analyses use the posterior means of the longitude and latitude estimates.

The processed SSM location estimates were used to create kernel density estimates to visualize habitat utilization using the kernal density estimation (KDE) function from the kernel smoothing package in R. A separate KDE was performed for each month in the GOM, which included locations from all available years. All location estimates were weighted equally. We used the kernel smoothing package's plug-in bandwidth selector. This selector uses an unconstrained, or full, bandwidth matrix allowing arbitrary orientation of the kernel function as described in Duong (2007).

Results

Pop-up satellite archival tags ($n = 135$) were attached to Atlantic bluefin tuna ($n = 125$) caught by commercial fishing boats using rod and reel in the fall months, from 2007 to 2013, in the southern GSL. Ten of these Atlantic bluefin tuna were double-tagged with MK10 and miniPAT tags. In total, 100 satellite tags from 94 Atlantic bluefin tuna, including six double-tagged fish, successfully transmitted data after fish left GSL waters (Table 1). The tagged Atlantic bluefin tuna ranged in size from 187 to 313 cm and had a mean measured length of 268 ± 20 cm (CFL ± SD, $n = 94$). Collectively, these 94 PAT tags recorded over 18 800 days of location and behavioral time-series data on Atlantic bluefin tuna in the Atlantic Ocean, GOM, and Mediterranean Sea. Twenty-five of the PAT tags were physically recovered following detachment, and their full archival records were obtained for further analyses. Recovery of the tags resulted in the acquisition of an archival time series that included 5800 days of location position, oceanographic profiles, diving, and behavioral data. Over the 7-year study, 35 PAT tags (including 28 MK10s) did not report, malfunctioned, or were attached to animals that were presumed to have died. Results from these tags are not reported further in this study.

The best tag retention duration on giant Atlantic bluefin tuna was obtained using the trilayer leader attachment, two titanium darts, and miniPAT tags in years 2010 to 2013. The mean attachment duration for these tag deployments was 7.60 ± 2.50 months (±SD, *n* = 41) (Fig. 1). These miniPAT-tagged fish provided tracks during occupation of the GOM and also provided an opportunity for recovery of the miniPAT tag upon return to the GSL foraging ground. Some (45.5%) of the miniPATs attached to large GSL Atlantic bluefin tuna were recovered after an extensive trip away from the foraging ground, providing evidence of fidelity to the foraging region. The MK10 tags had a significantly lower mean attachment duration of 4.65 ± 2.72 months (±SD, *n* = 71) (Supplementary Fig. 3).[1] Only a few of these larger MK10 tags remained attached on Atlantic bluefin tuna more than 6 months after deployment, reducing the capacity to capture the round trip. Importantly, only 8.9% of the miniPATs did not report compared with 19.3% of the MK10s not reporting. Atlantic bluefin tuna tagged with satellite tags in the GSL (*n* = 94) displayed migration patterns that involved movements to the GOM (*n* = 49), the Mediterranean Sea (*n* = 2), and the North Atlantic Ocean (*n* = 43). We report the results of these movements and behaviors in the geographic regions below separately.

GOM

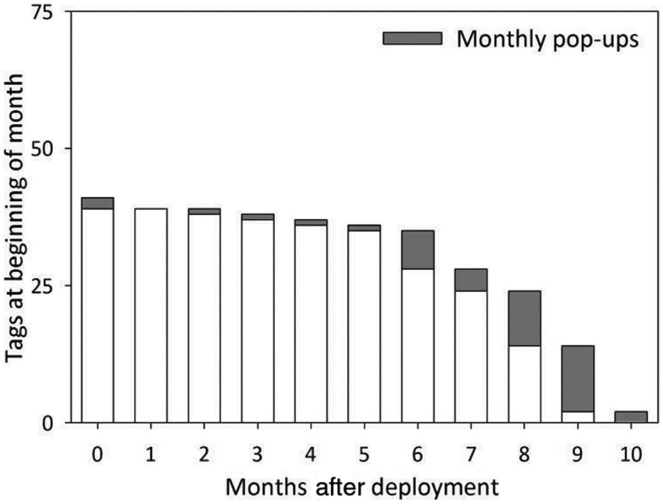
Many of the tagged Atlantic bluefin tuna (*n* = 49) moved from the Canadian foraging ground to the GOM spawning ground (Fig. 2*a*). All of these electronically tagged Atlantic bluefin tuna remained within the western management area after release. Their mean size was 275 ± 14 cm (CFL ± SD, *n* = 49), with their measured length ranging from 243 to 302 cm CFL (Table 1; Fig. 3*a*).

Of the 49 Atlantic bluefin tuna with tracks from the GSL to the GOM, five individuals entered and moved to the waters of the eastern GOM (Figs. 2*b*, 2*d*), 23 showed residency in the western GOM (Fig. 2*c*), 18 visited both regions (Fig. 2*e*), and three detached shortly after entering the GOM. The mean foraging ground exit date from the GSL of Atlantic bluefin tuna that visited the GOM was 14 October ± 13 days (SD) (*n* = 49). Travel duration between leaving the GSL and entering the GOM ranged from 30 to 184 days (mean duration of trip = 93 ± 39 days (SD), *n* = 49). Atlantic bluefin tuna entered the GOM over an extended period, ranging from 9 November to 6 April (mean entry date = 14 January ± 42 days (SD), *n* = 49), and exited the GOM from 4 April to 13 June (mean exit date = 22 May ± 18 days (SD), *n* = 22) (Fig. 4). Both entry and exit dates were available for 22 individual Atlantic bluefin tuna (Fig. 5). The mean residency period within the GOM for these 22 fish was 123 ± 49 days (SD) and ranged from a minimum of 44 days to a maximum of 194 days. The peak GOM residency, measured by the number of tagged Atlantic bluefin tuna in the GOM each month, occurred during the months of April and May.

In this study, complete round-trip tracks from the GSL foraging ground to the GOM spawning ground and back were obtained for nine Atlantic bluefin tuna (Figs. 2*b*–2*e*). These fish exited the GOM from 10 May to 11 June (mean exit date = 25 May ± 11 days (SD), *n* = 9) and returned back to the GSL from 10 June to 18 July (mean entry date = 28 June ± 11 days (SD), *n* = 9). Travel duration from the GOM to the GSL ranged from 20 to 44 days (mean return travel duration = 34 ± 7 days (SD), *n* = 9).

To examine the high-use areas of the GOM, a kernel density analysis of Atlantic bluefin tuna geolocations in the GOM was generated for the January to June period (Fig. 6). The kernel density analyses revealed two hotspots in the GOM during April and May, the hypothesized peak GOM spawning period based on catch data and larval surveys (Muhling et al. 2010; Teo et al. 2007*a*), located in slope waters of the northern GOM: one in the western GOM, and the other in the eastern GOM in the vicinity of the Macondo Well. Two of the Atlantic bluefin tuna electronically tagged in the fall of 2009 (Figs. 2*d*, 2*e*) were in the vicinity of the Macondo Well on 20 April 2010 when the Deepwater Horizon oil-drilling rig accident occurred.

Fig. 1. Reporting number of miniPAT tags by months after deployment.



Mediterranean Sea

Of the 94 Atlantic bluefin tuna tagged in GSL waters with records long enough to visit a spawning ground, two individuals traveled to the Mediterranean Sea spawning grounds (Figs. 7*a*, 7*b*). These two Atlantic bluefin tuna measured 267 and 261 cm (CFL) when tagged in the GSL in 2008 and 2011, respectively (Table 1; Fig. 3). Both fish first traveled to waters north of the Bahamas in December and February, respectively, before initiating their Atlantic crossings during the months of February and March, respectively. They crossed the 45°W meridian into the eastern management area on 15 March and 8 April, respectively. They entered the Mediterranean Sea on 28 and 19 May, respectively, and were both in Mediterranean Sea locations known to be spawning grounds (Tyrrhenian Sea) when their tags detached on 14 and 20 June, respectively. Both fish were in Mediterranean Sea waters and their tags recorded SSTs of 22–23 °C when their tags detached. Travel durations from the GSL to the Mediterranean Sea for the two fish were 210 and 234 days, respectively.

Neutral

We categorized 43 of the 94 Atlantic bluefin tuna as “neutrals”, i.e., their tracks did not permit assignment to either the GOM or Mediterranean Sea spawning grounds (Table 1; Fig. 8*a*). The Atlantic bluefin tuna designated as neutrals had a mean length of 259 ± 23 cm (CFL ± SD, *n* = 43) and ranged from 187 to 313 cm (Table 1; Fig. 3*a*). Many of these fish (65.1%, 28 of 43 individuals) had their tags detach prior to the month of May, the peak time for spawning on the GOM spawning ground (Table 1). We did not assign these 28 neutral fish to a spawning ground and eliminated these tracks from further consideration as the results are due to malfunction of tags or attachments. Some neutral fish remained completely within the western management area for the duration of their programmed tag attachments (Fig. 8*b*), whereas others moved east of the 45°W meridian (Figs. 8*c*–8*e*). Eight Atlantic bluefin tuna from the neutral group reported from just outside the GOM, most often off the coast of Florida, and may have subsequently moved into this spawning region. Prior work has shown Atlantic bluefin tuna dive repeatedly to deep depths (500–1000 m) in this region upon entrance to the GOM, and premature release is common here (Teo et al. 2007*a*). The mean size of this group of eight fish was 267 ± 16 cm (CFL ± SD, *n* = 8), and the mean detachment date was 11 Feb ± 37 days (±SD, *n* = 8). One tag reported in the month of

Fig. 2. (*a*) Positions derived from a state–space model for geolocations (circles) from the PAT tags attached to Atlantic bluefin tuna that went to the Gulf of Mexico (GOM) spawning ground after deployment in Canada (square indicates deployment; triangles indicate pop-up end points from Argos); (*b*) track of an Atlantic bluefin tuna that went to the eastern GOM (ID 5111034); (*c*) Atlantic bluefin tuna track that went to the western GOM (ID 5111025); (*d*) Atlantic bluefin tuna track that went the eastern GOM during the year of the Deepwater Horizon oil spill (ID 5109029); and (*e*) tracks that went to both sides of the GOM during the year of the oil spill (ID 5109026). The red positions in the two lower panels show Atlantic bluefin locations during the first week of the oil spill and "×" marks the position of the Macondo Well.

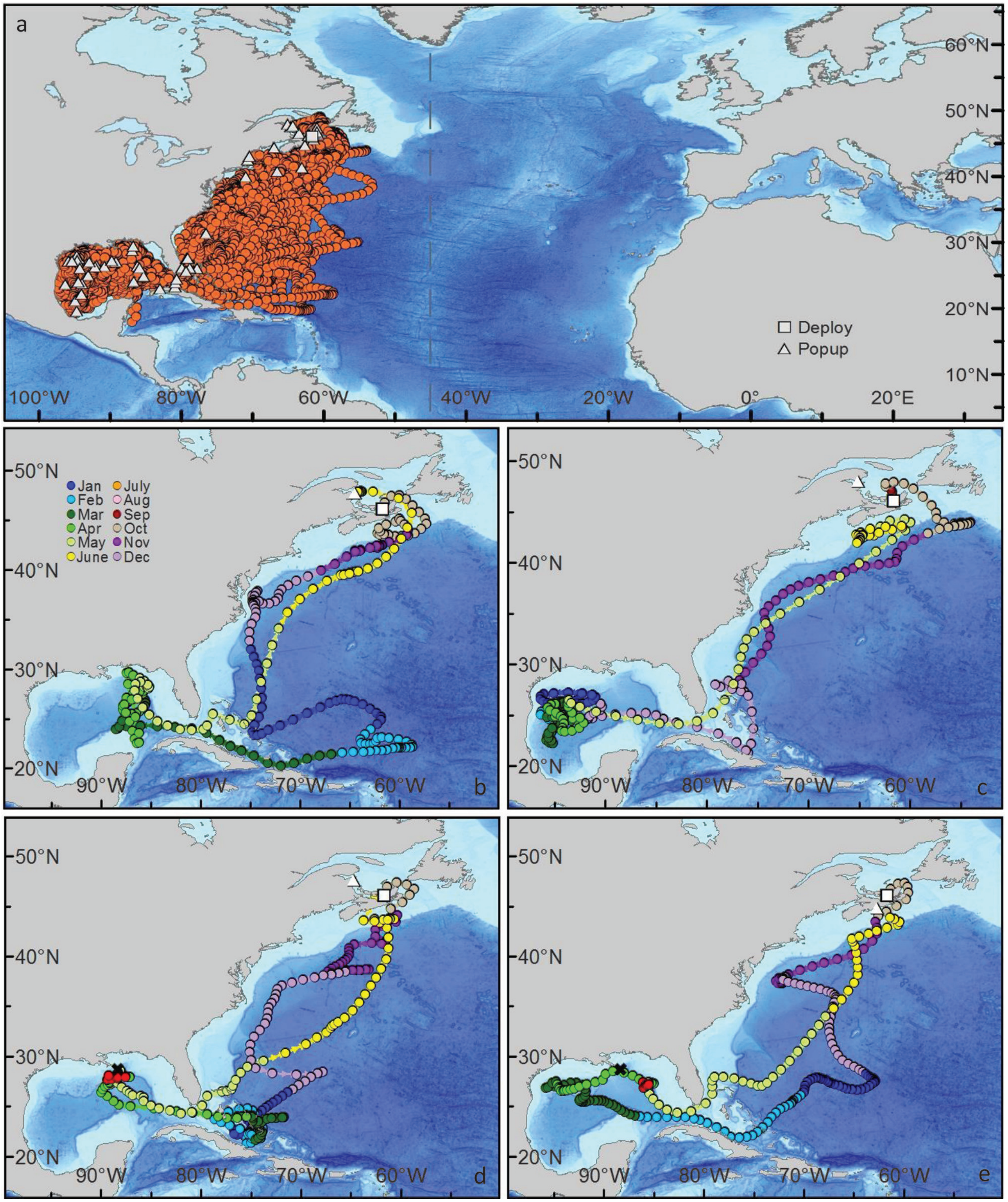
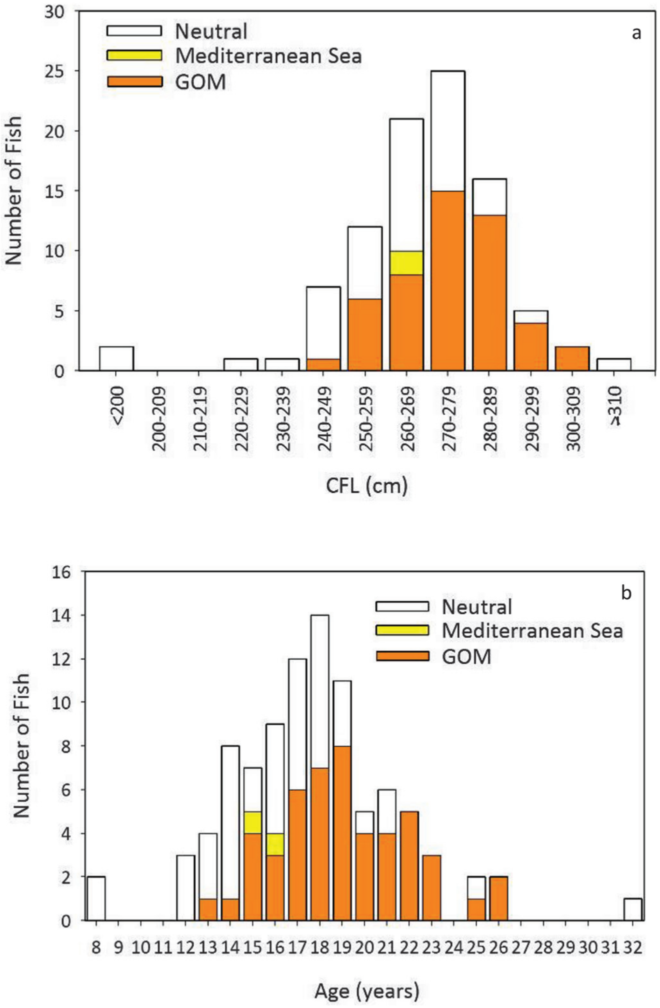


Fig. 3. Number of Atlantic bluefin tuna by (*a*) size class (CFL in cm) and (*b*) age at visit to the Gulf of Mexico (GOM), Mediterranean Sea, or neither location (neutral). The western growth curve (Restrepo et al. 2010) was used to calculate the age of GOM and neutral Atlantic bluefin tuna, and the eastern growth curve (Cort 1991) was used to calculate the age of the Mediterranean fish.



May just outside the Strait of Gibraltar and may have subsequently entered the Mediterranean Sea (Fig. 8*e*). Here, also, tag records indicate repeated oscillatory diving (Wilson and Block 2009) that may be a major source for premature release of MK10 PAT tags. The neutral group included some of the smallest fish tagged in this study (Table 1; Fig. 3*a*). If the neutrals whose tags came off prematurely prior to May are eliminated, 15 Atlantic bluefin tuna remain as neutrals that did not visit a known spawning ground during the spawning season. These 15 neutrals measured between 187 and 273 cm CFL. In summary, excluding the 28 neutrals whose tags came off prematurely, 74% (49 of 66) of the Atlantic bluefin visited the GOM spawning ground, 3% (2 of 66) visited the Mediterranean Sea spawning ground, and 23% (15 of 66) did not visit a known spawning ground during the spawning season. Some of these fish are potentially of eastern origin, and only genetic analyses of the fin clips removed at the time of tagging can help resolve this.

Time-series data

Twenty of the 25 fish whose tags were physically recovered had tracks revealing that they had traveled to the GOM spawning ground. High-resolution time-series data (ambient water temperature and depth) from these Atlantic bluefin tuna were summarized by region (Fig. 9). The time-series data allowed more in-depth analyses of the water temperature and depth records along the track. Time-series data were organized into the following track categories: the GSL in the fall, the migration from the GSL to the GOM, the entry and exit from the GOM, the period in the GOM, the migration from the GOM to the GSL, and the GSL in the summer. From the box plots of time-series data, several patterns emerge: (*i*) the shallowest depths and coldest median SSTs and ambient temperatures were experienced in the shelf waters of the GSL foraging area; (*ii*) the warmest median SSTs and ambient temperatures were experienced during the GOM entry and exit phases in waters of the Florida Straits or adjacent areas; and (*iii*) once in the GOM, Atlantic bluefin tuna experienced the highest SSTs (>30 °C) and ambient temperatures.

Ambient temperature – depth profiles of four Atlantic bluefin tuna that traveled to and presumably spawned in the GOM are shown in Fig. 10. Upon exiting the cold waters of the GSL, some of these fish move directly to the south and into the warm Gulf Stream waters very soon after departing (Figs. 2*d*, 10*c*), whereas others remain inshore of the western wall of the Gulf Stream as they travel southwards (Figs. 2*b*, 10*a*). Western Atlantic bluefin tuna are reported to spawn in surface waters in SSTs of at least 24 °C or warmer (Block et al. 2001; Mather et al. 1995). The putative period when the Atlantic bluefin tuna may be spawning can be seen during the months of April and May in waters with SSTs ≥ 24 °C, followed by a series of deep-diving behaviors that are characteristic of Atlantic bluefin tuna exiting the GOM (Teo et al. 2007*a*).

Discussion

Extensive efforts in recent years utilizing new biological techniques have led to a significant advancement in our understanding of the biology of Atlantic bluefin tuna. Electronic tags, genetics, and otolith microchemistry analyses provide clear evidence that Atlantic bluefin tuna have a complicated population structure involving three or more discrete populations that show fidelity to spawning grounds in the GOM and the western and eastern Mediterranean Sea.

In this paper, we use electronic tagging to further examine the spatial and temporal movements of Atlantic bluefin tuna utilizing the GOM spawning area. Despite recent advances in understanding of the biology of Atlantic bluefin tuna (e.g., Fromentin and Lopuszanski 2013; Rooker et al. 2014), numerous questions exist about visitation to the spawning grounds, mixing in Canadian waters, the temporal period of residency of Atlantic bluefin tuna in the GOM, and the size of first entrance to the GOM spawning grounds. We demonstrate strong linkages between the Atlantic bluefin tuna from the GSL foraging assemblage and the GOM spawning ground. Furthermore, we show here that fish tracked to the GOM spawning ground show little movement across the 45°W meridian during the period of time that they carried the tag. Utilizing these data in stock assessment models that incorporate explicit spatial and temporal movement patterns will improve our capacity to corroborate the population structure of the region during the year of tagging.

The Canadian assemblage of Atlantic bluefin tuna in the GSL has formed the basis of a strong commercial fishery in Canada in which over 500 t of Atlantic bluefin tuna have been landed annually over the past 4 years (ICCAT 2012). Atlantic bluefin catch per unit effort (CPUE) in the southern GSL has increased in recent years, while remaining stable in the southwest Nova Scotia fishery, which is primarily on the Scotian Shelf and declining in US waters (Neilson et al. 2007; Paul et al. 2008; ICCAT 2014). Studies have described a shift in the distribution of Atlantic bluefin tuna from the Gulf of Maine to areas farther east and north (Golet et al. 2013). Hypotheses proposed to explain this trend include

Fig. 4. Pooled monthly geolocations from all electronic tags that showed visitation to the Gulf of Mexico (GOM) spawning site. Movement into the GOM begins as early as November by some individuals. Exit from the GOM is by early July.

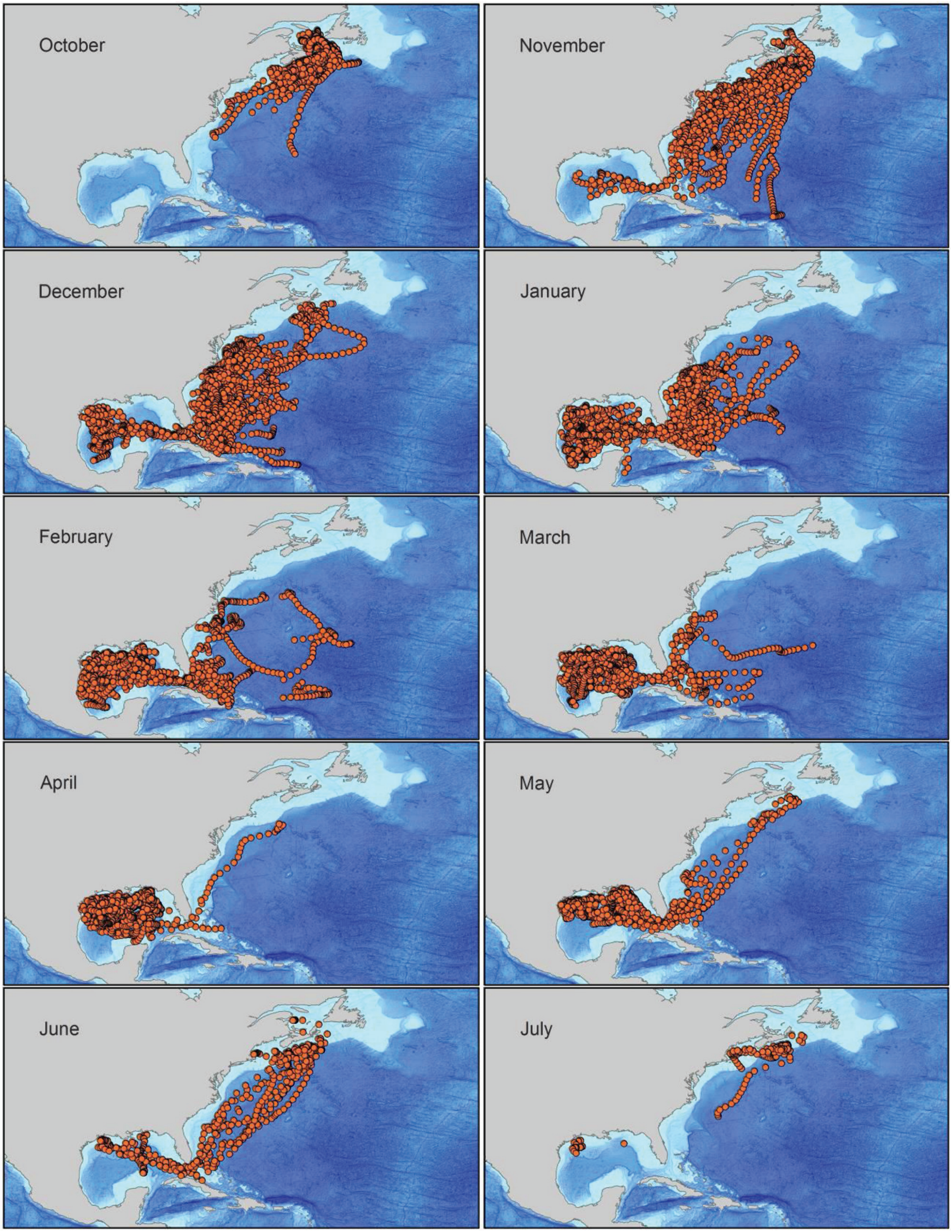
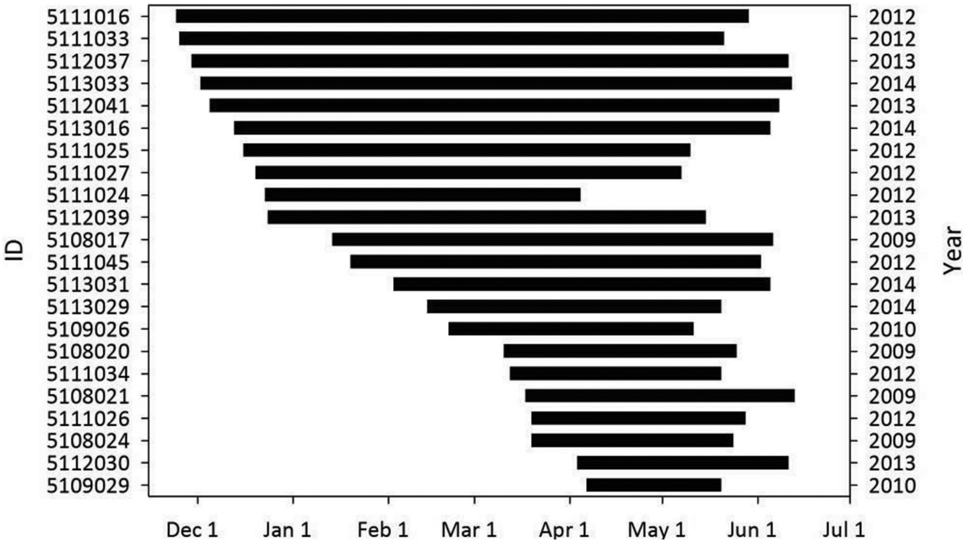


Fig. 5. Pop-up satellite archival tagging reveals entrance and exit dates from the Gulf of Mexico and the residency period of Atlantic bluefin tuna on the spawning grounds.



the following: (*i*) a year-class effect in which strong year classes are represented in the older age classes, which may be expanding their niche to the north as body size increases (B.A. Block, unpublished data); (*ii*) a warming of water temperatures in the western North Atlantic associated with global climate change has resulted in Atlantic bluefin tuna expanding their range into more northern habitats (MacKenzie et al. 2014); and (*iii*) a declining forage base on historical feeding grounds (McAllister et al. 2008). Furthermore, a recent study attributes the CPUE increase to an increase in the available Atlantic bluefin tuna habitat in the GSL in association with a deepening of the cold intermediate layer (CIL) and a decline in the proportion of the water column that it occupies (Vanderlaan et al. 2014).

The GSL assemblage provides an exceptional opportunity to examine migrations of Atlantic bluefin tuna. Previous studies have shown that Atlantic bluefin tuna in the GSL are primarily western in origin (Schloesser et al. 2010). By electronically tagging these larger Atlantic bluefin tuna, we hypothesized that we would acquire direct tracks to the GOM spawning ground with minimal time for satellite tags to be attached. In addition, our prior research suggested that the strong year classes that provided opportunities for extensive electronic tagging in the coastal waters of North Carolina in the mid- to late-1990s (e.g., 1989 and 1994 year classes) had moved into Canadian maritime waters. Finally, the Deepwater Horizon incident helped underline the importance of developing techniques to study Atlantic bluefin tuna utilizing the GOM to examine the potential impacts of the oil spill on the habitat utilization of adult Atlantic bluefin tuna in the GOM. We conducted seven consecutive years of satellite tagging in the Canadian Maritime Provinces and extended tag retention on large Atlantic bluefin to the point where complete tracks from foraging grounds to spawning grounds could be reliably obtained.

Improvements in tag retention were associated with a reduction in tag size (with miniPATs) and retention rates significantly improved over time (Fig. 1; Supplementary Fig. 3).[1] Additional techniques that potentially improved retention involved the addition of a layer of abrasion-resistant synthetic cord (aramide) between the monofilament and the shrink wrap. This refinement was introduced into the methods in the year before switching to the miniPATs. We hypothesize that this newly incorporated leader material, used regularly in military and aerospace applications, strengthened the connections between the titanium dart and the tag, as well as the loop.

The key results emerging from the tracking of GSL Atlantic bluefin tuna include: (*i*) confirmation of the linkage between the GSL and GOM populations of Atlantic bluefin tuna; (*ii*) the western residency displayed by GOM spawners in which they remain west of the 45°W meridian; (*iii*) the extended use of the GOM spawning grounds by mature fish from the GSL with residency in the GOM up to 194 days (6 months); (*iv*) confirmation of use of the Mediterranean Sea spawning ground by GSL Atlantic bluefin; and (*v*) the use of waters surrounding the Macondo Well, site of the oil spill, as potential spawning habitat of Atlantic bluefin tuna.

Fidelity

Tagged Atlantic bluefin tuna released in the GSL showed strong linkage to the GOM spawning ground. Importantly, two fish also traveled to the Mediterranean Sea spawning grounds, and some fish that were not assigned to a spawning population moved east of the 45°W meridian. This is consistent with the results of otolith microconstituent studies that suggested that GSL Atlantic bluefin were primarily of western origin (Rooker et al. 2008; Schloesser et al. 2010). Interestingly, fish that visited the GOM showed fidelity to the western Atlantic, and for the period that they carried the satellite tags, they never crossed the 45°W meridian. Combining these satellite tag results with prior research utilizing archival tags, only a single fish that has shown a pattern of visitation to the GOM has crossed the 45°W management boundary, either before or after being tracked to the GOM. This fish, archivally tagged off the coast of North Carolina as a juvenile, crossed the 45°W meridian three times prior to entering into the GOM, where it was captured (B.A. Block, unpublished data).

Excluding the 28 neutrals whose tags came off prematurely, 74% of the GSL-tagged Atlantic bluefin tuna went to the GOM spawning ground. Results from previous studies have reported that fish tagged on foraging grounds have dispersed to both sides of the Atlantic Ocean (e.g., Lutcavage et al. 1999; Block et al. 2005; Walli et al. 2009; Galuardi et al. 2010). This new study is consistent with prior work (Block et al. 2005) in which Atlantic bluefin tuna of GOM origin tagged in US waters did not cross from the western Atlantic to eastern waters as frequently as Atlantic bluefin of Mediterranean origin moved westward across the management boundary. Block et al. (2005) and Taylor et al. (2011) provided probabilities of west to east crossing of 10% for GOM origin fish and east to west probabilities of crossing of Mediterranean Sea origin fish of over 30%. The new electronic tagging results presented

Fig. 6. Kernel density estimations of all Atlantic bluefin tuna satellite-derived tracking data in the Gulf of Mexico (GOM) by month showing 25% and 50% utilization distributions in the GOM from the months of January to June. The two boxes show those areas that Amendment 7 to the 2006 Consolidated HMS Fishery Management Plan (NOAA 2014) intends to close to fishing during the months of April and May.

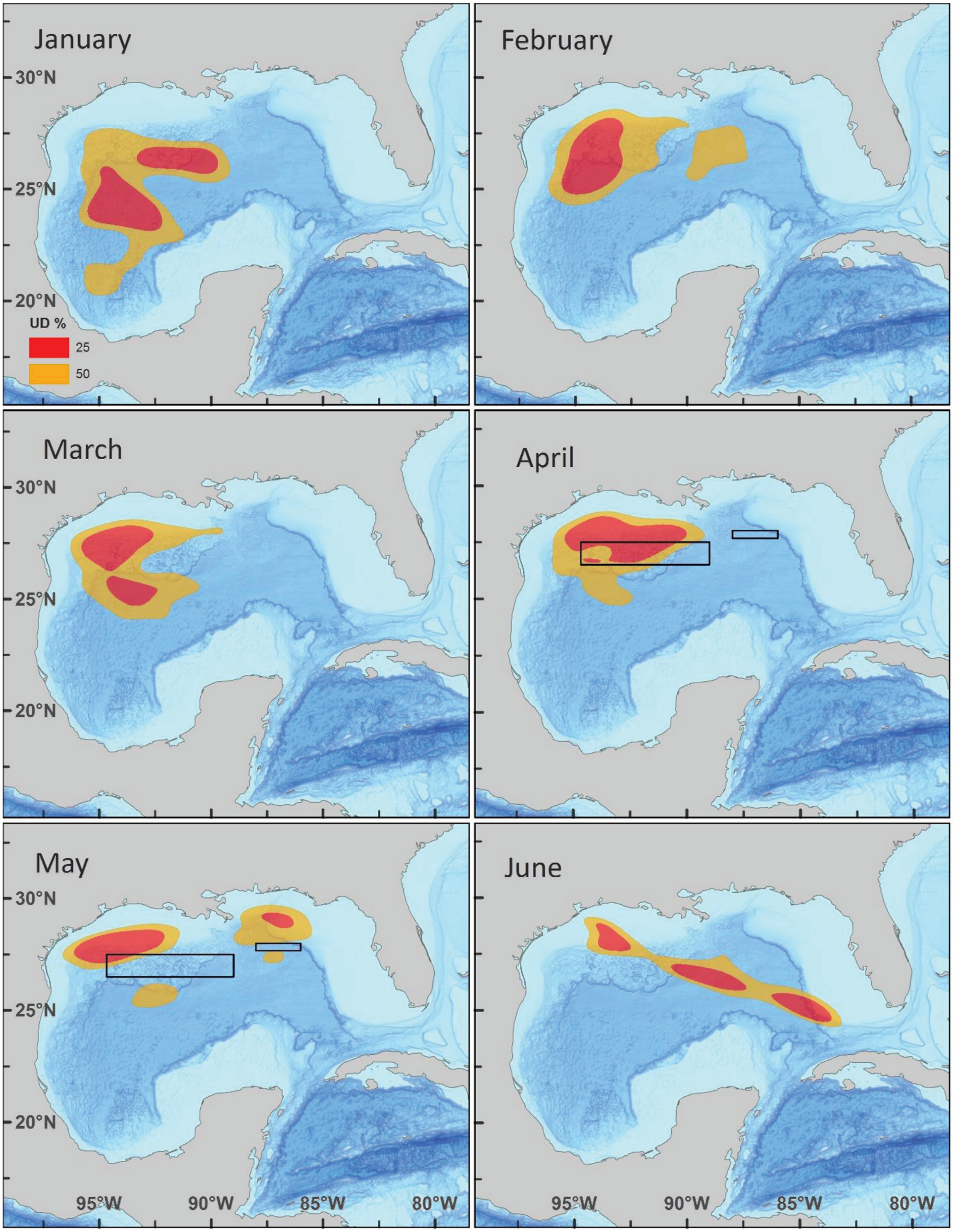
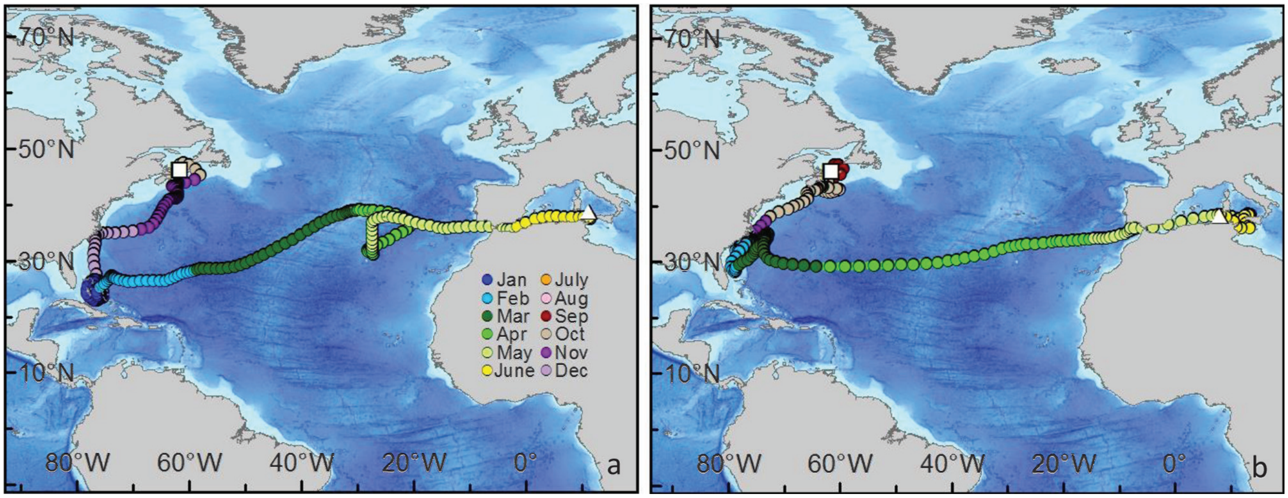


Fig. 7. Atlantic bluefin tuna satellite archival tag PAT tracks that went from deployment in the Gulf of St. Lawrence (square) to the Mediterranean Sea spawning ground (triangle): (*a*) ID 5108022; (*b*) ID 5111017.



here suggest that (*i*) fish of GOM origin, when mature, are not crossing the 45°W meridian with high regularity, and (*ii*) as these GOM spawning fish age, they may be restricting their habitat utilization completely to the western management unit. Block et al. (2005) also hypothesized that eastern Atlantic fish with multiyear spawning tracks demonstrated more site-directed fidelity to the Mediterranean Sea. In these long-term archival datasets (2–4 years of repeat spawning), fish always remained in the eastern spawning unit (east of the 45°W meridian) after the first year of spawning. Spawning is energy intensive, and females, in particular, may be focused on an annual schedule of foraging and spawning such that additional migratory movements across the ocean basin may be energetically unfavorable. Ontogenetic restriction of the Atlantic bluefin tuna into the western or eastern management unit once first spawning occurs may be of high importance to future management models that are able to sort age, origin, and catch datasets with ontogenetic information (Taylor et al. 2011). This emphasizes the overall need for increased use of electronic tags on mature fish to obtain information on spawning location or behaviors. To date, despite over 1000 tag deployments in the western North Atlantic, most tags have not been placed on western spawning-sized fish, based on length and visitation to known spawning grounds. PAT tags are, in general, only capable of recording a year of data at most, and early archival tags were limited to 2–4 years of battery performance. Thus, increased efforts to tag fish of spawning size with newer tagging techniques can increase the capacity to obtain these valuable tracks from mature fish.

For Atlantic bluefin not assigned to a spawning ground (neutrals), it is difficult to know to which management unit a fish belongs. In this paper, we use visitation to either the GOM or Mediterranean Sea spawning grounds for assignment to population of origin, and in the future, we can compare this assignment to genetic data (from a fin clip taken at the time of tagging) for assignment testing. This will help clarify if neutral fish in the eastern Atlantic are from Mediterranean Sea spawning populations. To date, both archival and satellite tagging data from the Tag-A-Giant program (Stokesbury et al. 2004; Block et al. 2005; this paper) suggest that GOM spawners have a restricted geographic distribution after spawning. Utilization distributions of prespawning Atlantic bluefin tuna may not match those of fish that have begun to spawn, which needs to be considered ontogenetically in spatially explicit models that incorporate ontogeny (Taylor et al. 2011). Tagging is a vital tool for defining how fish utilize the ocean during their various phases of ontogenetic growth, and modeling requires incorporating these types of data.

In this study, GOM spawners tagged in the GSL region displayed linkages between their foraging and spawning grounds. Complete tracks indicate that Atlantic bluefin tuna spend the summer and fall months in the GSL (mean entry and exit dates: 28 June and 14 October) and winter and spring in the GOM (mean entry and exit dates: 14 January and 22 May) (Figs. 4, 5). We also observed fidelity to the GSL region, with individual fish having been tracked to this region over multiple years. This was documented in a recaptured fish (5110072) that was twice handled on deck and measured in consecutive years in the GSL. This 298 cm (CFL) Atlantic bluefin tuna, initially caught and PAT tagged on 24 September 2010 on Fishermen's Bank in the GSL, was recaptured and acoustically tagged on 24 September 2011 at the same location. The fish was measured on deck in 2010 and 2011 and had grown only 1 cm during the one year at liberty, in line with asymptotic growth curves for large Atlantic bluefin tuna.

The tracks of Atlantic bluefin tuna allow estimation of the mean travel duration between the GSL and the GOM, which we estimated to be 93 days for the entry leg and 34 days for the return trip. The quicker northward migration may be aided by the predominately northward-flowing Gulf Stream. Some Atlantic bluefin tuna made the GSL to GOM transit in as little as 30 days versus 20 days for the GOM to GSL trip. The movement from high-latitude foraging grounds to low-latitude spawning grounds results in a rapid change in ambient temperatures from SSTs in the GSL of 9–10 °C upon departure and temperatures at depth as cool as 1 °C to median SSTs of 22–25 °C in the GOM (Fig. 9*b*). Time-series data reveal a substantial warming period of the tracks prior to entry when fish are moving through the Gulf Stream, Florida Straits, and Bahamian waters (Fig. 10). This warm period may in fact be a pre-acclimation period that improves the capacity of Atlantic bluefin tuna to physiologically experience the warmer temperatures (e.g., cardiac acclimation) and may also be a trigger for mobilizing lipid stores in the fat pad of females into the eggs. Most of these large fish displayed a preference for open ocean and (or) slope waters with little use of traditional foraging grounds along the eastern seaboard of the US (e.g., the Gulf of Maine and North Carolina).

Age at first spawning

For stock assessment purposes, ICCAT currently assumes that 100% of the western population spawns at age 9 (ICCAT 2014).

Fig. 8. (*a*) Pooled geolocations from the "neutral" Atlantic bluefin tuna that did not visit the Gulf of Mexico (GOM) or Mediterranean Sea spawning grounds, with premature release in blue; (*b*) track of a 231 cm (CFL) Atlantic bluefin tuna that remained within the western management area (ID 5110061); (*c*–*d*) tracks of 266 cm and 270 cm Atlantic bluefin that went to the eastern management area (ID 5111028, ID 5112034, respectively); and (*e*) track of a 250 cm Atlantic bluefin that popped up in May near the Strait of Gibraltar (ID 5111032).

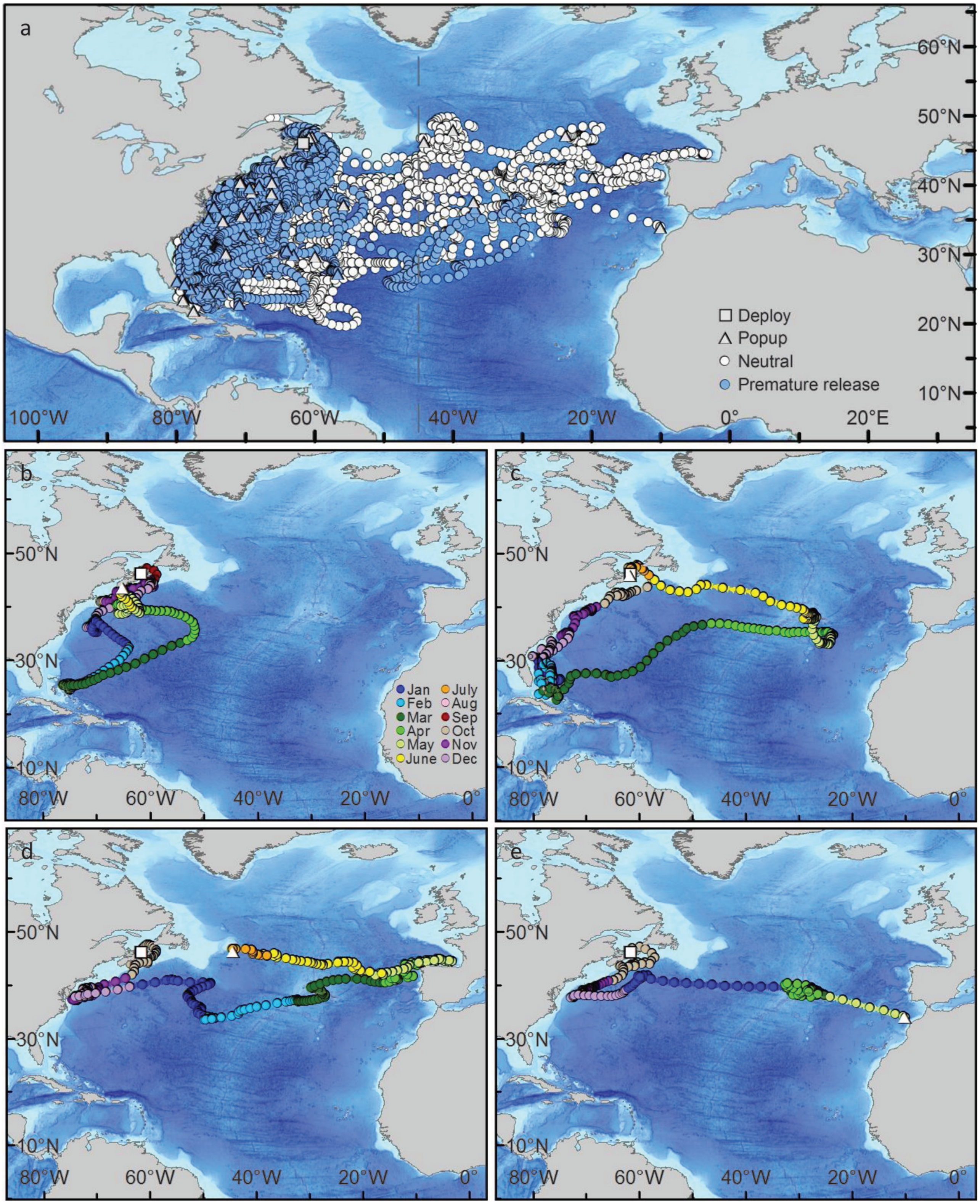
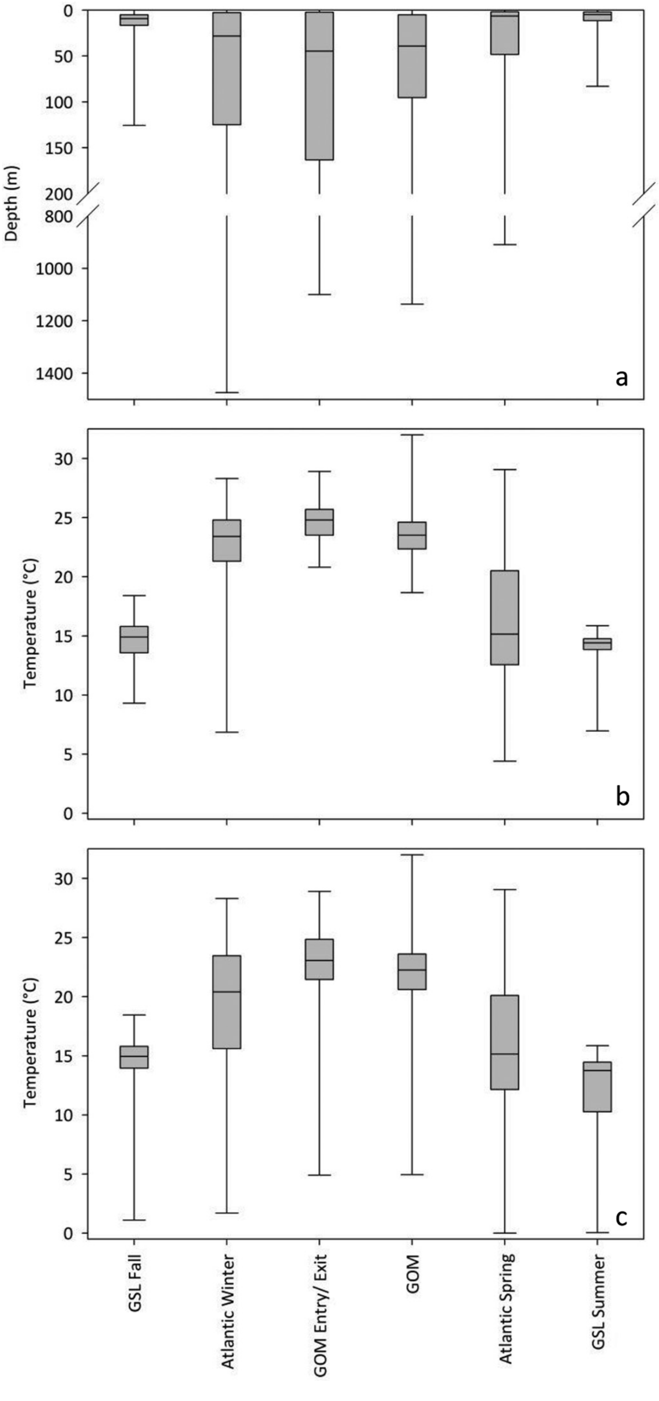


Fig. 9. Time-series data reveal preferences for (*a*) depth, (*b*) sea surface temperatures, and (*c*) ambient temperatures experienced by Atlantic bluefin at different locations in the North Atlantic Ocean. Box plots: interquartile ranges and medians from 20 recovered PAT tags that showed visitation to the GOM. Whiskers: the most extreme values (minimum and maximum). GSL, Gulf of St. Lawrence; GOM, Gulf of Mexico.



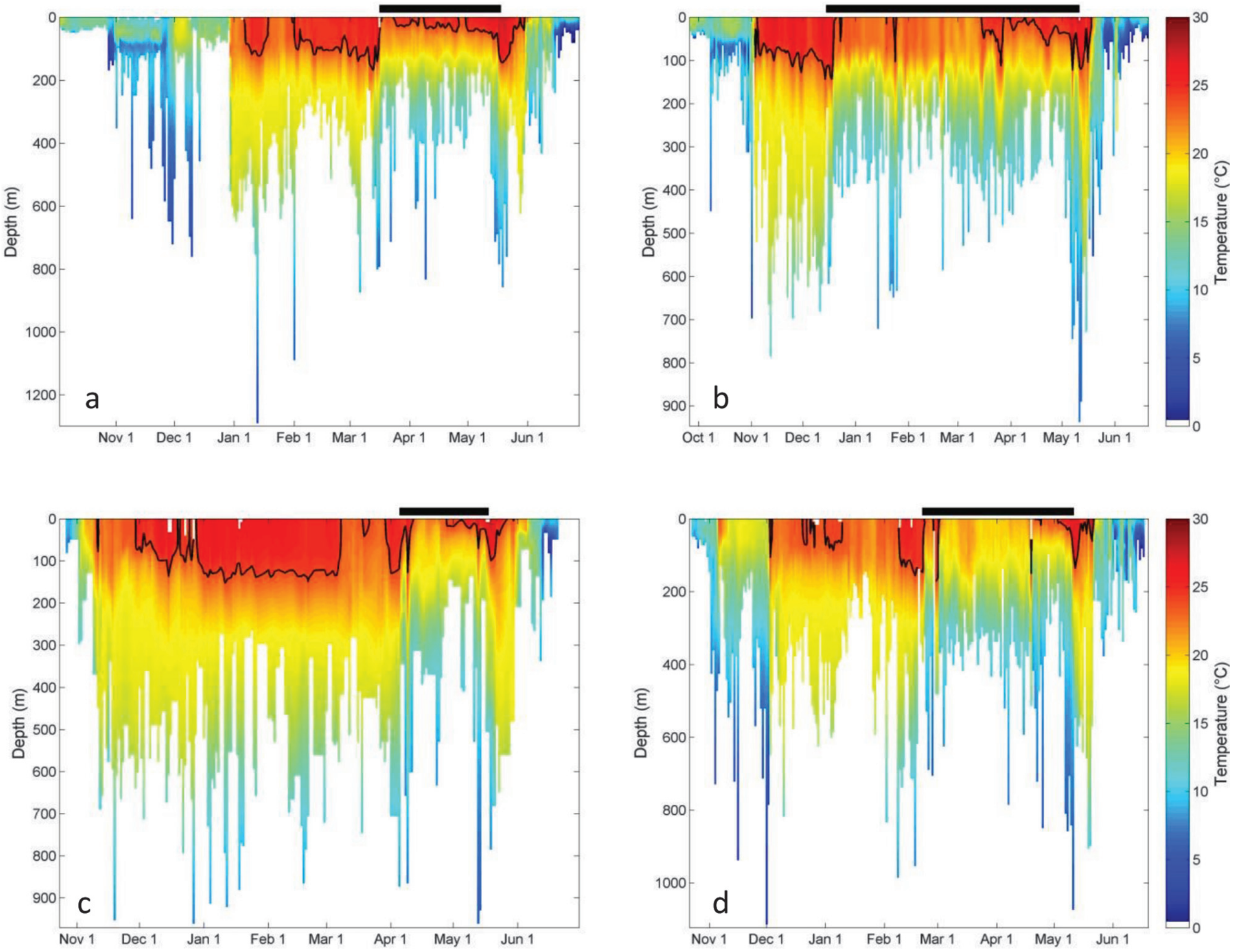
Western Atlantic bluefin tuna do not remain on their spawning ground throughout the year, and it is reasonable to believe that all Atlantic bluefin tuna found in the GOM are spawning adults (ICCAT 2013). Consequently, electronic tag data showing which fish travel to the GOM and which fish do not can be used to inform the maturity schedules of western Atlantic bluefin tuna. The same method cannot be applied to eastern Atlantic bluefin tuna, as the Mediterranean Sea contains year-round resident Atlantic bluefin tuna, as well as transient fish that move into the North Atlantic Ocean and return to the Mediterranean Sea to spawn (Cermeño et al. 2015; Fromentin and Lopuszanski 2013).

The age of first spawning (the youngest individual fish within a population that spawns) for western Atlantic bluefin tuna is unresolved, but estimates range from 4 to 8 years (Baglin 1982; Diaz 2011; Goldstein et al. 2007; Heinisch et al. 2014) depending on sample methodology. The age to 50% spawning is reported to be ~16 years in the GOM population (Diaz 2011). Electronic tagging can inform maturity studies by determining when, during ontogeny from adolescents to adults, Atlantic bluefin tuna first move into a spawning ground (Block et al. 2005; Teo et al. 2007*a*). In the eastern Atlantic, because some Atlantic bluefin tuna reside in the Mediterranean Sea year round, it is difficult to assess mean maturity of the distinct populations, and to date, few, if any, studies have resolved this. However, first maturity of some Mediterranean spawned fish is reported to be 3 to 4 years of age (Mather et al. 1995; Corriero et al. 2005).

In the present study, we tagged Atlantic bluefin tuna ranging from 187 to 313 cm on their GSL foraging grounds. The smallest fish that entered the GOM was 243 cm (~age 14; Restrepo et al. 2010), suggesting that few fish younger than age 14 spawn in the GOM (Fig. 3*b*). However, this study was not designed to identify age at first spawning, and the number of fish <243 cm that were tagged was small (n = 7) (Fig. 3*a*). Nevertheless, these tagging results are consistent with length frequency analyses of Atlantic bluefin tuna commercially caught on the GOM spawning ground that suggest age at 50% spawning of ~16 years (Diaz 2011). Thus, two independent methods (electronic tagging and pelagic long line fisheries capture) indicate an older age to mean and 100% spawning than is currently assumed by ICCAT assessments in population models (ICCAT 2014). A prior study using implanted archival tags on fish (primarily adolescents) tagged off North Carolina found that the mean size of fish that entered the GOM was 241 cm CFL when tagged, or ~14 years of age (Block et al. 2005), consistent with the results of the current study. In that previous archival tagging work, the smallest fish to enter the GOM was 207 cm when tagged, or ~10 years of age (Teo et al. 2007*a*). To date, our electronic tagging indicates that fish enter the GOM at ages of approximately 10–26 years and supports recent studies that have suggested later spawning schedules for GOM spawning fish (Diaz and Turner 2007; Diaz 2011).

Recent studies examining the maturity schedules of western Atlantic bluefin tuna, based on histology and endocrine levels, have suggested much younger ages of maturity for the GOM fish (i.e., ages 5–6; Goldstein et al. 2007; Heinisch et al. 2014). However, these studies used measures of maturity (stage 3 ovaries, ratios of follicle stimulating hormone to luteinizing hormone (FSH/LH) < 0.4) that may not indicate recent or approaching spawning activity but do provide information about hormone expression and gonad development. When compared with samples from the GOM spawning grounds, the values for these measures were quite different (presence of ovaries in stages 4 and 5 and FSH/LH = 0), as were measures of gonado-somatic index (mean GSI < 1 for samples outside the GOM and GSI > 3 for samples within the GOM; Baglin 1982; Goldstein et al. 2007; Knapp et al. 2013; Heinisch et al. 2014). Management models using earlier ages to maturity for GOM spawning fish may be overestimating the production of the population. Stock assessment models for western Atlantic bluefin tuna have consistently estimated stock recovery trajectories that have not been achieved in subsequent years, even though management advice was followed (Magnuson et al. 2001). This overestimation of the Atlantic bluefin tuna population growth rates may be due to the tradition of underestimating the mean age of spawning and therefore overestimating intrinsic rate of growth in this population.

Fig. 10. Daily ambient temperature – depth profiles of Atlantic bluefin tuna that (*a*) went to the eastern Gulf of Mexico (GOM) (ID 5111034), (*b*) went to the western GOM (ID 5111025), (*c*) went the eastern GOM during the year of the Deepwater Horizon oil spill year (ID 5109029), and (*d*) went to both sides of the GOM during oil spill year (ID 5109026). The 24 °C contour (the minimum SST reported for spawning in the western population) is shown. The bar at the top of each profile indicates residency period in the GOM based on location.



GOM spawning ground

By conducting tagging operations on the GSL assemblage of Atlantic bluefin tuna, the acquisition of electronic tagging tracks that provide data on entering and occupation of the GOM spawning ground from the western North Atlantic waters has increased substantially, providing new information on habitat utilization of these waters. These utilization data indicate that Atlantic bluefin tuna occupy the GOM spawning grounds from as early as late November through the first week of July, with peak residency occurring during the months of April and May. The mean length of GOM residency was 123 days. These findings are similar to those from studies using implantable archival electronic tags and pelagic longline catch data (Block et al. 2005; Teo and Block 2010; Teo et al. 2007*a*). Histological examination of gonads from Atlantic bluefin tuna caught on pelagic longlines observed ripe ovaries in April and May (Block et al. 2005; Gardner et al. 2012; Knapp et al. 2013). Similarly, larval surveys conducted in the GOM since 1982 by the National Marine Fisheries Service have shown that Atlantic bluefin tuna spawn there from April through June, with a peak thought to occur in May (Muhling et al. 2010, 2012). This does not explain why Atlantic bluefin tuna are present in the GOM from November to March and what role this early entry may play in final maturation before spawning.

Tagged Atlantic bluefin tuna also utilized a larger region in the prespawning period than during the peak spawning months. This larger range may also increase the probability of Atlantic bluefin catch in the pelagic longline fishery in the GOM before the spawning period. Directed fishing for Atlantic bluefin in the GOM is prohibited. However, significant numbers of Atlantic bluefin tuna are reportedly taken as bycatch (100 t in 2012) and landed by pelagic longline fishermen targeting yellowfin tuna and swordfish (Brown 2001; Ramírez-López and Abad Uribarren 2012). New regulations have closed parts of the GOM spawning ground to fishing from April through May and have implemented caps on Atlantic bluefin bycatch caught by individual boats and the fleet (National Oceanic and Atmospheric Administration (NOAA) 2014). However, kernel density plots for the months of April and May show that the spawning hotspots are centered to the north of the closure boxes and extend well beyond their boundaries (Fig. 6). As individual Atlantic bluefin residency in the GOM spans extensive periods before the spawning season, extending the closure into the winter months would have additional conservation benefit. Alternatively, the development of dynamic closure areas based on predictable GOM habitats defined by environmental signatures associated with spawning, e.g., bathmetry, SST, cyclonic and anticyclonic frontal zones, etc., may more effectively protect the population from unintentional bycatch during peak spawning periods.

Two regions of the GOM are known as Atlantic bluefin tuna spawning areas and both span the northern continental shelf slope waters: (*i*) the northern boundary of the Loop Current in the eastern GOM; and (*ii*) the northern boundary of mesoscale eddies in the western GOM (Block et al. 2005; Teo et al. 2007*a*, 2007*b*). The eastern hotspot identified by kernel analysis is consistent with the northern boundary of the Loop Current (Fig. 6). The Loop Current dominates the oceanography of the eastern GOM, entering from the Caribbean Sea, forming an anticyclonic loop, and then exiting through the Florida Straits (Sturges and Leben 2000). The western hotspot is situated along the northern boundary of anticyclonic eddies that spin across the western GOM. These are regular features of the western GOM and form once or twice per year when the Loop Current pinches off and forms a rotating ring of warm water (Sturges and Leben 2000). These rings travel from east to west and disintegrate once they cross the edge of the continental shelf and interact with the sea floor (Zimmerman and Biggs 1999). Smaller, cyclonic eddies spin off the Loop Current, upwelling nutrient-rich water at their centers and providing localized production (Zimmerman and Biggs 1999). Add to this the larger scale pattern of convergence associated with the anticyclonic flow of the Loop Current, and the result is enrichment followed by concentration and retention (Bakun 1996). The unidirectional flow of the Loop Current may also provide population maintenance problems for predators and competitors of Atlantic bluefin larvae. Larval surveys have found high concentrations of Atlantic bluefin along the northern edge of the Loop Current (Richards et al. 1989).

Deepwater Horizon oil spill

The Deepwater Horizon oil spill disaster led to approximately 3.19 million barrels of oil being spilled into the slope and coastal environments in the northeastern GOM between 20 April and 14 July 2010. Two Atlantic bluefin tuna tagged in Canada in 2009 were in close proximity to the Macondo Well on the day of the accident and remained nearby for several weeks (Figs. 2*d*, 2*e*). Oil from the wellhead formed surface slicks in the area, and these fish were potentially located in the oil-affected waters. Both fish, based on previous work using algorithms for surface and oscillatory behaviors exhibited by archival tagged Atlantic bluefin (Teo et al. 2007*a*), putatively spawned in late April – early May in waters impacted by the spill (Figs. 10*c*, 10*d*). If these Atlantic bluefin did spawn, their positively buoyant embryos would have risen to the surface where the slicks were observed. The toxic effects of Deepwater Horizon oil to early life stages of Atlantic bluefin tuna include bradycardia, arrhythmia, and edema (Brette et al. 2014; Incardona et al. 2014). The adult Atlantic bluefin tuna exited the GOM on 11 and 20 May 2010 and returned to Canadian waters by mid-June 2010, showing survivorship after potential interaction with oiled waters.

Mediterranean Sea

Canadian Atlantic bluefin tuna tagged in the GSL also moved to the eastern Atlantic and Mediterranean Sea. Two tags surfaced in the central Mediterranean Sea, and one popped up just outside the Strait of Gibraltar (Figs. 7*a*, 7*b*, 8*e*). This finding clearly links the Canadian Maritime fishery with fish of Mediterranean origin. These data contradict the earlier otolith analyses suggesting that all of the fish in this assemblage are of western origin (Rooker et al. 2008; Schloesser et al. 2010) and are more consistent with the recent data indicating that admixture may be increasing in this location (Hanke et al. 2015). Prior studies have reported on smaller Atlantic bluefin (mean size = 207 cm CFL) tagged in the western Atlantic that traveled to the Mediterranean Sea spawning ground (Block et al. 2005). Both of the Atlantic bluefin that entered the Mediterranean Sea spawning ground first traveled to Bahamian waters, as did some of the fish reported on in the earlier study. The Bahamas are recognized as a western Atlantic spawning region (Richards 1976). However, the Mediterranean Sea fish that traveled here did so in December through February, whereas spawning in this region is thought to occur in April through June (Richards 1976).

Neutral

A portion (43 of 94) of the electronically tagged fish did not visit the GOM or Mediterranean Sea spawning grounds. This resulted primarily from the premature release of MK10 PAT tags prior to their programmed pop-up date. The mean attachment duration of these 43 tags was 178 days. Many of these fish, based on size, were older than the age 5 or age 9 that ICCAT uses as ages of maturity for Mediterranean Sea and GOM Atlantic bluefin tuna, respectively (ICCAT 2013). Previous tagging studies in the western Atlantic have found "mature-sized" Atlantic bluefin tuna outside the known spawning grounds during the spawning season. Hypotheses proposed to explain this include the following: (*i*) spawning occurs at other locations in the Atlantic Ocean (Lutcavage et al. 1999; Block et al. 2001; Secor 2006); (*ii*) age at maturity is older than previously assumed (Block et al. 2005); or (*iii*) some Atlantic bluefin may "skip" spawning in some years, i.e., they are not obligate annual spawners (Lutcavage et al. 1999; Secor 2006). In the case of the 15 fish that were located in the North Atlantic during the spawning season, the mean size of the fish was 254 ± 22 cm (CFL ± SD, $n = 15$). This size corresponds with an age of ~15 years, close to the age of 50% spawning estimated by Diaz (2011) for GOM Atlantic bluefin tuna. Thus, it is possible that some of these fish are simply western spawners that have not yet started to spawn (adults that are just entering the top bracket in size for maturity). Alternatively, some may be eastern spawners that, if followed for longer periods of time, may have entered the Mediterranean Sea. Variability in first and mean spawning age, not knowing the prior history of individual fish as they proceed through ontogeny with variable access to prey resources, and the lack of knowledge of gender-specific schedules makes it challenging to know exactly when a fish begins regular spawning. Discerning between subadult and adult may vary by gender, particularly in the GOM lineage, and genetics on fin clips removed at the time of tagging may be the only method for population assignment of these particular tracks. However, precautionary approaches should recognize that this variability in maturation schedules is present, and this should be incorporated into modeling and population assessments to assure the future of the GOM population.

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