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Contribution to the Themed Section: ‘*Beyond ocean connectivity: new frontiers in early life stages and adult connectivity to meet assessment and management*’

Original Article

Seasonal movements and connectivity of an Atlantic cod (*Gadus morhua*) spawning component in the western Gulf of Maine

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Movement patterns of marine fishes can have considerable impacts on their population dynamics. A thorough understanding of fish movements is therefore required for informing stock identification, stock assessment, and fishery management. This study investigated the seasonal movements and connectivity of a spring-spawning component of Atlantic cod (*Gadus morhua*) in the western Gulf of Maine. From 2010 through 2013, spawning cod were sampled within an inshore spawning closure and tagged with conventional tags ($n = 2368$), acoustic transmitters ($n = 106$), and archival data storage tags ($n = 266$). Acoustic receivers were deployed on three inshore spawning sites to test for connectivity among sites. Data from archival tags were used to describe seasonal habitat occupancy and movement patterns via geolocation to statistical areas. Tagging data indicated that cod were primarily residential in the western Gulf of Maine, moving inshore to spawn during the spring (April–July), followed by an offshore migration to their feeding grounds for summer and fall. Cod generally inhabited waters from 45 to 175 m, with the deep offshore basins (>150 m) serving as overwintering habitat. Occupied water temperatures ranged from 4.0 to 13.3 °C, with the coldest temperatures experienced from March through July and the warmest temperatures experienced from September through January. Results provided evidence of spawning site fidelity and connectivity among spawning sites, with some fish visiting multiple spawning sites within or between years. The movements observed during and after the spring-spawning season serve as important mechanisms influencing metapopulation dynamics in the Gulf of Maine region, including both fine- and broad-scale population structure. The improved understanding of cod movement patterns will assist fishery managers in developing management plans, including spawning protection measures, and help to address remaining uncertainties with respect to cod population structure in the Gulf of Maine and other regions.

Keywords: acoustic telemetry, Atlantic cod, data storage tags, *Gadus morhua*, geolocation, metapopulation, population connectivity.

Introduction

Many marine fishes exhibit complex seasonal movement patterns that are centralized around their spawning and feeding grounds (Harden-Jones, 1968; Secor, 2015). Such movements present important implications for fishery management, stock assessment, and our understanding of the ecosystem. For example, fish movements can influence their vulnerability to fishing pressure (Olsen *et al.*, 2012) and impact the efficacy of closed areas (Sale *et al.*, 2005; West *et al.*, 2009). Fish movements also have implications for stock identification (Secor, 2014), because they can influence

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the biological relevance of management unit boundaries (Campana *et al.*, 1999; Zemeckis *et al.*, 2014c). Although the movements of many marine fishes have been extensively investigated, an improved understanding of the movements of individual population components, including the level of connectivity among them, is often required to inform the development of spatially explicit fishery management plans and stock assessment models (Goethel *et al.*, 2011).

There has been increasing attention among fishery biologists and managers on the population structure of marine fishes (Cadrin *et al.*, 2014), including adoption of the "population thinking" paradigm, which attributes fluctuations in abundance to local recruitment patterns and complex population structures, rather than to large-scale movements of a single, homogenous population (Sinclair, 1988; Sinclair and Smith, 2002; Cadrin and Secor, 2009). Complex population structures have typically been described using contingents (Secor, 1999) or metapopulation theory (McQuinn, 1997; Thorrold *et al.*, 2001). For example, the Atlantic cod (*Gadus morhua*) stocks off Newfoundland (Smedbol and Wroblewski, 2002) and in the North Sea (Wright *et al.*, 2006) have been described as metapopulations that consist of multiple subpopulations and many finer-scale spawning components. An important characteristic of a metapopulation is that there is some degree of demographic connectivity among semi-discrete subpopulations (Smedbol *et al.*, 2002; Kritzer and Sale, 2004), which is typically believed to occur during the early life stages (Cowen and Sponaugle, 2009). However, connectivity can also result from adult movements (Svedäng and Svenson, 2006; Rose *et al.*, 2011; Frisk *et al.*, 2014).

Fish movements have been most commonly investigated through fishery-dependent recaptures of conventional tags (Hall, 2014). However, conventional tagging data can bias perceptions of movement patterns, because the distribution of fishery recaptures is dependent upon the location and intensity of fishing effort and nothing is known about the period when the tagged fish is at liberty (Bolle *et al.*, 2005). Several types of electronic tags have been developed that provide a more detailed, fishery-independent view of movement patterns (Arnold and Dewar, 2001). For example, acoustic transmitters are frequently used to monitor movements and space use without requiring animals to be recaptured (DeCelles and Zemeckis, 2014). Pop-up satellite archival tags (PSATs) also allow for the investigation of movement patterns by using environmental data to estimate positions, referred to as geolocation. Data storage tags (DSTs) which archive environmental data present another option for geolocation, but in contrast to PSATs, DSTs rely on fishery recaptures to recover the archived data.

In the Gulf of Maine, efforts to eliminate overfishing and manage the rebuilding of Atlantic cod have not been effective (Rothschild *et al.*, 2014; NEFSC, 2015). Previous studies have described the Gulf of Maine cod stock as a metapopulation that consists of many semi-discrete spawning components (Ames, 2004), which can be grouped into genetically distinct spring- and winter-spawning subpopulations (Kovach *et al.*, 2010; Zemeckis *et al.*, 2014c). Declines in abundance have been associated with the depletion of historical spawning components (Ames, 2004) and contraction of the resource into the western portion of the stock area (Palmer, 2014; Richardson *et al.*, 2014). Once abandoned, most spawning sites have not been recolonized and the resulting decline in spawning diversity has compromised stock productivity and stability (Kerr *et al.*, 2010, 2014). In response, recent research has focused on cod population structure (Zemeckis *et al.*, 2014b, c) and spawning dynamics (Dean *et al.*, 2012, 2014; Gurshin *et al.*, 2013; Hernandez *et al.*, 2013; Siceloff and Howell, 2013) to improve stock assessments and fishery management plans (Armstrong *et al.*, 2013; Cao *et al.*, 2014; Kerr *et al.*, 2014; Zemeckis *et al.*, 2014a).

Despite multiple conventional (Hunt *et al.*, 1999; Howell *et al.*, 2008; Tallack, 2011) and electronic tagging studies (Gröger *et al.*, 2007), the seasonal movement patterns and connectivity among cod spawning components in the Gulf of Maine are uncertain. As a result, we employed several tagging methods to investigate the seasonal movement patterns of cod that utilize a spawning site in northern Massachusetts Bay, western Gulf of Maine. This spring-spawning component is protected by a seasonal fishery closure (currently 16 April–21 July), known as the Spring Cod Conservation Zone (SCCZ; Figure 1) (Armstrong *et al.*, 2013). Previous studies used acoustic telemetry to describe cod spawning behaviour in the SCCZ, including fine-scale, interannual spawning site fidelity (Zemeckis *et al.*, 2014b) and complex, sex-specific spawning behaviours (Dean *et al.*, 2014) that are vulnerable to disruption (Dean *et al.*, 2012). However, the movements of cod from this spawning component outside of the SCCZ are not well understood, both during and after the spawning season. Therefore, the objectives of this study were to describe the seasonal movement patterns of this spawning component and to examine the connectivity among adjacent spawning sites using multiple tagging technologies.

Methods

Sampling and tagging

Sampling was conducted in the SCCZ during the months of April through July from 2010 through 2013 aboard the Massachusetts Division of Marine Fisheries' *R/V Alosa*. Cod were primarily caught at a depth of 50–55 m with rod-and-reel fishing gear using jigs and teasers. Longlines (250 hooks per day) were also used to capture fish in 2012 and 2013. Total length (*L*; nearest cm) was measured for all fish, and their sex and maturity stage were determined via visual inspection or cannulation. Each fish was assigned a maturity stage based on guidelines from Burnett *et al.* (1989). Cod that were Developing, Ripe, Ripe and Running, or Spent were considered part of the SCCZ spring-spawning component and included in analyses.

Spawning cod were selected for electronic tagging, with preference for Ripe or Ripe and Running fish. Coded 69 kHz acoustic transmitters (models V16-6H and V16P-6H) with a battery life > 1500 d and a 60 s mean transmission rate (Vemco Division, AMIRIX Systems, Inc., Nova Scotia, Canada) were surgically implanted following the procedures of Dean *et al.* (2012, 2014). Nearly all cod (98%) tagged with acoustic transmitters in 2010 and 2011 were also tagged externally beneath the first dorsal fin with an archival DST (Zemeckis *et al.*, 2014b). The DSTs were model DSTmilli-L (39.4 × 13 mm, depth range = 1–250 m: Star-ODDI, Inc., Reykjavik, Iceland). The resolution and accuracy of pressure (depth) measurements was 0.03% and ±0.8%, respectively. The resolution of temperature measurements was 0.032°C, and the accuracy was ±0.1°C. The DSTs were programmed to record pressure and temperature measurements every 15 min and 2 h 45 min, respectively.

Cod ≥ 55 cm were selected for surgical implantation of acoustic transmitters, and fish ≥ 65 cm were selected for double-

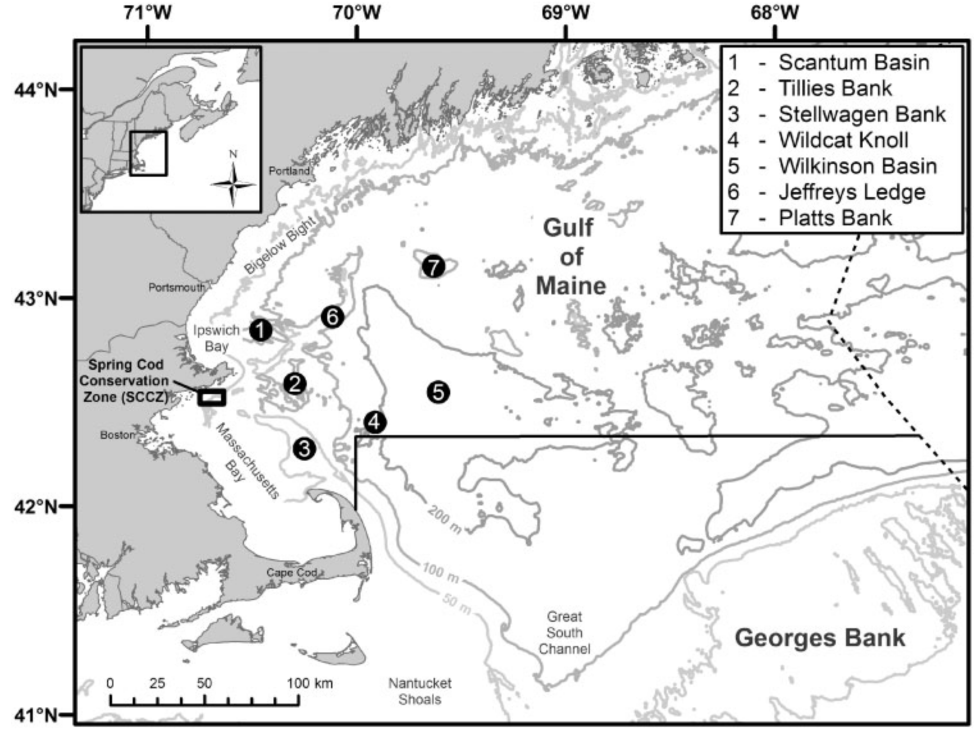

Figure 1. Map of the Gulf of Maine region, including borders of the SCCZ in northern Massachusetts Bay, identification of fishing grounds referred to in the text, multiple lines of bathymetry (50, 100, and 200 m), the boundary between the Gulf of Maine and Georges Bank cod management units (solid line), and the international boundary between the United States and Canada (dashed line).

electronic-tagging with an acoustic transmitter and DST. From 2010 through 2012, additional spawning cod ≥ 55 cm were tagged only with DSTs. In 2010 and 2011, all DSTs were externally attached beneath the first dorsal fin using Star-ODDI plastic saddles and stainless steel wire. These cod were also tagged with a conventional t-bar anchor tag beneath the second dorsal fin. Fishery recaptures indicated that externally attached DSTs were being shed during longer deployments (>8 months at liberty) and only the conventional tags were being reported. As a result, DSTs released in 2012 were surgically implanted into the peritoneal cavity to improve long-term tag retention. Surgically implanted DSTs were attached to modified billfish dart tags (BFIM-96) with plastic disc backings (Floy Tag and Mfg., Inc., Seattle, WA, USA). Cod tagged with surgically implanted DSTs also had t-bar anchor tags attached beneath the first dorsal fin. After all electronic tags were released during a given trip, the remaining cod were tagged with t-bar anchor tags (92% were double t-bar tagged). Two types of conventional t-bar anchor tags were used type FD-94 (Floy Tag Mfg., Inc.) and type TBA (Hallprint Inc., Australia).

Mark–recapture

A reward of a hat or a t-shirt ($15 USD value) was offered to incentivize fishers to report recovered conventional tags. For the return of electronic tags, both a gift card and hooded sweatshirt ($85 USD value) were distributed. Biological information (e.g. maturity stage, physical condition) and recapture data (e.g. location, depth) were collected from fishers when available. Some recaptured cod did not have reliable location data, so the recovery rate for each tag type was calculated using only recaptures with reliable positions.

Tag recapture rates were not adjusted for the distribution of fishing effort or catch, because of the low samples sizes for a given year, season, and region, which can impose further uncertainty (Loehrke, 2013). In addition, the reliability of data to inform the spatial/temporal distribution of the fishery was considered insufficient to provide a meaningful improvement due to uncertainties arising from changes in fishery management (Meredith, 2012), unreliable data for the recreational sector, which accounted for up to 42% of the total catch (NEFSC, 2015), and regional variability in tag reporting rates (Miller and Tallack, 2007). Therefore, all tag recaptures were grouped into four 3-month periods, aligned with the spring-spawning season, to describe the seasonality of movement patterns: 16 April–15 July, 16 July–15 October, 16 October–15 January, and 16 January–15 April. The total days at liberty and distance travelled were calculated using the release and recapture dates and positions. As performed by Loehrke (2013), a "bagplot" (or bivariate boxplot), which is a convex polygon fit around the bivariate median of a distribution (Rousseeuw *et al.,* 1999), was created using the "aplpack" package (version 1.3.0; Wolf and Bielefeld, 2015) of the R statistical software (version 3.1.2; R Development Core Team, 2014) to provide a two-dimensional representation of the distribution of tag recapture positions.

Acoustic telemetry

Vemco VR2W acoustic receivers were deployed during the spring-spawning seasons from 2012 through 2014 to test for connectivity among multiple inshore spawning sites (Figure 2 and Table 1). The Whaleback area (~45 km north of the SCCZ) is the focal point of spring-spawning activity in Ipswich Bay (Siceloff

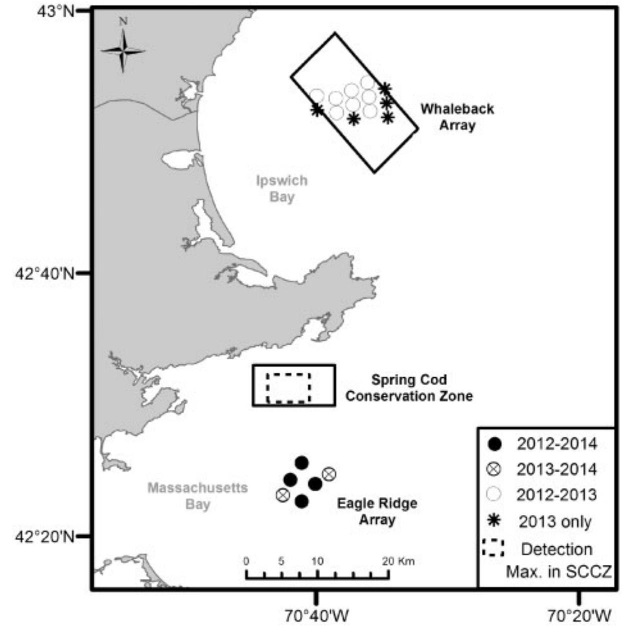

Figure 2. Schematic of the acoustic receiver arrays deployed to investigate connectivity among spawning sites. Included are the acoustic receivers deployed on Whaleback in 2012 and 2013 in relation to the boundaries of the spawning closure, the maximum detection radius of the largest acoustic receiver array deployed in the SCCZ between 2012 and 2014, and the arrays of acoustic receivers deployed on Eagle Ridge from 2012 through 2014.

Table 1. Deployment and retrieval dates of acoustic receivers in the SCCZ, on Eagle Ridge, and on Whaleback from 2012 through 2014.

Year	Location	Receivers	Deployment	Retrieval	Lost receivers
2012	SCCZ	25	3 April	30 August	4
	Eagle Ridge	4	2 April	8 August	0
	Whaleback	8	1 April	19 June	0
2013	SCCZ	4	29 March	16 July	1
	Eagle Ridge	6	29 March	18 July	1
	Whaleback	13	4 April	25 June	0
2014	SCCZ	28	2 April	15 July	2
	Eagle Ridge	6	3 April	15 July	2
	Whaleback	0	–	–	–

The number of receivers lost each year is in included for each study site.

and Howell, 2013) and has been protected by a spawning closure since 2011 (Armstrong *et al.*, 2013). In 2012, an array of eight acoustic receivers was deployed on Whaleback and the array was expanded to 13 receivers in 2013. Eagle Ridge ($\sim$15 km south of the SCCZ) was identified as a putative cod spawning site based upon tag recaptures from this study, an industry-based trawl survey (Hoffman *et al.*, 2012), and commercial fishery observer data which documented high catch rates of spawning cod from 2011 through 2014 (Massachusetts Division of Marine Fisheries, personal communication). Four receivers were deployed on Eagle Ridge in 2012 and 6 receivers in 2013 and 2014. In the SCCZ, a 25 receiver array was deployed in 2012, a 4 receiver array in 2013, and a 28 receiver array in 2014 (Zemeckis *et al.*, 2014b). Range test results from in the SCCZ indicated that the receivers had a detection radius of $\sim$1 km throughout a wide variety of weather conditions.

Individual detection histories were generated to describe spawning site fidelity behaviour (i.e. detected at the same spawning site during multiple years) and connectivity among spawning sites (i.e. detected at multiple spawning sites either during the year they were tagged or subsequent years). A detection event was defined as any period when a fish was detected at least two times by an acoustic receiver(s) within a 30-min period. To provide an estimate of connectivity among spawning sites, the proportion of cod tagged in the SCCZ from 2010 through 2013 and detected on either Eagle Ridge or Whaleback during any year was calculated. Cod recaptured by the fishery before the receivers were deployed were not included in calculations. Estimates were not adjusted for natural mortality or skipped spawning, because of low sample sizes, timing of receiver deployments, and varying detection probabilities. Alternatively, in an attempt to account for these factors, the percentage of cod that were detected at multiple spawning sites during a given year was calculated as the number of fish detected at multiple spawning sites divided by the number of cod that were tagged during a previous year and detected at any of the monitored spawning sites. Residence times were calculated as the total number of days an individual was detected at a given spawning site. Partial residence times were reported for the season during which a fish was tagged, because their time at the spawning site prior to tagging was unknown. In contrast, complete residence times were reported for cod detected in years after they were tagged, because their movements were monitored during the entire spawning period.

Data storage tags

Seasonal habitat occupancy

Seasonal patterns in the habitat occupied by cod were investigated using depth and temperature data from recovered DSTs. The monthly trends from the recovered tags were examined using boxplots, excluding data only from the day on which each fish was tagged. The DST data includes periods when cod were both active (i.e. moving horizontally and vertically) and sedentary on the bottom (i.e. little net horizontal or vertical movement). The DST data were plotted with inclusion of all data and also only data from periods when cod were identified as sedentary on the bottom to represent occupancy of benthic habitat. As performed in previous geolocation (Gröger *et al.*, 2007; Pedersen *et al.*, 2008) and behavioural studies (Hobson *et al.*, 2007, 2009), sedentary periods were identified based on the presence of a discernable tidal pattern in the depth data. The tidal extraction algorithm was based on Pedersen *et al.* (2008) and involved estimating the least-squares fit of a sine function to the observations over a sliding 5-h period. This 5-h period was chosen based on the period of the M_2 tidal constituent (12.4 h), which is the dominant tidal constituent in the Gulf of Maine, as well as sensitivity analyses using data from DSTs moored on the bottom at fixed positions. Data were extracted from periods that were $\geq$5 h and considered to represent sedentary activity when the model fit met the following criteria, which were modified from Pedersen *et al.* (2008) to account for regional oceanographic conditions: root mean square error ($RMSE$) $<$0.22 m, $R^2 > 0.85$, and tidal amplitude between 0.2 and 2.0 m.

Geolocation

The daily positions of cod tagged with DSTs were initially estimated using a tidal-based geolocation approach based on a hidden Markov model (HMM) (Pedersen *et al.,* 2008). Two validation approaches tested the accuracy of this HMM in the Gulf of Maine: (i) data from DSTs deployed on the bottom at fixed locations and (ii) acoustic telemetry data which provided known positions (±1 km) while at liberty for double-electronic-tagged fish ($n = 10$). Validation results indicated that the accuracy of the HMM was not satisfactory, due primarily to inadequate spatial contrast in tidal characteristics, fish activity levels, and regional oceanographic conditions (Liu *et al.,* in review). Therefore, a depth and temperature geolocation approach with tidal-based exclusion was developed using an observational likelihood model with movement constraints to assign daily positions on a broader spatial scale (Zemeckis, 2016). Positions were assigned to the statistical areas used to collect fisheries-dependent data (Figure 3), which were originally based on historical fishing grounds and roughly corresponded to the distribution of primary target species such as cod (Halliday and Pinhorn, 1990). This approach was developed and validated by comparing chosen statistical areas to known positions of double-electronic-tagged fish.

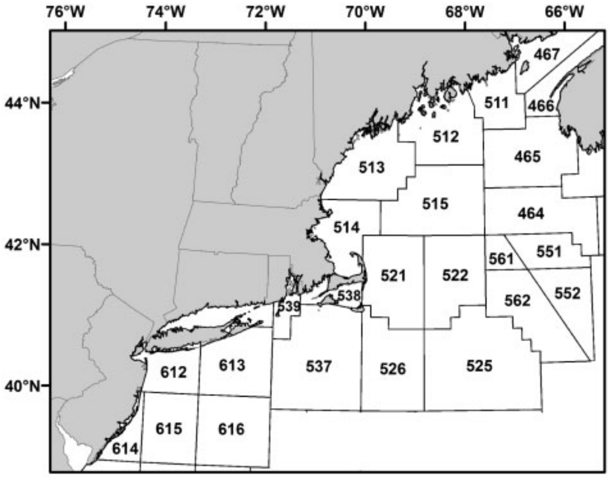

Figure 3. Statistical areas ($n = 25$) typically used for reporting fishery landings (Halliday and Pinhorn, 1990), which were included as potential areas to which cod positions could be assigned as part of geolocation analyses.

Building on the work of Pedersen *et al.* (2008), daily activity levels were categorized as low, moderate, or high using the DST pressure data (Figure 4). Low activity days were those with satisfactory fits of the tidal extraction algorithm over a 13-h period, moderate activity days were those with satisfactory fits over a 5-h period, and high activity days were those with no reliable tidal fits. The tidal fitting criteria for identifying low activity days was stricter than that used when extracting data to investigate patterns in seasonal habitat occupancy (i.e. $R^2 > 0.92$, rather than $R^2 > 0.85$), because the more relaxed criteria frequently resulted in false tidal fits which compromised estimates of tidal phase and geographic position. The same tidal fitting criteria from the seasonal habitat occupancy analysis were used for identifying moderate activity days, because tidal characteristics were not used for geolocation on moderate activity days.

An observational model compared the depth, bottom water temperature, and tidal information from DSTs with estimates from the Northeast Coastal Ocean Forecasting System (NeCOFS, 2013), which is based on the Finite-Volume Community Ocean Model (FVCOM: Chen *et al.,* 2006). The NeCOFS domain includes all locations where tagged cod would have likely been found based on previous tagging studies (Zemeckis *et al.*, 2014c). Tidal harmonics were derived from a barotropic configuration of NeCOFS, which has a standard deviation of 3.21 cm for the model-data elevation difference of the M_2 tidal constituent (Chen *et al.,* 2011). Daily positions were assigned based on a likelihood distribution $L(\boldsymbol{x})$ representing the probability of the observed data given the horizontal geographical location $\boldsymbol{x}$ for each day. The observation likelihood distributions $L(\boldsymbol{x})$ were constructed using the NeCOFS unstructured grid, which has a horizontal resolution of 5 km near the open boundary to 0.5 km along the coast and tidal mixing fronts. Assuming that depth and temperature were independent, the likelihood distribution given the observed depth and temperature (z, tp) was obtained by the

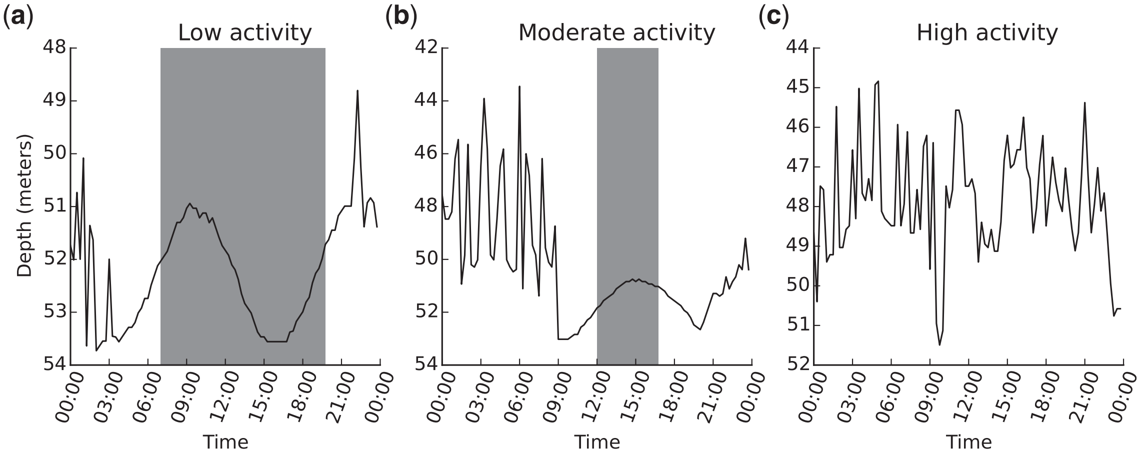

Figure 4. Examples of the three activity levels identified in data from the archival DSTs using the tidal fitting algorithm: (a) low activity, (b) moderate activity, and (c) high activity. The shaded areas represent the 13-h period used to identify low activity days and the 5-h period used to identify moderate activity days.

product of two normal distribution functions integrated inside defined intervals (modified from Le Bris *et al.*, 2013):

$$L_{\mathrm{dt}}\left(z, tp, \boldsymbol{x}\right) = \int_{z-\Delta z}^{z+\Delta z} N(z; \mu_z(\boldsymbol{x}), \sigma_z(\boldsymbol{x}))\mathrm{d}z \cdot \int_{tp-\Delta tp}^{tp+\Delta tp} N(tp; \mu_{tp}(\boldsymbol{x}), \sigma_{tp}(\boldsymbol{x}))\mathrm{d}tp \qquad (1)$$

where Δz and Δtp are measurement error for depth and bottom water temperature, respectively; $N(w; \mu, \sigma)$ is a normal distribution function for variable w with mean μ and standard deviation σ; μ_z and μ_{tp} are FVCOM depth and temperature estimates. The standard deviations of bathymetry (σ_z) and temperature (σ_{tp}) were determined using estimates from neighbouring grid points in FVCOM.

Limited regional variation of the tidal characteristics in the western Gulf of Maine (Chen *et al.*, 2011) reduces their utility for geolocation but estimates of tidal amplitude and phase were still helpful for excluding unlikely regions. The tidal signals ($\hat{\eta}$) extracted on low activity days were compared with the tidal signal for the same period at FVCOM grid points ($\eta(\boldsymbol{x})$) reconstructed from tidal harmonic constants (Chen *et al.*, 2011) by computing the RMSE as a function of horizontal location ($\boldsymbol{x}$):

$$RMSE(\boldsymbol{x}) = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\eta_i(\boldsymbol{x}) - \hat{\eta}_i)^2} \qquad (2)$$

where n is the number of measurements in a time series of η and $\hat{\eta}$. To eliminate unlikely regions and reduce computation time, the likelihood distribution was assigned a zero value at grid points where (i) the tidal amplitude from the tag signal $A(\hat{\eta})$ was not in between FVCOM estimates for the amplitude of the M2 tidal constituent ± the sum of the other seven tidal constituents and (ii) the RMSE was greater than a threshold Θ, which was chosen as the 30th percentile of the RMSE for the remaining grid points. This threshold was selected because it removed spurious position assignments (i.e. Scotian Shelf) which occasionally occurred as part of apparent long-distance movements over very short periods (<3 d), and it also preserved $L(\boldsymbol{x})$ within a fairly broad horizontal scale comparable to but greater than that of the observed error of the HMM method.

For each statistical area i, a score of likelihood (S_i) was determined by integrating $L(\boldsymbol{x})$ over the area of this statistical area (A_i):

$$S_i = \iint_{A_i} L(\boldsymbol{x})\mathrm{d}\boldsymbol{x}. \qquad (3)$$

The statistical area with the highest S_i was selected as the most likely daily position for that fish (Supplementary Material, Section 1). Movement constraints based on cod behaviour, physiology (i.e. swimming capabilities), and geolocation limitations were used to assign these most likely daily positions to statistical areas on (i) days of release and recapture, and when cod were in states of (ii) low activity or (iii) moderate activity on days adjacent to a low activity day (Supplementary Material, Section 2). Positions were automatically assigned to the statistical areas that included the reported release and recapture locations. For low activity days, estimated positions could have been in any statistical area unless there were at least five sequential low activity days, in which case positions were confined to either the most frequent statistical area during this period or an adjacent statistical area. This was based on the assumption that within 1 d a low activity fish could not have moved more than one statistical area. A 5-d period was chosen because it was long enough to not be influenced by a spurious position assignment and to identify the most frequent position to reliably constrain other days. For moderate activity days adjacent to low activity days, a similar constraint was applied where fish could not move more than one statistical area per day. Therefore, positions were confined to the statistical area of the neighbouring low activity day or an adjacent statistical area. Positions were not assigned on high activity or other moderate activity days, because validation results indicated that position estimates on these days were frequently unreliable.

Surgically implanted DST's were omitted from geolocation analyses, because the lower resolution pressure data compromised the tidal fitting procedure and frequently resulted in spurious position assignments with greater movement rates than cod tagged externally with DSTs (Zemeckis, 2016). To investigate seasonal movement patterns, assignments to statistical areas were grouped among all individuals and summarized by seasonal period. The proportion of days, number of days, and number of fish were reported for each statistical area and season. Results were also plotted separately for each fish to permit further interpretation of movement patterns.

Results

Sampling and tagging

A total of 2684 cod that were considered part of the SCCZ spawning component were tagged from 2010 through 2013 (Table 2 and Figure 5). Tag releases included 2368 cod tagged with conventional tags ($\bar{L} = 72 \pm 16$ cm; 975 males; 1393 females), as well as the release of 106 acoustic transmitters ($\bar{L} = 80 \pm 16$ cm; 56 males; 50 females) and 266 DSTs ($\bar{L} = 86 \pm 16$ cm; 118 males; 148 females). A total of 56 of these fish were double-electronic-tagged ($n = 51$ in 2010, $n = 4$ in 2011, $n = 1$ in 2012).

Mark-recapture

There were 223 reported recaptures, including 196 with reliable recapture positions. Recovery rates were 5% of t-bar tags, 23% of DSTs, and 22% of acoustic transmitters (Table 3). Recapture

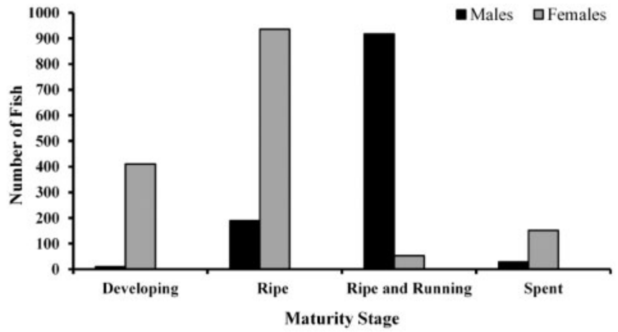

Figure 5. Maturity stages of tagged cod from 2010 through 2013 that were considered part of the SCCZ spawning component (black = males, females = grey).

Table 2. Number of tag releases in the SCCZ for each tag type from 2010 through 2013.

	2010			2011			2012			2013		
	t-bar	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**
Males												
Number	276	24	49	353	3	42	228	7	27	118	22	0
Mean length	67	80	77	67	115	84	62	78	74	54	66	–
s.d. length	13	9	12	14	4	13	11	15	14	9	7	–
Females												
Number	513	28	83	460	1	46	378	7	19	42	14	0
Mean length	81	93	92	82	97	92	70	80	82	57	69	–
s.d. length	13	15	15	15	–	19	14	13	12	12	5	–

The mean length (cm) and standard deviation (*s.d.*) are included by sex for each tag type and year. Note that there were 56 of these fish double-electronic-tagged with both an acoustic transmitter and an archival DST ($n = 51$ in 2010, $n = 4$ in 2011, and $n = 1$ in 2012).

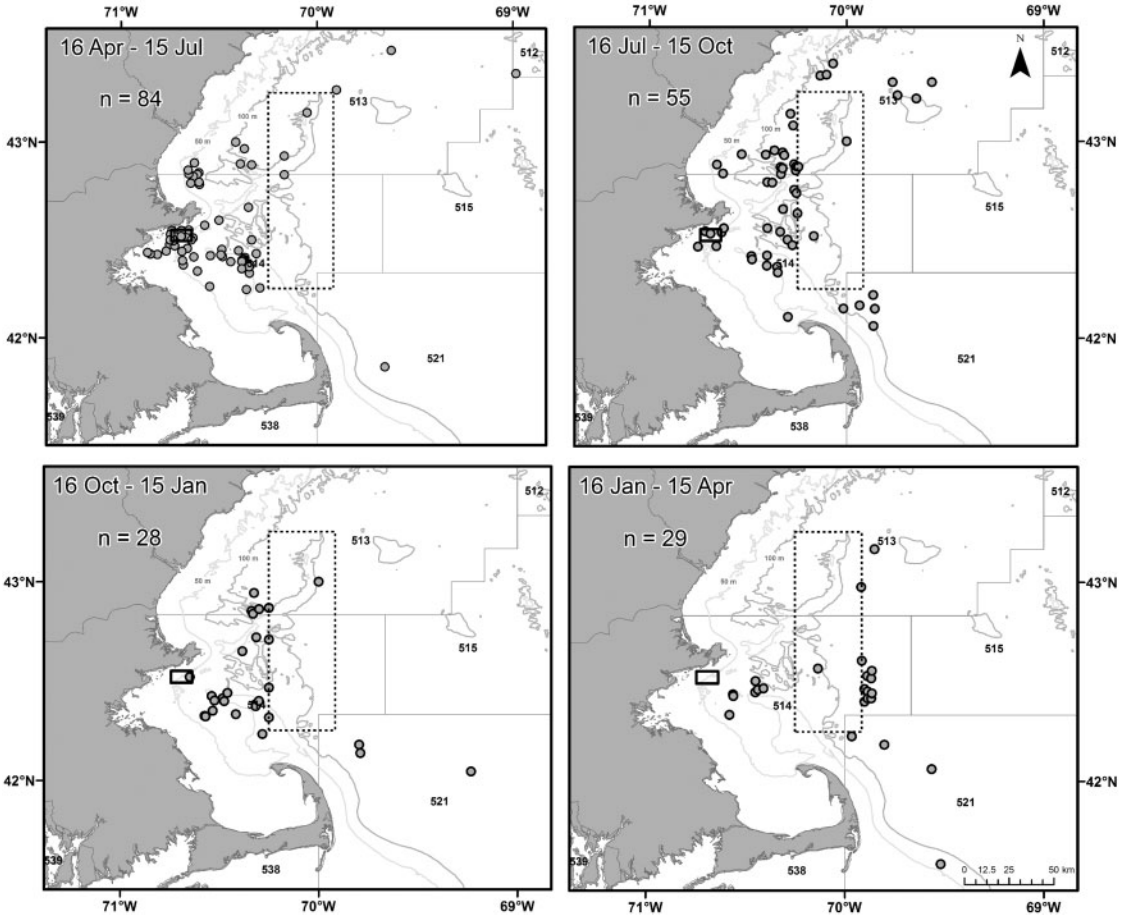

Figure 6. Recapture positions of cod tagged in the SCCZ (black rectangle, northern Massachusetts Bay). Recaptures are divided into four time periods using the approximate spring-spawning season as a starting point: 16 April–15 July, 16 July–15 October, 16 October–15 January, and 16 January–15 April. The dashed rectangle represents the Western Gulf of Maine Closure Area, which is closed year-round to commercial fishing activity.

positions were primarily within the western Gulf of Maine (Figure 6), and the mean distance between release and recapture was 42.6 ± 32.2 km (median = 34.3 km, range = 0.1–166 km). Fish were at liberty on average of 192 ± 175 d (median = 133 d, range = 8–1117 d).

There were 84 recaptures during the spring-spawning season (16 April–15 July; Figure 6). During this period, ten cod were recaptured ≤6 km from their release position after being tagged during a previous field season, providing evidence of spawning site fidelity. Tag recaptures during spring also provided evidence of connectivity among spawning sites, with individuals being recaptured in the vicinity of the Whaleback spawning closure ($n = 9$) and Eagle Ridge ($n = 6$). Additional recaptures ($n = 4$) came from another site in Massachusetts Bay where spawning

Table 3. Releases, recaptures, and recovery rate of cod that were tagged from 2010 through 2013 with conventional t-bar anchor tags, acoustic transmitters, and archival DSTs.

	Tag year											
	2010			**2011**			**2012**			**2013**		
	t-bar	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**	**t-bar**	**Acoustic**	**DST**
Releases	789	52[a]	132	813	4[a]	88	606	14	46	160	36	0
Recaptures	38	13	26	49	1	22	31	5	12	8	4	–
Recovery rate	0.05	0.25	0.20[b]	0.06	0.25	0.25[b]	0.05	0.36	0.26[c]	0.05	0.11	–

The recaptures and recovery rate only include recaptures for which reliable positions were available.

[a] Most fish were double-tagged with an acoustic transmitter and DST.

[b] Externally attached DSTs were being shed, for some only t-bar tags were reported and DST's were not recovered.

[c] DSTs were surgically implanted.

cod were caught in large numbers before this study (i.e. the "99 Hump", ~11 km southwest of the SCCZ). Recaptures late in the spring-spawning season suggest that cod moved offshore after spawning, with recaptures most commonly from Stellwagen Bank but also around Jeffreys Ledge and Scantum Basin (Figure 1).

There were 55 recaptures during the 16 July–15 October period (Figure 6). Some cod were still recaptured around the SCCZ and Whaleback during late July, but most recaptures were from offshore feeding grounds around the actively fished areas of Stellwagen Bank, Tillies Bank, and Jeffreys Ledge (Figure 1), which are all near the western edge of the Western Gulf of Maine Closure Area, inside of which commercial fishing is prohibited year-round. Multiple recaptures also came from Platts Bank and just northeast of Cape Cod (i.e. Highland Ground). There were 28 recaptures during the 16 October–15 January period. These recaptures came primarily from fishing grounds around Stellwagen Bank and Jeffreys Ledge. However, a few recaptures during early winter suggested a migration to deeper waters east of Cape Cod. This pattern continued with most recaptures (18 of 29 recaptures, 62%) during the 16 January–15 April period coming from deep waters (>150 m) along the eastern edge of the Western Gulf of Maine Closure Area.

The home range estimated for the SCCZ spawning component using fishery-dependent recaptures indicates that movements were primarily restricted to the western Gulf of Maine (Figure 7). The centre of gravity of the bagplot was in the vicinity of Tillies Bank. Recaptures east of Cape Cod and off the Maine coast were statistical outliers.

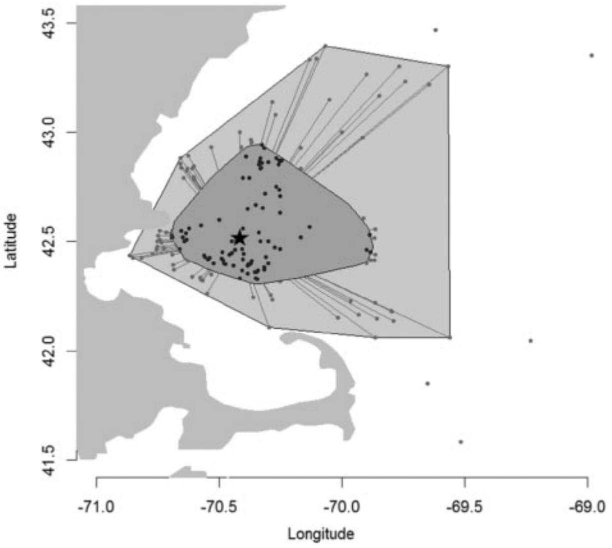

Figure 7. Bagplot of recapture positions. The bagplot includes a centre of gravity represented by a star, a dark grey "bag" which encompasses 50% of the recapture positions (i.e. the interquartile range), a light grey "loop" which is ~1.5 times the interquartile range, and a "fence" which separates outliers (Rousseeuw *et al.*, 1999; Potter, 2006). Lines connect the centre of gravity to each recapture position in the "loop".

Acoustic telemetry

Ten acoustic receivers were lost during this study (Table 1). However, detection data from part of the spring-spawning season were acquired from five prior to their loss. Fourteen acoustically tagged cod were recaptured before the receivers were deployed in 2012. Nineteen of the remaining 92 (21%) acoustically tagged cod were detected on either Whaleback or Eagle Ridge (Table 4 and Figure 8). Three of the 14 cod tagged (21%) in 2012 were detected on Eagle Ridge that year. Six of 36 fish (17%) tagged in 2013 were detected on other spawning sites during that year, including five on Eagle Ridge and one fish detected on 1 d on Whaleback (ID # 458). Only one other cod was detected on Whaleback, which was also only detected on 1 d, but during a year after tagging (ID # 177) (Table 4). In contrast, 18 cod were detected on Eagle Ridge, including ten during year(s) after tagging.

In 2012, seven cod tagged during previous years were detected, five (71%) of which were detected at multiple spawning sites. In 2013, nine cod tagged during previous years were detected, including one that was detected at multiple spawning sites (11%). In 2014, 11 cod that were tagged during a previous year were detected, including four at multiple spawning sites (36%). The mean partial residence time of cod on Eagle Ridge (mean = 6 ± 9 d, median = 2 d) was similar to that of cod in the SCCZ (mean = 7 ± 11 d, median = 3 d: Table 4). Cod that exhibited spawning site fidelity to the SCCZ had a mean complete residence time of 16 ± 13 d (median = 15 d), while cod detected on Eagle Ridge during a season after tagging had a mean complete residence time of 9 ± 11 d (median = 5 d: Table 4). Four cod had longer complete residence times on Eagle Ridge than in the SCCZ, while four other cod had longer partial residence times on Eagle Ridge than in the SCCZ (Table 4 and Figure 8). Three cod exhibited spawning site fidelity with respect to Eagle Ridge. However, eight cod

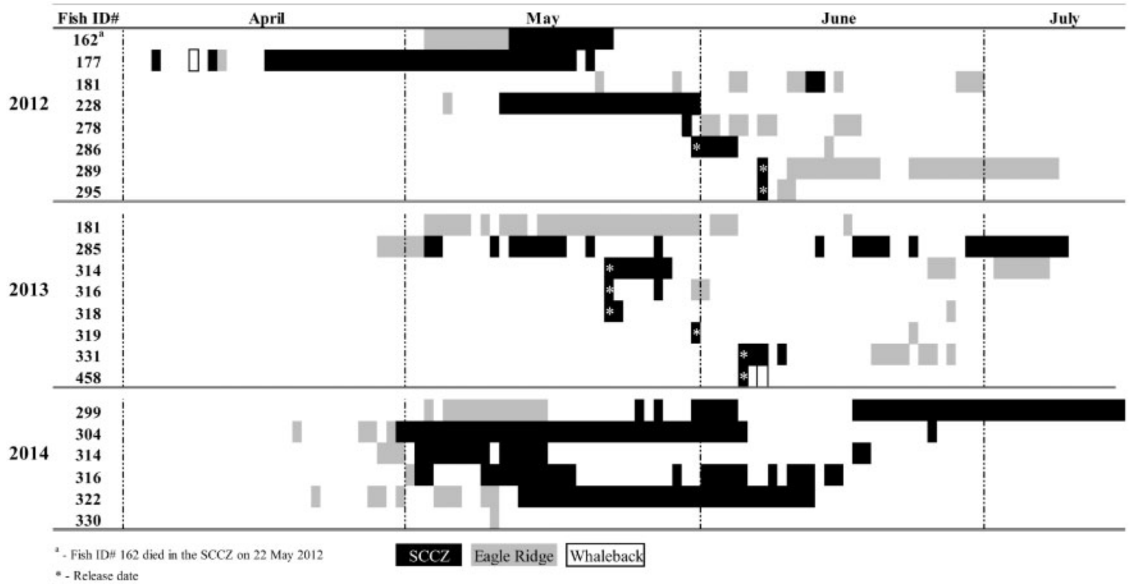

Figure 8. Detection histories of cod that were tagged with acoustic transmitters in the SCCZ and detected on Eagle Ridge or Whaleback from 2012 through 2014. Days when fish were detected in the SCCZ are presented in black, detections on Eagle Ride are in grey, and detections on Whaleback are in white. The days on which fish were tagged are represented by white asterisks.

were detected on Eagle Ridge during one spawning season but then only in the SCCZ during another season (see shaded cells of Table 4).

There was considerable variability in the movements of individuals. For example, some cod visited Eagle Ridge before moving north and being detected in the SCCZ (including all fish in 2014), while other fish moved south from the SCCZ to Eagle Ridge (Figure 8). In general, individuals did not appear to make repeated transits between spawning sites within a year. However, a single fish (ID # 177) was detected moving between all monitored spawning sites within a 4-d period in April 2012. In 2014, cod detected in the SCCZ tended to be resident for longer than fish detected in 2012 or 2013 (Figure 8) but detection probability in the SCCZ varied among years.

Data storage tags

There were 49 DSTs recovered (22 males; 27 females) with data suitable for analysis (38 external; 11 internal). A total of 5630 d of data were collected, with the mean days at liberty being 115 ± 133 d (median = 57 d, range = 9–635 d). The mean length of fish from which DSTs were recovered was 82 ± 13 cm (median = 79 cm, range = 58–118 cm).

Seasonal habitat occupancy

Cod were identified as sedentary for 28% of the measurements recorded by DSTs (13 585 of 48 217 temperature measurements; 149 387 of 530 389 depth measurements). Cod inhabited waters ranging from 4.0 to 13.3°C (mean = 7.0 ± 1.6°C, median = 6.8°C: Figure 9a). A similar seasonal trend was observed when including all temperature data and also only data when cod were sedentary on the bottom but there were more statistical outliers when including all data (Figure 9). The coldest temperatures were experienced from March through July, which roughly overlaps with the spring-spawning season, with an increase over the summer and fall to the warmest months from September through January. The median water temperatures occupied when cod were sedentary on the bottom were often warmer than when all data were included (e.g. July, October, and November: Figure 9). The range of occupied thermal habitat was narrowest in the sedentary data during February and March (Figure 9b) but results for these months were the most uncertain given the low sample size.

Cod typically inhabited waters from 45 to 175 m in depth, representing 90% of all depth measurements (mean = 93 ± 45 m, median = 84 m, range = 3–268 m: Figure 10a). The deepest waters were generally occupied in February and March. Depths recorded in May were shallower than those from March when including all data (Figure 10a), while depths in May and June were shallower than February when including only data from sedentary periods (Figure 10b). However, sample sizes for February, March, and April were low, making these inferences the most uncertain. The shallowest depths (<25 m) recorded by DSTs were frequently within 1 week of their release dates. The depth of periods when cod were identified as sedentary on the bottom tended to be shallower than depths when including all data (Figure 10). The range of depths occupied was narrowest during the spawning months of May and June (mean = 65 ± 32 m: Figure 10a).

Geolocation

Validation results indicated that the double-electronic-tagged fish were accurately assigned to statistical area 514 on 97% of days for which positions were available from acoustic telemetry detections (148 of 153 d). For the incorrectly assigned positions, there were three positions assigned to statistical area 513 and two to statistical area 512 (Supplementary Material, Section 3: Fish ID's 156, 172, and 282).

For the recovered externally attached DSTs ($n = 38$), positions were determined for 1210 d of the 2981 d (41%) with available data, including 76 d of release/recapture (6.3%), 802 d of low activity (66.3%), and 332 d of moderate activity (27.4%). Results

Table 4. Residence times (days) at each spawning site from 2012 to 2014 for cod that were tagged in the SCCZ and detected at Eagle Ridge or Whaleback.

					Residence time							
					2012			2013			2014	
ID #	**Tag date**	**Length**	**Sex**	**Maturity**	**SCCZ**	**Eagle Ridge**	**Whaleback**	**SCCZ**	**Eagle Ridge**	**Whaleback**	**SCCZ**	**Eagle Ridge**
162	7 May 2010	80	M	U	11	9	0	–	–	–	–	–
177	11 May 2010	109	F	D	36	1	1	1	0	0	–	–
181	8 June 2010	77	F	R	2	10	0	0	30	0	–	–
228	18 June 2010	81	F	R	21	1	0	1	0	0	–	–
278	10 June 2011	97	F	R	1	9	0	–	–	–	–	–
285	31 May 2012	63	M	U	37^a	0	0	28	5	0	–	–
286	31 May 2012	67	M	U	5^a	1	0	4	0	0	18	0
289	7 June 2012	65	M	U	1^a	26	0	–	–	–	–	–
295	7 June 2012	94	F	S	1^a	2	0	–	–	–	–	–
299	2 May 2013	59	M	U	–	–	–	8^a	0	0	12	36
304	2 May 2013	65	M	R	–	–	–	26^a	0	0	38	4
314	22 May 2013	68	M	U	–	–	–	7^a	9	0	15	3
316	22 May 2013	68	F	R	–	–	–	2^a	2	0	24	1
318	22 May 2013	67	F	D	–	–	–	2^a	1	0	–	–
319	31 May 2013	73	F	R	–	–	–	1^a	1	0	–	–
322	31 May 2013	68	M	U	–	–	–	2^a	0	0	31	9
330	5 June 2013	66	M	U	–	–	–	5^a	0	0	0	1
331	5 June 2013	58	M	U	–	–	–	4^a	7	0	–	–
458	5 June 2013	58	M	U	–	–	–	1^a	0	1	–	–

Included for each fish are an ID #, date tagged, length (cm), sex, and maturity stage (D, developing; R, ripe; U, ripe and running; S, spent). Shaded fields signify years when these cod were only detected in the SCCZ and not on Eagle Ridge or Whaleback.

[a] Year in which the fish was tagged in the SCCZ.

suggest that cod were primarily residential within the Gulf of Maine (Figure 11; Supplementary Material, Section 3). There were 751 positions determined for 36 fish during the spring-spawning season (16 April–15 July). Cod were mainly located in statistical areas 514 (92%) and 513 (6%) during this period. Cod also demonstrated a high degree of residency in the Gulf of Maine after the spawning season but a greater proportion of positions came from other statistical areas. For example, from 16 July – 15 October (365 positions, 18 fish), 62% of positions were in 514, 17% in 513, 9% in 512, and 3% in 465. One fish, ID # 231, occupied statistical area 521 for 35 d during this time period, which represents ~10% of days during this period and movement into the Georges Bank management unit (Supplementary Material, Section 3). However, little movement south of Cape Cod or to Georges Bank was observed for other individuals. During the 16 October–15 January period (70 positions, 4 fish), the majority of positions were assigned to statistical areas 514 (17%), 512 (64%), and 465 (11%). Most positions during the 16 January–15 April period (24 positions, 4 fish) were assigned to statistical area 514 (46%) or 512 (42%).

Discussion

Combining data from multiple tagging technologies provided a robust description of the seasonal movement patterns and connectivity of a spring-spawning component of Atlantic cod in the western Gulf of Maine. Acoustic telemetry data and tag recaptures provided evidence of spawning site fidelity and connectivity among spawning sites. Tag recapture positions demonstrated that movements were primarily restricted to the western Gulf of Maine, with tagged fish moving from their inshore spawning sites to offshore feeding grounds and overwintering in deep (>150 m) offshore basins. This seasonal movement pattern was corroborated by habitat occupancy data from recovered DSTs, and it was largely consistent with movements identified by geolocation. However, geolocation results also suggested a higher rate of movement to portions of Georges Bank and the central and eastern areas of the Gulf of Maine but there is considerable uncertainty in these position assignments.

The acoustic telemetry data provided evidence of spawning site fidelity with respect to both the SCCZ and Eagle Ridge. The estimate of connectivity (21%) among spawning sites is conservative, because tagged cod could have moved to other unmonitored spawning sites and this does not account for factors such as non-reporting of recaptured cod, natural mortality, or skipped spawning. Our attempts to account for these factors produced a range of connectivity estimates (11–71%), which suggests that movements to multiple spawning sites can frequently occur within a given spawning season. Based on the acoustic telemetry data, there was greater evidence of connectivity within Massachusetts Bay than between Massachusetts Bay and Ipswich Bay, which was likely influenced by the further distance between the SCCZ and Whaleback. However, within the vicinity of the Whaleback spawning closure, more fish were recaptured ($n = 9$) than detected by the acoustic receivers ($n = 2$). This provides some additional evidence of conservative connectivity estimates based on acoustic telemetry detections, but it is difficult to compare estimates between the two tag types due to the inherent biases with fishery-dependent recaptures, the differential timing between receiver deployments and the majority of tagging, the implementation of spawning closures, and potentially variable spatial or temporal distribution in cod spawning activity. Furthermore, there was a similar number of reported tag recaptures from the

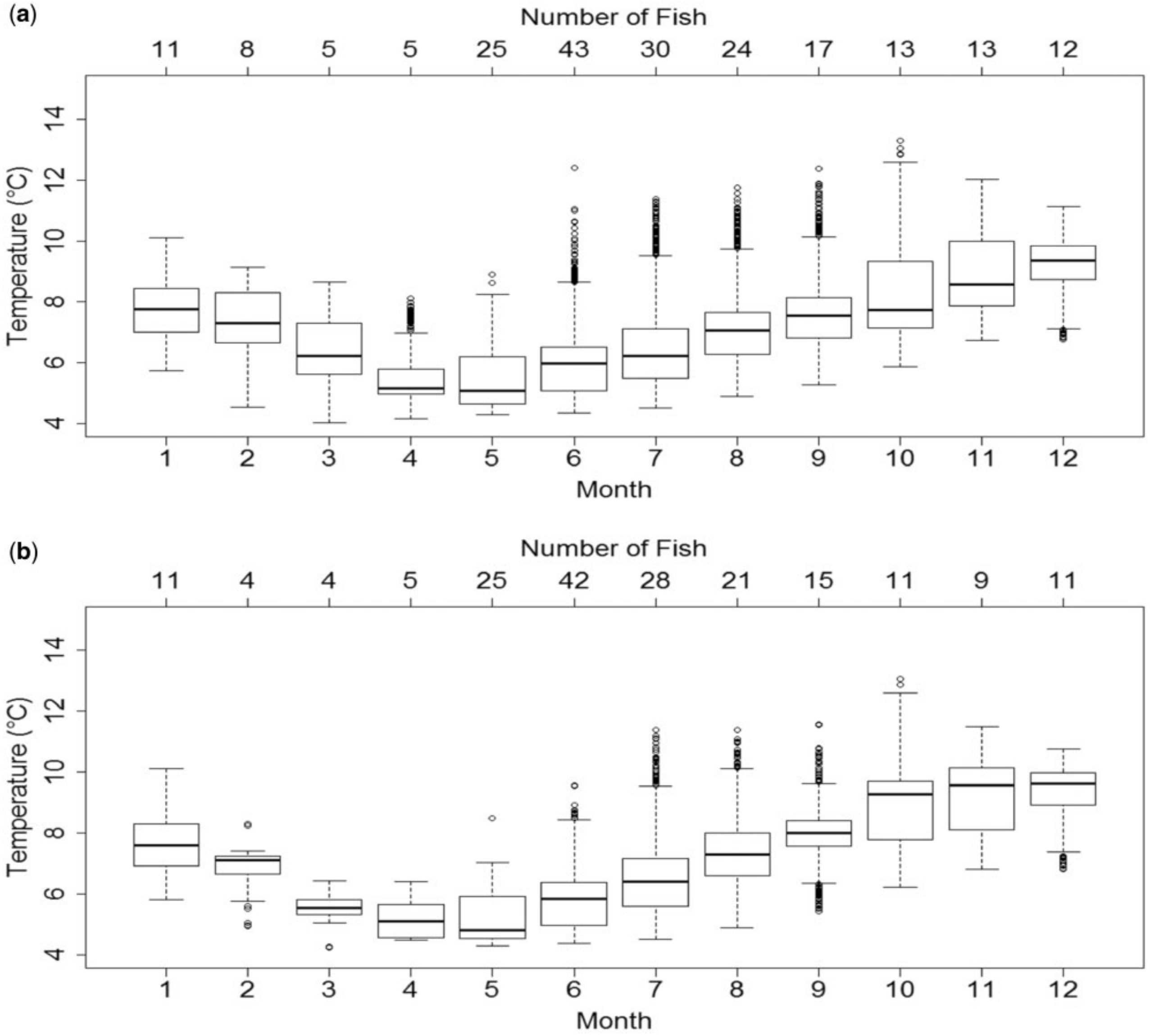

Figure 9. Boxplots of monthly temperature data for recovered DSTs, including (a) all data and (b) data only from periods when cod were identified as sedentary on the bottom using the tidal fitting procedure. The number of fish for which data were available in each month is included on the upper *x*-axes. Solid black lines within each box (i.e. the interquartile range) represent the median monthly temperature.

SCCZ ($n = 10$) and Whaleback, with only slightly fewer from Eagle Ridge ($n = 6$). This provides additional insight into the frequency of movements between locations, but similar caveats must be considered when interpreting these recapture data, in particular the variable spatial and temporal distribution in fishing activity and the implementation of spawning closures.

The evidence of spawning site fidelity and connectivity among spawning sites provides additional support to conclusions of Zemeckis *et al.* (2014b), whereby these movements function as important mechanisms influencing cod metapopulation processes. Spawning site fidelity promotes the formation of semi-discrete spawning components but the connectivity among spawning sites via adult movements contributes to the gene flow among spring-spawning components. Genetic analyses grouped spring-spawning cod from Massachusetts Bay, Ipswich Bay, and southern Maine into a "northern Spring Spawning" subpopulation (Kovach *et al.*, 2010), suggesting that the observed connectivity promotes this genetic relatedness despite evidence of strong fidelity to specific spawning sites (Dean *et al.*, 2014; Zemeckis *et al.*, 2014b). However, the connectivity within this subpopulation, which is also influenced by larval dispersal dynamics (e.g. Huret *et al.*, 2007; Churchill *et al.*, 2011), includes spawning components from areas with the greatest biomass in recent years and there is apparently insufficient connectivity to stimulate recolonization of inactive spawning sites within neighbouring subpopulations, particularly along coastal Maine (Ames, 2004; NEFSC, 2015). Based on these findings, we refer to each fine-scale location where spawning cod are observed to aggregate in large numbers as a "spawning site" (e.g. the SCCZ), and the overall inshore area where these connected sites are located can be grouped into a

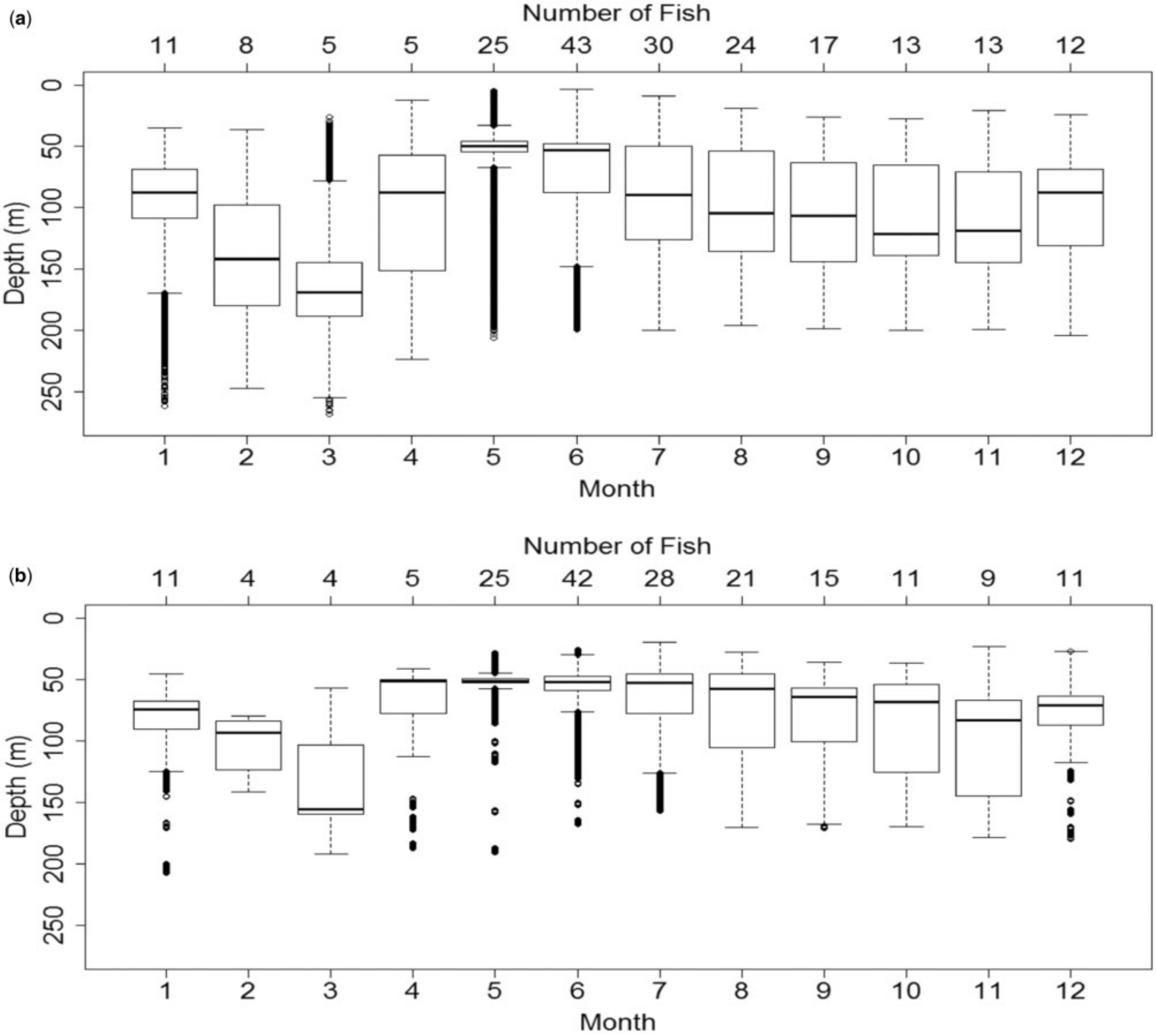

Figure 10. Boxplots of monthly depth data for recovered DSTs, including (a) all data and (b) data only from periods when cod were identified as sedentary on the bottom using the tidal fitting procedure. The number of fish for which data were available in each month is included on the upper *x*-axes. Solid black lines within each box (i.e. the interquartile range) represent the median monthly depth.

"spawning ground" (e.g. Massachusetts and Ipswich Bays). The connectivity among spawning sites complicates determination of the appropriate spatial scales for developing spawning protection measures and this terminology helps to communicate our findings of connectivity to fishery managers. Consideration of these movement patterns and the distribution of spawning activity can help fishery managers evaluate whether small-scale (e.g. Armstrong *et al.*, 2013) or broader-scale spawning closures (e.g. Department of Commerce, 2015) would be more effective for achieving management objectives (e.g. Clarke *et al.*, 2015), including balancing tradeoffs with respect to permitting access to other interacting fisheries.

Geolocation results from the spring-spawning season corroborated acoustic telemetry data and tag recapture positions by demonstrating that tagged cod primarily remained in the western Gulf of Maine during this period (i.e. statistical areas 513 and 514). After spawning, tagged cod typically moved further offshore to their feeding grounds. The distributions of tag recapture and geolocation positions during the period from 16 July through 15 October were generally in agreement, with most positions being in the western Gulf of Maine and in the Great South Channel. However, the geolocation results identified apparent movements that were not evident from tag recapture positions (e.g. Scotian Shelf, eastern Gulf of Maine, and eastern Georges Bank). This inconsistency could be due to regional variability in fishing effort or tag reporting rates resulting in a lack of recaptures in these areas. However, these differences are more likely due to geolocation error. Similarly, for the 16 October–15 January period, all recapture positions were from the western Gulf of Maine and in the Great South Channel but the geolocation results suggested frequent movement also occurred further east. The least amount of data was available for the 16 January–15 April period, when tag

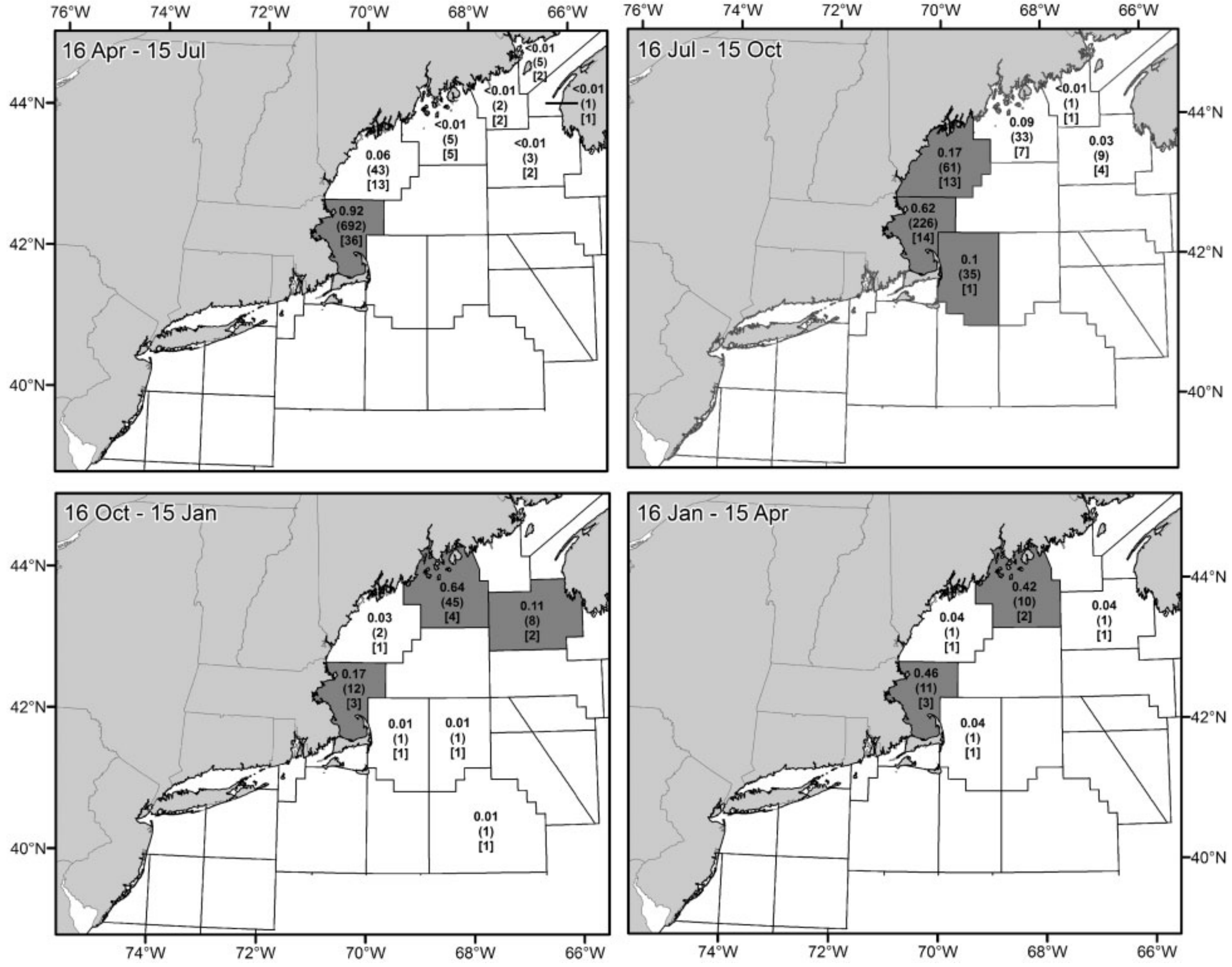

Figure 11. Geolocation results for externally attached DSTs by statistical area and season. In each statistical area, the upper number represents the proportion of days assigned to that area during a given season, the numbers in parentheses are the total number of days in that area during that season, and the numbers in brackets are the number of fish which were assigned positions to that area during that season. Shaded statistical areas are those which had ≥10% of positions assigned during a given season.

recapture positions and geolocation results suggested similar movement patterns as the previous period but an increased proportion of recaptures came from deep basins east of Stellwagen Bank (i.e. >150 m: Wilkinson Basin, Wildcat Knoll). Seasonal habitat occupancy data corroborated this pattern by indicating that the deep offshore basins served as overwintering habitat.

The frequency by which geolocation positions were assigned to statistical areas where no tag recapture positions were recorded was likely overestimated by error in the geolocation method (Zemeckis, 2016). Previous conventional tagging studies also found limited or no movement from the western Gulf of Maine to these other regions (e.g. Tallack, 2011; Loehrke, 2013), and trawl surveys suggest extremely low abundance of cod along coastal Maine (NEFSC, 2015). Therefore, despite the high accuracy of the geolocation method for assigning positions of double-electronic-tagged fish to statistical area 514 during the spring and summer (97%), it was apparent that the geolocation error varied spatially and temporally. The primary factors influencing geolocation error were DST data resolution and limitations of the tidal fitting procedure (Supplementary Material, Section 4; Zemeckis, 2016). Oceanographic conditions also influenced the geolocation accuracy. For example, bathymetry in the western Gulf of Maine is roughly parallel to the coast, and the Western Maine Coastal Current approximately follows the bathymetry (Manning *et al.*, 2009). As a result, there is relatively little geographic variability in depth and temperature over a broad region, which complicates estimation of geographic position when combined with regional tidal dynamics and limitations of the oceanographic model.

Tagged cod inhabited a relatively wide range of temperatures (∼4–13°C), which is similar to cod from other regions and this broad range suggests that adult cod might have appreciable tolerance for adapting to warming seas (Righton *et al.*, 2010). It is possible that shifts in movement patterns and behaviour can occur in response to changing oceanographic conditions, such as the recent warming trend in the Gulf of Maine (Mills *et al.*, 2013; Pershing *et al.*, 2015). Future research should continue to investigate the thermal habitat preferences of cod in the Gulf of Maine, including habitats utilized relative to those available and potential shifts in distribution due to warming conditions (e.g. Freitas *et al.*, 2015). The narrow range of the vertical habitat occupied during May and June was likely due to prolonged residency in the SCCZ (∼50–55 m depth), which is consistent with observations of cod spawning behaviour (Dean *et al.*, 2014). The shallowest depths (<20 m; Figure 10) were typically within 1 week of release and are likely due to variable recovery behaviour following tagging and release, similar to van der Kooij *et al.* (2007). The median depths observed when cod were determined to be sedentary on the bottom were frequently shallower than the median depths when all data were plotted (Figure 10). This could result from variability in activity levels, whereas, cod may be more active when in deeper areas. Another factor could be lower resolution pressure data at the extreme of the DST calibration range (i.e. up to 250 m). However, if cod do exhibit less frequent demersal behaviour when in deeper areas, then they may be less vulnerable to capture by demersal fishing gears.

The observed movement patterns are generally consistent with previous classification of cod in the Gulf of Maine as being "sedentary" (Howell *et al.*, 2008), which based on Robichaud and Rose (2004) refers to a group of cod that exhibits strong site fidelity and is found year-round within a relatively small area compared with other cod groups. Based upon comparison with previous conventional tagging studies (e.g. Hunt *et al.*, 1999; Tallack, 2011; Loehrke, 2013), it is apparent that cod from the SCCZ spawning component have limited connectivity with subpopulations beyond the western Gulf of Maine. This finding will be valuable for informing future fishery management decisions and ongoing investigations into cod population structure that are building on previous efforts (Annala, 2012; Zemeckis *et al.*, 2014c) by focusing on describing the connectivity among subpopulations. In some instances, the temporal and spatial scales of our observations were relatively coarse due to data and model limitations. For example, all recapture and geolocation positions were grouped among years, thereby preventing investigations into interannual variability. Also, aggregating data into 3 month time blocks may have grouped fish that were in different stages of their annual migration pattern (Loehrke, 2013; Sólmundsson *et al.*, 2015). Therefore, future studies should continue to investigate cod spatial ecology in the western Gulf of Maine, including other spring- and winter-spawning components, because cod might be mobile despite remaining residential in this area (Gröger *et al.*, 2007), and different movement patterns can exist among spawning components (Thorsteinsson *et al.*, 2012; Neat *et al.*, 2014).

In conclusion, we analysed data from multiple tagging technologies to describe the seasonal movements and connectivity of a spring-spawning component of Atlantic cod in the western Gulf of Maine. We documented evidence of spawning site fidelity and connectivity among spawning sites. The observed movements influence the connectivity among spawning components and promote gene flow within the spring-spawning western Gulf of Maine subpopulation but apparently limited connectivity exists to promote recolonization of inactive spawning sites in other subpopulations. Movements after the spawning season were primarily concentrated in the western Gulf of Maine, with cod moving to offshore feeding grounds and overwintering in deep offshore basins. Based upon comparison with previous tagging studies, adult cod from the SCCZ spawning component appear to have limited overlap with cod subpopulations from outside of the western Gulf of Maine. Results from this study have therefore advanced our understanding of cod population dynamics in the Gulf of Maine. The available evidence of connectivity among spawning sites will be valuable for consideration by fishery managers when determining the appropriate spatial scales for designing spawning protection measures. Furthermore, the improved understanding of processes that regulate cod population structure on multiple spatial scales will be helpful for informing ongoing investigations into cod population structure in the Gulf of Maine region, as well as other cod stocks throughout the North Atlantic.

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Supplementary data

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

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