



Assimilating electronic tagging, oceanographic modelling, and fisheries data to estimate movements and connectivity of swordfish in the North Atlantic

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Broadbill swordfish (*Xiphias gladius*) is a key species in commercial fisheries, but management efforts continue to be hindered by data gaps in their basic biology, including ongoing debate over stock boundaries and movement between management zones. We deployed 20 pop-up satellite archival transmitting (PSAT) tags on juvenile swordfish in the Azores and adults in the northwest Atlantic (NWA). We applied a recently developed geolocation approach that synthesizes tag data with a global observation-assimilating ocean model to improve geolocation accuracy. Resulting tracks from 16 individuals averaged 3751 km (range 345–7247 km) over 93 days (range 17–181 days). Juveniles tagged in the Azores made regional movements while adults tagged in the NWA moved between summer foraging grounds near the Grand Banks to winter habitats near the Antillean Arc. All individuals spent considerable time in the mesopelagic zone during the day, and this behaviour increased with fish size. We integrate results from our PSAT-based movements with conventional tag and catch-per-unit effort data, which indicates complex stock structure within the North Atlantic that largely supports current stock boundaries. Our work demonstrates the utility in synthesizing fishery-independent electronic tag data and fisheries datasets to improve our understanding of large pelagic fish ecology.

Keywords: movement ecology, oceanography, satellite telemetry, state-space model

Introduction

Swordfish have the broadest geographical distribution of all billfishes (Braun *et al.*, 2015) and are found worldwide from 45°S to

45°N (Rich, 1947; Wise and Davis, 1973; Palko *et al.*, 1981). The species is the target of the most valuable and ubiquitous commercial billfish fishery in the world (FAO, 2012) that has historically led to

the overexploitation of swordfish stocks. Despite their economic value, swordfish now appear to be adequately managed in the North Atlantic after years of overfishing, but the South Atlantic and Mediterranean stocks are considered overfished with overfishing occurring (Collette *et al.*, 2011; Neilson *et al.*, 2013; ICCAT, 2017a, b). These three Atlantic swordfish stocks (North, South, and Mediterranean) have been defined based on deployment of conventional “spaghetti” tags (Garcia-Cortes and Quintans, 2003) and pop-up satellite archival transmitting (PSAT) tags (Neilson *et al.*, 2009; Abascal *et al.*, 2015) as well as analyses of population genetics (Bremer *et al.*, 1996; Alvarado Bremer *et al.*, 2005; Smith *et al.*, 2015). However, recent genetic evidence suggests that the boundary between north and south stocks may require revision (Smith *et al.*, 2015), and tagging studies by Neilson *et al.* (2009) and Abascal *et al.* (2015) observed movements consistent with potential population structure within the North Atlantic.

Most of the existing research on Atlantic swordfish is driven by stock assessment needs. Nearly all biological and ecological parameters are derived from the extensive work in the northwest Atlantic (NWA). Tagging studies indicate North Atlantic swordfish exhibit north–south movements for feeding and reproduction driven by contrasting ocean regimes (Sedberry and Loefer, 2001; Neilson *et al.*, 2009; Abascal *et al.*, 2015) during which they migrate from productive foraging grounds in the far north in summer to warm tropical and subtropical waters in winter to spawn and where larval growth rates are optimal (Arocha and Lee, 1995). Swordfish also have the physiological mechanisms that facilitate their ability to occupy a 15°C daily temperature range (Galli *et al.*, 2009) during regular diel vertical migrations (DVM; Carey and Robison, 1981; Lerner *et al.*, 2013) to the deep scattering layer (Carey, 1990; Josse *et al.*, 1998).

A thorough understanding of animal movements and habitat use is critical for formulating reliable stock assessments, including habitat-based vulnerability models and cpue corrections (Hinton and Nakano, 1996; Bigelow and Maunder, 2007), and detecting effects of climate changes (Schirripa *et al.*, 2017). Despite significant tagging effort in the NWA (>90 tags deployed in the Atlantic; Abascal *et al.*, 2015; Braun *et al.*, 2015), movement ecology of swordfish remains poorly understood, and no movement data are currently reported from the central Atlantic near the mid-Atlantic Ridge. In addition, relatively few studies combine fisheries-dependent and independent datasets to synthesize inference across data types. We analysed >1500 tracking days and 230 000 time-series data points from 16 swordfish equipped with PSATs in the NWA ($n = 10$) and the Azores ($n = 6$) and integrated these fisheries-independent data with inference from movements of 72 swordfish derived from PSAT tag records, >15 000 conventional tag deployments and cpue data from nearly 2 billion longline hooks to address swordfish movements and connectivity in the North Atlantic.

Material and methods

Satellite tagging

We deployed 20 PSAT tags (17 miniPAT, 3 Mk10-AF; Wildlife Computers Inc., Redmond, WA, USA) on swordfish (*Xiphias gladius*) in the North Atlantic between 2009 and 2014, including eight near the Grand Banks, five in the southern Sargasso Sea, and seven around the Azores (Table 1). PSAT tags archived depth, temperature, and light-level data every 10 s (Mk10-AF) or 15 s (miniPAT). All tags recorded light data for geolocation purposes, and the Mk10-AF tags also housed a Fastloc GPS receiver

for acquiring high-resolution location information. Juvenile swordfish in the Azores were caught by a research vessel using a modified longline (light tackle, small hooks, and short soak times) and brought alongside a smaller tagging skiff for restraining and tagging in the water. Larger NWA swordfish were caught by a commercial longline vessel, brought alongside the boat, and tagged if judged to be in good condition by the vessel captain. Weight and lower jaw fork length were measured or estimated by the tagging teams. Maturity stage was estimated based on maturity-at-age 4–6 and weighing ~60 kg (subadult 40–60 kg at age 2–3 and juveniles <40 kg at age 1; Neilson *et al.*, 2013). Anchoring devices (titanium plate or nylon umbrella dart) were placed in the dorsal musculature near the base of the dorsal fin. Tags were released from the swordfish using a corrosive burn wire at pre-programmed dates (range of programmed deployment duration 90–181 days). After the tags released and floated to the surface, summarized data were transmitted to Argos satellites until battery failure. Transmitted data were decoded with manufacturer software (WC-DAP 3.0, Wildlife Computers, Inc.). Data from tags that released prematurely after <10 days were not analysed. This research was performed in accordance with the Woods Hole Oceanographic Institution’s Animal Care and Use Committee (IACUC) protocol #16518.

Geolocation methods

Most probable tracks for PSAT-tagged swordfish were constructed using the HMMoce package (Braun *et al.*, 2018) for R (R Development Core Team, 2015). This approach combines measurements of light-levels, sea surface temperature (SST), and depth-temperature profiles recorded by archival tags, with bathymetry and oceanographic observations and model outputs, to construct likelihoods of the tagged individual’s movements. Likelihoods are convolved in a gridded hidden Markov model that computes posterior probability distributions to estimate the most likely state (position and behaviour) of the animal at each time point.

Observation-based likelihoods were derived from remotely-sensed SST, light-based longitude, and depth-temperature profile data collected by the tags, using four separate likelihood calculations: (i) An SST likelihood was generated for tag-based SST values integrated according to an error term ($\pm 1\%$) and compared with remotely-sensed SST from daily optimally-interpolated sea surface temperature (OI-SST, 0.25° resolution) fields (Reynolds *et al.*, 2007; Banzon *et al.*, 2016); (ii) Light-based longitude likelihood was derived using estimates of longitude from GPE2 software (Wildlife Computers, Inc.) that allowed visual checking of light curves; (iii) Depth-temperature profiles recorded by the tag were compared with daily reanalysis model depth-temperature products from the HYbrid Coordinate Ocean Model (HYCOM, 0.08° resolution; Bleck, 2002; Chassignet *et al.*, 2007) at standard depth levels available in these products. Individual likelihood surfaces for each depth level were then multiplied together for an overall profile likelihood at that time point; (iv) Ocean heat content (OHC) was obtained by integrating the heat content of the water column above the minimum daily temperature to the most shallow depth recorded by the PSAT and included in the HYCOM fields (Luo *et al.*, 2015). Start and end locations were known in all model runs.

The resulting observation likelihoods, in all possible pairwise and triplicate combinations, were convolved with two different

Table 1. Summary of swordfish tagged with PSATs (this study) in the North Atlantic Ocean.

Tag ID	Tag date	Tag lat. (°N)	Tag lon. (°E)	Est. wt. (kg)	Stage	Tag type	Region	TAL	Pop lat. (°N)	Pop lon. (°E)	Cum. dist. (km)	PDT (%)	Light (%)	SST (%)	Geoloc. obs.
98751	2009-12-02	38.44	−28.52	11.0	J	mP	AZ	17	32.92	−28.18	773	88	47	82	LSH
104668	2011-10-21	38.41	−28.51	19.5	J	mP	AZ	35	27.17	−30.92	2590	91	9	89	LSH
104670	2011-10-21	38.44	−28.56	23.5	J	mP	AZ	26	31.9	−30.89	902	88	85	42	LSH
98721	2011-10-26	38.44	−28.54	12.0	J	mP	AZ	DD ^a							
98722	2011-10-26	38.43	−28.53	11.0	J	mP	AZ	150	38.17	−28.56	5335	60	24	81	LSH
104671	2011-11-15	37.84	−27.17	17.5	J	mP	AZ	150	37.84	−27.17	4816	71	33	91	LSH
104672	2011-11-15	37.84	−27.17	10.0	J	mP	AZ	41 ^b	33.54	−28.53	2357	96	38	98	LSH
100976	2010-11-25	28.20	−66.92	50.0	SA	mP	FL	24	20.27	−65.05	979	92	0	92	LH
100980	2010-11-30	28.34	−67.52	68.2	A	mP	FL	90	30.84	−75.17	3828	94	1	73	LSH
100978	2011-01-10	27.57	−67.92	45.5	SA	mP	FL	DD							
95975	2011-01-20	24.61	−68.58	56.8	SA	mP	FL	181	38.93	−53.2	6782	83	9	81	LSH
95983	2011-01-31	25.90	−69.53	56.8	SA	mP	FL	DNR							
110490	2011-09-15	43.67	−48.81	81.8	A	mP	GB	90	30.29	−63.63	4449	79	39	96	LSH
110491	2011-09-15	43.65	−48.82	81.8	A	mP	GB	180	12.35	−60.04	6914	36	33	64	LSH
110497	2011-09-19	43.94	−48.57	65.9	A	mP	GB	90	18.7	−76.16	4869	72	21	70	LH
110498	2011-09-22	43.90	−48.40	100.0	A	mP	GB	90	32.38	−59.38	2718	74	14	83	LSH
110496	2011-10-17	44.57	−46.90	61.4	A	mP	GB	149 ^c	34.95	−50.37	7247	99	32	97	LSO
106788	2013-09-27	46.69	−45.80	90.9	A	fl	GB	180	20	−74.28	6714	27	1	3	LSH
106795	2013-09-27	46.48	−45.56	90.9	A	fl	GB	40	31.03	−39.68	2146	95	28	70	FLSH
106797	2013-09-27	46.62	−45.64	68.2	A	fl	GB	DNR							

Est. wt., estimated weight (kg). Stage, stage of maturity for juvenile (J); subadult (SA); and adult (A) swordfish. Tag types are miniPAT (mP) or Fastloc (fl). Region indicates where an individual was tagged and refers to the Grand Banks (GB), the Azores (AZ) or offshore from Florida in the southern Sargasso Sea (FL). Time-at-liberty (TAL) is in days. Distance (Cum. dist.) is cumulative track distance in km. PDT, Light, and SST = per cent of deployment period with depth-temperature profiles (PDT), light, and sea surface temperature (SST) data, respectively. Observation likelihoods (Geoloc. obs.) indicates observations used in HMMocean to construct the most probable track: L, light-based longitude; S, sea surface temperature; H, HYCOM depth-temperature profiles; O, integrated ocean heat content; F, Fastloc GPS; DD, data deficient. Graphical representation of some variables is shown in [Supplementary Figure S1](#).

^aPredation after release.

^bPredation by lamnid shark after 41 days.

^cCaptured by Spanish longline vessel 149 days after release. Tag was physically recovered.

movement kernels representing resident and migratory behaviour “states” of tagged fish. For full details of the convolution, filtering and smoothing components of the model see [Braun et al. \(2018\)](#). Parameter estimation was performed using an Expectation–Maximization algorithm following [Wouillez et al. \(2016\)](#), and model selection used Akaike Information Criterion. Results from the final smoothing step of the selected model represent the posterior distribution of each state over time. Distributions were summed for each behaviour state and time-step to determine the most likely behaviour state at each time. The mean of the daily distributions was used to calculate a most probable track.

Fisheries data

To evaluate movements of satellite-tagged fish in relation to the swordfish longline fishery in the North Atlantic, we obtained fisheries data (Task II catch–effort; version November 2016) from the ICCAT Secretariat (<http://www.iccat.int/en/accesingdb.htm>). We extracted longline data for the years 1990–2010 in the North Atlantic west of 20°W at two different spatial resolutions: (i) 1° × 1° for the US fleet and (ii) 5° × 5° resolution data available for the international fleets from Brazil, China, Cuba, Greece, Japan, Korea, Libya, Mexico, Spain, UK, and Uruguay. Longline catch data were used to calculate mean catch-per-unit effort (cpue; number of fish per 1000 hooks) in each grid cell. Cpue data resulting in >200 fish per 1000 hooks were considered an error and removed from the dataset. We also obtained conventional tag data from the ICCAT Secretariat tag database for swordfish in the North Atlantic from 1940 to 2016.

Data analysis

All analyses were conducted in R ([R Development Core Team, 2015](#)). Vertical movements of archival-tagged swordfish were analysed by aggregating depth and temperature data in seasonal (Spring, 20 March–19 June; Summer, 20 June–19 September; Fall, 20 September–19 December; Winter, 20 December–19 March) bins every 25 m and 1°C, respectively. Further analyses used remotely-sensed, modelled, and tag-based *in situ* data to summarize typical environmental characteristics relevant to swordfish vertical movements. SST and temperature-at-depth data were derived from HYCOM (see Geolocation methods). Diffuse attenuation coefficient (K490) indicates how strongly light intensity at 490 nm is attenuated within the water column and was used as a proxy for scattering layer depth following [Dewar et al. \(2011\)](#). K490 is a derivative product of MODIS Aqua (8-day composite, Global, 4 km; accessed at NOAA’s ERDDAP server using dataset ID erdMH1kd4908day) calculated using an empirical relationship between K490 and reflectance. Night-time habitat use was compared with lunar illumination using the lunar package in R ([Lazaridis, 2014](#)). Occupation of the mesopelagic was quantified by summarizing the percent time individuals spent below 200 m for each deployment day. Non-linear regression analysis was used to characterize the relationships between maximum depth and K490, lunar illumination and mean night-time depth, and swordfish size with time spent in the mesopelagic. Fork lengths were estimated using empirical weight–length relationships from ICCAT for North Atlantic swordfish ([Lombardo et al., 2017](#)). Connectivity was quantified by comparing conventional tag releases and recaptures among ICCAT sampling zones. These were overlaid with fishery-independent satellite tag data from published swordfish tracks in the Atlantic by updating a

recent review ([Braun et al., 2015](#)) with tracking data published since ([Abascal et al., 2015](#)).

Results

Sixteen of the 20 PSAT tags deployed reported and transmitted useable data, 7 of which were shed prematurely ([Table 1](#)). Fifteen of the reporting tags transmitted data after an average deployment of 93 days (range 17–181 days), and one tag was recovered after 149 days at liberty (PTT 110496; [Table 1](#)). All individuals ($n = 7$) tagged near the Azores were juveniles with a mean estimated weight of 15 kg (range 10–24 kg). The largest individuals were adults tagged near the Grand Banks ($n = 8$), which averaged 80 kg (range 61–100 kg), and those tagged in the western Atlantic were a mix of adult ($n = 1$) and subadult ($n = 4$) fish averaging 55 kg (range 46–68 kg; [Supplementary Figure S1](#)).

Varying amounts of each data type were obtained from the PSATs for estimating most probable tracks ([Table 1](#), [Supplementary Figure S1](#)). Light data recorded by the tags were rarely sufficient for traditional light-level geolocation (mean 25% of deployment days, range 0–85%). Both SST and depth-temperature profile data were generally available for a higher percentage of deployment days than light data and, on average, comprised 72 and 79% of deployment days, respectively (SST range 3–98% and profile range 27–99%). Two of three Fastloc tags reported data, but only one (PTT 106795) reported two realistic GPS positions collected during deployment. Geolocation model selection favoured HYCOM-based profile likelihoods in 15 of 16 track calculations. The remaining geolocation analysis leveraged OHC-based profile likelihoods to generate the most likely track estimate ([Table 1](#)).

Horizontal movements

Overall movements of PSAT-tagged swordfish ranged from 345 to 7247 km in up to 181 days at liberty ([Supplementary Figure S1](#)) and were predominantly oriented north–south ([Figure 1](#)). We found no relationship between fish size and displacement using regression, and we found no difference in movement rates among fish from the different regions. The PSAT-tagged adults in the NWA moved across a 35° latitudinal range between temperate waters in summer as far north as the Grand Banks and tropical or subtropical waters during winter from the Caribbean to coastal Florida (10–30°N; [Figure 1](#)). These habitats were connected by long-range, relatively directed movements through the Sargasso Sea with the majority of more tortuous movements occurring in the Gulf Stream and from the Bahamas southeast along the Antillean Arc and southern Sargasso Sea (track distance 979–7247 km).

All of the seven tags deployed on adults near the Grand Banks in September and October had left the tagging region by mid-October. Six individuals crossed the Gulf Stream and moved southwest into warm tropical waters (~28–30°C) in early November and were located south of 30°N by December. The remaining individual tagged on the Grand Banks (PTT 110491) moved into the Gulf Stream in early November and remained mostly along the north boundary until late December. Overwintering habitat was centred on ~20–25°N but spanned 30° of longitude from the eastern Caribbean and the NE coast of Venezuela to as far east as the mid-Atlantic Ridge. The individual tagged on the Grand Banks that moved SE to the mid-Atlantic Ridge began a return migration to the north in mid-February,

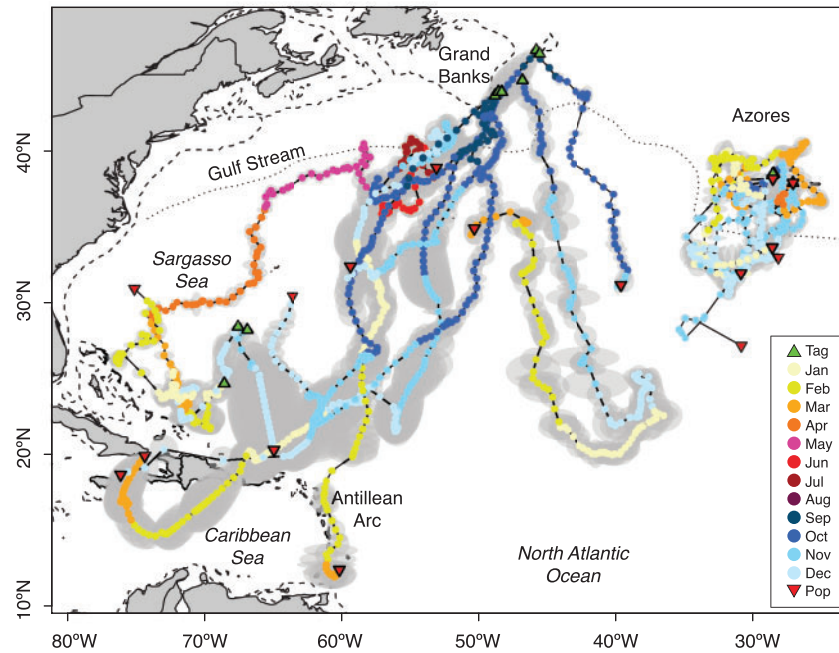


Figure 1. Movements of satellite-tagged swordfish in the North Atlantic. Most probable track estimates for swordfish in which point colour indicates month. Upwards (green) and downwards (red) pointing triangles represent release and pop-up positions, respectively. Dashed point and line contours represent the mean Gulf Stream position (15°C contour at 200 m in World Ocean Atlas mean temperature climatology) and the 200 m bathymetric contour, respectively. Grey ellipses indicate 90% likelihood interval for position estimates.

but this tag popped up prematurely in mid-March along the 20°C isotherm near 35°N. A single tag from January deployments off Florida transmitted reliable data (PTT 95975). This dataset comprised the only spring movements observed in this study and indicated northward migration began in mid-April arriving to the Gulf Stream by May.

Juveniles and subadults tagged near the Azores exhibited relatively restricted movements, in both latitudinal range (27–40°N) and overall distance (345–5335 km), as compared with the larger fish tagged in the NWA. These individuals were tagged in late October and early November around 38°N and, in general, moved south into the warmer Azores Front region at ~32°N. Of the three tags at liberty in January, one returned to the Azores in late December followed by a second that returned in mid-February. A third tag deployment ended in early January at 33°S, and movements did not suggest a return migration to the Azores.

Vertical movements

Maximum depth observed was 1664 m by an adult in the NWA, and five more adults made excursions deeper than 1000 m. Although maximum depths recorded by tagged juveniles were considerably shallower than the adults, all tagged individuals made excursions to at least 600 m (Table 2). Diel vertical migration was consistently recorded in all individuals (except for PTT 104672, which experienced mortality because of predation shortly after tagging) with daytime depths (mean 507 ± 152 m) significantly deeper than night (67.6 ± 54 m; t -test $p < 0.001$). During diel vertical migrations, all individuals regularly occupied the mesopelagic (>200 m) during daytime, but adults in the NWA spent significantly more time deep in the water column ($51 \pm 17\%$ daily average below 200 m) than smaller individuals in the Azores

($30 \pm 21\%$). This difference appeared to be driven primarily by body size (non-linear regression $R^2 = 0.59$, $p = 0.002$; Figure 2) rather than temperature at depth ($p > 0.05$ using regression; Supplementary Figure S4). Histograms of time-at-depth demonstrate clear diel vertical migration by all adults in the NWA (Figure 3, Supplementary Figure S3). Depth distribution among juveniles in the Azores exhibited some bimodality (Figure 3, Supplementary Figure S3) with a primary DVM signal and a smaller (~20% of time) but apparent signal of contrasting surface occupation during daytime.

Swordfish experienced a 27°C temperature range (2.7–29.6°C) by occupying warmer surface waters at night (median temperature range 17.3–25.9°C) than during deep vertical excursions during daytime (median temperature range 11–20.3°C). Overall, daily temperature differences relative to SST (ΔT) exhibited a bimodal distribution in which nearly half (46%) of time-series temperature data was $\pm 1^\circ\text{C}$ ΔT and nearly 30% was between 8 and 15°C ΔT . Juveniles in the Azores consistently occupied colder water at the surface and exhibited less seasonal fluctuation in vertical and thermal habitat envelopes compared with adults in the NWA (Figure 4). Adults occupied a wider range of temperatures both at the surface and at depth as their movements spanned >30° of latitude during seasonal migrations. Swordfish also tended to occupy greater depths during day and night in the Sargasso Sea and at the southern extent of the movements exhibited by fish tagged in the Azores relative to shallower movements at the northern extent of both tagging regions (Gulf Stream/Grand Banks and north of Azores archipelago; Figure 5). Some individuals exhibited deeper median night-time depths with increasing lunar illumination, but correlation was highly variable ($R^2 = 0.03$ –0.76; Table 2). Aggregated vertical movements by region indicated no

Table 2. Summary of depth and temperature records of PSAT-tagged swordfish.

ID	Stage	Region	Data days	Max depth (m)	Median day depth (m)	Median night depth (m)	Median day temp (°)	Median night temp (°)	Median daily meso time (%)	Lunar R ²
98722	J	AZ	150	760	494	54	13.0	17.8	29.8	0.03
98751	J	AZ	17	632	291	46	14.3	18.7	22.0	0.55 ^a
104668	J	AZ	35	792	683	48	11.0	22.2	43.8	0.04
104670	J	AZ	26	648	131	42	16.7	20.9	9.9	0.04
104671	J	AZ	150	728	526	41	12.0	17.3	43.3	0.03
104672	J	AZ	41	688	6	30	20.3	20.4	15.0	0.03
95975	SA	FL	181	1024	566	22	13.1	21.2	59.3	0.08 ^a
100976	SA	FL	24	1182	683	23	12.0	25.3	50.5	0.35 ^a
100980	A	FL	90	1064	637	30	13.3	24.0	50.0	0.51 ^a
106788	A	GB	180	824	582	44	15.0	25.9	50.0	0.25 ^a
106795	A	GB	40	680	516	25	11.6	19.5	50.1	0.22 ^a
110490	A	GB	90	1008	591	47	13.6	25.3	49.9	0.03
110491	A	GB	180	1008	417	26	11.6	24.3	47.7	0.16 ^a
110496	A	GB	149	1664	576	40	12.4	23.8	48.9	0.37 ^a
110497	A	GB	90	896	599	63	13.1	24.3	51.3	0.17 ^a
110498	A	GB	90	800	585	38	14.1	24.0	48.0	0.12 ^a

See [Supplementary Figure S2](#) for the complete depth-temperature time-series data from which most of these summary statistics were calculated.

^aLinear regression between lunar illumination and median nightly depth $p < 0.01$.

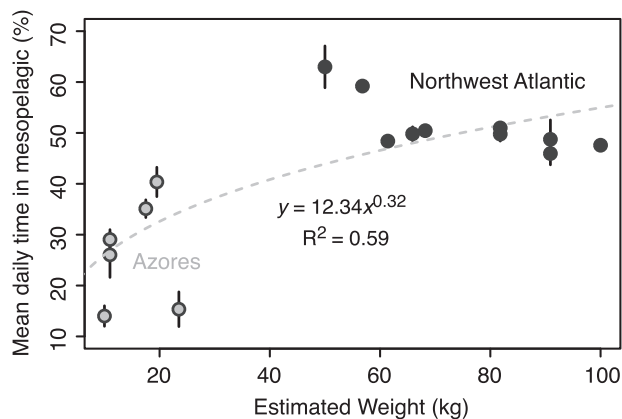


Figure 2. Mean (\pm s.e.) daily time individuals occupied the mesopelagic (>200 m) as a function of estimated body weight for immature fish tagged in the Azores (grey) and larger individuals from the northwest Atlantic (black).

correlation with lunar illumination as a group, and we found no relationship between maximum depth and K490.

Fishery-based inference

The ICCAT Task II database contained catch and effort data consisting of ~ 135 million hooks set by the US longline fleet from 1990 to 2009 gridded at 1° spatial resolution ([Figure 6](#)). This effort resulted in a catch of 1.2 million swordfish with a mean cpue of 12 fish per 1000 hooks (range 0–200). Data were available for longline vessels from other flag countries that set ~ 1.7 billion hooks in the North Atlantic from 1990 to 2009. Approximately 4 million swordfish were harvested during this time with mean cpue of 3.4 fish per 1000 hooks (range 0–72). Most of the reported non-US catch data came from the Japanese (52%), Chinese (23%), and Spanish (22%) fleets. Seasonality observed in catch data was broadly similar to the movements

exhibited by the satellite-tagged fish ([Figure 6](#)) and from conventional tag data ([Supplementary Figure S5](#)). In general, cpue was highest along the Grand Banks, the central North Atlantic, and around Bermuda in summer and moved south from northern latitudes in winter ([Figure 6](#)). During winter and spring months, cpue was focused from the Gulf of Mexico, east to the southeastern United States, Caribbean Sea, and along the Antilles. Effort began returning north in spring, particularly by the international (non-US) fleet, and returned to the Grand Banks and south to $\sim 20^\circ\text{N}$ in the central North Atlantic by summer ([Figure 6](#)). Catch rates in the Caribbean and Gulf of Mexico were low to moderate for the US fleet during Fall, Winter, and Spring but were particularly low during summer and did not appear to yield any cpue to the international fleet using the ICCAT dataset. The Azores did not appear to exhibit high cpue during any season.

The conventional tag database contained 568 recaptures from 15 101 conventional tag deployments on swordfish from 1940 to 2016. The majority of conventional tags was deployed and recovered along the eastern seaboard of the United States but spanned the North Atlantic from the Gulf coast of Texas to Europe and from the Amazon Delta to the Grand Banks ([Figure 7](#)). Conventional tag displacements exhibited north–south seasonality similar to those derived from PSAT data in which winter conventional tag releases were spread between $\sim 10^\circ$ and 35°N , moving almost exclusively north of 30°N and concentrated around 45°N during summer and fall, before moving south again starting in November ([Supplementary Figure S5](#)).

Connectivity

We observed no overlap in movements of PSAT-tagged fish from the NWA with those tagged in the Azores and little overlap with previously published swordfish PSAT tracks ([Figure 7](#)). Conventional and satellite tag-based displacements suggested virtually no movement across the north–south stock boundary at 5°N but suggested some exchange across the boundary proposed by [Smith et al. \(2015\)](#), particularly east of 35°N and south of the

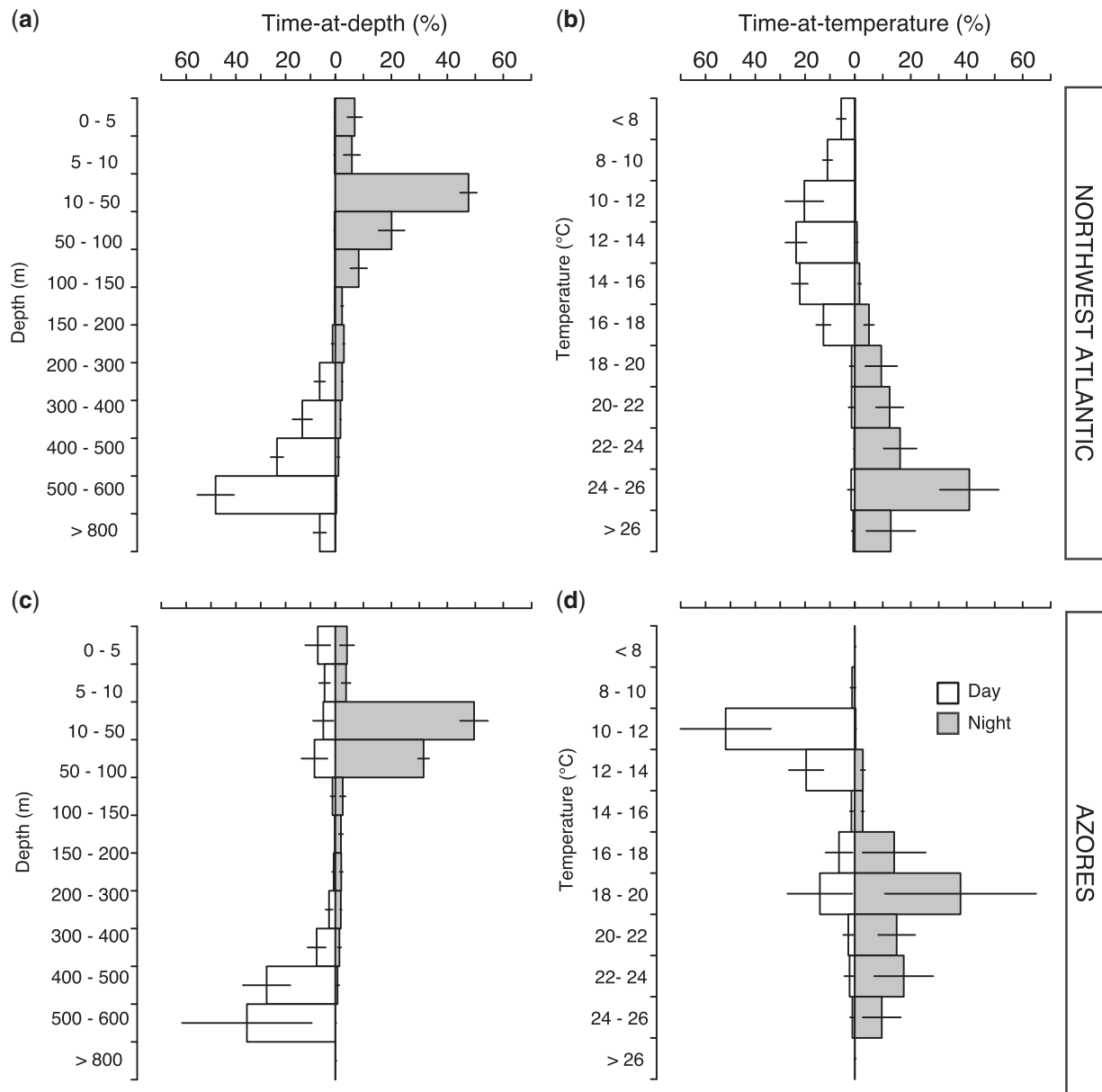


Figure 3. Frequency (%) histograms of mean (\pm s.e.) time-at-depth (a, c) and time-at-temperature (b, d) exhibited by swordfish tagged in the northwest Atlantic (panels a, b; $n = 10$) and the Azores (panels c, d; $n = 6$).

Azores. Displacement of recaptured conventional tags indicated limited connectivity between the NWA and NEA and between any of the ICCAT sampling zones except between the Gulf of Mexico (BIL91) and the eastern United States (BIL92) (Figure 7). The east-west division was most prominent around $\sim 35^\circ$ W, as $< 3\%$ of conventional tag recoveries (out of 568 total recovered tags) and only 2 PSATs ($< 2\%$) exhibited movement across this boundary.

Discussion

Horizontal movements of swordfish in the Atlantic remain poorly understood despite the deployment of PSATs on > 110 individuals (Abascal *et al.*, 2015; Braun *et al.*, 2015). This is at least partially because of a consistent pattern of crepuscular descents by swordfish that often render traditional light-based geolocation difficult (Dewar *et al.*, 2011; Lerner *et al.*, 2013). Many studies

have therefore focused on the vertical habitat of swordfish in isolation from the geographic space where the vertical behaviours occurred (Loefer *et al.*, 2007; Dewar *et al.*, 2011; Abecassis *et al.*, 2012; Lerner *et al.*, 2013; Evans *et al.*, 2014).

Here, we employed a recent advance in geolocation analysis methods to supplement missing light data with other forms of data recorded by the PSATs (Braun *et al.*, 2018). Although we were unable to quantify reconstructed track error using known tracks, Braun *et al.* (2018) suggested that the root-mean-square error for similar quality datasets is ~ 100 – 150 km, which is significantly more accurate than traditional geolocation approaches with higher quality data. This is primarily because of the functionality in HMMoce that uses daily depth-temperature profiles collected by deep diving swordfish to inform geolocation estimates despite low-quality light data. Indeed, using likelihood-

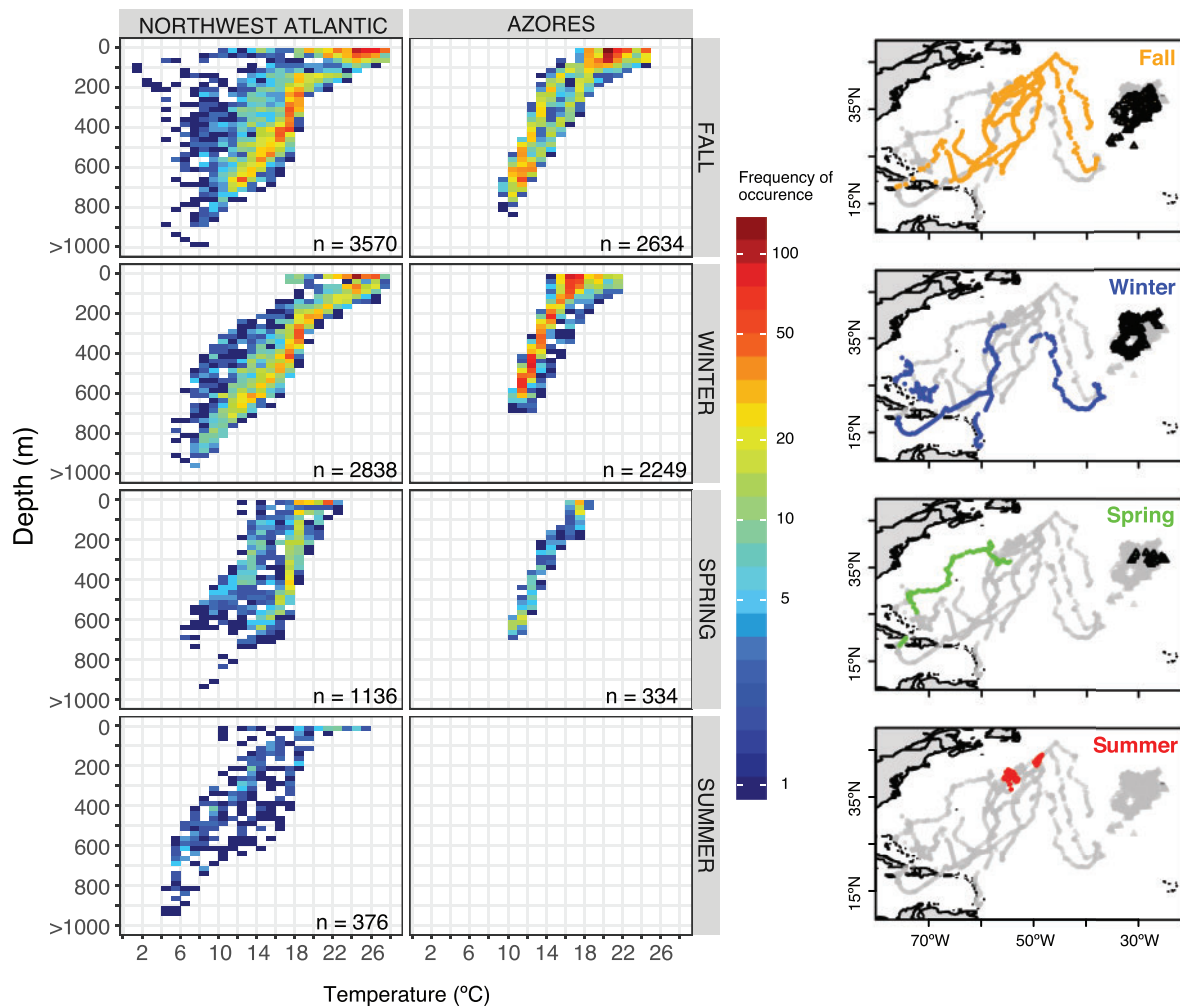


Figure 4. Vertical habitat envelopes occupied by PSAT-tagged swordfish in the northwest Atlantic (column 1) and Azores (column 2). Temperature and depth data are binned every 1°C and 25 m, respectively. Corresponding movement data for each seasonal habitat envelope are shown in column 3 (northwest Atlantic, circles; Azores, triangles).

based model selection, all model runs in this study suggest those that leveraged three-dimensional oceanographic data were superior to otherwise identical two-dimensional models. These results highlight the need to leverage depth-temperature profiles in data-poor geolocation models (e.g. [Liu et al., 2017](#)).

Movements

Most swordfish movement studies around the world report broad, cyclic movements of adult swordfish from known spawning habitats in warm (>24°C), tropical, or subtropical waters during winter to more productive foraging habitats (e.g. upwelling zones and productive banks, [Sedberry and Loefer, 2001](#); [Abascal et al., 2015](#)) during summer [northwest Pacific ([Takahashi et al., 2003](#)), southeast Pacific ([Abascal et al., 2010](#)), and NWA ([Neilson et al., 2009](#))]. Our results provide additional support for such long-range, periodic pelagic movements, but most individuals occupied a distinct longitudinal gap in the existing literature on swordfish movements (~40–60°W; except see [Abascal et al., 2015](#)). Synthesis across several large-scale tagging studies in the NWA has previously shown primarily north–south movements by individuals tagged further west than most of the swordfish in our study ([Neilson et al., 2014](#)).

Swordfish in the western North Atlantic typically exhibited north–south movements from productive foraging grounds in the far north during summer to tropical and subtropical waters in winter, presumably to spawn in warm waters that promote larval growth ([Arocha and Lee, 1995](#); [Suca et al., 2018](#)). The timing of migration varied among individuals, but, in general, adults occupied a relatively restricted area within temperate waters from Cape Cod to the Grand Banks during June to October then performed directed movements south to a wider region in the (sub)tropics to the Sargasso Sea, Caribbean, and Gulf of Mexico from December to March ([Neilson et al., 2009](#)). Mature individuals moved into known spawning areas of the southern Sargasso Sea and Antillean Arc during the spawning period (December through February; [Neilson et al., 2013](#)). However, these individuals were typically tagged months earlier and thousands of kilometres away and were not sexed nor was maturity assessed. As such, we are unable to determine the contribution of reproduction to the observed movements.

Relatively little is known about juvenile swordfish movements and habitat use. Tagged juveniles in our study made relatively restricted movements between the Azores Front and the Azores archipelago. Previous work has suggested juveniles primarily occupy

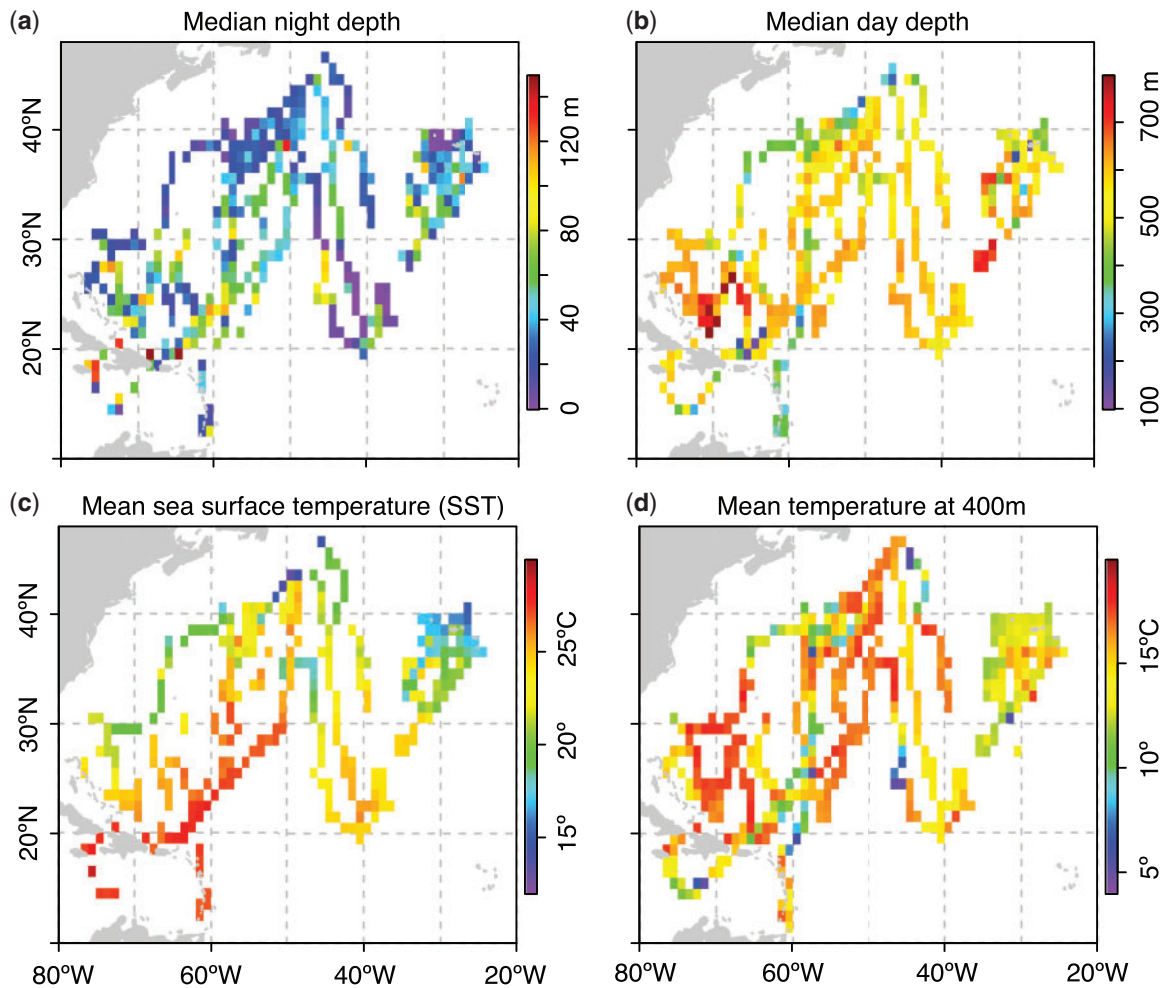


Figure 5. Depths (a: median night depth, b: median day depth) and environmental characteristics (c: mean sea surface temperature, d: mean temperature at 400 m) occupied by PSAT-tagged swordfish summarized on a $1^\circ \times 1^\circ$ grid.

warm, subtropical habitats and likely exhibit more variable movements compared with the largely north–south migration observed by most tagged adults (Abascal *et al.*, 2015; Neilson *et al.*, 2009). This may reflect the importance of foraging needs among immature individuals that subsequently changes with ontogeny to incorporate larger-scale movements related to spawning. In addition, in contrast to Palko *et al.* (1981) who found individuals <90 kg were rarely observed in SST <20°C and concluded these smaller individuals had lower thermal plasticity, we observed juvenile swordfish 10–25 kg consistently occupied waters with mean SST <20°C for extended periods. Our observations suggest juveniles may seek a more thermally-stable habitat (as opposed to warm water or oceanographic regimes with significant seasonality) instead of requiring warmer water than adults, as previously hypothesized.

Vertical activity

Although previous studies have included broad analyses of vertical movements by adult swordfish (e.g. Loefer *et al.*, 2007; Dewar *et al.*, 2011), we found evidence of similar diel behaviour by juvenile swordfish. This behaviour may be developing in younger individuals, as juveniles typically spent less time-at-depth and the

DVM was less consistent than in adults. Time spent in the mesopelagic zone increased with body size implying that larger individuals have the physiological abilities to withstand the acute changes in temperature that accompany their daily vertical movements. These findings suggest an ontogenetic component to the development of DVM behaviour in swordfish that may be related to the ongoing development of specific cardiac functions (Galli *et al.*, 2009) or their highly specialized extraocular musculature and vascular system that warms the eyes and brain up to 15°C above ambient water temperature (Carey, 1982, 1990). It should also both influence and reflect the progressive development of behavioural ability in pursuing and capturing prey at depth. This development and its influence on habitat use by juvenile swordfish may make them more available to surface-oriented fishing fleets and has implications for size selectivity in a fishery that, in the Atlantic, prohibits the landing of smaller individuals.

Temperature has long been hypothesized as a primary driver of vertical habitat use for swordfish (e.g. Carey and Robison, 1981; Abecassis *et al.*, 2012). Takahashi *et al.* (2003) suggested cooler SSTs (<20°C) may inhibit diel vertical migrations, but, similar to Dewar *et al.* (2011), we observed swordfish at SSTs ~15°C diving below 400 m during the day into water <10°C.

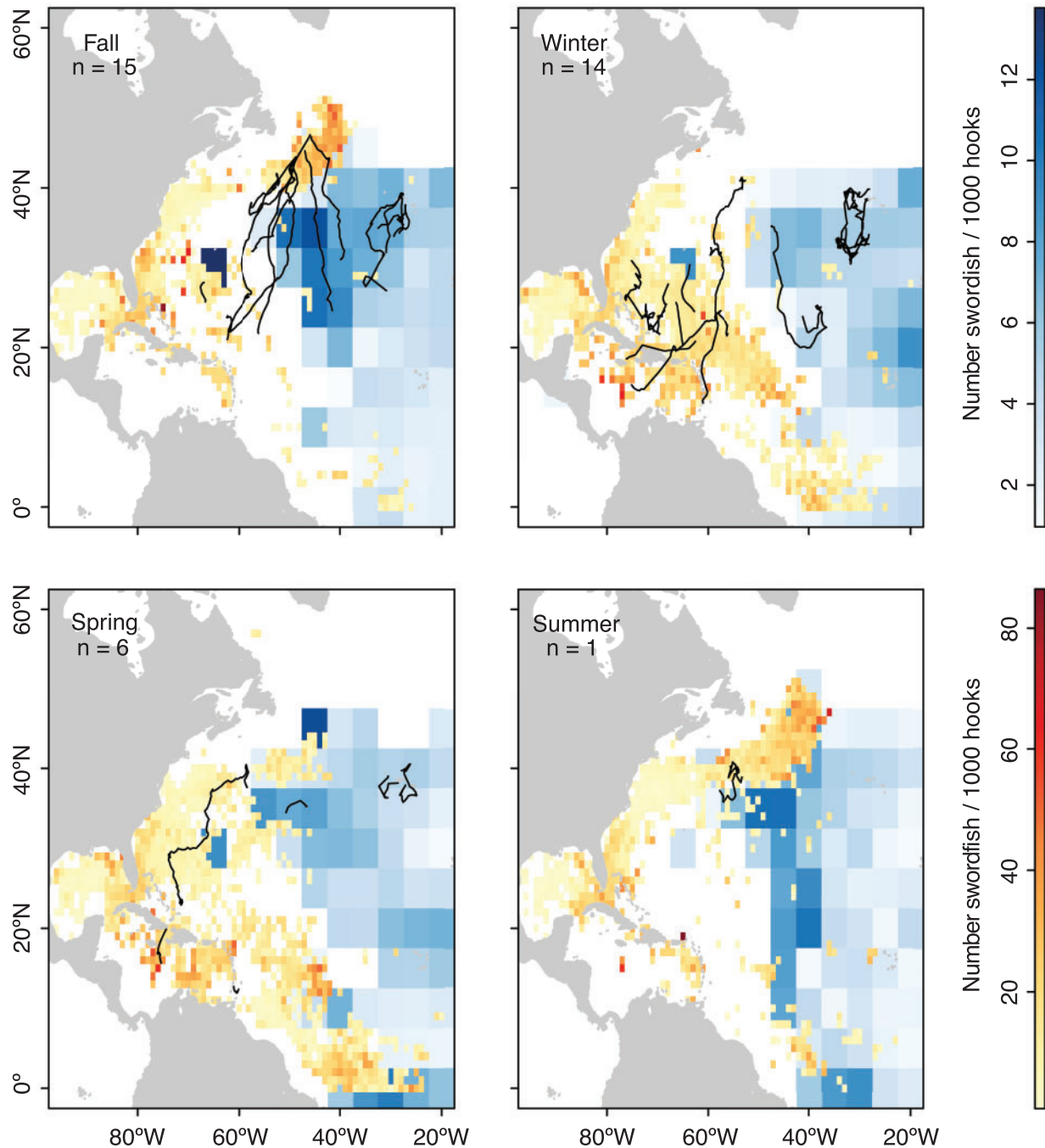


Figure 6. Seasonal distribution (Fall: September–November, Winter: December–February, Spring: March–May, Summer: June–August) of catch-per-unit effort (number of fish per 1000 hooks) of the longline swordfish fishery in the North Atlantic between 1990 and 2010 at $5^\circ \times 5^\circ$ resolution for the international fleet (blue colour scale) and $1^\circ \times 1^\circ$ resolution for the US fleet (red/yellow colour scale). Tracks of tagged swordfish (this study) shown in black lines (n = number of tagged individuals).

Similarly, minimum temperature observed was similar to the coldest ambient temperature ever recorded for swordfish (2°C ; Takahashi *et al.*, 2003) suggesting cold water may not inhibit swordfish movements as much as previously thought. Some authors have proposed that warm temperatures can also constrain vertical movements of large pelagic fish (Teo *et al.*, 2007). Dewar *et al.* (2011) observed that swordfish in the western North

Atlantic and Caribbean regularly used cooler habitats below the warm surface mixed layer during night-time, possibly to thermoregulate, but evidence for active avoidance of warmer waters was not available. In our study, fish tended to be deeper at night in warmer regimes (e.g. Sargasso Sea) and shallower in colder water (e.g. Grand Banks), but individuals also were regularly found near the surface at night, even in SSTs $>25^\circ\text{C}$. Observations of

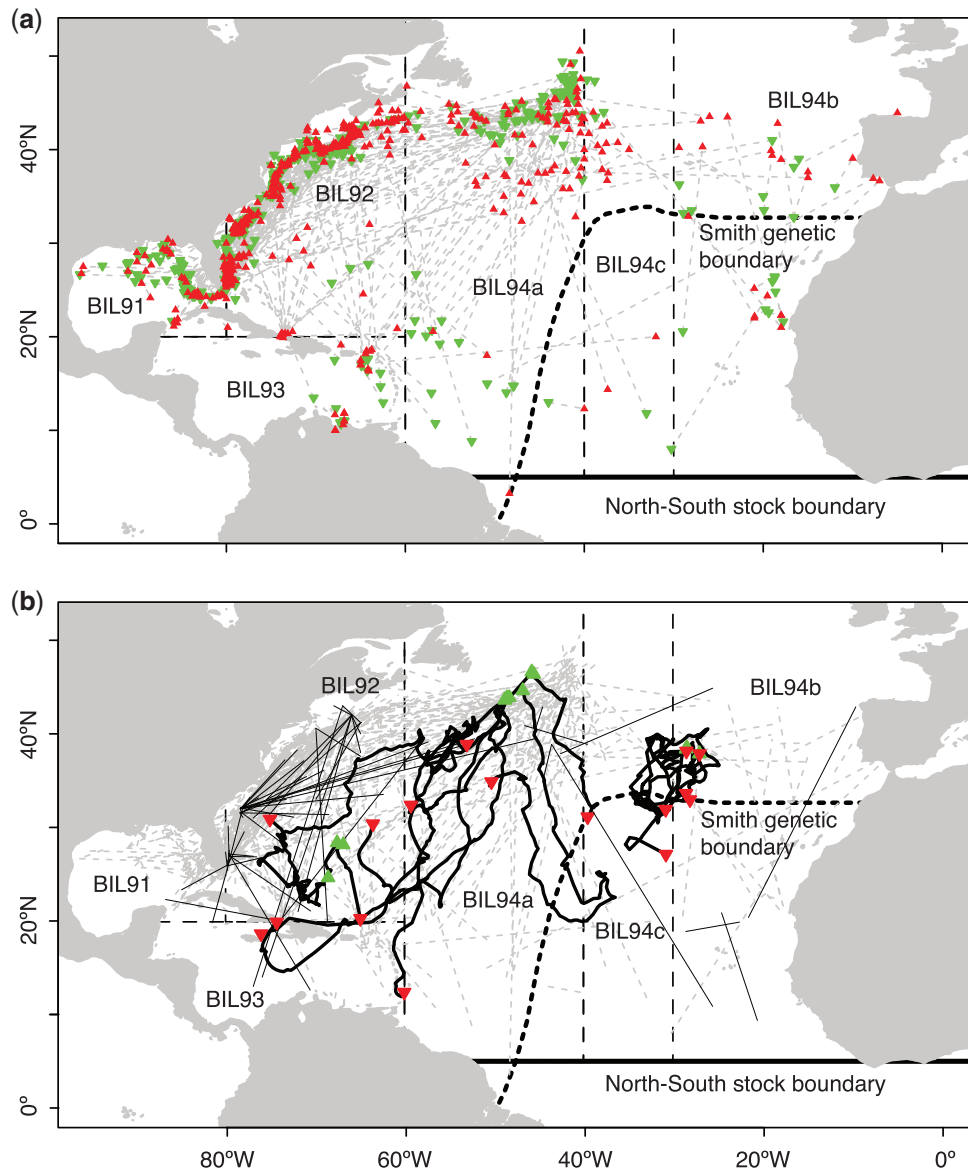


Figure 7. Movements of (a) conventional-tagged (dashed grey lines) and (b) satellite-tagged swordfish in the literature (thin black lines, no endpoints; see Material and methods) and in this study (thick black lines) in the North Atlantic relative to ICCAT sampling areas (black dashed lines, labelled “BIL9x”). Green triangles indicate release locations and red triangles show recapture (conventional tags) or pop-up (satellite tags) positions. Heavy latitudinal line at 5°N indicates current north–south stock boundary, and dashed black line from South America to northern Africa is the boundary line from genetic evidence in [Smith et al. \(2015\)](#).

the effect of temperature on the vertical movements of swordfish have been considered evidence for behavioural thermoregulation (e.g. [Teo et al., 2007](#)). Based on the extreme plasticity of thermal habitat use exhibited by swordfish and evidence for sufficient dissolved oxygen at depth in this region ([Prince et al., 2010](#)), we suggest prey distribution may be the primary driver of swordfish habitat use in this region, at least within their broad thermal limits. It is clear additional information on thermal limits and physiological function of swordfish across a range of habitats is still needed. Further work on the mechanistic drivers of swordfish movement and behaviour, including specific oceanographic associations and physical–biological interactions, are necessary to quantify specific vulnerability to various fishing gear types and

susceptibility to change in a dynamic ocean ([Horodysky et al., 2016](#)).

Connectivity

A recent review of swordfish population connectivity and stock boundaries ([Neilson et al., 2013](#)) suggested that Atlantic swordfish stocks have recovered from historical overfishing impacts, but complex connectivity patterns complicate stock assessments. Genetic evidence supports separation of North Atlantic, South Atlantic, and Mediterranean stocks ([Bremer et al., 1996](#); [Alvarado Bremer et al., 2005](#); [Smith et al., 2015](#)), and recent work recommended moving the North–South stock boundary as far north as 25°N east of 45°W ([Smith et al., 2015](#)). However, tagging studies

(Abascal *et al.*, 2015) suggest a more complex stock structure within the North Atlantic. Our results provide further support for the current North–South stock boundary at 5°N (Neilson *et al.*, 2014). No satellite-tagged individuals in our study, or published PSAT tracks, crossed the boundary, and only one conventional tag deployed near the Grand Banks was recovered across this boundary along the Amazon Delta. In contrast, when considering the proposed boundary based on genetic evidence (Smith *et al.*, 2015), several PSAT-tagged individuals and 11 carrying conventional tags traversed the 50% probability contour proposed by Smith *et al.* (2015) based on single nucleotide polymorphism markers. Existing work on swordfish connectivity using tagging has primarily focused on the western North Atlantic (e.g. Neilson *et al.*, 2014; Braun *et al.*, 2015); however, our results and those of Abascal *et al.* (2015) provide empirical evidence of active movement across the boundary suggested by Smith *et al.* (2015). The ICCAT cpue data presented here indicates significant swordfish catch adjacent to the current 5°N boundary and on both sides of 35°W with relatively little catch overlying the actual boundaries. Our synthesis across these fisheries-dependent and independent datasets support the current North–South division while highlighting the complexity in stock designation in the Atlantic to incorporate limited, but apparent, east–west connectivity. However, the limited duration of satellite tagging studies renders direct comparison with longer term datasets difficult. Longer duration tagging and simulation studies capable of assessing inter-annual individual variability and transition probabilities (Galuardi *et al.*, 2014, 2018) may be needed to further clarify the appropriate placement of the meridional stock boundary and to estimate potential exchange.

Supplementary data

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

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