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Electronic tags reveal high migratory diversity within the largest Atlantic halibut (*Hippoglossus hippoglossus*) stock

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Abstract

Growing evidence suggests that complex spatial structure occurs within the Scotian Shelf and southern Grand Banks (SSGB) Atlantic halibut stock, yet large knowledge gaps remain about diversity of migratory and spawning behaviors. Here, 71 pop-up satellite archival tags were deployed on large Atlantic halibut (FL: 87–166 cm) between 2012 and 2020. Migration tracks were successfully reconstructed for 43 fish using a hidden Markov geolocation model, and temperature and depth time series were available for an additional nine fish (total $n = 52$). Five migratory behavior categories were identified: shelf residency, slope residency, shelf-channel migration, shelf-slope migration, and dispersal. High-resolution data for four of 20 physically recovered tags provided evidence of putative spawning behavior in deep channels on the continental shelf and along the continental slope between January and February. Additionally, four halibut displayed previously undocumented periods of sustained, oscillatory vertical movements along the continental slope between November and February. The high migratory diversity observed in this study provides support for the existence of multiple resident and migratory contingents in the SSGB stock in the apparent absence of significant genetic structure.

Key words: Atlantic halibut, PSAT, electronic tag, migratory behavior, geolocation

1. Introduction

The need to characterize life cycle diversity and to incorporate it into spatial fisheries assessments and management (Goethel et al. 2011) has stimulated the documentation of the variation in migratory and spawning behavior at the individual and population levels across a wide range of fish species (Secor 2015). Through the portfolio effect, migratory diversity (*i.e.*, within population diversity in migratory behaviors) can increase long-term population stability (Kerr et al. 2010), and preserving this diversity may help reduce risk of population collapse or promote recovery (Petitgas et al. 2010). Indeed, documented local extirpation of migratory and spawning groups is believed to have contributed to the collapse of marine fish stocks, and to have delayed their subsequent recovery (e.g., Gulf of Maine cod, Ames 1997; Northern cod, Smedbol and Wroblewski 2002; Northwest Atlantic herring, Smedbol and Stphenson 2001), leading to calls for better consideration of migratory diversity within fish stock management.

Several theories have been proposed to explain this diversity including metapopulation, partial migration, and contingent theory. While metapopulation structure applies to a set of geographically or ecologically isolated subpopulations with some degree of connectivity (Harrison and Taylor 1997; Stacey et al. 1997), partial migration focuses on variation in individual propensity to migrate within the same population (Brodersen et al. 2008; Chapman et al. 2012*a*, 2012*b*). The contingent theory centers on multiple groups of fish in a population (contingents) whose members exhibit similar migratory behaviors that differ among contingents (Clark 1968; Secor 1999).

Atlantic halibut (*Hippoglossus hippoglossus*) in the Northwest Atlantic has been the subject of particular attention in recent years, especially its migratory and spawning behaviors (Gauthier et al. 2021; Shackell et al. 2021), stimulated by lucrative fisheries and rapid growth in landings and biomass estimates since the early 2000s (Cox et al. 2016; Trzcinski and Bowen 2016). Halibut is currently the groundfish fishery with the highest landed value in Atlantic Canada (DFO 2022). Knowledge of Atlantic halibut stock structure and migration has been gained through genetic studies (Kess et al. 2021) and the analyses of electronic tags (Armsworthy et al.

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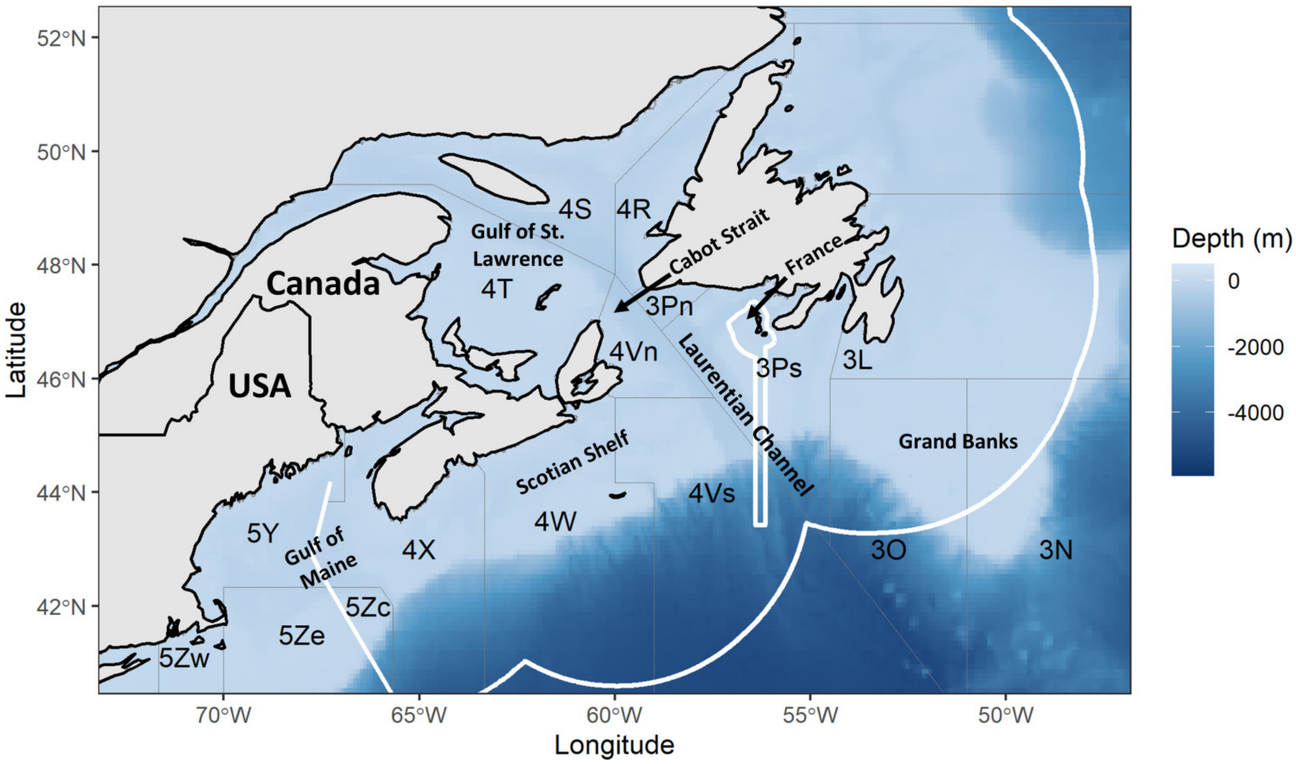
Fig. 1. Map of the Northwest Atlantic showing the Northwest Atlantic Fisheries Organization (NAFO) divisions that make up the Scotian Shelf and southern Grand Banks (3NOPs4VWXZc), Gulf of St. Lawrence (4RST), and US (5YZe) Atlantic halibut stocks. The white line indicates the Canadian, American, and French Exclusive Economic Zones (EEZs). Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022).



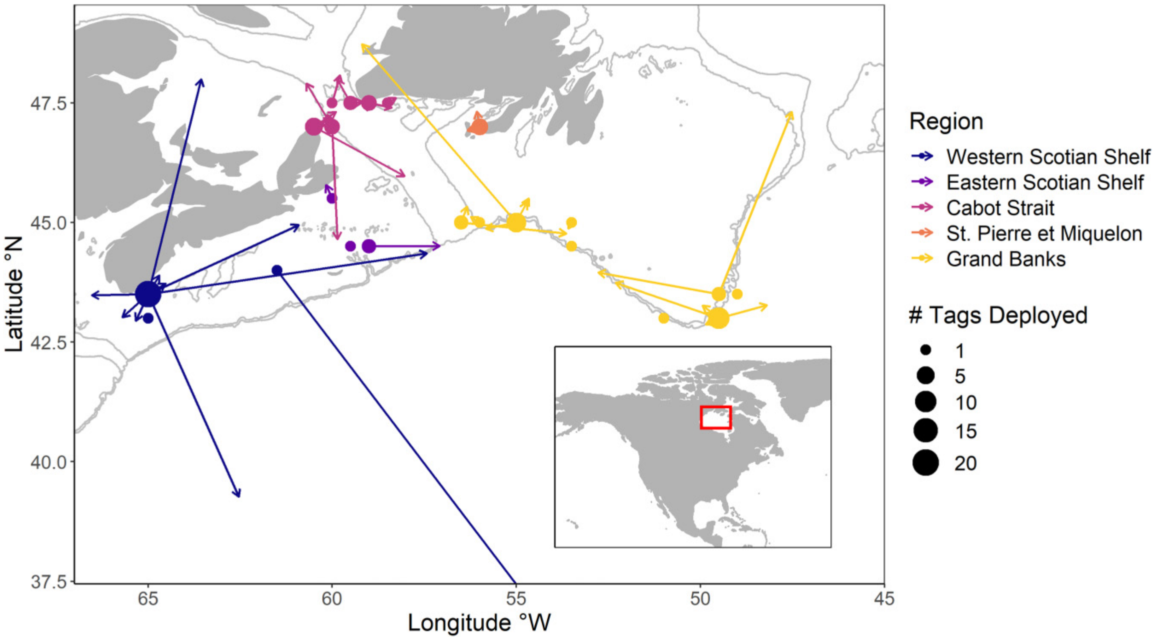
2014; Seitz et al. 2016; Le Bris et al. 2018; Liu et al. 2019; Gatti et al. 2020; James et al. 2020; Marshall et al. 2023) and conventional tags (Stobo et al. 1988; Kanwit 2007; den Heyer et al. 2012; Kersula and Seitz 2019; James et al. 2020), particularly in the Gulf of Maine (GoM) and the Gulf of St. Lawrence (GSL), where in the GSL, the existence of multiple migratory contingents has been suggested (Gatti et al. 2020).

The current Northwest Atlantic halibut stock structure consists of three stocks: the GSL stock encompassing Northwest Atlantic Fisheries Organization (NAFO) divisions 4RST, the Scotian Shelf and southern Grand Banks Stock (SSGB, NAFO Divisions 3NOPs4VXW5YZc), and the United States (US) stock (NAFO Divisions 5YZw) (Fig. 1). Support for the continued separation of the two Canadian stocks, defined in 1988, has come from a combination of differences in growth rates (Sigourney et al. 2006; Armsworthy et al. 2014; Shackell et al. 2019) and size and age composition of commercial landings (McCracken 1958), limited mixing between the two stocks (McCracken 1958; Stobo et al. 1988; den Heyer et al. 2012; Shackell et al. 2016; Le Bris et al. 2018; James et al. 2020), subtle but significant genomic differences (Kess et al. 2021), and possibly differing peak spawning times (Neilson et al. 1993; Armsworthy et al. 2014; Murphy et al. 2017; Le Bris et al. 2018; James et al. 2020). However, questions remain about the possibility of a more complex spatial structure within SSGB stock boundaries (Shackell et al. 2021), about the movement rates across the SSGB and US stock boundary (Kersula and Seitz 2019) and across the Canada–France (*i.e.,* territory of Saint Pierre and Miquelon) boundary, and also about the possible connectivity between SSGB and GSL stocks (Armsworthy et al. 2014).

These questions of population structure and connectivity are important given that the SSGB stock is the largest of the three stocks in area, biomass, and landings. Recent genomic analyses did not find detectable differences among regions within the SSGB stock (Kess et al. 2021); however, non-genetic evidence of spatial structure within the stock is growing. On the warmer Scotian Shelf, halibut grow faster (Armsworthy and Campana 2010; Shackell et al. 2019) and mature at smaller sizes (Sigourney et al. 2006; Shackell et al. 2019) than on the cooler Grand Banks (GB). Furthermore, connectivity of juvenile habitat (250 km) (Boudreau et al. 2017) and the median distance at recapture (∼3–90 km) estimated from multiple conventional tagging studies (McCracken 1958; Stobo et al. 1988; Kanwit 2007; den Heyer et al. 2013; Kersula and Seitz 2019) are far less than the scale of the SSGB stock (2000 km), suggesting differential habitat use and limited mixing.

Given the emphasis on electronic tagging applications and geolocation within the GSL and US stocks, far less is known about the migratory behaviors of halibut across the SSGB region. Prior to this study, only 17 pop-up satellite archival tags (PSATs) had been deployed between 2007 and 2010 on Atlantic halibut in the SSGB, and only on halibut larger than 118 cm (Armsworthy et al. 2014). Their temperature and depth time series data showed that many halibut migrated

Fig. 2. Deployment locations of pop-up satellite archival tag ($n = 71$ total) colored by deployment region. Bubble sizes correspond to the number of tags deployed at each location. The thin grey lines represent the 200 and 500 m isobaths. Arrows are positioned from tag deployment location (bubble) to tag pop-off location (arrowhead) for all tags with a known pop-up location. The red box on the map inset highlights the Northwest Atlantic study region. Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022).



seasonally between the shallower continental shelf in the summer and deeper waters on the continental slope in the winter where some fish may have spawned (Armsworthy et al. 2014). At that time, however, no geolocation model for the northwest Atlantic was available, making it difficult to reconstruct movement tracks, nor to identify spawning locations. With the recent expansions of PSAT tagging of halibut within the SSGB, and the development of geolocation tools applied to halibut migration (Le Bris et al. 2018; Gatti et al. 2020), we can now further characterize migratory diversity and spawning areas in SSGB to provide new understanding and inputs for sustainable management of the stock.

In this study, we examined the data collected from 71 pop-up satellite tags to characterize the diversity of migratory behavior, habitat use, and putative spawning areas of Atlantic halibut across the SSGB stock. We hypothesize that because of the extent and diversity of habitat in the stock area, SSGB halibut display a high diversity of migratory behaviors, encompassing the migratory diversity observed in other stocks.

2. Materials and methods

2.1. Tagging operations

Between 2012 and 2020, 71 pop-up satellite archival tags were deployed on large (fork length: median = 130 cm, min = 87 cm, max = 166 cm) Atlantic halibut across the SSGB stock (Supplementary Table S1). Sex was determined for a small subset of halibut ($n = 10$) with a single nucleotide polymorphism (SNP) panel and genomic identification (Weise et al. 2023). Tagging locations were selected primarily based on their importance to the fishery, management of the stock, and ecology of the species. Halibut were tagged at the edge of the GB and southwest Nova Scotia, which are important fishing locations, near the Cabot Strait (CS), which is the boundary of the SSGB and GSL stocks, and off Saint Pierre and Miquelon (SPM), an archipelago within the French exclusive economic zone in NAFO division 3Ps (Fig. 2; Supplementary Table S1). Additionally, tags were deployed around the Gully, a submarine canyon and marine protected area (MPA) on the Scotian Shelf slope of interest because it is a putative spawning location (Stobo et al. 1988) and a juvenile halibut hotspot (Boudreau et al. 2017). In subsequent analyses, halibut were binned in five groups based on tagging location: western Scotian Shelf (WSS), eastern Scotian Shelf (ESS), the CS, SPM, and the GB. Halibut were caught using longlines equipped with circle hooks (no. 12, no. 14, or no. 16) on commercial vessels either chartered specifically for PSAT tag deployment or part of the halibut longline survey (den Heyer et al. 2015) or the 4Vn sentinel survey (Lambert 2019). The care and use of experimental animals complied with Canadian Council on Animal Care's animal welfare laws, guidelines, and policies as approved by Memorial University's Animal Care Committee, protocol 19-02-AL.

MiniPat PSATs and Mk-10 PSATs (Wildlife Computers Inc., Redmond, WA, USA) deployed before 2018 were anchored using barbed plastic anchor (umbrella dart) (Armsworthy et al. 2014); later, MiniPat (384 F) tags were tethered just below the pterygiophores on the dorsal, eyed-side of the fish using a titanium dart (Murphy et al. 2017). Tags were programmed to pop-off after 8 ($n = 14$), 9 ($n = 5$), 10 ($n = 16$), 11 ($n = 28$), or 12 months ($n = 8$). The differences in programmed deployment lengths were due to delays in deployment and opportunities for at-sea recovery. PSATs recorded temperature (±0.05 °C), depth (±0.5 m to 1700 m), and light (5×10^{-12} to 5×10^{-2} W·cm^{-2}) continuously throughout the deployment period (hereafter, archived data). For tags deployed in 2018 or later, the data resolution was 15 s and data transmitted via the Argos satellite system (hereafter, transmitted data) were summarized in 10 min intervals. For tags deployed prior to 2018, the data had 10 s resolution and 6 h summaries when transmitted. Tag recovery missions took place on preprogrammed pop-up dates on board-chartered commercial vessels with the aid of a goniometer (RGX-134 digital receiver with RG-58 direction finding antenna; CLS America Inc. Lanham, MD, USA) as described by Fisher et al. (2017) and Gatti et al. (2020). Archived data at 10–15 s continuous recording resolution were downloaded from physically recovered tags.

In addition to the PSATs, 32 fish were double tagged with a mark-report pop-off satellite archival transmitting tag (mrPATs, Wildlife Computers, Redmond, Washington, USA) programmed to pop-off on a date between December and February to provide a single pop-off location per halibut during the presumed spawning period. Those locations were also used to measure the error of reconstructed geolocation positions for the subset of halibut for which data from both tags were available (Gatti et al. 2021). Additionally, three of the halibut tagged in 2020 on the ESS had a VEMCO V16 (length: 66 mm, weight: 24 g in air) acoustic transmitter surgically implanted.

2.2. Geolocation

Reconstruction of Atlantic halibut migration routes was performed using a hidden Markov model (HMM) originally developed to track Atlantic cod movements in the North Sea (Pedersen et al. 2008; Thygesen et al. 2009) and since adapted for Atlantic cod (Le Bris et al. 2013) and Atlantic halibut (Le Bris et al. 2018; Gatti et al. 2020) in the GSL. HMMs couple a process and an observation model. For each track day, the process model simulated fish movement using a diffusion equation and priors about swimming speed. Then, the observation model refined the estimated probability of fish position from the movement model by comparing data recorded by the tag with environmental data from ca. 4 km^2 resolution grids, built using data from SRTM30 PLUS global bathymetry grid (Version 1) (Becker et al. 2009). Because Atlantic halibut is an epi-benthic species, light data were not used for geolocation. In prior utilization of the HMM geolocation model in the region, daily maximum depth and associated temperature were used in the observation model (Le Bris et al. 2013); however, sensitivity analyses conducted by Gatti et al. (2021) demonstrated that the model performed as well in the GSL with depth only rather than with both depth and temperature data. Therefore, in this study, only daily maximum depths were used and compared with 4 km^2 resolution bathymetric grids from the Canadian Hydrographic Service. Previous validation efforts of this model revealed that, on average, a geolocation error of 50 km is obtained with this model configuration in the region for Atlantic halibut (Gatti et al. 2021). The output of the geolocation model was the posterior probability density function of fish position for each day. For data visualization purposes, we reported the most probable position for each day using the grid cell with the highest likelihood values. Tracks with probability densities are available on Supplementary Fig. S1.

2.3. Model validation using mrPATs and acoustic tags

The mrPATs popped-off at a pre-programmed date and transmitted their location via satellite. This specific preprogrammed date provided one day during the tag deployment period when the halibut's location was known. When data were received from a fish tagged with an mrPAT, the model was run first without forcing the mrPAT location for the day the mrPAT popped off. This analysis allowed us to compare the distance between where the geolocation model predicted the fish would be that day to the halibut's known location. Additionally, one of the three acoustically tagged fish was detected in the halibut receiver array by four different receivers on four days in December 2020 and January 2021. We estimated the mean distance between the predicted and known locations (both the transmitted mrPAT and acoustic receiver locations) on corresponding day. This was done by first calculating the distance between each grid cell from the grid cell corresponding to the location where the mrPATs surfaced, or where the acoustic receiver was located when a detection occurred. Then this distance for each cell was weighted by multiplying the distance by the posterior probability value of the cell for that day as estimated by the geolocation model. The weighed distances of each cells were then summed. The geolocation output from the model when the mrPAT location was forced was the only trajectory used in all further analyses for all fish that were tagged with an mrPAT that transmitted to the satellite successfully.

Data from one halibut outfitted with three electronic tags were treated differently. Fish 19P1446 was tagged with a PSAT and an mrPAT and equipped with a V16 acoustic transmitter (length: 68 mm, weight: 24 g in air). This fish was detected four times during tag deployment by an array of VEMCO VR4 receivers in The Gully. The geolocation model was run (i) with only the PSAT and pop-off locations forced, and (ii) with the PSAT tag and pop-off, mrPAT pop-off, and four acoustic detection locations all forced. The latter geolocation output was used in all further analyses for this fish.

2.4. Measuring distance traveled

Based on geolocation model outputs, distance traveled between tagging and pop-off locations of miniPAT and mrPAT was estimated as the sum of the distance between daily locations. Each cell on the grid used for geolocation was assigned coordinates that corresponded to the latitude and longitude of the central point of the cell. The coordinates of the cell with the highest probability on a given day was assigned as the fish's location on that day. Distance traveled each day was calculated as the great circle distance between fish locations on day i and day $i - 1$. The total distance was then estimated as the sum of daily distances traveled.

2.5. Identifying putative spawning rises

Halibut have yet to be observed spawning in their natural habitat. However, Seitz et al. (2005) identified putative spawning behavior in Pacific halibut by comparing time series data from PSATs deployed on Pacific halibut to the spawning behavior of seven other flatfish species that was directly observed by humans using self-contained underwater breathing apparatus (SCUBA). Seitz et al. (2005) characterized the spawning rises as large and abrupt vertical ascents and descents that were regularly spaced every 2 to 3 days over a period of roughly two weeks. Similar putative spawning behavior has since been observed in Atlantic halibut using PSATs (Armsworthy et al. 2014; Le Bris et al. 2018).

In this study, spawning rises were detected through visual inspection of the full depth archived time series. Spawning rises were defined as a series of abrupt vertical ascents of 25–100 m with a pronounced apex and duration of only 10–20 min (Marshall et al. 2023). Since transmitted data has maximum 10 min resolution and large data gaps and detecting spawning rises requires data resolution on the temporal scales of minutes or seconds, it is not likely that spawning rises will be detected (Fisher et al. 2017). For this reason, only archived data were inspected for spawning rises.

3. Results

3.1. Tracking success

Of the 71 PSATs deployed, 38 tags popped off within one day of their pre-programmed date or were recaptured by fishermen, four tags popped off less than 2 months after deployment, 21 tags popped off after 2 months but before their pre-programmed date, 7 tags did not report, and 1 tag did not report but was physically recovered by a fish harvester (Table 1). Among the premature releases, we identified six instances of possible fish mortality within 2 months of deployment and one instance of possible fish mortality 9 months after deployment. Halibut mortality was assumed when the fish's depth profile showed an oscillation of 1–2 m in time with the tides for the remainder of the tag's lifespan. Twenty tags were physically recovered that provided 15 s data resolution for their entire deployment periods. Despite extensive recovery efforts, several tags that transmitted were unable to be recovered due to battery failures with the miniPATs series deployed in 2019 and storms that pushed tags offshore in the fall of 2020. In summary, of the 71 deployed PSATs, we had access to 55 PSAT datasets: 20 archived datasets and 35 transmitted datasets (Table 1).

3.2. Geolocation success

Migration tracks were successfully reconstructed for 46 fish, 16 archived (WSS, $n = 2$; ESS, $n = 0$; CS, $n = 2$; SPM, $n = 3$; GB, $n = 9$) and 30 transmitted (WSS, $n = 6$; ESS, $n = 2$; CS, $n = 10$; SPM, $n = 1$; GB, $n = 11$). Geolocation attempts were unsuccessful for 9 fish, meaning the model could not produce location predictions. These fish were tagged on the WSS ($n = 3$), on the ESS ($n = 2$), and on the GB ($n = 4$).

Among the 32 fish double tagged with a PSAT and an mrPAT, we had access to data for both tags and with successful geolocation for 12 fish (Table 2). Distance between the known location of the fish on the mrPAT pop-off date and the location-predicted geolocation model without the mrPAT location forced informed on geolocation model performance. The mean distance between the known and predicted locations was 47.96 ± 25.22 km. Two examples of the trajectories produced by the model with the known mrPAT location forced versus unforced are available in the supplementary materials (S3–S6).

3.3. Seasonal distribution and migratory behavior categories

Time series data were available for 55 fish (Table 1). Depth and temperature distributions varied by region, although halibut from all regions tended to exhibit maximum depths in the late fall and early winter months (Figs. 3 and 4). We identified five migratory behavior categories from the depth and temperature profile and with the help of reconstructed tracks (Fig. 5, Table 3): shelf residency, slope residency, shelf-channel migration, shelf-slope migration, and dispersal. Shelf residents ($n = 16$) remained on the continental shelf throughout the year in waters shallower than 250 m. Tag 18P1571 (Fig. 5) shows a typical profile of shelf residents with relatively little differences in depth distribution throughout the year. Of these shelf residents, seven were tagged on the WSS, two on the ESS, one in the CS, and six on the GB. The second category, slope residents ($n = 12$), were halibut that remained along the continental slope in water deeper than 300 m all year, with a similar depth profile as fish 19P1430 (Fig. 5). During winter months, slope residents experienced less variable temperature (typical variation between 2 °C and 6 °C) than shelf residents (2–10 °C) (Fig. 5). All 12 slope residents were tagged on the GB.

The third category, shelf-channel migrants ($n = 14$), was characterized by a seasonal shift from shallower (<200 m) waters in the summer to deeper waters (400–500 m) in the channels on the continental shelf in the winter (Fig. 6). During the winter, the depth was relatively stable and rarely varied by more than 50 m per day (Fig. 5). This behavior was seen in halibut tagged in each of the four regions, most frequently in halibut tagged in the CS and off of St. Pierre et Miquelon (SPM). Temperatures occupied in the CS were mostly constant (~5–6 °C). In contrast, thermal habitat was more variable year-round off SPM. Indeed, some crossed the cold intermediate layer in the spring and fall and were in very shallow depths in the summer where temperature was more variable.

The fourth category, shelf-slope migrants, shifted from shallow (>300 m) water in the summer to deeper (>700 m) water on the edge of the continental slope in the fall and/or winter ($n = 7$). Of these shelf residents, one was tagged on the WSS, one in SPM, and three on the GB. The migration distance and the depth profile varied depending on the summer shelf residency location, with halibut tagged on the GB migrating shorter distance, due to the proximity of the slope, than halibut tagged in coastal waters, which needed to undergo longer migration to reach the continental slope (Fig. 6). Temperatures were relatively constant (~4.5 °C) in the deep waters of the slope and varied between ~1 °C and 10 °C, while

Table 1. Tag summary for 55 pop-up satellite archival tags (PSATs) deployed on Atlantic halibut on the Scotian Shelf and southern Grand Banks for which the time series data were available.

				Deployment			Pop-up						
PSAT ID	mrPAT ID	Length (cm)	Sex	Date (dd/mm/yyyy)	Lat (°N)	Lon (°W)	Date (dd/mm/yyyy)	Lat (°N)	Lon (°W)	Data type	Days at large	Total dist. (km)	Behavior
Western Scotian Shelf													
18P1571		118	NA	08/06/2019	43.519	−65.003	NA	NA	NA	A	302	429.8	Shelf Res.
18P1572		143	NA	08/06/2019	43.519	−65.012	28/01/2020	44.354	−57.435	T	235	360.4	Dispersal
18P1575	18U1937	120	NA	08/06/2019	47.167	−60.225	09/12/2019	43.614	−64.797	T	185	164.9	Shelf Res.
18P1577	18U1468	123	NA	08/06/2019	43.575	−64.905	12/05/2020	43.022	−65.698	T	340	827.5	Shelf Res.
18P1579[b]	18U1933	125	NA	08/06/2019	43.543	−64.917	12/05/2020	43.480	−66.531	T	340	496.8	Shelf Res.
19P1319		130	F	22/07/2020	43.615	−65.126	01/04/2021	39.270	−62.538	T	254	286.2	Shelf Res.
19P1350[a]	19U2466	142	NA	22/07/2020	45.738	−60.136	16/05/2021	47.995	−63.559	T	299	NA	Dispersal
19P1440[a]		144	F	22/07/2020	47.052	−60.282	28/03/2021	43.715	−65.148	A	250	NA	Shelf Res.
19P1444		130	NA	22/07/2020	47.052	−60.283	16/05/2021	44.944	−60.914	A	299	1366.5	Dispersal*
19P1699	19U2465	136	NA	22/07/2020	47.063	−60.293	23/10/2020	43.509	−64.923	T	94	86.8	Shelf Res.
119962[a]		87	F	02/07/2012	43.25	−64.78	12/06/2012	NA	NA	T	346	NA	Shelf-Slope
Eastern Scotian Shelf													
18P1607[a]	19U1403	156	NA	25/09/2019	45.738	−60.136	06/08/2020	45.784	−60.164	A	327	NA	Shelf-Channel
19P1446	19U2454	110	NA	13/09/2020	47.052	−60.282	08/06/2021	44.632	−59.954	T	269	346.5	Shelf Res.
19P1538		120	NA	13/09/2020	47.052	−60.283	08/06/2021	44.498	−56.566	T	269	1012.6	Dispersal
119967[a]		93	F	05/07/2012	43.25	−64.78	13/01/2013	43.69	−51.29	T	193	NA	Shelf Res
Cabot Strait													
18P1219		99	NA	24/09/2019	47.485	−59.028	26/08/2020	43.344	−59.056	T	338	563.1	Shelf-Channel
18P1220	19U1399	126	NA	24/09/2019	47.488	−59.011	09/08/2020	47.404	−53.382	T	321	527.9	Shelf-Channel
18P1570	18U2411	133	NA	11/09/2019	47.487	−59.013	07/07/2020	48.078	−59.793	T	301	474.2	Shelf-Channel
18P1573		130	NA	20/09/2019	43.516	−64.979	26/08/2020	47.249	−60.133	T	342	222.5	Shelf-Channel
18P1576		150	NA	11/09/2019	43.516	−64.982	26/08/2020	47.905	−60.699	T	351	557.9	Shelf-Channel
18P1608	19U1398	140	NA	18/11/2019	43.516	−64.982	26/08/2020	47.049	−60.208	T	283	215.6	Shelf Res.
18P1609		115	NA	18/11/2019	43.516	−64.981	26/08/2020	47.106	−60.248	T	283	183.1	Shelf-Channel
18P1663	19U1351	120	NA	18/11/2019	47.167	−60.225	26/08/2020	47.172	−60.030	T	283	554.5	Shelf-Channel
18P1667		149	NA	18/11/2019	47.256	−60.150	26/08/2020	45.968	−58.041	T	283	494.4	Dispersal
19P0260	19U1440	158	NA	26/09/2019	43.519	−65.004	26/08/2020	47.602	−58.267	A	336	784.3	Shelf-Channel*
19P0457		87	NA	24/09/2019	43.520	−65.012	26/08/2020	47.988	−59.861	T	334	1481.8	Shelf-Channel
19P0470		105	NA	24/09/2019	47.167	−60.225	26/08/2020	47.521	−59.179	A	334	1263.3	Shelf-Slope+

Table 1. (*concluded*).

				Deployment			Pop-up						
PSAT ID	mrPAT ID	Length (cm)	Sex	Date (dd/mm/yyyy)	Lat (°N)	Lon (°W)	Date (dd/mm/yyyy)	Lat (°N)	Lon (°W)	Data type	Days at large	Total dist. (km)	Behavior
St. Pierre et Miquelon													
17P0146	18U0599	147	NA	23/09/2018	46.888	−56.211	27/08/2019	46.925	−56.320	A	339	802.5	Shelf-Channel*
17P0167		126	NA	23/09/2018	46.893	−56.212	27/08/2019	46.928	−56.320	A	339	1051.7	Shelf-Slope+
17P0168		128	NA	23/09/2018	46.891	−56.212	27/08/2019	46.922	−56.325	A	339	338.7	Shelf-Channel
18P0368	18U0671	152	NA	21/09/2018	46.894	−56.214	21/03/2019	47.321	−56.078	T	182	718.8	Shelf-Channel
Grand Banks													
19P1422	19U2456	135	NA	29/09/2020	43.153	−49.674	02/06/2021	43.170	−49.704	A	247	154.3	Slope Res.
19P1424	19U2333	151	NA	29/09/2020	43.161	−49.697	06/02/2021	43.110	−49.843	T	131	263.1	Slope Res.
19P1430	19U2467	146	NA	29/09/2020	43.651	−65.011	02/06/2021	42.871	−49.857	T	247	303.4	Slope Res.
19P1436[a]	19U2331	140	NA	29/09/2020	43.153	−49.674	11/06/2021	45.232	−27.392	T	256	NA	Dispersal
19P1479	19U2468	133	NA	29/09/2020	43.151	−49.546	02/06/2021	43.176	−49.544	A	247	337.3	Slope Res.
19P1487		130	NA	29/09/2020	43.660	−65.001	02/06/2021	42.985	−50.900	A	247	148.7	Slope Res.
19P1491[a]		121	NA	29/09/2020	43.612	−65.142	02/06/2021	43.261	−49.946	A	256	NA	Shelf-Slope
19P1492		140	NA	29/09/2020	43.612	−65.142	02/06/2021	43.124	−49.535	A	256	210.5	Slope Res.
19P1494		157	NA	29/09/2020	44.421	−59.458	02/06/2021	43.740	−52.307	A	247	487.1	Slope Res.*
19P1496		135	F	01/08/2020	43.151	−49.546	02/06/2021	45.063	−55.130	A	306	296.3	Slope Res.
19P1540	19U2453	138	F	13/09/2020	47.063	−60.293	15/10/2020	44.871	−55.834	T	76	377.4	Shelf Res.
19P1542[a]	19U2330	124	NA	29/09/2020	42.973	−50.898	20/04/2021	43.273	−48.199	A	204	NA	Slope Res.
19P1544	19U2329	132	NA	01/08/2020	43.161	−49.697	02/06/2021	45.064	−55.115	T	306	431.2	Shelf-Slope
19P1546		135	F	29/09/2020	43.183	−49.543	02/06/2021	43.140	−49.550	A	247	1317.1	Slope Res.
19P1547		136	F	01/08/2020	43.183	−49.543	02/06/2021	45.426	−54.716	T	306	1075.9	Shelf-Channel
19P1548		152	NA	29/09/2020	45.054	−55.125	02/06/ 2021	43.957	−52.782	A	247	413.5	Slope Res+
19P1549		135	M	01/08/2020	45.026	−55.135	02/06/2021	48.724	−59.191	A	306	1239.3	Dispersal+
19P1696		124	F	29/09/2020	44.664	−59.000	08/05/2021	47.318	−47.525	T	222	159.9	Slope Res.
106702		88	NA	22/07/2012	45.02	−56.59	11/06/2013	45.33	−56.34	T	325	1307.8	Shelf Res.
106703		97	NA	21/06/2012	44.85	−56.13	10/06/2013	45.12	−56.24	T	355	348.0	Shelf-Slope
119960		118	NA	04/07/2012	44.87	−56.11	25/06/2013	44.77	−53.65	T	357	1267.6	Shelf Res.
119968[a]		102	F	25/07/2013	44.01	−52.68	13/11/2013	42.23	−60.30	T	60	NA	Shelf Res.
119970		109	NA	26/06/2013	43.39	−61.39	04/06/2014	44.44	−53.61	T	344	1264.6	Shelf Res.
119975		108	NA	04/07/2012	47.17	−60.14	25/06/2013	44.87	−53.59	T	357	137.2	Shelf Res.

Notes: Behaviors are abbreviated as follows: Data type: A, archived; T, transmitted; Shelf Res., Shelf residency; Slope Res., Slope residency; Shelf-Channel, Shelf-channel migration; Shelf-Slope, Shelf-slope migration. Total distance is the estimated total distance measured from the geolocation model. [a]Geolocation attempts unsuccessful

[b]One month of archived data recovered by Wildlife Computers, but 10 months of data transmitted so transmitted data used in analysis

*Putative spawning

+Offshore behavior

Table 2. Tag summary for mrPATs deployed as well as acoustic tag detections (ACD) on Atlantic halibut on the Scotian Shelf and southern Grand Banks and the distance between mrPAT pop-offs reported by the ARGOS satellite or acoustic receiver (AR) locations and the location estimated by the geolocation model without mrPAT pop-off or ACD locations forced.

				Pop-off or AR location		Model-estimated location		
PSAT ID	mrPAT ID	Data type	mrPAT pop-off/ACD date (dd/mm/yyyy)	Lat (°N)	Lon (°W)	Lat (°N)	Lon (°W)	Mean distance (km) and 95%CI between pop-off/AR location and model estimate
mrPAT Pop-Offs								
17P0146	18U0599	A	16/02/2019	46.857	−57.919	47.414	−56.482	125.89 ± 0.03
19P0260	19U1440	A	10/02/2020	47.526	−59.505	47.121	−58.395	97.24 ± 0.08
19P1422	19U2456	A	21/12/2020	43.143	−49.720	43.214	−49.516	19.32 ± 0.05
19P1430	19U2467	A	30/09/2020	43.136	−49.666	43.157	−49.543	11.76 ± 0.05
19P1479	19U2468	A	21/12/2020	42.733	−50.085	43.063	−51.343	108.87 ± 0.13
18P0368	18U0671	T	26/01/2019	46.846	−57.920	46.492	−57.587	47.23 ± 0.05
18P1220	19U1399	T	09/09/2020	47.529	−59.339	47.103	−58.557	75.04 ± 0.04
18P1570	18U2411	T	22/12/2019	47.306	−60.189	47.305	−60.201	2.81 ± 0.01
18P1608	19U1398	T	10/02/2020	47.164	−60.101	47.103	−60.120	8.17 ± 0.06
18P1663	19U1351	T	10/02/2020	47.245	−58.886	46.678	−58.988	58.32 ± 0.07
19P1424	19U2333	T	21/12/2020	43.094	−49.670	43.119	−49.516	13.28 ± 0.06
19P1446	19U2454	T	21/12/ 2020	44.231	−59.253	44.232	−59.257	0.39 ± 0.00
19P1262	19U2465	T	31/09/2020	43.395	−64.990	43.308	−65.025	7.27 ± 0.07
Acoustic tag detections								
19P1446	4	T	23/12/2020	43.300	−59.087	43.383	−59.662	129.51 ± 0.02
19P1446	5	T	24/12/2020	44.300	−59.050	44.403	−59.689	132.65 ± 0.02
19P1446	16	T	24/01/2021	44.381	−59.049	44.553	−60.039	150.95 ± 0.02
19P1446	24	T	24/01/2021	44.408	−59.087	44.553	−60.039	74.41 ± 0.04

Fig. 3. Monthly depth distributions recorded by PSAT recovered and transmitted since 2019 in the WSS ($n = 11$), ESS ($n = 4$), CS ($n = 12$), SPM ($n = 4$), and GB ($n = 24$). PSAT, pop-up satellite archival tag; WSS, western Scotian Shelf; ESS, eastern Scotian Shelf; CS, Cabot Strait; SPM, Saint Pierre et Miquelon; GB, Grand Banks.

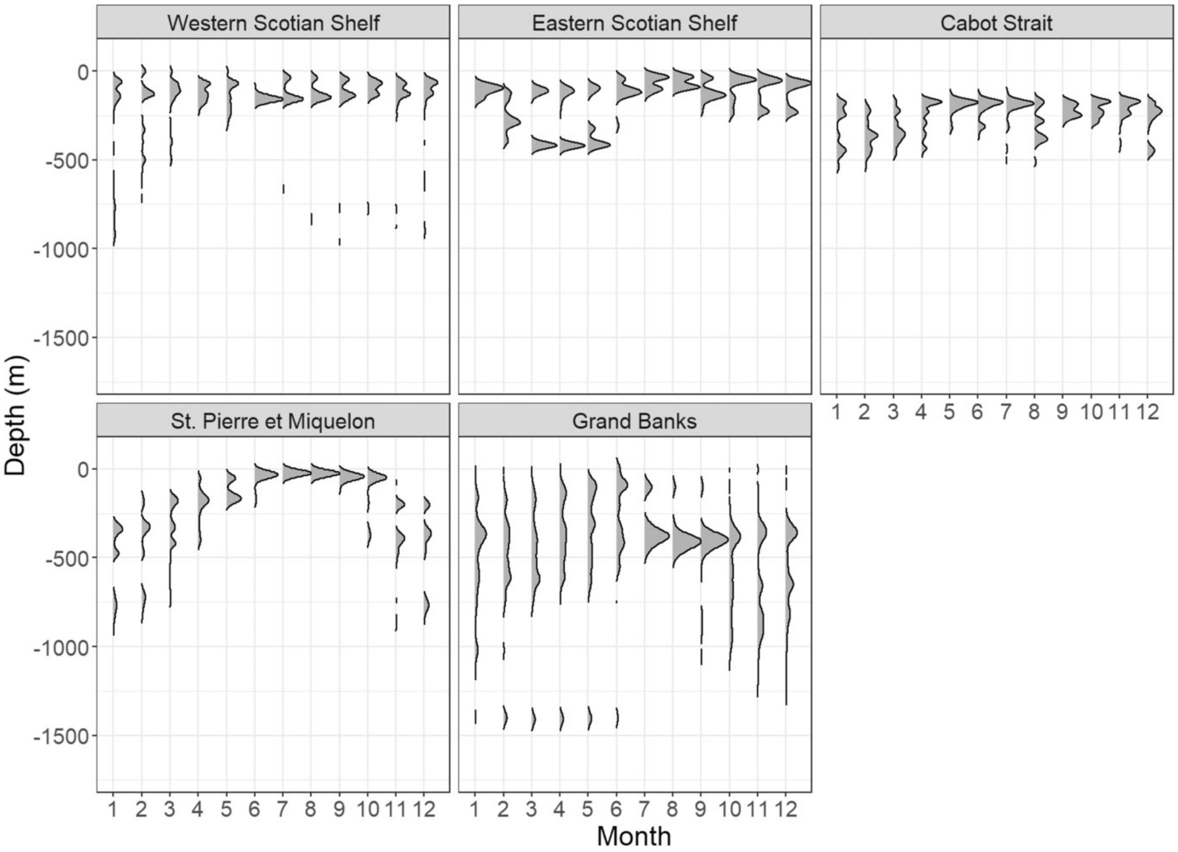
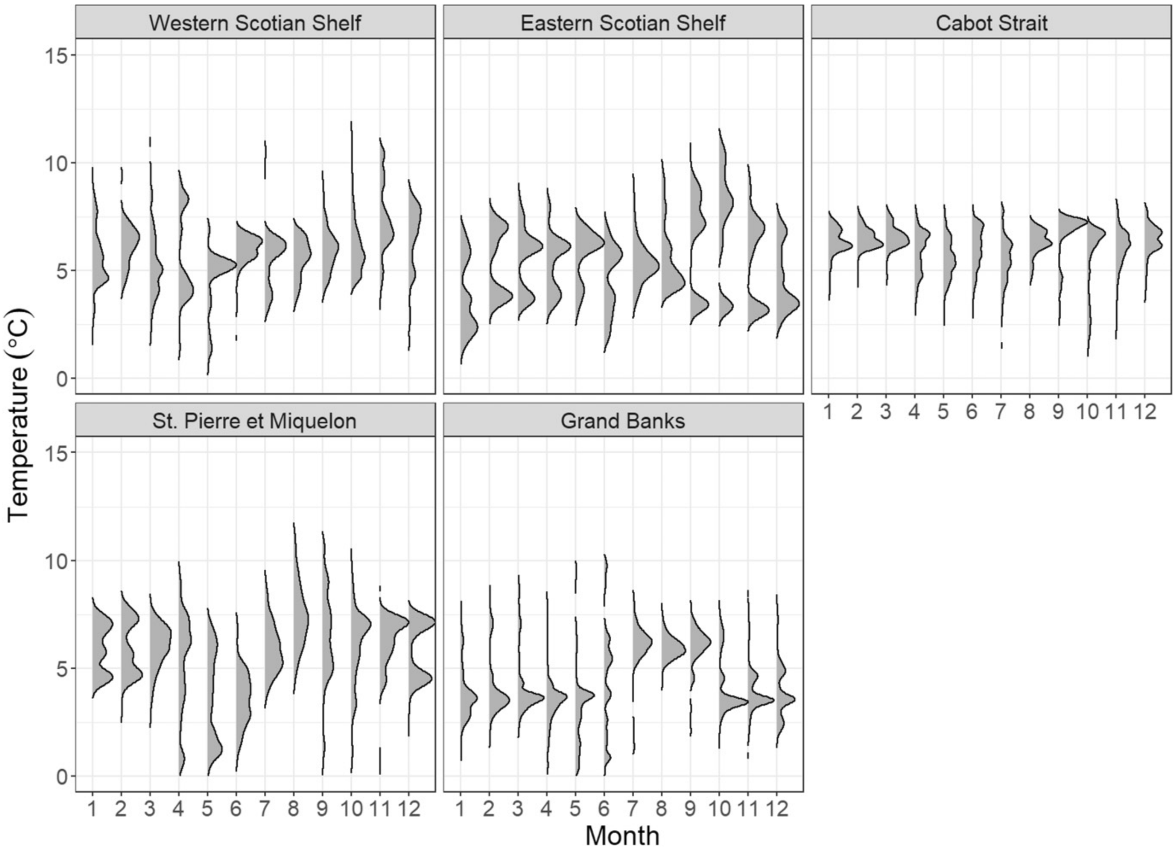


Fig. 4. Monthly temperature distributions recorded by PSAT recovered and transmitted since 2019 in the WSS ($n = 11$), ESS ($n = 4$), CS ($n = 12$), SPM ($n = 4$), and GB ($n = 24$). WSS, western Scotian Shelf; ESS, eastern Scotian Shelf; CS, Cabot Strait; SPM, Saint Pierre et Miquelon; GB, Grand Banks.



the fish were on the shelf and migrating from the shelf to the slope.

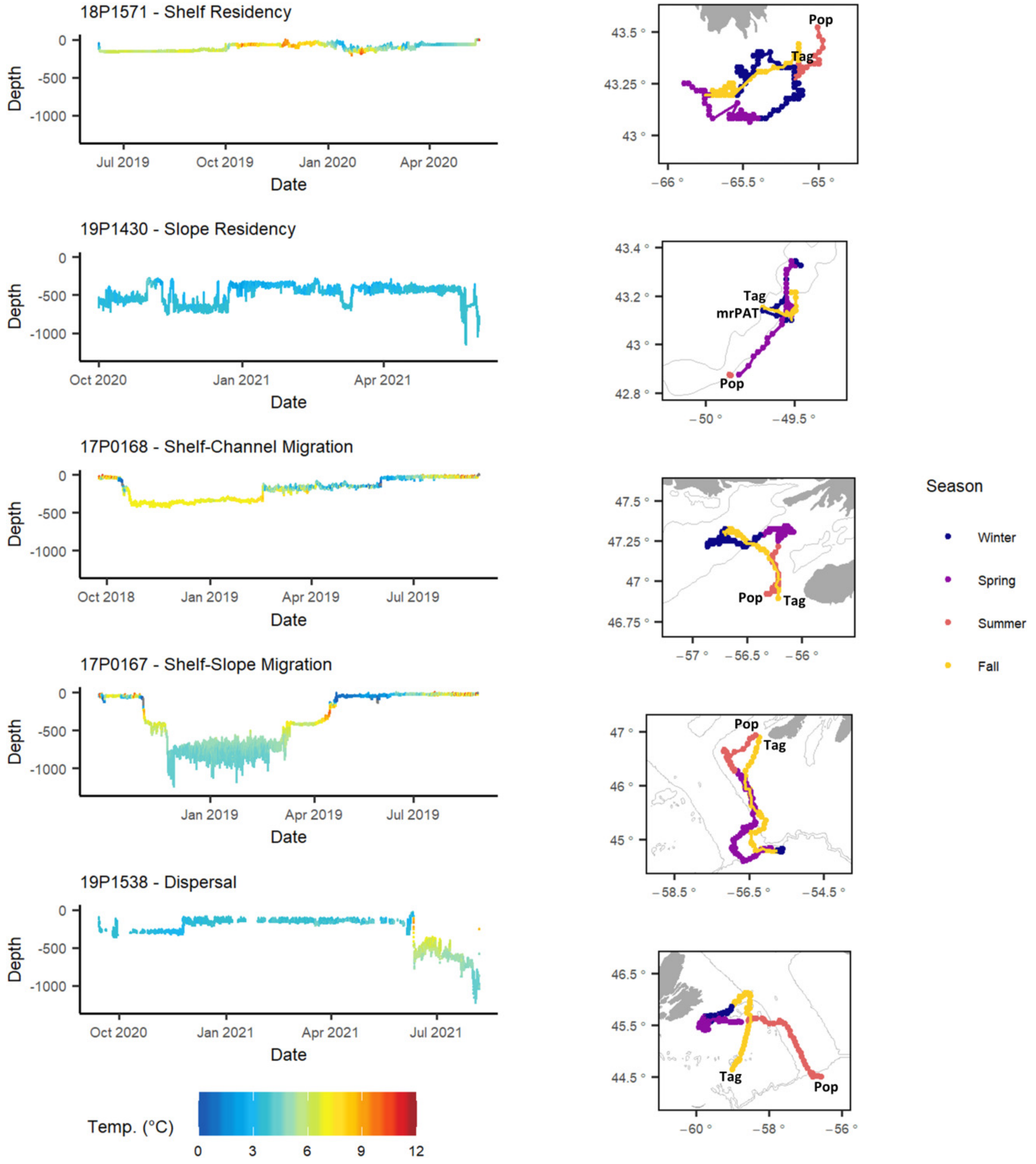
Finally, the fifth behavior category observed was dispersal. On the contrary to shelf-channel and shelf-slope migrants, who displayed a homing behavior by returning to their tagging locations, six halibut in total, tagged on the WSS ($n = 2$), ESS ($n = 1$), and on the GB ($n = 2$) and in the CS ($n = 1$), traveled hundreds of kilometers from where they were originally tagged and did not return to their tagging location during the tag deployment period. The depth profiles of these dispersers varied. Two halibut stayed shallower than 400 m throughout the year, while the four remaining dispersers ventured into water greater than 900 m at times.

Interestingly, two fish (17P0168 and 17P0167) with similar length, which were tagged on the same day and location, and for which both tags popped-up on the same day near their tagging location, displayed markedly different behaviors (Fig. 5). Fish 17P0168 exhibited a shelf-channel migration from about 50 m in the summer to around 400 m in the Hermitage Channel in the winter, where it displayed a putative spawning behavior. Meanwhile, fish 17P0167 exhibited a shelf-slope seasonal migration with a winter migration to much deeper waters on the continental slope, where it displayed extensive vertical movements but did not seem to conduct the typical patterns associated with spawning rises (Figs. 5 and 7).

3.4. Putative spawning behavior and other vertical movement behaviors

Of the 20 archived tags recovered, four (20%) showed evidence of putative female spawning behavior with spawning rises occurring 4–5 days apart each time (Fig. 7 and Supplementary Fig. S1). The four fish, each tagged at different locations, displayed putative spawning rises between 1 January and 10 February. Fish 19P0260, a shelf-channel migrant tagged off Port aux Basques in September, displayed spawning rises from 450 to 350 m between 3 January and 17 January while in the CS. Similar rises were observed in fish 17P0146, another shelf-channel migrant tagged off St. Pierre et Miquelon in September, while located in the Laurentian Channel in January. Fish 19P1494, a slope resident tagged on the GB in September, exhibited rises from 1100 m to about 700–800 m, while located on the continental slope between 9 January and 1 February. Finally, fish 19P1444, a shelf-slope migrant tagged on the WSS in July, exhibited 200 m rises while located in 600–900 m deep slope waters off the Scotian

Fig. 5. Depth and temperature profiles of five fish that displayed different characteristic migratory behaviors and corresponding movement track estimated with a geolocation model. The thin grey lines on the maps to the right represent the 200 and 500 m isobaths, "tag" marks where the pop-up satellite archival tag (PSAT) and mrPAT were deployed, "mrPAT" marks where the mrPAT popped-off, and "pop" marks where the PSAT popped off. Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022).



Shelf between 8 January and 1 February (Fig. 7 and Supplementary Fig. S1).

Additionally, four fish displayed frequent and rapid depth oscillations of as much as 200–400 m per day throughout the fall and/or the winter, while located on the continental slope. Of the four fish that displayed this pattern, one (17P0167) was tagged off St. Pierre et Miquelon in the summer, one (19P0470) was tagged in the CS, and the other two (19P1548 and 19P1549) were tagged on the GB (Table 1).These vertical migrations lasted for 2–4 months, were not periodic, and were conducted at any time of the day (Fig. 8). Despite large movements across the water column, temperature was relatively stable at about 4 °C.

4. Discussion

In this study, we used pop-up satellite archival tags to characterize the migratory diversity of Atlantic halibut across the SSSGB, the largest Northwest Atlantic halibut stock in area, biomass, and landings. Depth and temperature time series

Table 3. Summary of behaviors observed in Atlantic halibut tagged with PSATs on the Scotian Shelf and southern Grand Banks.

Region	*N* Released	*N* Dead	*N* Available data	Data Type % Arch.	% Trans.	% Showing migratory behavior type Shelf Res.	Slope Res.	Shelf to channel migrant	Shelf to slope migrant	Disperser	*N* Spawn	*N* Offshore behavior
WSS*	22	4	11*	27.3	72.7	0	63.6	0.0	27.3	9.1	1	0
ESS	5	0	4	25.0	75.0	50.0	0	25.0	0.0	25.0	0	0
Cabot Strait	15	2	12	16.7	83.3	8.3	0	75.0	8.3	8.3	1	1
SPM	4	0	4	75.0	25.0	0	0	75.0	25.0	0.0	1	1
Grand Banks	25	0	24	45.8	54.2	25.0	50.0	4.2	12.5	8.3	1	2

Note: *N* is the number of individuals. *For one tag, one month of archived data recovered by Wildlife Computers, but 10 months of data transmitted so transmitted data used in analysis. This tag is included in the %Transmitted estimate. PSAT, pop-up satellite archival tag; WSS, western Scotian Shelf; ESS, eastern Scotian Shelf; SPM, Saint Pierre et Miquelon.

and reconstructed migration tracks revealed five behavior categories: shelf residency, slope residency, shelf-channel migration, shelf-slope migration, and dispersal. These five migratory behaviors varied within and between regions. Like previous studies on the migration of Atlantic halibut (Stobo et al. 1988; Kanwit 2007; Armsworthy et al. 2014; Liu et al. 2019; Gatti et al. 2020) and Pacific halibut (Loher and Seitz 2006; Seitz et al. 2008; Loher 2008, 2022; Loher and Blood 2009; Nielsen and Seitz 2017), we observed both seasonal migrations and yearlong residencies suggestive of partial migration in the stock. Furthermore, putative spawning behavior was detected in four of the 20 halibut for which the archived data were available. Putative spawning was observed in shelf-channel migrants, shelf-slope migrants, and slope residents. Though each fish spawned in different areas within the SSGB stock, they all spawned between early January and early February. Altogether, this study supports the hypothesis that the SSGB Atlantic halibut stock is composed of multiple migratory and resident contingents, a migratory diversity observed that encompasses the diversity observed across all other halibut stocks in the Northwest Atlantic.

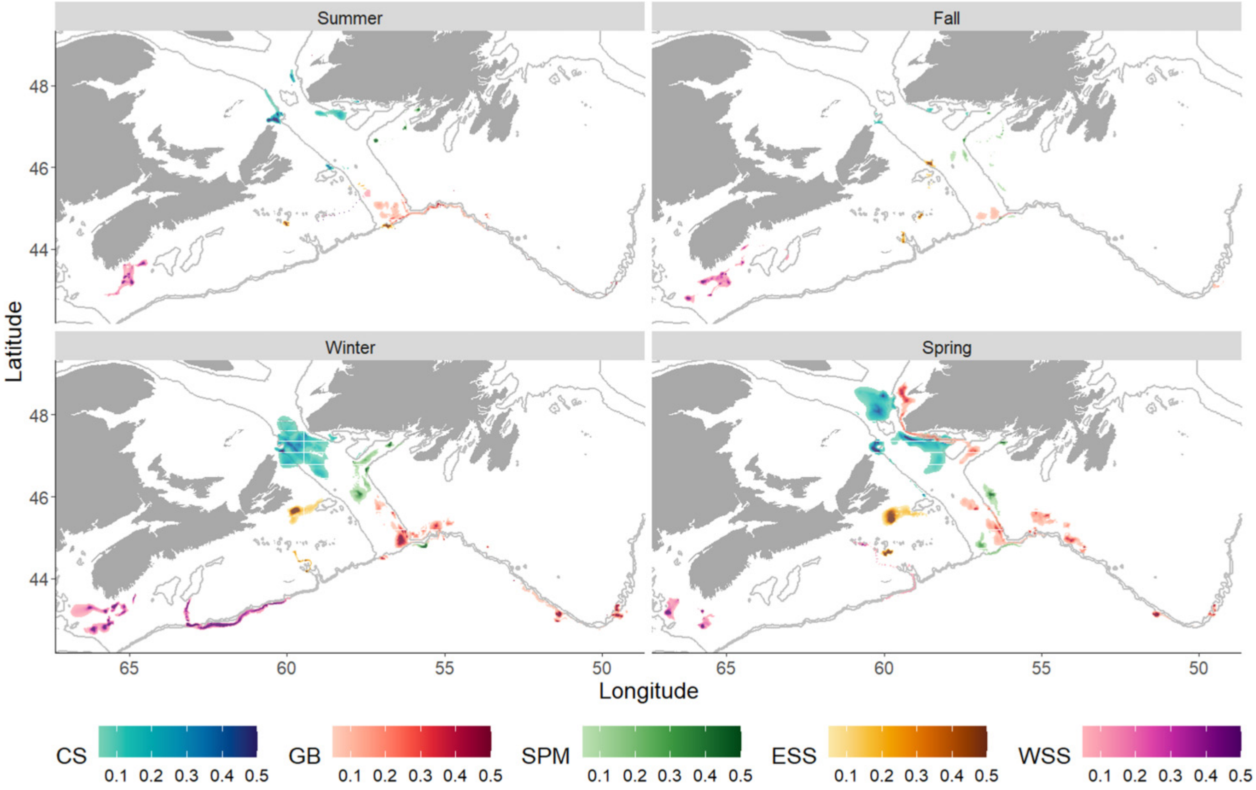
4.1. Migratory behavior

Using primarily variation in depth distribution throughout the year, we identified five categories of migratory behavior for Atlantic halibut:

1. Shelf residents: Halibut that remained in water shallower than 200 m on the continental shelf all year with limited variation in depth.
2. Slope residents: Halibut that remained in water deeper than 300 m along the continental slope all year with limited variation in depth.
3. Shelf-channel migrants: Halibut that migrated between shallow (<200 m) water on the continental shelf in summer and deeper (400–500 m) water in the channels of the sentinel shelf in winter.
4. Shelf-slope migrants: Halibut that migrated between shallow (<300 m) water on the continental shelf in summer and deep (>700 m) water along the continental slope in winter.
5. Dispersers: Halibut that were located >200 km from their release site on the pop-up date and changed stock areas.

Classifying individual behavior in categories requires to discretize a continuum, a process that can be arbitrary. However, it remains a valuable exercise, as it enables to reveal differences and similarities not only within and across regions of a fish stock (e.g., Loher 2022), but also across stocks of the same species (Robichaud and Rose 2004). A previous study categorizing migratory behavior of marine fish used distance and homing metrics (Robichaud and Rose 2004). In this study, we used a similar approach to Seitz et al. (2011) and categorized migratory behavior primarily based on depth time series and with tagging and pop-up locations. This allowed to classify behaviors even in the absence of a successfully geolocated migration tracks, although having access to reconstructed geolocation tracks helped better characterized be-

Fig. 6. Seasonal residency distribution plots showing the predicted spatial distribution of Atlantic halibut tagged with PSATs from 2012 to 2022 on the western Scotian Shelf (WSS, $n = 7$) and eastern Scotian Shelf (ESS, $n = 2$), in the Cabot Strait (CS, $n = 12$), off St. Pierre et Miquelon (SPM, $n = 4$), and on the Grand Banks (GB, $n = 20$), represented as the average density per grid cell. Tags were deployed in the summer (WSS, $n = 8$; ESS, $n = 0$; CS, $n = 0$; SPM, $n = 0$; GB, $n = 9$) and fall (WSS, $n = 0$; ESS, $n = 2$; CS, $n = 12$; SPM, $n = 4$; GB, $n = 11$). The thin grey lines represent the 200 and 500 m isobaths. Probabilities between 0.5 and 1 were binned together to increase image clarity. Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022).

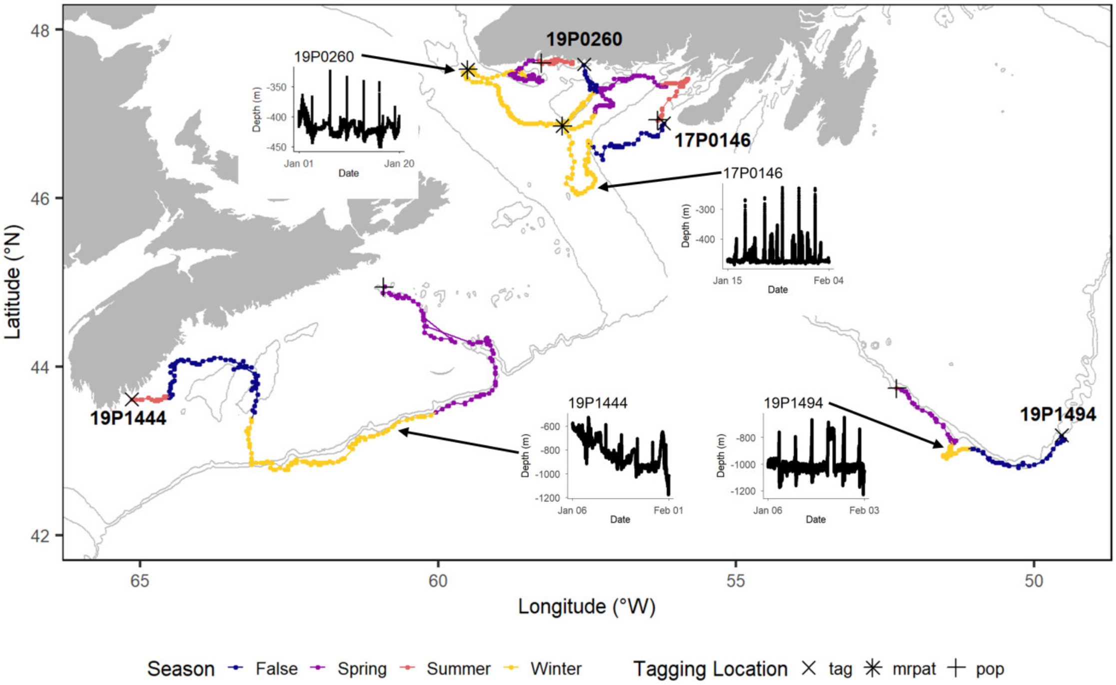


haviors. Furthermore, focusing primarily on depth profiles over distance traveled implied to identify seasonal changes in habitats irrespective of the distance between those habitats. For instance, most fish tagged in the CS area remained in that area all year long and thus would have been classified as "sedentary residents" using distance metrics such as those from Robichaud and Rose (2004). However, having access to depth time series indicated that some of the CS area halibut remain residents in shallow waters (shelf residents), while other changed habitats from shallower summer to deeper winter waters. The latter behavior is thus more similar to other shelf-channel migrants that need to migrate over longer distance because their summer foraging grounds are not close to suitable deeper wintering grounds, such as previous commonly observed in the southern GSL (James et al. 2020).

Our classification approach was inspired by the one used by Seitz et al. (2011) for Pacific halibut. A common category between the two studies was "shelf-residents," a behavior previously documented in both Atlantic and Pacific halibut (Nielsen and Seitz 2017; Le Bris et al. 2018). Specific to Atlantic halibut, shelf-residents have been observed in the GSL (Gatti et al. 2020), the GOM (Liu et al. 2019), and along the Norwegian Coast (Godø and Haug 1988). In this study we distinguished "slope-residents" from "shelf-residents" because, while both showed relatively limited seasonal variation in habitat use and horizontal movement, they occupied distinct habitats. Year-long residency along the continental slope had previously been documented in the SSGB stock (Armsworthy et al. 2014) but has not been documented yet in other Atlantic halibut stocks, probably because of the limited tagging efforts in distant offshore waters along the continental slope in those stocks.

Having access to annual time depth time series along with reconstructed migration tracks enabled to distinguished resident fish from fish that conducted seasonal migration and returned to the same area after a year. Homing to feeding areas for *Hippoglossus* species has been widely documented on both sides of the Atlantic (e.g., Godø and Haug 1988; Le Bris et al. 2018) and in the Pacific (Loher 2008). Seitz et al. (2011) classified as feeding-site returnees, Pacific halibut whose tag pop-up locations were on the shelf near the tagging location, but that had migrated to water deeper than 200 m. In this study, we separated Atlantic halibut that migrated to the deep channels of the continental shelf (shelf-channel migrants) from halibut that migrated to deeper waters along the continental slope (shelf-slope migrants). This distinction was necessary as winter habitat use on the continental shelf chan-

Fig. 7. Movement pathways of four halibut that displayed putative spawning behavior. The tracks are labeled with the corresponding fish's PSAT number and the arrows indicate the spawning locations. The thin grey lines represent the 200 and 500 m isobaths. Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022). PSAT, pop-up satellite archival tag.

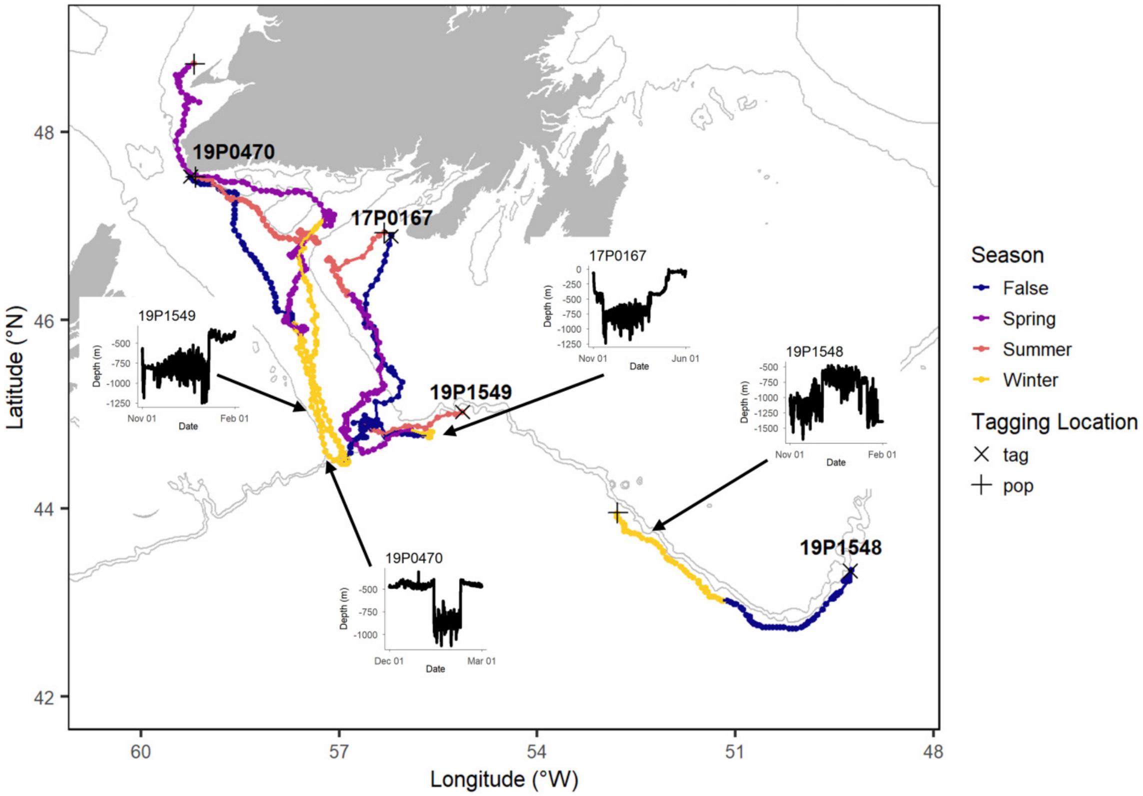


nels greatly differed from winter habitat use on the continental slope, as best exemplified by tags 17P0168 and 17P0167, which use very different winter habitats despite both being tagged and recaptured at almost the same dates and locations near SPM (Fig. 5). Shelf-channel migrants were observed in the GSL (Gatti et al. 2020) and in the GoM (Liu et al. 2019), while shelf-slope migrants were observed in the GoM but not in the GSL.

The last behavior category that we used was dispersal. Dispersal traditionally refers to the completion of a key life cycle event (e.g., recruitment and spawning) by an individual outside of the geographical distribution of a population (Petitgas et al. 2010) and as such the individual can be lost to the population (also termed "vagrants" by Sinclair and Iles 1989). In fish tagging studies, dispersal is often used to refer to individuals that have been recaptured (or whose tags have popped up) far away from the tagging site, typically in another management unit. Dispersal behavior have been documented in Atlantic halibut from the GSL (McCracken 1958), GoM (Kersula and Seitz 2019), SSGB (Stobo et al. 1988), and the Norwegian Coast (Godø and Haug 1988). It is important to note that using distance metrics between tagging and recapture/pop-up locations to classify dispersers can result in misclassification if the data do not cover the full year, because the distance of the tag pop-up or recapture may reflect more seasonal migration than true dispersal behavior. Seitz et al. (2011) used three dispersal behavior categories (slope dispersers, long-distance slop dispersers, and long-distance shelf dispersers) but acknowledged that a risk of misclassification occurred. In our study, we limited the use of dispersal to individual whose tag popped up in a different management unit, also recognizing that some fish may have been misclassified because their time series were shorter than 1 year.

The five behavior categories documented in this study encompass the diversity of migratory behaviors observed in the two other stocks of Atlantic halibut in the Northwest Atlantic. Interestingly, migratory behaviors varied across the SSGB stock area. Off southwest Nova Scotia, halibut primarily exhibited shelf residency similar to halibut observed in the GoM (Liu et al. 2019) and in the inshore waters of southeast Alaska for Pacific halibut (Nielsen and Seitz 2017). In contrast, most halibut tagged in the CS and off St. Pierre et Miquelon exhibited seasonal migration similar to those seen in many fish tagged in the GSL (Gatti et al. 2020; James et al. 2020). The stock's large geographic area and diversity in habitats likely contributes to the regional diversity in migratory behaviors observed in this study. The stock extends about 20° of longitude (~2000 km) and 6° of latitude (~650 km) and includes a multitude of habitats, from shallow shelves to deep channels and slopes with decreasing degree days from south to north (Shackell et al. 2019). Previous studies using electronic tags observed that, in the GSL, migration distances between summer and winter habitats were primarily influenced by the proximity of suitable overwintering habitats (Gatti et al. 2020). Furthermore, seasonal migrations were often shown to be spawning migrations but can also be driven by the need for thermal refuge in the winter when the temperature in shallow waters can drop below Atlantic halibut's lower thermal tolerance limit of -1.5 °C (Davies et al. 1988). In the CS and on the GB, the summer and winter habitats are relatively close,

Fig. 8. Movement pathways of four fish that displayed extensive vertical movements. The tracks are labeled with the corresponding fish's PSAT number, and the arrows point to the center of the period during which the extensive vertical patterns were exhibited. The thin grey lines represent the 200 and 500 m isobaths. Base map from Wickham (2016) and bathymetric data from NOAA National Centers for Environmental Information (2022). PSAT, pop-up satellite archival tag.



allowing for shorter migrations. In contrast, fish that reside SPM in the summer must migrate farther to reach deeper waters in which to overwinter. Like the shallow waters off Prince Edward Island (PEI) in the GSL (James et al. 2020), the bottom temperatures of nearshore waters off SPM are likely too cold for Atlantic halibut in the winter. This would necessitate seasonal migration, whether the halibut spawned that year or not, and could explain why no residency behavior was seen in the SPM region. However, that we did not observe year-round residents off SPM could also be attributed to the low number of individuals tagged in that region ($n = 4$). Based on our limited sample size (tagged and archived data, $n = 14$), the environmental conditions on the Scotian Shelf do not appear to necessitate seasonal migrations as most fish tagged were year-round residents.

Migratory diversity was also observed at the scale of the tagging location, raising the question, of "What is driving the observed migratory diversity?" Fish tagged on the same day in nearly the exact same location, and that came back a year after at the same locations where tagged, sometimes displayed very different migratory behaviors and, in some cases, separate winter spawning areas, as has been seen with Atlantic halibut in the north-east GSL (Gatti et al. 2020) and southern GSL (James et al. 2020) and with Pacific halibut in the Bering Sea (Loher 2011). Differences in body size is one of the most documented traits in partial migration studies, with smaller individuals being more likely to migrate (Chapman et al. 2012*a*). However, this was not obviously the case for tagged halibut. In many instances, such as with the fish tagged on the GB, the length ranges of shelf and slope residents (99–158 cm length) and the migrators or dispersers (97–140 cm length) were similar. In addition, the tagging protocol primarily targeted large mature females, thus limiting our ability to investigate the effects of length or life stage on migration behavior. In the GSL, halibut displaying a spawning behavior migrated to deeper and further away wintering grounds than individuals not displaying a spawning behavior (Gatti et al. 2020). Though most halibut tagged in this study are likely to be mature, only a few exhibited spawning behavior. It is possible that some exhibited skipped-breeding partial migration, whereby individuals do not migrate to spawn each year (Chapman et al. 2012*a*), which could explain some of the partial migration observed. However, several large halibut in this study migrated without exhibiting spawning behavior, indicating that additional mechanisms may be responsible for the alternative migratory strategies observed within the population, or simply that other types of spawning behaviors not as distinctive as the ones documented here exist, and that we did not detect them.

The observed diversity of migratory behaviors supports the contingency hypothesis, whereby there is potential for both resident contingents and multiple different migratory contingents within the SSGB stock. However, the ability of this study to definitively test the contingent hypothesis, as was done with striped bass acoustically tagged in the Hudson River (n tagged = 51, >500 000 detections) (Gahagan et al. 2015), is limited by both sample size and the spatial distribution of tags. Interestingly, migratory halibut (i.e., shelf-channel and/or shelf slope migrants) were observed in every region within the stock area, ensuring some connectivity between the regions, and potentially contributing to the absence of genetic structuring across the stock areas (Kess et al. 2021). The presence of multiple migratory contingents and the absence of genetic structuring are not mutually exclusive hypotheses. Indeed, the contingent theory centers on the existence of multiple groups of fish in a population, whose members exhibit similar migratory behaviors, but that differ among groups (Clark 1968; Secor 1999). Gene flow between these groups can be maintained by larvae connectivity or if the groups share similar spawning grounds. For instance, Gatti et al. (2020) documented that contingents of halibut in the GSL differ in their summer feeding grounds but share common winter spawning grounds. Interestingly, there is a growing body of research suggesting that alternative migratory phenotypes in highly connected fish species could be maintained by variation in migratory-associated supergenes (Kess et al. 2019; Pearse et al. 2019), but further examination on this is needed for Atlantic halibut (Kess et al. 2021).

4.2. Putative spawning and other specific vertical movements

Putative spawning rises were detected in four fish of unknown sex, which were tagged in different regions. In all four cases, halibut were in relatively deep waters either in the Laurentian Channel or off the Continental Shelf. Because the tags were deployed in the summer and fall for less than a year and therefore did not cover multiple spawning seasons, it is not possible to comment on spawning site fidelity. Despite the four fish spawning hundreds of kilometers apart, they all displayed putative spawning behavior between early January and early February. This timing falls within the time range of spawning rises previously suggested on the GB between November and February (Armsworthy et al. 2014). Historically, general observations have indicated that Atlantic halibut spawn primarily from November to April on the continental slope and along the deep-water margins of offshore banks (McCracken 1958; Neilson et al. 1993). In the GSL, a stock-wide electronic tagging study found evidence of spawning between January and March with a peak in mid-February (Gatti et al. 2020), with concurrent spawning behavior by both male and female halibut (Marshall et al. 2023). Spawning was suggested at multiple spawning locations within the deep channels of the GSL, a result subsequently confirmed by the first catches of halibut larvae in the GSL at the locations predicted from electronic tag data (Ghinter et al. 2023).

Though the timing of halibut spawning observed here is the same as in the GSL (Gatti et al. 2020), the proportion of halibut that have presumably spawned is much lower. Of the 62 PSATS that were physically recovered in Gatti et al. (2020), 40 (65%) exhibited putative spawning behavior. In contrast, only 4 out of 20 (20%) of physically recovered tags in this study show presumed spawning patterns. Studies of both Pacific halibut (Seitz et al. 2005, 2011; Nielsen and Seitz 2017) and Atlantic halibut (Seitz et al. 2014, 2016) did not observe evidence of spawning (i.e., not occupying deep water spawning grounds or undertaking spawning rises) in large proportion of highly likely mature halibut. This could in part be explained by skipped spawning (Loher and Seitz 2008), which is common among iteroparous fish (Rideout and Tomkiewicz 2011). Another potential explanation is that some spawning behavior is going undetected, for instance, if the spawning behavior of halibut residing in shallow waters on the continental shelf differs from distinct spawning rises off the sea floor (Loher and Seitz 2008).

Differences in spawning behavior between male and female halibut can further complicate detecting spawning rises. In the Gulf of St. Lawrence, female Atlantic halibut engage in distinct rapid rises with a median between-rise interval of 3.15 days (Marshall et al. 2023), which corresponds to the time required between spawning rises to hydrate the next batch of eggs (Finn et al. 2002). Males, on the other hand, do not face the physiological constraints associated with developing eggs (Coleman and Jones 2011), which results in more random and frequent spawning rises (Marshall et al. 2023). As a result, male spawning behavior is harder to detect with confidence than female spawning behavior (Marshall et al. 2023). In the GSL, females exhibited a median of seven spawning rises over a median of 16 days, while males exhibited a median of 57 rises over 61 days. Though the sex of the putative spawners observed here is unknown, based on the regular 4-day intervals between spawning rises they displayed, it is likely that the four halibut for which we detected spawning behavior were females, and that we possibly could not identify spawning behavior in male fish. However, out of the 15 halibut we tagged for which sex was identified, only one was male, suggesting that most tagged halibut were female. Further research is needed to get a clearer picture of spawning behavior and locations across the SSGB stock.

One behavior not previously reported in the literature and that remains challenging to interpret was the rapid depth oscillations of as much as 200–400 m per day exhibited by some individuals while located offshore, in deep waters along the continental slope. This pattern was observed for several weeks to several months during the fall and winter. Boje et al. (2014) and Hunter et al. (2003) observed in Greenland halibut, *Reinhardtius hippoglossoides*, seasonal variation in vertical activity with periods of high vertical activity (100s meters of change in a day) occurring between December and February that they attributed to foraging behavior. While there are reported examples of Pacific halibut conducting rapid vertical excursions throughout the water column between 200 and 600 m, which were also interpreted as a foraging behavior (Loher and Seitz 2006; Seitz et al. 2011), these rapid rises have never reported at the depths observed here (600–1000 m). It is possible that Atlantic halibut are distributed along the continental slope during fall and winter to feed on cephalopods or mesopelagic species, as documented in other migratory top predators (Schaber et al. 2022; Skomal et al. 2021). An additional possible explanation for this behavior may be exploration-related movements up and down the shelf slope and using vertical movements to aid in transportation or navigation (Hunter et al. 2003; Gleiss et al. 2011).

The last possible explanation is that it corresponds to a spawning behavior. In the GSL, male halibut exhibited a median of 57 spawning rises over a median 61 days, and the difference between mean minimum peak depth and mean maximum peak depth ranged from 40.9 to 132.5 m (Marshall et al. 2023). It is possible that the depth oscillations observed here could be male spawning behavior as the timing of the rises does overlap with the spawning period; however, the frequency of rises here is much higher than was observed in the GSL. We observed fish conducting over a hundred rises per month, and there was typically about 300 m between the maximum and minimum peaks. This behavior may not have been observed in previous studies because the data acquisition frequency may have been too low to capture the behavior. The hundreds of meter depth oscillations occurred multiple times a day, meaning they may not be captured by low-resolution transmitted data (Supplementary Fig. S2). If halibut in Seitz et al. (2011) or Armsworthy et al. (2014) were displaying the offshore behavior, it is unlikely that it would have been detectable in their time series because the transmitted data were summarized over 12 and 6 h periods, respectively.

5. Conclusions

Our study provides evidence that the SSGB Atlantic halibut population comprises multiple migratory and resident contingents with multiple spawning locations across the stock area. The high migratory diversity observed in the SSGB stock, including five general types of migratory behaviors, encompassed the diversity of migratory behaviors described in all the other Atlantic halibut stocks. Maintaining this diversity of contingents and spawning grounds is important to preserve the capacity of the population to withstand and recover from environmental conditions (Kerr et al. 2010).

Multi-year electronic tagging data would be beneficial to test if individual behaviors observed in this study are consistent within contingents across several years, and if individuals exhibit site fidelity not only to summer feeding areas, but also to winter spawning areas. This would further inform of possible spatial structure within the population. Finally, comparing the timing and geographical distribution of the fishery to the migratory diversity observed in this study would help to better understand the management implications of halibut migratory diversity and connectivity among stocks.

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0282.

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