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Stock-of-origin catch estimation of Atlantic bluefin tuna (*Thunnus thynnus*) based on observed spatial distributions

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Abstract: Atlantic bluefin tuna (*Thunnus thynnus*) are a large, highly migratory fish distributed throughout the North Atlantic Ocean and adjacent seas currently managed as two discrete stocks: western and eastern. Both stocks forage in the North Atlantic, and a high degree of intermixing occurs, which combined with limited single-stock survey data makes it difficult to assess the abundance and status of individual populations. In this study, we used movement patterns from a multidecadal tagging dataset to create monthly distribution maps for these two major stocks. We then used these maps to separate the overall catch records into stock-specific catch (catch per unit effort, CPUE) time series. We identified an increase in the past two decades in the proportion of catch estimated to come from the eastern stock, attributable to a decrease in CPUE in regions dominated by the western stock, relative to other regions. The stock-specific catch series can be used to improve the accuracy of stock assessments and inform spatial management.

Résumé : Les thons rouges de l'Atlantique (*Thunnus thynnus*) sont de grands poissons très migrateurs présents dans tout l'océan Atlantique Nord et les mers attenantes et ils sont actuellement gérés comme s'ils faisaient partie de deux stocks distincts, les stocks ouest et est. Les individus de ces deux stocks s'approvisionnent dans l'Atlantique Nord où un important mélange des deux stocks se produit qui, combiné à des données d'évaluation limitées sur chacun des stocks, complique l'évaluation de l'abondance et de l'état des différentes populations. Nous avons utilisé les motifs de déplacement obtenus d'un ensemble de données de marquage couvrant plusieurs décennies pour produire des cartes de répartition mensuelles pour ces deux grands stocks. Nous avons ensuite utilisé ces cartes pour séparer les prises rapportées globales en des séries chronologiques de prises (CPUE) propres à chacun des stocks. Nous relevons une augmentation, au cours des deux dernières décennies, de la proportion estimée des prises provenant du stock est, attribuable à une baisse de la CPUE dans des régions où le stock ouest est dominant par rapport aux autres régions. Les séries de données de prises propres au stock peuvent être utilisées pour améliorer l'exactitude des évaluations de stock et éclairer la gestion spatiale. [Traduit par la Rédaction]

Introduction

Atlantic bluefin tuna (*Thunnus thynnus*; ABT) is a moderately long-lived, large highly migratory species distributed throughout epi- and mesopelagic waters of the northern Atlantic Ocean (Fig. 1*a*; Mather et al. 1995). Mature ABT migrations follow an annual cycle of foraging in temperate and subpolar waters with spawning in the subtropical and warm temperate waters of adjacent seas and the North Atlantic. Distinct seasonal movement patterns are driven by seasonally productive foraging areas (Stokesbury et al. 2004; Block et al. 2005; Fromentin et al. 2014; Druon et al. 2016) and migrations into spawning areas (Teo et al. 2007; Cermeño et al. 2015; Hazen et al. 2016).

Electronic tagging, otolith microchemistry, and genetics have confirmed that ABT is composed of at least two stocks, each with its own spatially separated spawning ground (Block et al. 2005; Rooker et al. 2008; Rodríguez-Ezpeleta et al. 2019). The western stock primarily spawns in the Gulf of Mexico (GOM) during spring months (Block et al. 2005; Teo et al. 2007; Wilson et al. 2015) and the eastern Atlantic stock spawns primarily in the western Mediterranean Sea (WestMed.; Abascal et al. 2016) during summer. Additional spawning sites have been identified in the slope waters between the Gulf Stream and the northeastern United States continental shelf, as well as in the eastern Mediterranean Sea; however, these events are not well-documented and the spatial and temporal extents of spawning in those locations are still being investigated (Karakulak et al. 2004; Richardson et al. 2016; Aalto et al., unpublished data). Thus, International Commission for the Conservation of Atlantic Tunas (ICCAT) management currently includes only the two primary spawning grounds. For both western and eastern stocks, most mature individuals leave the northern portion of their North Atlantic range by late December and migrate to their respective spawning grounds or midlatitude North Atlantic foraging regions during winter and spring, followed by a return migration to temperate and subpolar oceanic areas as summer commences (Walli et al. 2009). Western ABT are unique, with biological traits that include the largest body size of the *Thunnus* clade (Mather et al. 1995), latest onset of maturity (Corriero et al. 2005; Diaz and Turner 2007), and potentially higher thermal tolerances for spawning, as evidenced by observations of the species in the lower latitude and warm waters of the GOM

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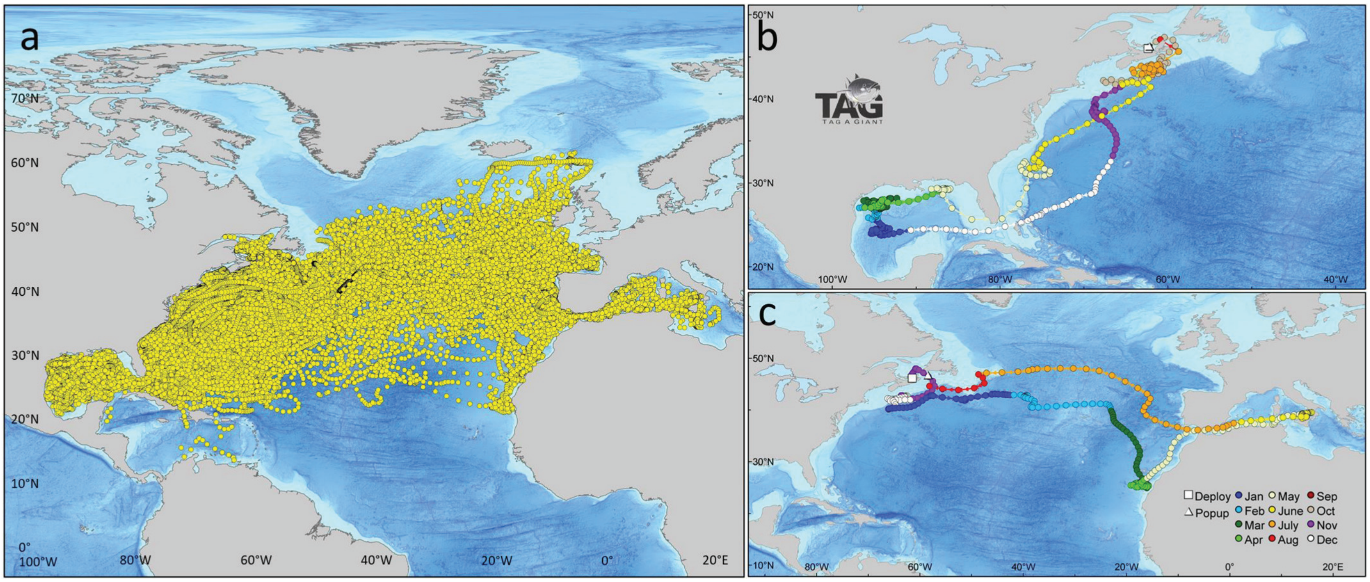
Fig. 1. Atlantic bluefin electronic tag tracks (*n* = 411) revealing the geolocation positions from satellite and archival tagged bluefin tuna from western deployments. (*a*) Total daily locations for all 411 tracks, demonstrating full range of both Atlantic bluefin tuna stocks. (*b*) Example track for a western stock individual tagged in the Gulf of St. Lawrence (GSL), showing annual migration from northern foraging grounds to the Gulf of Mexico spawning grounds and return. (*c*) Example track for an eastern stock individual tagged in the GSL, with migration to and from the Mediterranean Sea spawning grounds. Map created using ArcGIS software from Esri (2011). Land layer source: ArcWorld Supplement. Bathymetry data source: GEBCO_08 Grid (GEBCO 2021).



(25–31 °C; Teo et al. 2007). The western stock is genetically distinct, and several studies have differentiated this stock, though not fully, from the eastern stock (Carlsson et al. 2006; Boustany et al. 2008; Puncher et al. 2018). Given differences in stock status (eastern–western), stock abundance, and stock differentiation, conservation of distinct reproductive stock units and their associated unique properties is important to the species long-term survival and genetic biodiversity in the North Atlantic.

As one of the most highly valued fish in the world, ABT have experienced heavy fishing pressure from international distant-water fishing fleets, as well as trap and net fisheries (Rooker et al. 2007; Fromentin 2009). The eastern stock, which has been fished for >2000 years, was estimated to be at ~40% of unfished levels during the last decade (Rouyer et al. 2018). Such depleted levels prompted ICCAT to implement a rebuilding plan. Recent ICCAT stock assessments suggest that the eastern stock has grown "substantially" (Rouyer et al. 2018; Rouyer and Miller 2019), leading ICCAT to revise the multi-annual recovery plan and increase total allowable catches to 28 200 t beginning in 2018 followed by further increases to 36 000 t by 2020 (ICCAT 2018; Rouyer and Miller 2019). The western stock has been severely depleted following heavy fishing for 50+ years, with one estimate of ~18% of its historical unfished level (ICCAT 2017; though the past biomass is challenging to estimate). However, there is considerable uncertainty about the status of the western stock, due in part to frequent immigration of the eastern stock-of-origin fish into the West Atlantic, and thus the success of its recovery (ICCAT 2017).

Stock mixing is a major challenge for properly assessing and sustainably managing ABT fisheries in the West Atlantic. Historically, the western stock was considered the primary component of biomass harvested by US and Canadian fishers in the West Atlantic. Isotopic microconstituent analyses of otolith data from the 1960s–1970s suggests that foraging grounds off Canada, such as the Gulf of St. Lawrence (GSL), were once composed of 100% western stock fish (Rooker et al. 2008; Schloesser et al. 2010). Electronic tagging (Block et al. 2005), otolith microchemistry (Schloesser et al. 2010), and genetics (Puncher et al. 2018) have all demonstrated that since the 1990s the West Atlantic (demarcated by the 45°W meridian) has become a zone of intense mixing of mature and immature ABT of both stocks that forage together along the North American continental shelf (Kerr et al. 2020). Electronic tagging data indicated that during the late 1990s and early 2000s, 46% of the fish tagged and released off the eastern North American seaboard that traveled to a known spawning ground went to the Mediterranean Sea to spawn (Block et al. 2005). ABT of both stocks are caught by fleets throughout the Atlantic and adjacent seas, complicating the reporting of catch, stock assessment, and management. In addition, there is bycatch associated with gears targeting swordfish (*Xiphias gladius*) and other tuna species which catch ABT incidentally (Block et al. 2005; Teo and Block 2010).

The western ABT stock is estimated to be approximately ten times less abundant than the eastern stock and experienced a precipitous decline in spawning biomass during the 1960s–1980s (ICCAT 2017). Both stocks were recently estimated to be recovering (ICCAT 2018), but current assessments are challenging to interpret because of conflicting indices of abundance and potential bias from mixing of the stocks on the North Atlantic foraging grounds. Because the eastern stock is much larger than the western stock and may be recovering more quickly, even a small mixing rate from east to west could greatly inflate the abundance in the West Atlantic and thus distort estimates of western stock recruitment (Kerr et al. 2012). Assumptions about mixing rate and spatial structure, in turn, greatly affect the outcomes of stock management models (Cadrin 2020), especially for the western stock (Taylor et al. 2011; Kerr et al. 2017; Cadrin et al. 2018; Morse et al. 2018). Consequently, management of these stocks relies heavily on the few available stock-specific, fishery-independent abundance indicators, which, for the western stock, means primarily the GOM spring plankton survey (Scott et al. 1993; Ingram et al. 2010).

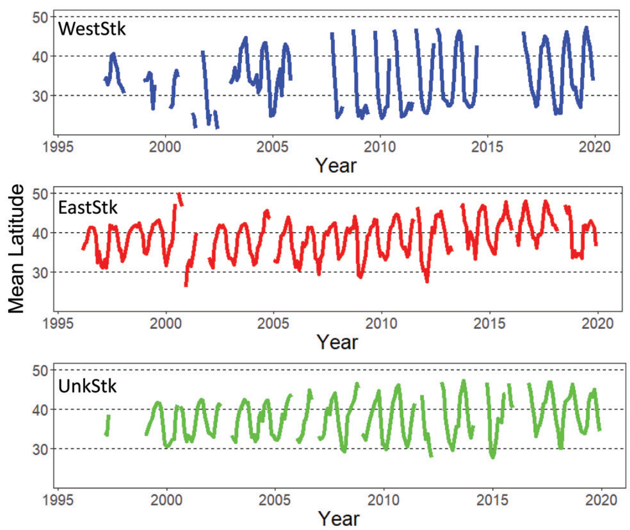
In this study, we propose a novel method to augment fishery observation datasets by using annual movement patterns from

Table 1. Atlantic bluefin tuna tag data.

Years	Tag type	WestStk	EastStk	UnkStk	Total	West:East:Unk
1996–1999	Archival	3	8	23	34	0.38:1:2.86
2000–2009	Archival	2	18	22	42	1.48:1:9.19
	Satellite	29	3	171	203	
2010–2018	Archival	0	6	3	9	3.40:1:4.40
	Satellite	51	9	63	123	
Total		85	44	282	411	1.93:1:6.41

Note: WestStk, western stock from Gulf of Mexico; EastStk, eastern stock from western Mediterranean; UnkStk, unknown stock-of-origin.

Fig. 2. Mean latitude over time for each stock. Note that the broken nature of the WestStk line prior to 2006 is due to the low mean duration of WestStk tracks from those years.



tagging data to separate combined-stock catch series into estimated single-stock components. We identified western and eastern stocks using electronic tag track data, then combined individual tracks to create monthly density contours in the West Atlantic for the two stocks, as well as a third "unknown origin" category. We used the density-based regional stock likelihoods to estimate stock composition for catch data based on time and location of catches. We then were able to produce stock-specific catch series that can be used as an index of stock removals, in conjunction with stock-of-origin indices (larval and aerial surveys in the GOM and WestMed., respectively), to conduct stock-of-origin assessments and better define population trends over the period of removals.

Methods

Spatial distribution data and analysis

For this analysis, we used 411 individual electronic tag tracks from the Stanford University Block lab and TAG A Giant ABT database spanning the period 1996 to 2018 (Fig. 1*a*; Table 1). The archival and pop-up satellite archival tags measure physical variables such as light, pressure, and ambient water temperature and have an accurate clock (time) that enables subsequently processing the data using geolocation techniques to produce estimated daily positions from threshold light models (Block et al. 2005; Teo et al. 2007). We focused exclusively on ABT track data points in the GOM and the West Atlantic (defined as locations to the west of 45°W) to determine relative stock likelihoods in the regions of maximum overlap. For fish double-tagged with archival and pop-up satellite archival tags, we used the track generated with the longest time-at-liberty. Individual fish that entered the GOM or WestMed. were designated as western (WestStk) or eastern (EastStk) stock (presumed origin), respectively, while all other individuals were initially labeled as unknown stock-of-origin (UnkStk). We used a secondary spatial range analysis (described below) to identify a subset of the UnkStk tracks that were likely EastStk.

We took the state-space-modelled outputs from each track (Wilson et al. 2015; Hazen et al. 2016) and then analyzed spatial distributions of each stock on an annual time scale, split into monthly intervals. Preliminary analysis found that annual latitudinal migration patterns were relatively unchanged across the three decades covered by the tag data (Fig. 2); we thus aggregated all tracks together when generating monthly distributions. We divided the observed spatial domains of fish in the West Atlantic into 1°×1° cells, then treated the daily mean positions of individuals as independent data points for the purpose of estimating stock density by month. Using this method, an ABT that lingered in a cell for most of January would increase stock density there proportionally to the time spent, while one that spent the month traveling south along the Atlantic coast would contribute roughly equally across its range. We considered this assumption appropriate because ABT have been observed making rapid transitions between spatial cells on the scale of hours to days. We calculated a monthly spatial distribution map for each stock category (WestStk, EastStk, and UnkStk) using the two-dimensional kernel density estimator function (Venables and Ripley 2013) in the MASS R package (version 7.3-49; Ripley 2011). The resulting contours indicated probable distributions **within** each stock category (for example, the likelihood of a WestStk individual being near New England in March), but not likelihoods **across** stocks (the likelihood of an individual caught near New England in March being WestStk). To calculate the latter, we weighted the monthly probability contours by the relative proportion of each stock category in the tag data for that month to create density contours, which allowed direct comparison by combining both spatial distribution and relative abundance. When overlaid, the maps allowed us to estimate the degree of stock overlap for each month and spatial cell and thus to split West Atlantic catch records into estimated WestStk, EastStk, and UnkStk proportions.

Stock designation by spatial range analysis

Stock-of-origin was defined by movement of an individual into a known spawning area (GOM or WestMed.). However, 70% of the tagged individuals did not enter either spawning ground and were not assigned a stock-of-origin, leaving the majority of the data not initially usable for the known stock-of-origin analysis. In more than half the cases, the tags released prematurely (and before the spawning period), and only a short track was obtained (n = 150, mean curved fork length (CFL) = 225 cm). In a few cases, the animals were presumed to be immature (CFL $<$ 175 cm; n = 5, mean CFL = 167 cm) and thus not spawning, and the rest (n = 127, mean CFL = 218 cm) may have either skipped spawning or may be

Table 2. International Commission for the Conservation of Atlantic Tunas (ICCAT) catch and origin data.

Dataset	Years available	Type	Filters used (all data)
Catch series			
US longline	1986–2018	Catch (number); effort (no. of hooks)	Latitude >20°N, <55°N; longitude <45°W
US rod and reel	1972–2018	Catch (number); effort (hours fished)	1987+; must have both catch and effort
Canada longline	2008–2018	Catch (kg); effort (no. of hooks)	
Canada rod and reel	2008–2018	Catch (kg); effort (hours fished, days fished)	
Japan longline	1972–2018	Catch (kg); effort (no. of hooks)	
Stock-of-origin			
US–Canada	1996–2002, 2009–2015	Otolith; genetics	Regions GOM, W_ATL, and GSL

Note: For the analysis, all data were in one catch unit (kg) and one effort type (number of hooks for longline, hours fished for rod and reel). Catch data (number of individuals) were converted to kilograms using mean Atlantic bluefin tuna kilograms per individual from ICCAT longline and rod and reel samples in the West Atlantic, specific to decade (1986–1995, 1996–2005, 2006–2018) and north–south (represented by ICCAT sampling regions BF51 and BF55, respectively). Effort in units of "days fished" were converted into "hours fished" using the assumption of 8 h active fishing per day. We tested values ranging from 6 to 12 and found little noticeable effect on the results.

associated with newly identified spawning sites (e.g., the continental slope waters in the Atlantic). To classify some of the UnkStk individuals into either WestStk or EastStk, we explored whether there were aspects of an individual track's spatial range that were stock-specific in nature. We compared the following characteristics for each stock: latitudinal range (total degrees covered); longitudinal range; and furthest North, South, East, and West.

The UnkStk individuals remaining unassigned following this analysis could not be assumed to be 100% WestStk, as multiyear tracks show that EastStk fish do not always return to the East Atlantic every year. We treated these individuals as a separate category, a conservative approach that still allowed us to compare the UnkStk distribution with the two known stocks.

Comparison with stock-of-origin data

We tested the accuracy of the stock distribution maps by comparing the monthly outputs with independent stock-of-origin estimates from otolith microchemistry analysis of individuals caught in US and Canadian waters across two periods (1996–2002, 2009–2015; Rooker et al. 2008; Schloesser et al. 2010; Hanke et al. 2016). Because these data were only available at the regional scale, we aggregated both the stock estimates and our distribution maps by month and region. We then compared the mean estimated probability of WestStk across months for each of the three western Atlantic management regions: GOM, West Atlantic, and GSL. This was calculated as the ratio of density for western-assigned individuals in month *i* and region *j* to total density for WestStk and EastStk as follows:

$$\text{Prob.WestStk}_{i,j} = \frac{\text{Density.WestStk}_{i,j}}{\text{Density.WestStk}_{i,j} + \text{Density.EastStk}_{i,j}}$$

To eliminate unreliable proportions (i.e., high variance stemming from low numbers of fish), we excluded month–region combinations in which the combined total density of WestStk and EastStk individuals was <5% of total density across all regions.

Stock-specific catch series estimation

One potential use of the stock distribution map is to estimate the stock proportion within a given catch based on the month and location. For example, an ABT caught offshore of North Carolina in March is more likely to be an EastStk fish than a WestStk fish, whereas one caught off of New England in September could be from either stock. Annual catch trends (measured as catch per unit effort, CPUE) can be disaggregated based on the estimated stock probabilities into stock-specific time series. By applying this calculation across the series of CPUE records and summing annually, it is possible to divide the original combined-stock catch series into distinct stock-specific removals.

For this analysis, we used West Atlantic ABT catch data for 1987–2018 provided by ICCAT via the Task 1 total catches and Task 2 Catch-Effort databases (Table 2; https://www.iccat.int/en/t2ce.asp). We focused exclusively on the US and Canadian longline and rod and reel fisheries and Japanese longline because they were responsible for a combined 87% of the overall ABT catch in the West Atlantic in 2016 (ICCAT 2017), and both catch and effort data are available for over three decades (refer to online Supplementary Figs. S1–S3[1]; note that Canadian data are available for only 2008–2018). We standardized the CPUE data by dividing by the peak value (in 2008 for longline and 2005 for rod and reel). We assigned estimated catch composition for each catch record using its month and location, aggregated by stock, to create stock-specific estimated CPUE series for 1987–2018. We then compared both CPUE and year-to-year change to determine when and how the stock-specific catch series components differed from the original combined series. Finally, we compared the WestStk-specific component with two independent surveys intended to serve as indices of WestStk abundance, the Canadian Acoustic Survey (1994–2015), and the GOM Larval Survey (1986–2015). We normalized each index and catch series by dividing by its maximum value within the comparison period.

All analyses were performed using R (version 3.4.4; R Core Team 2018).

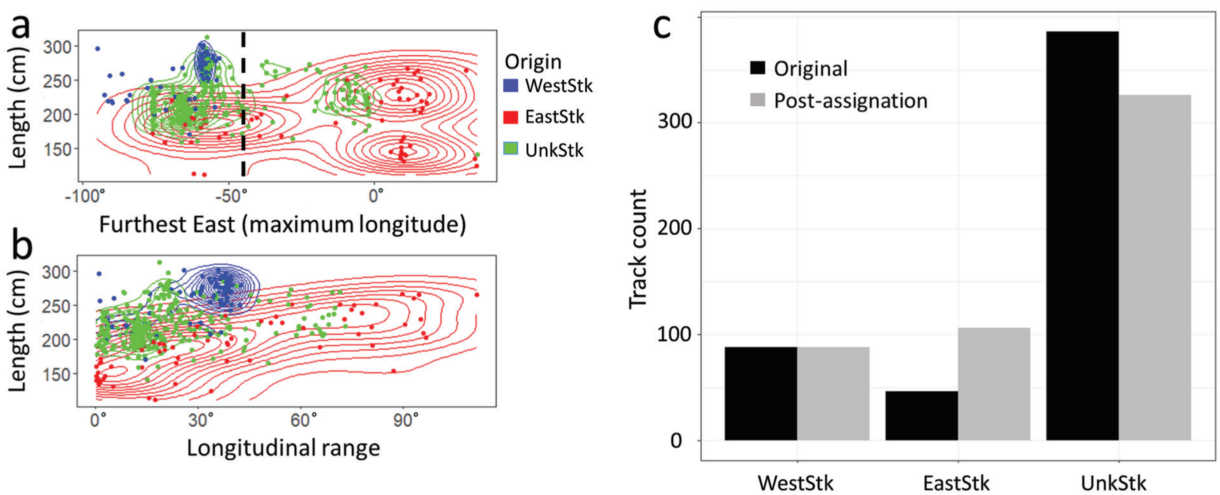
Results

Stock assignment by spatial range analysis

There was little difference between the two stocks in furthest North, furthest South, or furthest West (without entering the GOM, defined as crossing 80°W) or latitudinal range. In general, the EastStk had a much wider longitudinal range than the WestStk (Fig. 3*b*). The clearest distinction, however, was using furthest East: none of the WestStk assigned individuals were ever observed crossing 50°W, while all the EastStk (by definition) and a good number of the UnkStk tracks did make this transition (Fig. 3*a*). To be conservative, and in keeping with historical ABT management guidelines, we used 45°W as the threshold for classifying an UnkStk individual as EastStk. This allowed us to include 62 additional tracks as estimated EastStk, which was ~22% of the UnkStk individuals (Fig. 3*c*; see Supplementary material[1] for the sensitivity of results to this assignment).

[1]Supplementary material is available with the article at https://doi.org/10.1139/cjfas-2019-0445.

Fig. 3. Estimation of stock-of-origin for UnkStk individuals. (*a*) Use of furthest East location, or maximum longitude reached, to assign EastStk origin. The *x* axis indicates maximum longitude reached within a particular track, and the *y* axis indicates fish body length. The vertical dashed line indicates the 45°W meridian used to assign EastStk status to UnkStk individuals. Contours indicate relative concentrations for each stock. (*b*) Longitudinal range for EastStk, WestStk, and UnkStk. The axes are the same as for panel (*a*), except that the *x* axis indicates total longitudinal range (maximum – minimum). (*c*) Change in track counts for different origin categories after assignation of origin based on furthest East value.



Stock distribution and stock-specific catch series estimation

The monthly stock distribution maps (Fig. 4) show that both WestStk and EastStk overlap almost completely when foraging in the North Atlantic (July through November), but begin to show spatial separation in December as the WestStk spawners return to the GOM along the eastern US seaboard, shelf, or slope waters, and the remaining individuals migrate to the southeast coast of the United States. This separation in stock overlap reaches its peak by March, and the WestStk spawners remain predominantly in the GOM until June (though entry and exit times and length of stay vary widely; Fig. 5*b* and Wilson et al. 2015), when they rejoin the other individuals in the West Atlantic as they return to the northern foraging grounds. The EastStk and UnkStk distributions overlap throughout the year in the North Atlantic off New England during warmer months (April–November) and near the Carolinas in the winter (December–March), with the EastStk individuals ranging further to the east. Note that these maps only show EastStk individuals that have remained in the West Atlantic during each month, and there are numerous EastStk fish that travel to the East Atlantic and Mediterranean Sea during May through November (Supplementary Fig. S4[1]). The two sets of contours thus represent primarily individuals that did not spawn during the tag year (except potential spawning occurring in the Atlantic Ocean), whether due to immaturity or having skipped a year, and instead migrated along the western Atlantic coast to forage. They are, on average, smaller in size than the WestStk spawners (Fig. 5*a*).

Regional estimates of monthly stock composition were similar to those produced by otolith microchemistry, but with a higher variance in the West Atlantic (Fig. 6). For the tagging data, GOM residents are 100% WestStk by definition, and the available months of otolith data showed a consistently low probability of EastStk (Fig. 6*a*). In the GSL, both approaches showed mostly WestStk fish in the late summer with an increasing proportion EastStk by November (Figs. 6*c* and 6*f*). In the West Atlantic, which has ABT year-round, the tagging data had much greater variation in stock composition than the fairly consistent WestStk–EastStk mix seen in the otolith data (Fig. 6*b*). The biggest differences in stock mixing were observed in the West Atlantic, where the otolith data suggested fairly consistent WestSTk presence (*i*) during the spawning season in the late spring, when our model shows ~75%–80% of the WestStk density within the GOM (Fig. 6*d*), and (*ii*) in the early fall, when many WestStk tags are in the GSL (Fig. 6*f*). This is likely due to the movement-based distinction between spawning individuals (WestStkand EastStk) and nonspawning individuals (usually labeled UnkStk, unless later harvested in a spawning region) in the tagging data, whereas the otolith data attempt to classify every fish by stock and thus can include nonspawning WestStk individuals during those months. In addition, most WestStk fish were tagged initially in the GSL in the fall, which, due to the ~1-year life-span of the pop-up tags, may bias the distribution against WestStk individuals in other locations during that period.

Using the species distribution maps, we assigned longline CPUE records by month and location into the three stock categories proportionally to their relative likelihoods (Fig. 7*a*). By aggregating across months, we produced the estimated stock-specific components WestStk and EastStk, as well as UnkStk, which together formed the combined longline CPUE series (Fig. 8*a*). Separating CPUE by stock unit showed that while the combined series was representative of the WestStk in the 1990s and early 2000s, the WestStk CPUE was substantially different in later years, with a larger decline in 2005 and a poor recovery in 2011. EastStk fish were less numerous in the late 1980s and 1990s than suggested by the combined series, but became a larger component of the catch in the West Atlantic during the 2000s. While year-to-year changes were usually in sync across stocks (possibly due to non-stock-specific factors such as fleet distribution; Fig. 8*b*), there were years when WestStk and EastStk catch showed different trajectories (e.g., 1991, 1993, 2003, 2005) or similar directions but at different rates (e.g., 2000, 2011). The overall proportion of total CPUE coming from WestStk decreased in the 2000s (Fig. 8*c*), and this was caused by a decrease in CPUE in WestStk regions and an increase in catch in regions dominated by EastStk and, to a lesser degree, UnkStk (Fig. 8*d*).

We then analyzed the rod and reel CPUE dataset, which was dominated by very high CPUE in 2005 and 2006 (Fig. 9*a*). The rod and reel catch is primarily coastal, and the effort is along the Atlantic seaboard rather than in the GOM (Supplementary Fig. S3[1]). Consequently, our model predicts that EastStk and UnkStk provide

Fig. 4. Monthly stock distribution maps for the West Atlantic. Contour lines indicate relative density for each stock (western (WestStk) and eastern (EastStk)) and the unknown individuals (UnkStk). Track data are aggregated across all tagging years (1996–2018). Note that many EastStk individuals leave the western Atlantic in the spring–summer to return to the eastern Atlantic and Mediterranean, meaning that absolute EastStk density declines substantially during those months. Map created with R package ggplot2 (Wickham 2016). Land layer source: mapdata package (Becker and Wilks 2018).

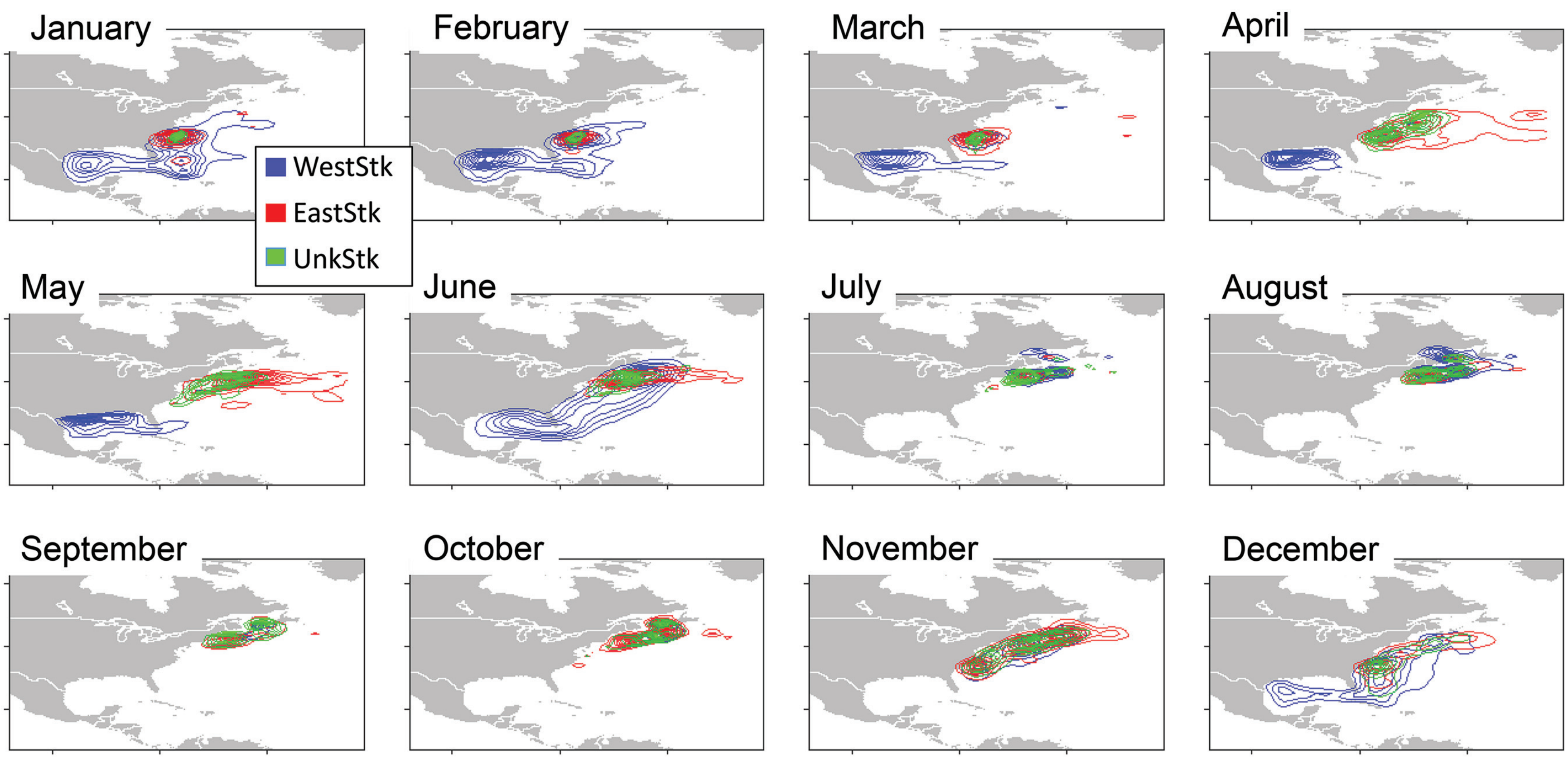


Fig. 5. (*a*) Size distribution of tagged individuals. The *x* axis indicates curved fork length (cm CFL) for each individual when initially tagged, with color indicates stock assigned based on later movement. (*b*) Gulf of Mexico (GOM) residency for western stock. Individual entry–exit lines are sorted by start date, with color indicating length at entry.

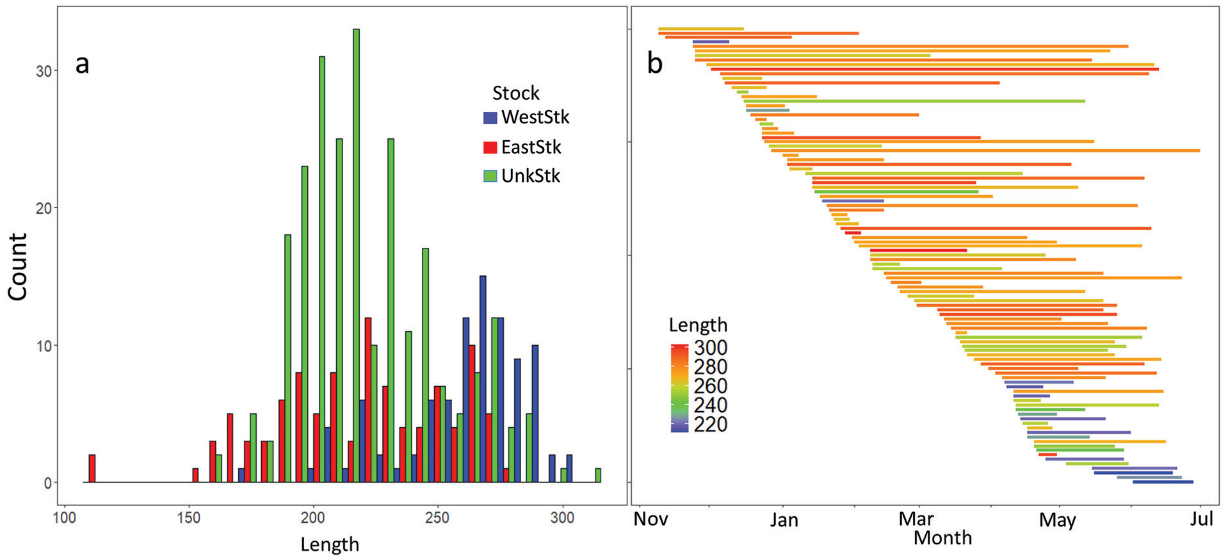
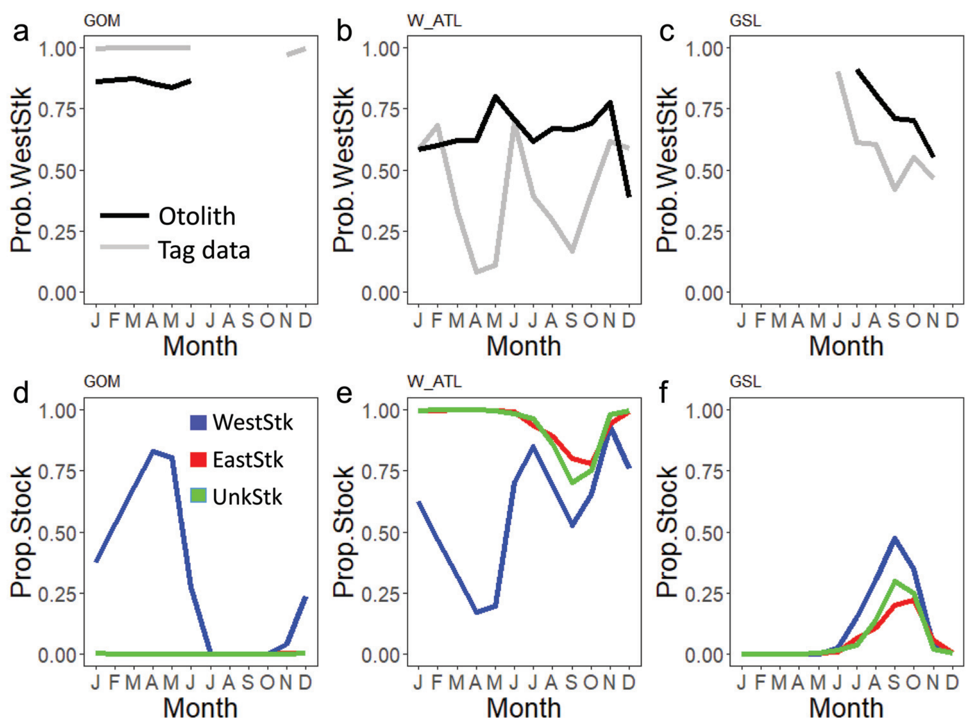


Fig. 6. Comparison with regional stock-of-origin. (*a*–*c*) Each panel represents a different management region, with the *x* axis indicating month and the *y* axis indicating mean probability of a fish in that region being of western stock. The three regions are Gulf of Mexico (GOM; *a*, *c*), the West Atlantic (W_ATL; *b*, *e*), and the Gulf of St. Lawrence (GSL; *c*, *f*). Black lines indicate the monthly stock-of-origin data taken from otolith microchemistry, while the gray lines show results from our tagging data analysis. (*d*–*f*) Proportion of each stock across the three regions (from tagging data). The proportion indicated is the proportion of the given stock located within the specific region (out of three) during each month, such that the sum of the three regions for each month is ~1.0 for each stock.



a greater proportion of the CPUE than for the longline fishery, with little change over the time period examined (Fig. 9*c*). However, as with the longline data there are years when the WestStk component trends differently from the other two (Fig. 9*b*), and CPUE in WestStk regions increases, though almost never exceeding CPUE in EastStk regions (Fig. 9*d*).

To determine whether our estimated stock-specific component behaves similarly to the prior WestStk abundance indicators

Fig. 7. Mean CPUE by month and year and gear type for the West Atlantic for (*a*) longline and (*b*) rod and reel. Point color indicates estimated likelihood of WestStk versus EastStk (i.e., excluding UnkStk individuals), and point size indicates mean CPUE for the specific month–year combination (differs for each panel). Background color indicates the proportion of UnkStk individuals.

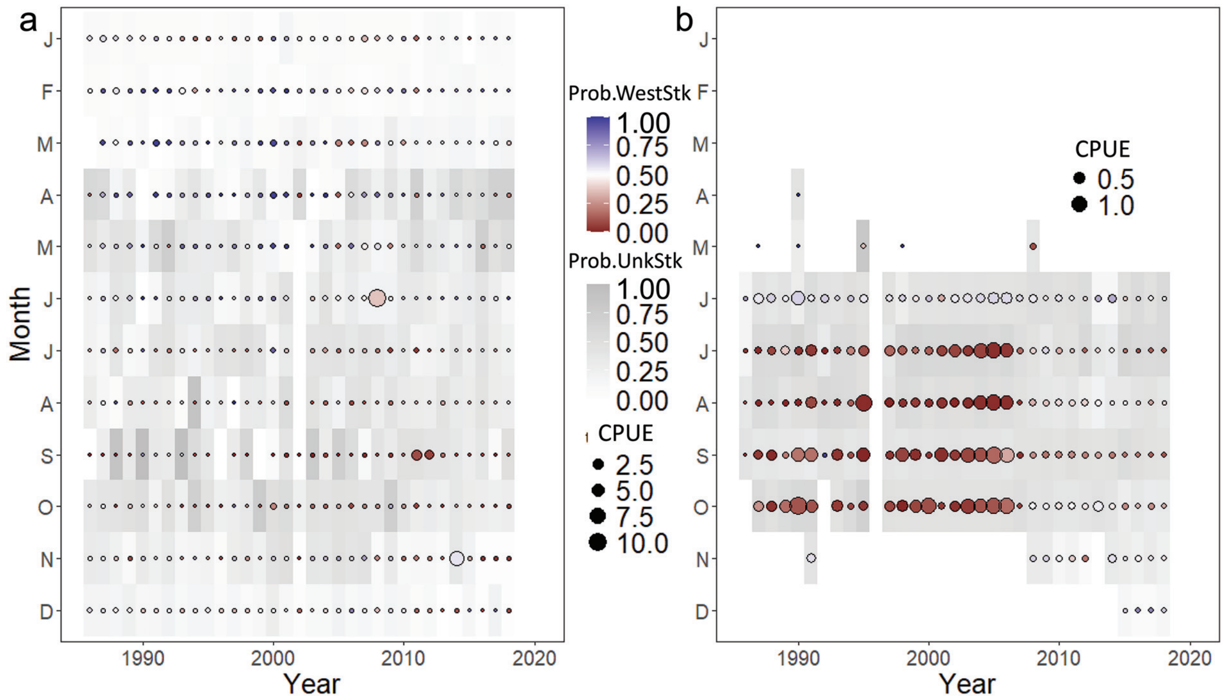


Fig. 8. Separation of longline catch series into stock-specific components. (*a*) Mean CPUE over time, separated into three "stocks". (*b*) Annual proportional change in log-scale for overall series and stock-specific components. (*c*) Proportion of overall CPUE for each stock category. (*d*) Mean dominant-stock CPUE. This differs from panel (*a*) in that mean annual stock CPUE is taken only from regions in which that stock is the dominant stock. Consequently, it represents change in CPUE in areas specifically associated with each stock and thus a change in "catchability" of each stock.

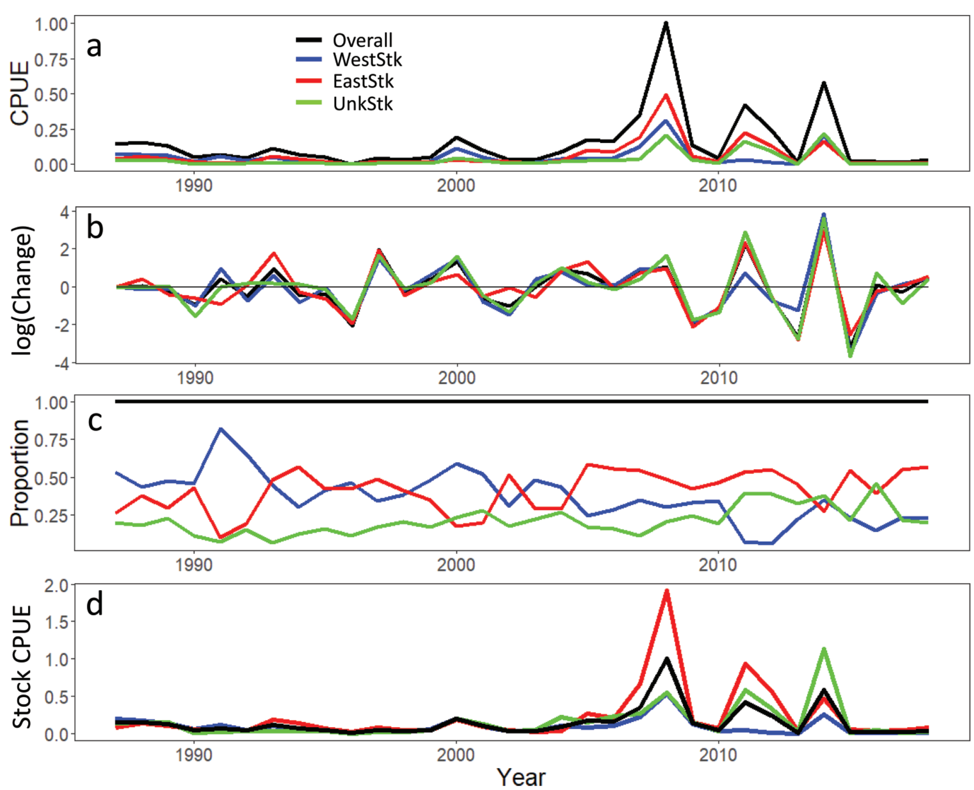


Fig. 9. Separation of rod and reel catch series into stock-specific components. All details are otherwise the same as in Fig. 8.

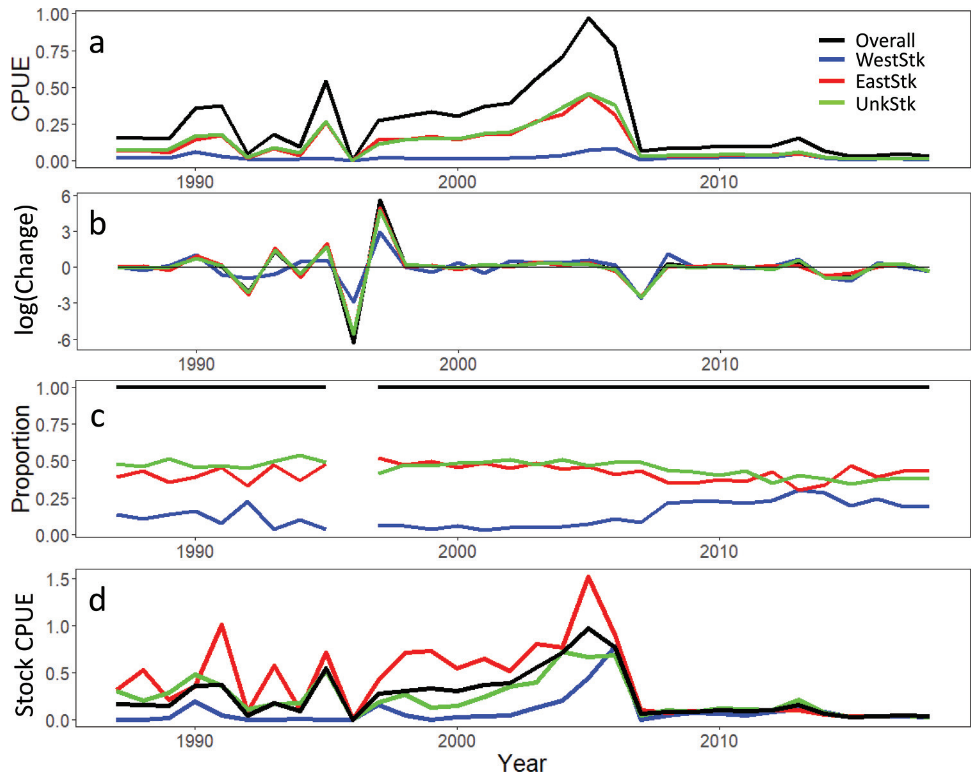
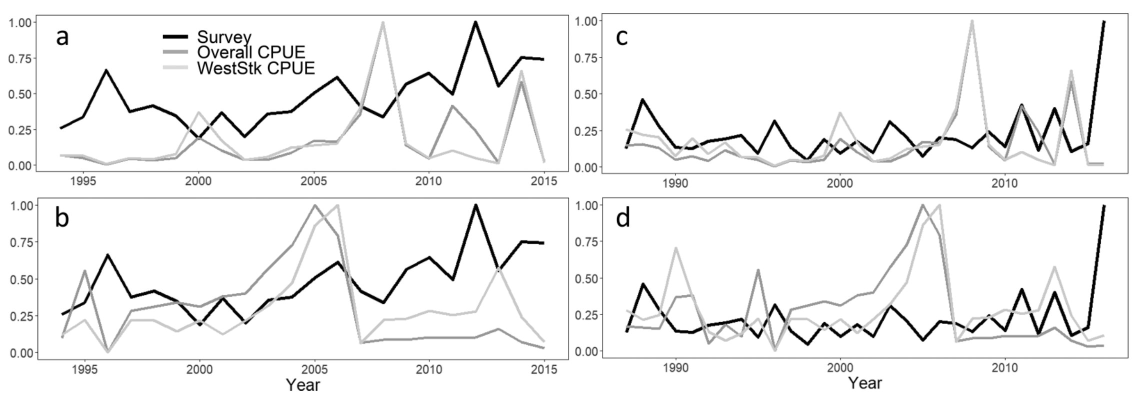


Fig. 10. Comparison of WestStk-specific CPUE series from with western stock surveys. The *y* axes indicate both survey values and CPUE values standardized to a maximum of 1.0 across the time period. (*a*, *b*) Canadian Acoustic Survey standardized index and CPUE series (overall and WestStk-specific) from (*a*) longline data and (*b*) rod and reel data. (*c*, *d*) GOM Larval Survey standardized index and CPUE series from (*c*) longline data and (*d*) rod and reel data.



being used in management models, we compared the original longline CPUE series and our estimated WestStk-specific series to two independent western stock surveys (the Canadian Acoustic Survey and the GOM Larval Survey). We standardized each time series and investigated whether the WestStk component was a better predictor of the survey values than the original CPUE series using a Granger causality test, a method for testing the usefulness of one time series to predict another (Granger 1969). The two CPUE series do not match either stock index particularly well (Fig. 10) and using the WestStk-specific component either did not improve the fit (longline data) or improved only marginally (rod and reel: original/GOM-specific sum-of-squares for Canadian survey: 3.855/2.610; Gulf survey: 3.566/2.974). Neither CPUE series was a statistically significant predictor of index time series from either survey.

Discussion

Biological datasets indicate that there is substantial mixing of ABT in North Atlantic foraging grounds, which complicates the interpretation of the West Atlantic stock assessment and regional fishery management decisions (Block et al. 2005; ICCAT 2017). In this paper, we provide a first attempt to separate ABT catch of unknown origin into estimated stock proportions based on spatial movements (month, location) and hypothesized stock distributions from electronic tagging data based on spawning ground residency. Although the harvest of ABT has been regulated and monitored for decades, for most of this period catch stock assignment has been simplistic; all ABT caught west of 45°W are assumed to be western stock fish, and all ABT caught to the east are eastern stock. The limitations of this approach are clear, as years of tagging data, as well as otolith microchemistry and genetic analyses, have provided ample evidence that the two stocks intermix across their foraging grounds in the North Atlantic. While genetics and otoliths can be used to assign stock-of-origin months later after processing samples, our methodology allows rapid estimation of stock-of-origin as soon as catch data are available, including areas where samples are absent (such as with historical data).

By retroactively estimating stock composition using catch month and location and stock-of-origin distributions, we were able to include both current and historical catch data series and assess how the stock-specific components have trended over time relative to the original combined catch series. Our results show that EastStk fish (and UnkStk fish) make up more of the West Atlantic longline landings in the last decade (2006–2018: 27%–57%, mean = 49%) than was observed historically (1986–1995: 10%–57%; mean = 35%; 1996–2005: 18%–58%, mean = 37%), which is consistent with a shift of mean CPUE (though not effort) north and east (Supplementary Fig. S5[1]) and potentially indicates either a decrease in western stock abundance or an increase in the abundance of EastStk fish moving into the West Atlantic. By tracking trends in CPUE in regions associated with each stock (Fig. 8*d*), we found evidence for both (i.e., CPUE in WestStk regions has decreased, while CPUE has increased in regions dominated by eastern stock fish). Although the magnitude of these differences is affected by how UnkStk individuals are assigned, the overall pattern is robust (Supplementary Fig. S6[1]). Conversely, EastStk proportion trended slightly down for the rod and reel landings (1986–1995: 33%–48%, mean = 41%; 1996–2005: 44%–52%, mean = 47%; 2006–2018: 30%–47%, mean = 39%), though this was mainly driven by high WestStk catch proportion during the post-2008 low CPUE period rather than during the peak catch years (2005 and 2006; Figs. 9*a* and 9*c*). Both mean effort and CPUE have shifted north and east in the rod and reel fishery (Supplementary Fig. S5[1]), but the late summer timing (Fig. 7*b*) and close proximity to the coast (Supplementary Fig. S3[1]) increase the catch of WestStk individuals because the two stocks overlap considerably (Fig. 3). These trends are also robust to changes in the assignation of UnkStk individuals (Supplementary Fig. S7[1]).

Potential biases in the CPUE series from the US longline and, to a lesser extent, rod and reel that are not accounted for in the analysis include regulatory effects (e.g., gear restrictions, bycatch allocations, size and bag limits, and fishery area closures) as well as gear technological advances on catch rates. Differences in gear and regulations could introduce error when aggregating catch and effort across fleets and regions. However, we note that these biases are not unique to our analysis and influence the current assessment and management advice for the stocks. The Canadian dataset presents an additional issue, as it is only available starting in 2008. Consequently, catch in this region suddenly "appears" in the final decade (Supplementary Figs. S2 and S3[1]), potentially biasing the spatiotemporal trends. Removing the Canadian data changes the CPUE observed from 2008 on (Supplementary Figs. S6.6a and S7.6a[1]); however, the shifts in proportion between WestStk and EastStk remain relatively the same, with similar year-to-year trends (Supplementary Figs. S6.6b, S6.6c, S7.6b, and S7.6c[1]).

The separation of catch into stock-specific components depends on the accuracy of two independent aspects of the tagging data. The first aspect, stock distribution, is created by the aggregation of all movement data for individuals of a specific stock to create monthly density maps. Inherent in this is the assumption that the distribution of movement patterns in the data are representative of the movements of the stock as a whole. Our assignment of stock for most individuals, however, is based on whether they visited one of the two primary spawning grounds, a method that excludes many nonspawners (placing both immature fish and mature fish that did not spawn that year in the UnkStk category) as well as excluding potential Slope Sea spawners. Consequently, our known-stock movement data are biased almost completely towards mature adult individuals, and if juveniles and other nonspawners exhibit different movement patterns, our results may represent only the spatial movement patterns of the GOM and WestMed spawning components. Juveniles, particularly of eastern stock origin, may have more wide-ranging movements (Stanford University Block lab, unpublished data) and the tagging data are biased towards larger individuals, as tags primarily went on fish close to or at mature size (Fig. 5*a*). Additionally, the majority of the WestStk tags were from satellite tags (up to a 1 year track), while the EastStk data were from archival tags (multiyear). This could cause one period of the year (near the end of the tag life-span) to be under-reported for WestStk individuals, potentially producing misleading movement and abundance estimates. These problems will not be fully solved until we are able to assign stock with high probability of genetic assignments using samples (fin clips) taken during deployment. Nonetheless, the findings of our analysis are a major advancement in the ability to assess the spawning abundance of western stock fish, which otherwise could only be estimated from larval surveys with high variance.

The second essential aspect of the data is the relative abundance of the two stocks. Each distribution map is standardized to indicate the likelihood of an individual of that stock being in a particular cell in a given month. However, these maps were then weighted by relative abundance to convert the standardized likelihoods for each stock (which summed to 1) into comparable density values (which summed to each stock's relative abundance), allowing us to determine the chance of an individual in any given cell belonging to each of the three stock categories. Because known-stock tags were few in number in any given time period, particularly 1996–1999, we used the overall ratios of West:East:Unk tags as proxies of stock abundance when weighting the distribution maps (Table 1). However, the West:East:Unk tag ratios are highly dependent on tagging location; of the two primary tagging sites used for these studies, more WestStk fish were seen in the northern location in the GSL tag dataset (West:East:Unk = 62:8:66) and more EastStk fish in North Carolina (West:East:Unk = 7:31:198). Consequently, the relative abundances of the stocks are potentially influenced by the amount of tagging effort in each location. However, using an alternate approach that weighted the two tagging locations equally did not qualitatively affect the results or the inference in stock-specific trends (Supplementary Figs. S5.3a–d and S6.3a–d[1]).

Potentially more important is the assumption that relative difference in abundance between the two stocks has stayed constant throughout the study period. If, for example, there were an influx of EastStk fish in the 2000s that raised their abundance relative to WestStk fish, as is suggested by otolith and genetic data (Rooker et al. 2008; Schloesser et al. 2010; Kerr et al. 2020), then we would expect the EastStk proportion of the catch to increase even further as CPUE increased in regions where EastStk fish aggregate. In the current analysis, there are insufficient known-stock fish to estimate year-specific relative abundances. However, the majority of the tag tracks are classified as "unknown stock" and thus represent a pool of potential data that will become available as genetic stock identification techniques are improved, work that is currently underway. Adding even 50% of these 282 tags would more than double our known-stock dataset and allow more detailed analysis of changes in relative abundance over time. We expect these spatial models and analyses to improve as genetic markers begin to confirm the identity of the tagged fish, filling in missing size classes. Many of the fish analyzed here have archived tissues that can be retrospectively analyzed to assign stock-of-origin based on genetic assignment. This is expected to improve the accuracy and resolution of stock-density distributions in the near future. Importantly, we have not addressed the slope water spawning area discovered recently. It is possible that with increased tagging and a focus on this area, some assignments could be made for these fish. However, it is unclear at this point how they fit genetically into the overall picture (Rodríguez-Ezpeleta et al. 2019).

Application to management

The method applied for separating unidentified catch into stock-specific components will aid in the assessment and management of ABT by providing better indices of population abundance to be used in estimates of stock biomass and trend, in addition to the relative abundance surveys currently used for assessing stock trends. Fleet catch records provide a longer-term, more spatially detailed measure of ABT abundance than annual surveys, but cannot be automatically associated with specific stocks because of the high level of mixing. Prior to the analysis described here, estimation of catch composition for a specific fleet required a lengthy analysis of catch samples. We hope that this methodology will allow an approximate but useful real-time attribution of catches to specific stocks and thus help improve the accuracy of future stock assessments and mixing models. Additionally, we hope that the stock-specific catch components will provide a valuable counterpoint to the fishery-independent surveys and highlight periods when trends in overall catch are poor predictors for changes in a specific stock. This is of particular importance to the western stock assessment, given its historically depleted status and the ease with which an influx of the numerically greater in abundance eastern stock fish can influence estimated abundance in the West Atlantic.

Generating stock-specific catch records will also improve the spatial management models used to set quotas and predict future stock status. Models such as the M3 mixing model (Carruthers et al. 2016). a candidate model for multistock management strategy evaluation, rely on catch records, stock-of-origin analysis, and movement data to estimate abundance of the two stocks in different regions across the Atlantic. Because the catch records have unassigned stock-of-origin, however, the relative stock abundances in the model output become highly sensitive to the few stock-specific time series available (the larval and aerial surveys; T. Carruthers, personal communication). By providing an additional time series of trends in the western and eastern stocks, and in particular one linked directly to the overall abundance data, we expect that including the stock-specific catch series from this approach will lessen that sensitivity and produce more accurate estimates and model predictions. This methodology can also be applied to the individual components of the overall CPUE data going into both stock assessments and mixing models to determine sensitivity to catch composition assumptions for each fleet. For example, estimating that one West Atlantic fleet was primarily targeting eastern stock fish while another was catching equally from both stocks could greatly affect the influence of those catch records on model outputs.

In addition to isolating stock-specific abundance indicators from the combined catch series, the distribution maps can also be used to inform current spatial management of the ABT fisheries in the West Atlantic. Because of the relatively depleted status of the western stock as well as the large relative difference in stock size, quota for ABT in the West Atlantic is set low compared with that in the East Atlantic (ranging from 1750 to 2350 t over the last decade) to aid recovery of this stock. Being able to selectively harvest individuals from the more abundant stock, however, would reduce the negative impact to the less abundant stock and would aid recovery of the weakest stock component. Consequently, it is theoretically possible to both maintain harvest in certain fishing areas and improve status of the limiting, or weak, stock by concentrating fishing effort in regions and times when the more productive stock predominates and (or) by targeting smaller size classes that maximize eastern stock likelihood.

In conclusion, the analyses conducted herein show that stock-specific movement data from the electronic tag tracks can be used to estimate stock composition for pre-existing catch records based on location and time of year. The resulting stock-specific catch series can be used to improve or evaluate the sensitivity of results from area-based stock assessments, as well as inform management decisions. Our approach will benefit from expected advances in genetic stock assignment and will yield improved estimates of catch composition, both current and historical, even if fast ship-board assignment methods are not feasible in the near future. It will work together with current methods of otolith- and genetic-based stock assignment by providing movement-based comparisons for stock-mixing estimates, as well as potentially using those methods to increase the usable movement data by identifying and incorporating more of the "unknown stock" tags. The methodology will improve with genetic assignments of tracks in the future. The method presented here provides a useful tool for the management of mixed-stock fisheries, and particularly ABT, an iconic fish of North Atlantic ocean ecosystems, commercial fisheries, and conservation importance.

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