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Original Article

Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding

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Rebuilding the Gulf of Maine stock of Atlantic cod (*Gadus morhua*) has been much slower than expected. An important source of scientific uncertainty contributing to the difficulties in managing rebuilding has been the lack of understanding of cod population structure. Previous research indicates that the stock functions as a metapopulation that is made up of multiple subpopulations and many finer-scale spawning components. This study investigated fine-scale, multiyear spawning site fidelity by a spring-spawning component of Atlantic cod in the western Gulf of Maine. Movements of acoustically tagged cod (*n* = 63) with respect to a known spawning site were tracked using passive acoustic telemetry. A large proportion (38–67%) of tagged cod exhibited spawning site fidelity between 2010 and 2012. After adjusting for fishing mortality, natural mortality, and skipped spawning, the estimated rate of spawning site fidelity ranged between 47 and 95% in 2011. Multiyear spawning site fidelity was also observed, with individuals being tracked for up to four consecutive spawning seasons. Spawning site fidelity serves as one of the multiple mechanisms that contribute to the formation and maintenance of the observed metapopulation structure. Spawning site fidelity also reduces the reproductive connectivity among spawning sites, thus delaying both recolonization of abandoned spawning sites and stock rebuilding. Future stock assessment models and fishery management plans that incorporate the metapopulation structure of cod in the Gulf of Maine are expected to be more effective at preventing continued declines in spawning diversity and promoting rebuilding.

Keywords: acoustic telemetry, Atlantic cod, *Gadus morhua*, Gulf of Maine, metapopulation, spawning site fidelity.

Introduction

Atlantic cod (*Gadus morhua*) have been a principal component of New England's fisheries since the seventeenth century (Serchuk and Wigley, 1992; Kurlansky, 1997; Leavenworth, 2008). In recent decades, the Gulf of Maine cod stock has experienced considerable declines in abundance due to interactions between overfishing (NEFSC, 2013), environmental variation (Rothschild, 2007; Fogarty *et al.*, 2008; Halliday and Pinhorn, 2009), and predator/prey dynamics (Frank *et al.*, 2011; Ames and Lichter, 2013; Friedland *et al.*, 2013). The most recent stock assessment models indicate that since at least 1982 the stock has been overfished and overfishing has been occurring (NEFSC, 2013). Stock assessment updates demonstrated that previous projections were overly-optimistic and the population did not increase as predicted (NEFSC, 2013). The ensuing shifts in perception with respect to stock status resulted in continued overfishing despite fishery management measures that successfully prevented the fishery from exceeding the acceptable biological catch (SSC, 2012a; Rothschild *et al.*, 2014).

Consequently, rebuilding the Gulf of Maine cod stock has been much slower than expected despite continuously evolving management strategies and considerable reductions in fishing effort (Serchuk and Wigley, 1992; Mayo *et al.*, 2009; NEFMC, 2009). An important source of scientific uncertainty for stock assessments and fishery management has been the lack of understanding of cod population structure in the Gulf of Maine (Annala, 2012; SSC, 2012b; Zemeckis *et al.*, 2014a). Previous research indicates

that the Gulf of Maine cod stock is not as homogeneously assumed (Ames, 2004; Wirgin *et al.*, 2007; Kovach *et al.*, 2010). In contrast, the stock appears to function as a metapopulation. Under this view, the stock can be described as a system of discrete local subpopulations, each of which determines its own internal dynamics to a large extent, but there remains an identifiable and non-trivial demographic influence from neighbouring subpopulations (Kritzer and Sale, 2004). On a finer scale, each subpopulation is made up of multiple semi-discrete spawning components that are grouped based upon their reproductive connectivity (Ames, 2004; Annala, 2012; Zemeckis *et al.*, 2014a). Ignoring this complex intra-stock diversity can bias perceptions of stock status and lead to inappropriate fishery management strategies that risk the extirpation of semi-discrete spawning components (Reich and DeAlteris, 2009; Kerr *et al.*, 2010). In fact, nearly half of the historical spawning components in the Gulf of Maine have been depleted and the abandoned spawning sites have not been recolonized despite many being inactive for over 70 years (Maine Dept. Sea and Shore, 1949; Ames, 1997, 2004). The substantial decline in spawning diversity has led to reductions in stock productivity and is likely contributing to difficulties in rebuilding (Reich and DeAlteris, 2009; Kerr *et al.*, 2010).

Bimodal peaks in cod spawning activity in the Gulf of Maine include spring (April–July) and winter (October–February) subpopulations (Berrien and Sibunka, 1999). Despite frequently occupying the same spawning sites, these subpopulations are genetically distinct due in part to their temporal variation in spawning (Wirgin *et al.*, 2007; Breton, 2008; Kovach *et al.*, 2010). Variable oceanographic conditions within and between spawning seasons also influence population structure by affecting the dispersal and retention of the early life stages (Huret *et al.*, 2007; Churchill *et al.*, 2011). Spawning site fidelity, in which cod return to the same spawning site each season, also contributes to the observed metapopulation structure (Perkins *et al.*, 1997; Howell *et al.*, 2008), because it limits the reproductive connectivity among spawning sites (e.g. Svedäng *et al.*, 2007).

Spawning site fidelity by Atlantic cod has been documented in other regions, using both conventional (Robichaud and Rose, 2004; Wright *et al.*, 2006) and electronic tagging (Green and Wroblewski, 2000; Robichaud and Rose, 2001; Svedäng *et al.*, 2010; Skjæraasen *et al.*, 2011). However, spawning site fidelity has only been documented in the Gulf of Maine over relatively broad spatial scales (tens of kilometers) using information acquired from conventional tagging studies (e.g. Perkins *et al.*, 1997; Howell *et al.*, 2008). Additional information regarding the prevalence, consistency, and precision of this behaviour will improve our understanding of cod population structure in the Gulf of Maine. The objectives of this study were to investigate fine-scale, multiyear spawning site fidelity by Atlantic cod in the western Gulf of Maine, and to discuss the implications with respect to population structure and rebuilding.

Methods
Study site
This study investigated spawning cod in the Spring Cod Conservation Zone (SCCZ) (depth range: 25–60 m), which is a seasonal spawning closure in northern Massachusetts Bay in the western Gulf of Maine (Figure 1) (Armstrong *et al.*, 2013). The closure was first implemented in 2009 (1 May–30 June) and covered a total area of 22.8 km². In 2010, the closure was increased in duration (1 May–21 July) to protect cod spawning later in the season. The

closure was adjusted again in 2011 by increasing the duration of the closure (16 April–21 July) and doubling the closure area (45.4 km²) (Figure 1). The timing and size of the SCCZ were maintained in 2012 and 2013.

Sampling and tagging
Cod were caught in the SCCZ with rod and reel using jigs and teasers, which was expected to maximize survival (Nøstvik and Pedersen, 1999; Milliken *et al.*, 2009) and minimize the disruption of cod spawning activity relative to other fishing gears (Morgan *et al.*, 1997; Dean *et al.*, 2012). Total length was measured for all captured fish and their sex and maturity stage were determined via visual inspection or cannulation (extraction of a gonadal biopsy using a plastic tube inserted through the genital pore). Each fish was assigned a maturity stage using guidelines set forth by Burnett *et al.* (1989): Immature, Resting, Developing, Ripe, Ripe and Running, Spent, Unknown.

Cod movements in the SCCZ were monitored using passive acoustic telemetry, which enables collection of high-resolution information on the movement and behaviour of individual fish (DeCelles and Zemeckis, 2014). Spawning cod (classified as Ripe or Ripe and Running) were tagged with Vemco V16P-6H coded acoustic transmitters (98 mm length, 36 g in air, 69 kHz) with a 60 s ($\pm$ 50%) transmission rate and an expected battery life of >1500 d (Vemco, Inc., Nova Scotia, Canada). In accordance with the protocol developed by Dean *et al.* (2012, 2014), all acoustic transmitters were surgically implanted into the peritoneal cavity and incisions were sealed using braided silk sutures (Figure 2). An internal anchor tag (FM-84, Floy Tag and Mfg., Inc., Seattle, WA, USA) was also inserted inside the incision to notify fishers that there is a transmitter inside the fish and to increase the likelihood of recovering the transmitter if the fish was recaptured. Nearly all cod that were tagged with a surgically implanted acoustic transmitter in 2010 and 2011 also received an externally attached archival data storage tag (milli-L, Star-ODDI, Reykjavik, Iceland) for a future study applying tidal-based geolocation. Given the intensive double-tagging procedure, fish $\geq$ 65 cm were targeted for electronic tagging. Cod that were not chosen for electronic tagging were instead doubled-tagged with two conventional t-bar anchor tags (FD-94, Floy Tag and Mfg., Inc.).

Acoustic telemetry
Results from a range test conducted at the study site in March 2010 indicated that the detection radius of each acoustic receiver was ~1 km throughout a wide variety of sea and weather conditions. These data informed the design of an acoustic array that consisted of 28 receivers (model VR2W, Vemco Inc., Nova Scotia, Canada) that were spaced 400 m apart (Figure 3a). The spacing between receivers permitted overlap in the detection radii of adjacent receivers and determination of fish positions over an ~9.5 km² area (Figure 3a) as part of a Vemco VR2W Positioning System (VPS) (e.g. Andrews *et al.*, 2011; Espinoza *et al.*, 2011). The 28-receiver array was deployed in 2010 (21 April–19 July) and in 2011 (14 April–20 July). After being hauled out, the 28-receiver array was reduced to four receivers with 400 m spacing (Figure 3b) to maintain our ability to monitor the study site after the opening of the fishery, while also reducing the risk of equipment loss during a period when intense fishing pressure was anticipated. The downsized VPS array was deployed until 31 August in 2010 and 24 August in 2011. In 2012, the VPS array was modified to include 25 receivers spaced 800 m apart (deployed from 3 April–16 July),
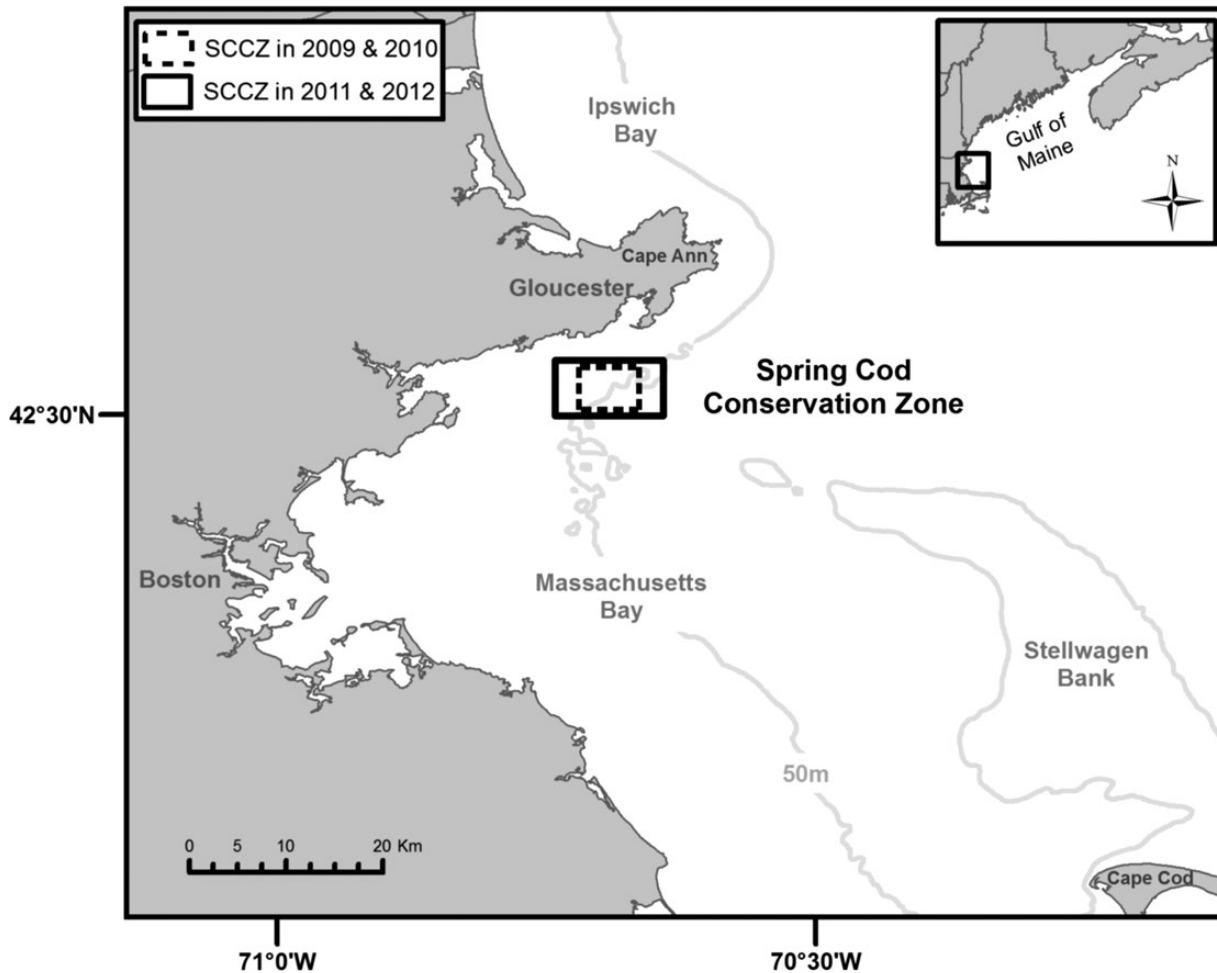
Figure 1. Map of the Spring Cod Conservation Zone (SCCZ), which is a seasonal spawning closure in northern Massachusetts Bay in the western Gulf of Maine. During its first year of implementation in 2009, the closure spanned from 1 May – 30 June and covered a 22.8 km² area. The duration of the closure was increased to 1 May – 21 July in 2010. The most recent modification to the closure came in 2011, when it was expanded longitudinally (45.4 km²) and the timing was increased to 16 April – 21 July.
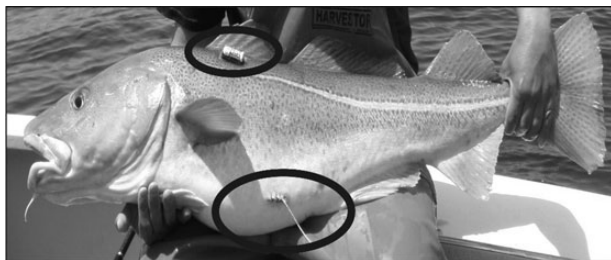
Figure 2. An example of a 110 cm Ripe and Running male double-tagged with an acoustic transmitter and an archival data storage tag. The acoustic transmitters (Vemco V16P-6H) were surgically implanted into the peritoneal cavity and an internal anchor tag (Floy FM-84) was inserted inside each incision. The archival data storage tags (Star-ODDI milli-L) were externally attached beneath the first dorsal fin using plastic saddles and stainless steel wire.

providing a total detection area of ∼15.9 km² (Figure 3c). The four-receiver VPS array (Figure 3b) was deployed until 30 August in 2012. Reference transmitters were deployed as a part of each configuration

of the VPS to ensure that the arrays were functioning properly throughout the study, thus supporting the assumption of a 100% detection probability of tag transmissions within their detection range (Figure 3). Results presented here focus on the inter-annual fidelity to this spawning site (presence/absence within the SCCZ). The fine-scale observations of spawning behaviour from these VPS data are described by Dean *et al.* (2014).

Data analysis

Cod were considered to have exhibited spawning site fidelity if they were detected in the SCCZ during a field season after tagging. It must be emphasized to note that this behaviour should not be confused with natal homing because no linkages to natal habitats were assumed (Bradbury and Laurel, 2007). Rates of spawning site fidelity were calculated for fish tagged in year i and returning to the SCCZ in year j ($SSF_{i,j}$), using the following equation:

$$SSF_{i,j} = \frac{\# \text{ observed}_{i,j}}{\# \text{ putatively alive}_{i,j}} \quad (1)$$

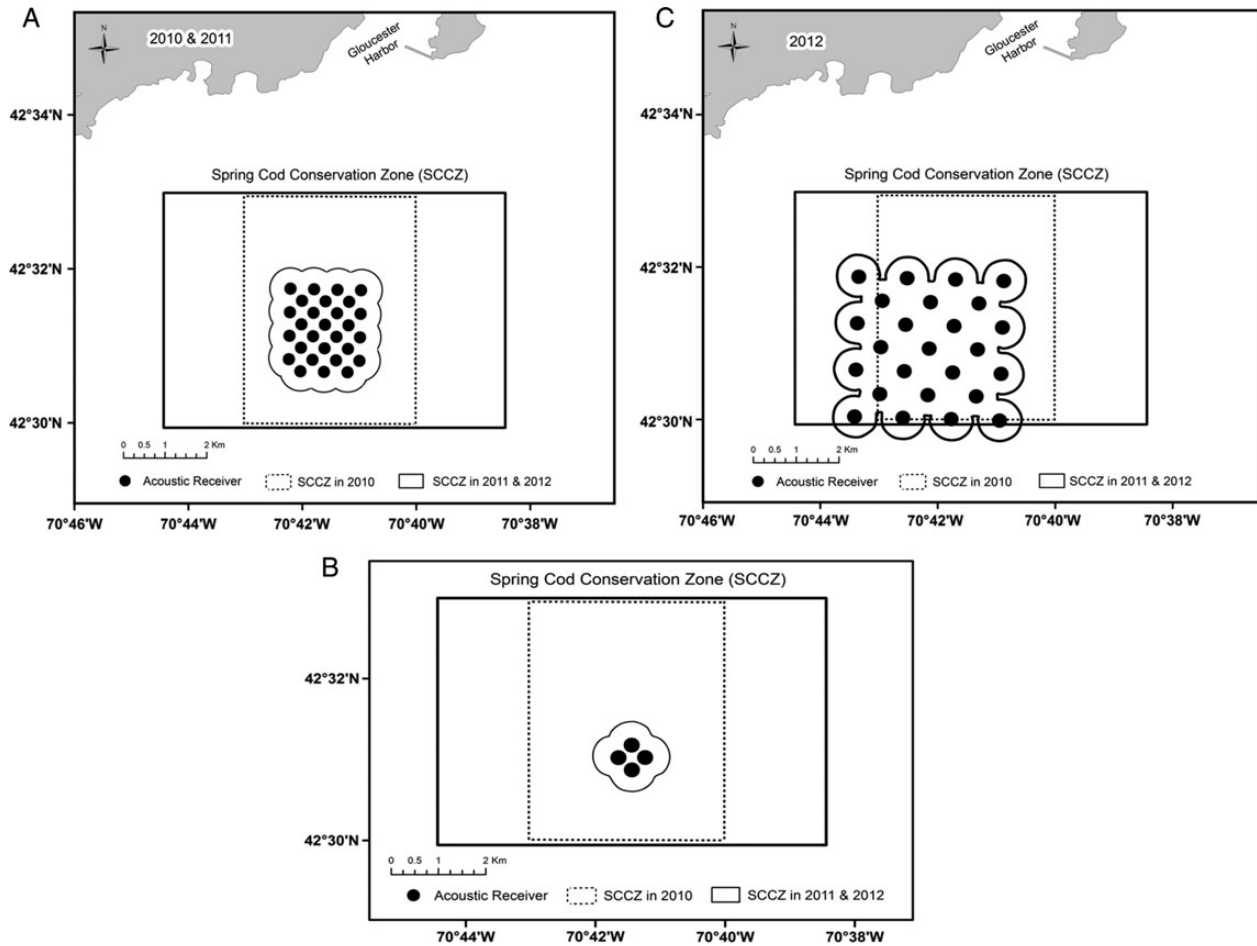The # observed$_{i,j}$ represents the number of cod tagged in year i and

Figure 3. (A) Schematic of the 28-receiver Vemco VR2W Positioning System (VPS) that was deployed in 2010 and 2011. Receivers were spaced 400 m apart, allowing fish to be tracked in three dimensions over an ~9.5 km² area. (B) Each year, the VPS was downsized to a four-receiver diamond-shaped array when the closure was lifted to reduce the risk of equipment loss when the fishery opened. (C) In 2012, the VPS array was reduced to 25 receivers, but receiver spacing was increased to 800 m, which provided a total detection area of ~15.9 km².

detected in the SCCZ during year j. The # putatively alive$_{i,j}$ represents the number of cod tagged in year i and expected to be alive in year j, which was calculated as the number of cod tagged in year i minus the number confirmed dead before the beginning of the spawning season (1 April) in year j. Fish were pronounced dead following fishery recaptures or observations of tagging-induced mortality (T), which were identified by a lack of horizontal (based upon VPS positions) and vertical movements (based upon depth data from acoustic transmitters). Multiyear spawning site fidelity was also described for fish that were detected in the SCCZ during more than two spawning seasons.

Similar to Robichaud and Rose (2001), an adjusted rate of spawning site fidelity (SSF$_{adj}$) was calculated to account for factors that would prevent fish from returning to the SCCZ. This calculation was performed with the following equation using 2011 acoustic telemetry data for fish that were tagged in 2010:

$$\text{SSF}_{adj} = \frac{\# \text{ observed}}{(\# \text{ tagged})(1 - A - T - S)} \quad (2)$$

The # observed represents the number of cod that were tagged with acoustic transmitters in 2010 and detected in the SCCZ in 2011.

The denominator includes the total number of cod tagged with acoustic transmitters in 2010 (# tagged), with adjustments for factors that would prevent individuals from returning to the SCCZ. An annual proportion of deaths (A) was calculated as $A = 1 - \exp[-(M + F)]$. Two estimated rates of instantaneous natural mortality (M) were used based on the most recent stock assessment models for Gulf of Maine cod ($M = 0.2$ and 0.4: NEFSC, 2013). An instantaneous rate of fishing mortality (F) was estimated using Equation (3) and an estimated proportion of tagging-induced mortality (T) was derived from 2010 tagging data. An estimated annual proportion of skipped spawning (S) was included, because cod that skip spawning are believed to not migrate to spawning sites (Skjæraasen et al., 2012). Estimated rates of skipped spawning are not available for the Gulf of Maine. Therefore, estimates from other regions were used, including an estimate of $S = 0.08$ based on the findings of Rideout and Rose (2006) for cod off Newfoundland and an estimate that $S = 0.24$ based on the findings of Skjæraasen et al. (2012) for Northeast Arctic cod.

Considering the large size of cod sampled in the SCCZ, this group may experience a different fishing mortality rate than the entire Gulf of Maine management unit. Therefore, fishing mortality (F) was estimated using recapture information from conventional

Table 1. Number of acoustic transmitters released each year in the SCCZ.

Tag year	Releases	Tagging mortality	Fishery recaptures	Putatively alive			Exhibited spawning site fidelity		
				2010	2011	2012	2010	2011	2012
2009	11	1	4	7	7	6	3	2	1
2010	55	3	13	–	39	39	–	15	5
2011	4	0	1	–	–	3	–	–	2

The number putatively alive during each spawning season was calculated by subtracting observations of tagging-induced mortality and fish recaptured in the fishery. The number of fish tagged in each year that exhibited spawning site fidelity is also included.

t-bar anchor tags released in 2010. Only tagged cod that were ≥65 cm and recaptured within 1 year of being released were included in this analysis. Calculations were performed by iteratively solving for *F* in the following derivation of Baranov's catch equation:

$$F = \frac{r/\lambda}{[(n(1-L^2))(1-\exp(-Z))]/Z} \quad (3)$$

The number of tag recoveries (*r*) was adjusted for a tag reporting rate (*λ*). Similarly, the number of tag releases (*n*) was adjusted for a tag-shedding rate (*L*), which was squared because fish were double-tagged with two conventional t-bar anchor tags. Estimates of the tag-shedding rate (*L* = 0.1494) and tag reporting rate in the Gulf of Maine (*λ* = 0.457) were obtained from Miller and Tallack (2007), which were derived from a conventional tagging study of Gulf of Maine cod (Tallack, 2011). The total mortality (*Z*) was calculated as the sum of *M* + *F*, using both available estimates of natural mortality.

Variability in spawning site fidelity between males and females would provide insights into cod spawning behaviour and their complex mating system (Zemeckis *et al.*, 2014b). An RxC test of independence using a G-test and a Williams' correction (Sokal and Rohlf, 2012) was used to determine whether there was a significant difference in the frequency of spawning site fidelity between males and females. This analysis was performed using 2011 acoustic telemetry data for fish that were tagged in 2010, because this was the year during which the most cod were observed. Cod have been documented following larger "scouts" during long-distance migrations (Rose, 1993), suggesting that larger, older cod might have an increased ability to follow learned migrations and accurately navigate to spawning sites. Therefore, the same test and data were used to determine whether there was a significant difference in the prevalence of spawning site fidelity among fish of different lengths. For this analysis, fish were arbitrarily divided into three size classes based on their lengths when tagged: medium (<80 cm), large (80–99 cm), and whale (>100 cm).

The residence times of cod that exhibited spawning site fidelity were calculated to infer the likelihood that cod spawned during their residency. Residence times were measured as the period between the first and last detection recorded for an individual during a given spawning season. Residence times were only reported for the season(s) during which a fish exhibited spawning site fidelity, because we were able to observe the entire spawning season by documenting dates of arrival and departure to and from the SCCZ. An *F*-test for equality of variances determined that the variances of the residence times were significantly different between males and females in 2011 (*p* = .001). Therefore, Welch's *t*-test was used to determine whether there was a significant
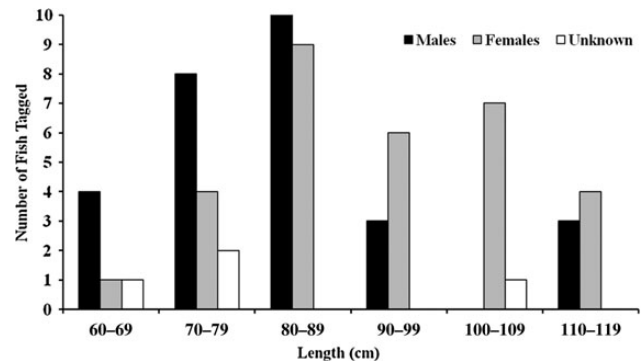

Figure 4. Length distribution of cod that were tagged with acoustic transmitters in the SCCZ from 2009 to 2011, excluding fish which were confirmed to be dead using acoustic telemetry data. A total of 63 fish were incorporated into analyses (28 males, 31 females, 4 unknown).

difference between males and females, because the assumptions of Student's *t*-test were not met. Data from 2011 were used in this analysis because this was the year from which the largest sample size was available.

Results

A total of 70 cod were tagged with acoustic transmitters from 2009 to 2011 (Table 1). As confirmed using the VPS data, three individuals tagged in 2009 were killed when the fishery opened on 1 July (Dean *et al.*, 2012), and one fish died after being released due to tagging-related effects. As a result, seven cod tagged in 2009 survived the full spawning season, including one male, two females, and four unknown (low availability of spawning cod in June 2009 resulted in four cod of unknown sex being tagged). In 2010, three acoustically tagged cod died shortly after release (<4 h) despite being in excellent physical condition (tagging-induced mortality, *T* = 0.055). All tagging-related mortalities in 2010 occurred on the same sampling date and perhaps these fish were preyed upon by the abundant spiny dogfish (*Squalus acanthias*) that were observed attacking cod while they were being reeled to the surface. Therefore, 52 releases from 2010 survived the full spawning season (24 males, 28 females). In 2011, four fish were tagged with acoustic transmitters and released (3 males, 1 female). As a result, a total of 63 cod that were tagged with acoustic transmitters from 2009 to 2011 were included in our analyses (28 males, 31 females, 4 unknown) ($\bar{x}$ = 88.4 cm ± 15.2 cm: Figure 4).

Three of the seven cod that were tagged with acoustic transmitters in 2009 were detected in the SCCZ for 39, 33, and 60 d in 2010 (SSF$_{2009,2010}$ = 43%: Table 1). Two of these same fish exhibited multiyear spawning site fidelity and were detected in the SCCZ

Table 2. Tagging date, sex, length (cm), and residence times (days) for fish that exhibited spawning site fidelity between 2010 and 2012.

ID #	Tag date	Sex	Length	Spawning site fidelity			Residence time		
				2010	2011	2012	2010	2011	2012
9	8 June 2009	M	73	Y	Y	N[a]	39	32	–
15	27 June 2009	F	94	Y	Y	Y	33	55	14
19	24 June 2009	U	77	Y	N	N	60	–	–
162	7 May 2010	M	80	–	Y	Y	–	46	11[b]
164	7 May 2010	M	77	–	Y	N	–	30	–
168	11 May 2010	M	74	–	Y	N	–	53	–
169	11 May 2010	M	69	–	Y	N	–	27	–
170	11 May 2010	M	84	–	Y	N	–	33	–
177	11 May 2010	F	109	–	Y	Y	–	28	47
181	8 June 2010	F	77	–	Y	Y	–	4	2
185	8 June 2010	M	82	–	Y	N	–	37	–
187	8 June 2010	F	104	–	Y	Y	–	51	39[b]
227	18 June 2010	F	99	–	Y	N	–	20	–
228	18 June 2010	F	81	–	Y	Y	–	19	21
233	18 June 2010	M	69	–	Y	N	–	52	–
241	2 July 2010	F	118	–	Y	N	–	106	–
247	16 July 2010	M	99	–	Y	N	–	34	–
249	20 July 2010	F	112	–	Y	N	–	21	–
278	10 June 2011	F	97	–	–	Y	–	–	1
281	20 May 2011	M	116	–	–	Y	–	–	41[b]

U = unknown sex. Whether or not a fish exhibited spawning site fidelity in a given season is indicated by Y = Yes or N = No.
[a]Fish was recaptured September 2011.
[b]Minimum residence time, died due to unexplained mortality.

again in 2011 (Fish ID #9 for 32 d and Fish ID #15 for 55 d) and one was detected in the SCCZ for the fourth consecutive year in 2012 (Fish ID #15 for 14 d) (Table 2). Fish ID #9 was recaptured in September 2011 and was therefore unable to return to the SCCZ in 2012.

Eleven cod tagged in 2010 were reported dead via fishery recaptures before the beginning of the 2011 spawning season (1 April). Two additional cod tagged in 2010 were recaptured in 2011 on 7 May and 14 May, ~14 km south of the SCCZ in an area known as Eagle Ridge. Because these fish were recaptured early in the 2011 spawning season and within 1 year of being released, they were included with the other reports of fishery recaptures because they were removed from the population and did not have a full spawning season during which they could return to the SCCZ. As a result, 39 of the 55 cod tagged in 2010 were putatively alive during the 2011 spawning season (18 males and 21 females). Fifteen of these 39 fish were observed in the SCCZ and exhibited spawning site fidelity in 2011 ($SSF_{2010,2011} = 38\%$: Table 1).

A total of 475 cod ≥ 65 cm were double-tagged with conventional t-bar anchor tags in 2010, 23 of which were reported through fishery recaptures within 1 year of being released. Including these data in Equation (3), the instantaneous rate of fishing mortality (F) was estimated to be 0.127 when $M = 0.2$ and 0.140 when $M = 0.4$. Based on these estimates, the annual proportion of deaths (A) was calculated to be 0.279 when $M = 0.2$ and 0.417 when $M = 0.4$. After including these estimates in Equation (2), the SSF_{adj} was calculated under four scenarios given the different combinations of natural mortality and skipped spawning (Table 3). The resulting values ranged from 47% (Scenario 1: most conservative) to 95% (Scenario 4: least conservative). These findings indicate that spawning site fidelity in 2011 was prevalent, and nearly universal under the least conservative scenario, among cod that were tagged in the SCCZ in 2010.

Table 3. Scenarios in which adjusted rates of spawning site fidelity (SSF_{adj}) were calculated using Equations (2) and (3).

Scenario	M	F	A	T	S	SSF_{adj}
1	0.2	0.127	0.279	0.055	0.08	0.465
2	0.2	0.127	0.279	0.055	0.24	0.640
3	0.4	0.140	0.417	0.055	0.08	0.609
4	0.4	0.140	0.417	0.055	0.24	0.948

Calculations were performed for fish that were tagged in 2010 and exhibited spawning site fidelity in 2011. Variables in the equations included estimates of natural mortality (M), fishing mortality (F), annual proportion of deaths (A), tagging-induced mortality (T), and skipped spawning (S).

There was no significant difference between the mean residence time of males ($\bar{x} = 38.2$ d ± 9.7 d) and females ($\bar{x} = 38.0 \pm 32.3$ d) that exhibited spawning site fidelity in 2011 ($t_{.05,[8]} = 0.019$; $t_{crit} = 2.306$; $p = 0.986$) (Table 2). There was also no significant difference in the frequency of spawning site fidelity between males (44%) and females (33%) in 2011 ($\chi^2_{.05,[1]} = 3.841$, $G_{adj} = 0.485$, $p = 0.486$) (Table 2). Similarly, the prevalence of spawning site fidelity was independent of fish length (medium: 45%, large: 32%, whale: 44%) ($\chi^2_{.05,[2]} = 5.991$, $G_{adj} = 0.704$, $p = 0.703$).

Five cod tagged in 2010 were detected in the SCCZ for the third consecutive spawning season in 2012 (Table 2), thus providing additional evidence of multiyear spawning site fidelity. All cod that exhibited multiyear spawning site fidelity were detected each consecutive spawning season and did not skip a year (i.e. there were no fish tagged in 2010 that returned in 2012 and were not also detected in 2011). One cod tagged in 2011 was recaptured in the fishery later that year. Therefore, two of the three fish that were tagged in 2011 and putatively alive were detected in the SCCZ in 2012 ($SSF_{2011,2012} = 67\%$: Table 1). Three of the eight fish that exhibited spawning site fidelity in 2012 died due to

unexplained mortality while in the SCCZ. These fish (Fish ID #'s 162, 187, and 281) returned to the SCCZ and exhibited spawning behaviour as described in Dean *et al.* (2014) for a period that was included in the calculation of minimum residence times (Table 2). In each case, this normal behaviour ceased abruptly and the fish displayed a complete lack of horizontal and vertical movement. Fish that exhibited spawning site fidelity in 2012 and survived the full spawning season had residence times ranging from 1 to 47 d (Table 2).

Discussion

Our results have documented multiyear spawning site fidelity on a finer spatial scale than previously described for Atlantic cod in the western Gulf of Maine (e.g. Perkins *et al.*, 1997; Howell *et al.*, 2008). The mean night-time position of females in the SCCZ between 2010 and 2011 varied by only 9 m (Dean *et al.*, 2014), which represents finer-scale spawning site fidelity than previously reported for Atlantic cod (e.g. <1 km off coastal Norway: Skjæraasen *et al.*, 2011). Similar observations of multiyear spawning site fidelity have also been documented for cod off southern Newfoundland (Robichaud and Rose, 2001), where transplantation studies suggest that cod are able to accurately home to spawning sites by navigating along learned migration routes using an omnidirectional attractor (i.e. effective cues from any direction, such as sound or magnetism) in combination with spatial memory of bathymetry or ocean currents (Robichaud and Rose, 2002; Windle and Rose, 2005).

The estimated rates of un-adjusted spawning site fidelity reported in this study ($SSF_{2009,2010} = 43\%$, $SSF_{2010,2011} = 38\%$, $SSF_{2011,2012} = 67\%$) are similar to those documented for cod off coastal Norway (55 and 37% in two separate seasons: Skjæraasen *et al.*, 2011). However, the adjusted rates of spawning site fidelity estimated for cod in the SCCZ (ranging from 47 to 95%: Table 3) are greater than the adjusted rate (39%) reported for cod off Newfoundland (Robichaud and Rose, 2001). Both studies used similar estimates for the parameters in their calculations, but Robichaud and Rose (2001) did not consider skipped spawning. Future work should evaluate the hypothesis that fish which skip spawning do not migrate to spawning sites, as well as investigate the prevalence of skipped spawning by cod in the Gulf of Maine to determine the applicability of estimates from other stocks. For example, observations of skipped spawning from a highly migratory stock such as the Northeast Arctic cod (Robichaud and Rose, 2004) might not be relevant to the less migratory cod in the western Gulf of Maine (Howell *et al.*, 2008). Future research should also investigate the origin of cod that spawn in the SCCZ, which may provide evidence of natal homing in addition to spawning site fidelity (e.g. Svedäng *et al.*, 2010), thus offering further insights into the mechanisms that influence the development and maintenance of population structure.

Ancillary information resulting from this study provides further support for the prevalent spawning site fidelity observed between 2010 and 2011. For example, none of the cod that were tagged with acoustic transmitters in 2010 that went un-detected in 2011 have since been recaptured in the fishery. These individuals were also not detected by nearby acoustic receivers off Cape Ann and Cape Cod that were maintained from 2011 to 2013 to monitor the movements of striped bass (*Morone saxatilis*) (Kneebone *et al.*, 2014). This was the case despite other cod that were tagged with acoustic transmitters in the SCCZ having been detected by the Cape Ann receivers, and multiple recaptures of cod tagged with conventional tags coming from within 15 km of these receivers. The lack of detection or reported recapture over multiple spawning seasons for these fish suggests that they either died of natural mortality or were recaptured in the fishery and not reported, thus corroborating the relatively high adjusted rates of spawning site fidelity calculated in this study.

The estimated rates of instantaneous fishing mortality calculated in this study (e.g. $F = 0.127$ when $M = 0.2$) were substantially lower than estimates of fully recruited fishing mortality (e.g. $F = 0.62$ in 2010 and $F = 0.59$ in 2011 when $M = 0.2$) from the most recent stock assessment models for Gulf of Maine cod (NEFSC, 2013). This may be due to age-related differences in fishing mortality (Butterworth and Rademeyer, 2008), because the cod tagged in this study represent the largest size classes found in the region (Tallack, 2009; NEFSC, 2013). Another potential source of uncertainty in our calculations results from the use of an estimated tag reporting rate from a previous study. Perhaps the reporting rate was lower in the present study due to a shift in the attitudes of fishers (e.g. tag saturation) or a decrease in advertising compared with the previous study. Additional sources of uncertainty also influenced calculations of the rates of fishing mortality and adjusted spawning site fidelity. For example, the rate of tagging-induced mortality may be an underestimate because these data do not account for fish that might have died outside of the detection range of our receivers. Our calculations were also influenced by the uncertainty surrounding natural mortality for Gulf of Maine cod, which is evidenced by the use of two different values in recent stock assessment models ($M = 0.2$ or 0.4: NEFSC, 2013).

The residence times of cod in the SCCZ during 2011 (range: 4–106 d, $\bar{x} = 38.1$ d) were similar to the residence times reported by Siceloff and Howell (2013) for cod spawning in nearby Ipswich Bay (range: 8–53 d, $\bar{x} = 30$ d), which is ∼45 km north of the SCCZ. In contrast to our results, they documented a marked difference between the mean residence time of males ($\bar{x} = 36.6$ d) and females ($\bar{x} = 23.4$ d). This discrepancy could be due to the inability of Siceloff and Howell (2013) to completely monitor the residency of tagged individuals on the spawning site (i.e. some fish were still resident at the termination of their experiment). Mean residence times documented for cod in the SCCZ were also considerably longer than the mean residence times (males: $\bar{x} = 10$ d, females: $\bar{x} = 19$ d) documented by Robichaud and Rose (2003) for cod spawning in coastal Newfoundland. The difference between studies may be due to regional variability in spawning behaviour or differences in the efficiency of tracking methods (i.e. active vs. passive tracking).

The small sample size of fish that exhibited spawning site fidelity influenced our finding of a lack of a difference in the mean residence time between males ($\bar{x} = 38.2$ d $\pm$ 9.7 d) and females ($\bar{x} = 38.0$ d $\pm$ 32.3 d) in 2011 by reducing the statistical power of the test and increasing the likelihood of committing a type II error. Similarly, the lack of a difference in the prevalence of spawning site fidelity between sexes could also be due to the relatively small sample size, which was limited by the high cost of acoustic transmitters. The lack of a relationship between fish length and spawning site fidelity may be due to the large size classes tagged in this study. The size of available acoustic transmitters with multiyear battery life necessitated the 65 cm minimum fish length for electronic tagging. If the current trend of progressively smaller and less expensive acoustic transmitters continues (DeCelles and Zemeckis, 2014), future studies could include larger sample sizes and a broader size range of individuals, which may more conclusively address the influence of sex and length on spawning site fidelity.

Our findings have provided some evidence of connectivity among inshore spawning sites via adult movements. For example, the residence times of three fish that exhibited spawning site fidelity during our study were less than 5 d, which was considerably shorter than other tagged individuals (Table 2). This suggests that these fish may have spawned at other locations in addition to the SCCZ. Observations from tagging trips indicate that there was relatively low abundance of spawning cod in the SCCZ when these fish stayed for only a short period. Perhaps these individuals were attracted to other nearby aggregations with more intensive spawning activity at that time. Interestingly, two fish tagged in the SCCZ were recaptured ∼14 km to the south on Eagle Ridge, which is an area where spring-spawning cod have been caught in recent years. These observations indicate that despite exhibiting prevalent spawning site fidelity, there may also be some connectivity among inshore spawning sites via adult movements. Therefore, adult choice appears to play an important role in population connectivity (e.g. Frisk *et al.*, 2014). Continued research using both acoustic telemetry and archival data storage tags is currently underway to more extensively investigate the connectivity among inshore spawning sites in the western Gulf of Maine.

Cod spawning dynamics in the Gulf of Maine (e.g. dense, predictable aggregations close to shore) increase the vulnerability of spawning aggregations to overexploitation and have contributed to the serial depletion of historical spawning components (Ames, 2004; Armstrong *et al.*, 2013; Zemeckis *et al.*, 2014b). Prevalent, fine-scale spawning site fidelity is believed to be another important factor contributing to the declines in spawning diversity, because this behaviour is one of the multiple mechanisms (e.g. temporal variation in spawning, larval dispersal dynamics) that limit the reproductive connectivity among spawning sites and promote the formation of semi-discrete spawning components that are vulnerable to extirpation. The genetic differentiation documented among cod subpopulations in the Gulf of Maine region has remained consistent across multiple years of samples (Wirgin *et al.*, 2007; Breton, 2008; Kovach *et al.*, 2010), despite the sensitivity of these techniques to mixing among population segments (Mariani and Bekkevold, 2014). Therefore, spawning site fidelity (both spatially and temporally), as well as the apparent movement of adults among spawning sites, is an important mechanism for the formation of the observed metapopulation structure, as well as maintaining it through multiple generations.

Recolonization of inactive spawning sites is critical for rebuilding and can occur through the resurgence of a remnant population or via immigration of adults from other regions (Frank and Brickman, 2000; Wroblewski *et al.*, 2005). Critical depletion and a lack of rebuilding of cod spawning components in the eastern Gulf of Maine (Ames, 2004; NEFSC, 2013) reduces the likelihood of a rapid resurgence by the remnant population. Recolonization of these inactive spawning sites might be more likely to occur via immigration from spawning sites that remain active, which are primarily found in the western Gulf of Maine. However, limited connectivity between subpopulations in the eastern and western Gulf of Maine (Zemeckis *et al.*, 2014a), which is due in part to spawning site fidelity, reduces the probability of rapid recolonization through immigration. Results from ongoing work investigating the connectivity among inshore spawning sites will provide further insights into potential mechanisms for recolonization. For example, frequent movement of adults between spawning sites would increase the reproductive connectivity among spawning components and promote recolonization on shorter time scales than

expected in a more isolated stock (Stephenson, 1999; Rose *et al.*, 2011). However, as evidenced by the lack of recolonization in the eastern Gulf of Maine (Ames, 1997, 2004), any level of connectivity that might exist either within or between subpopulations has evidently been too low for recolonization to occur within the observed time frame, suggesting that recolonization of abandoned spawning sites will remain a slow process.

Future stock assessments and fishery management plans should integrate substock-specific information to prevent continued declines in spawning diversity and promote rebuilding (Lindegren *et al.*, 2013; Zemeckis *et al.*, 2014b). For example, the fishery management plan applied to cod and other groundfish in New England has shifted from input controls (e.g. trip limits and days-at-sea) to a quota-based approach beginning in 2010 (NEFMC, 2009). In the Gulf of Maine, there has since been a relative increase in landings of larger vessels (NEFSC, 2013), for which it was economically less efficient to target cod when trip limits were regulated. Therefore, the removal of trip limits made it possible for all fishing vessels to harvest a greater number of cod during a shorter period. Much of the fishing effort has focused on cod spawning aggregations, which risks continued depletion of semi-discrete spawning components that are not included in current spawning closures. Future fishery management plans should consider additional spawning protection measures to protect the persistent spawning components that are crucial for rebuilding cod in the Gulf of Maine region (Armstrong *et al.*, 2013; Zemeckis *et al.*, 2014a, b).

This study has demonstrated that cod in the western Gulf of Maine can exhibit prevalent, fine-scale spawning site fidelity behaviour over multiple years. This behaviour limits the reproductive connectivity among spawning sites and promotes the formation of semi-discrete spawning components. Therefore, spawning site fidelity serves as one of the multiple mechanisms that contribute to the formation and maintenance of the observed metapopulation structure in the Gulf of Maine region. By limiting the reproductive connectivity among spawning sites, prevalent spawning site fidelity slows the recolonization of inactive spawning sites and contributes to the persistent difficulties in rebuilding. Future stock assessment models and fishery management plans that incorporate the metapopulation structure of cod in the Gulf of Maine are expected to be more effective at preventing continued declines in spawning diversity and promoting rebuilding.

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References

Ames, E. P. 1997. Cod and haddock spawning grounds of the Gulf of Maine from Grand Manan to Ipswich Bay. *In* The implications of localized fishery stocks, pp. 55–64. Ed. by I. H. von Herbing, and M. Tupper. Natural Resource, Agriculture, and Engineering Service, Ithaca, New York. 200 pp.

Ames, E. P. 2004. Atlantic cod stock structure in the Gulf of Maine. Fisheries, 29: 10–28.

Ames, E. P., and Lichter, J. 2013. Gadids and alewives: structure within complexity in the Gulf of Maine. Fisheries Research, 141: 70–78.

Andrews, K. S., Tolimieri, N., Williams, G. D., Samhouri, J. F., Harvey, C. J., and Levin, P. S. 2011. Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Marine Biology, 158: 2377–2387.

Annala, J. 2012. Report of the Workshop on Stock Structure of Atlantic Cod in the Gulf of Maine Region, 12–14 June 2012. Portsmouth, NH. http://www.gmri.org/mini/index.asp?ID=52&p=149 (last accessed 2 January 2014).

Armstrong, M. P., Dean, M. J., Hoffman, W. S., Zemeckis, D. R., Nies, T. A., Pierce, D. A., Diodati, P. J., *et al.* 2013. The application of small scale fishery closures to protect Atlantic cod spawning aggregations in the inshore Gulf of Maine. Fisheries Research, 141: 62–69.

Berrien, P., and Sibunka, J. 1999. Distribution patterns of fish eggs in the U.S. NE Continental Shelf Ecosystem, 1977–1987. NOAA Technical Report - National Marine Fisheries Service. 145 pp.

Bradbury, I. R., and Laurel, B. J. 2007. Defining "natal homing" in marine fish populations: comment on Svedäng et al. (2007). Marine Ecology Progress Series, 349: 307–308.

Breton, T. S. 2008. Spawning stock identification of Atlantic cod (*Gadus morhua*) in U.S. waters using *PANI* and microsatellite genetic markers. MS Thesis, University of New Hampshire, Durham, NH, USA.

Burnett, J., O'Brien, L., Mayo, R. K., Darde, J., and Bohan, M. 1989. Finfish maturity sampling and classification schemes used during Northeast Fisheries Center bottom trawl surveys, 1963–1989. NOAA Tech. Mem. NMFS-F/NEC, vol. 76. 14 p.

Butterworth, D. S., and Rademeyer, R. A. 2008. Statistical catch-at-age analysis vs. ADAPT-VPA: the case of Gulf of Maine cod. ICES Journal of Marine Science, 65: 1717–1732.

Churchill, J. H., Runge, J., and Chen, C. 2011. Processes controlling retention of spring-spawned Atlantic cod (*Gadus morhua*) in the western Gulf of Maine and their relationship to an index of recruitment success. Fisheries Oceanography, 20: 32–46.

Dean, M. J., Hoffman, W. S., and Armstrong, M. P. 2012. Disruption of an Atlantic cod spawning aggregation resulting from the opening of a directed gill-net fishery. North American Journal of Fisheries Management, 32: 124–134.

Dean, M. J., Hoffman, W. S., Zemeckis, D. R., and Armstrong, M. P. 2014. Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the western Gulf of Maine. ICES Journal of Marine Science, 71: 1474–1489.

DeCelles, G., and Zemeckis, D. 2014. Acoustic and radio telemetry. *In* Stock Identification Methods, 2nd edn, pp. 397–428. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Elsevier, San Diego. 566 pp.

Espinoza, M., Farrugia, T. J., Webber, D. M., Smith, F., and Lowe, C. G. 2011. Testing a new telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fisheries Research, 108: 364–371.

Fogarty, M., Incze, L., Hayhoe, K., Mountain, D., and Manning, J. 2008. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. Mitigation and Adaptive Strategies for Global Change, 13: 453–466.

Frank, K. T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, 57: 513–517.

Frank, K. T., Petrie, B., Fisher, J. A. D., and Leggett, W. C. 2011. Transient dynamics of an altered large marine ecosystem. Nature, 477: 86–91.

Friedland, K. D., Kane, J., Hare, J. A., Lough, R. G., Fratantoni, P. S., Fogarty, M. J., and Nye, J. A. 2013. Thermal habitat constraints on zooplankton species associated with Atlantic cod (*Gadus morhua*) on the US Northeast Continental Shelf. Progress in Oceanography, 116: 1–13.

Frisk, M. G., Jordaan, A., and Miller, T. J. 2014. Moving beyond the current paradigm in marine population connectivity: are adults the missing link? Fish and Fisheries, 15: 242–254.

Green, J. M., and Wroblewski, J. S. 2000. Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. Journal of the Marine Biological Association of the UK, 80: 1077–1085.

Halliday, R. G., and Pinhorn, A. T. 2009. The roles of fishing and environmental change in the decline of Northwest Atlantic groundfish populations in the early 1990s. Fisheries Research, 97: 163–182.

Howell, W. H., Morin, M., Rennels, N., and Goethel, D. 2008. Residency of adult Atlantic cod (*Gadus morhua*) in the western Gulf of Maine. Fisheries Research, 91: 123–132.

Huret, M., Runge, J. A., Chen, C., Cowles, G., Xu, G., and Pringle, J. M. 2007. Dispersal modeling of fish early life stages: sensitivity with application to Atlantic cod in the western Gulf of Maine. Marine Ecology Progress Series, 347: 261–274.

Kerr, L. A., Cadrin, S. X., and Secor, D. H. 2010. Simulation modelling as a tool for examining the consequences of spatial structure and connectivity on local and regional population dynamics. ICES Journal of Marine Science, 67: 1631–1639.

Kneebone, J., Hoffman, W. S., Dean, M. J., and Armstrong, M. P. 2014. Movements of striped bass between the Exclusive Economic Zone and Massachusetts state waters. North American Journal of Fisheries Management, 34: 524–534.

Kovach, A. I., Breton, T. S., Berlinsky, D. L., Maceda, L., and Wirgin, I. 2010. Fine-scale spatial and temporal genetic structure of Atlantic cod off the Atlantic coast of the USA. Marine Ecology Progress Series, 410: 177–195.

Kritzer, J. P., and Sale, P. F. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries, 5: 131–140.

Kurlansky, M. 1997. Cod: A biography of the fish that changed the world. Walker and Co., New York.

Leavenworth, W. B. 2008. The changing landscape of maritime resources in seventeenth-century New England. International Journal of Maritime History, XX, No. 1: 33–62.

Lindegren, M., Waldo, S., Nilsson, P. A., Svedäng, H., and Persson, A. 2013. Towards sustainable fisheries of the Öresund cod (Gadus morhua) through sub-stock-specific assessment and management recommendations. ICES Journal of Marine Science, 70: 1140–1150.

Maine Department of Sea and Shore Fisheries. 1949. Annual Report. Augusta, Maine.

Mariani, S., and Bekkevold, D. 2014. The nuclear genome: neutral and adaptive markers in fisheries science. *In* Stock Identification Methods, 2nd edn, pp. 397–428. Ed. by S. X. Cadrin, L. A. Kerr, and S. Mariani. Elsevier, San Diego. 566 pp.

Mayo, R. K., Shepherd, G., O'Brien, L., Col, L. A., and Traver, M. 2009. The 2008 assessment of the Gulf of Maine Atlantic cod (*Gadus morhua*) stock. Northeast Fisheries Science Center Reference Document 09–03. 136 pp.

Miller, T., and Tallack, S. 2007. Estimating instantaneous rates of regional migration and mortality from conventional tagging data. Groundfish Assessment Review Meeting Working Paper C3.

Milliken, H. O., Farrington, M., Rudolph, P., and Sanderson, M. 2009. Survival of discarded sublegal Atlantic cod in the Northwest Atlantic demersal longline fishery. North American Journal of Fisheries Management, 29: 985–995.

Morgan, M. J., DeBlois, E. M., and Rose, G. A. 1997. An observation of the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling. Canadian Journal of Fisheries and Aquatic Sciences, 54 (Suppl. 1): 217–223.

New England Fishery Management Council. 2009. Northeast Multispecies Fisheries Management Plan. Amendment 16. 905 pp.

Northeast Fisheries Science Center (NEFSC). 2013. 55th Northeast Regional Stock Assessment Workshop (55th SAW) Assessment Report. US Dept Commer., Northeast Fish Sci. Cent Ref Doc. 13–11; 845 pp. National Marine Fisheries Service, Woods Hole.

Nøstvik, F., and Pedersen, T. 1999. Catching cod for tagging experiments. Fisheries Research, 42: 57–66.

Perkins, H. C., Chenoweth, S. B., and Langton, R. W. 1997. The Gulf of Maine Atlantic cod complex, patterns of distribution and movement of the Sheepscot Bay substock. Bulletin of National Research Institute of Aquaculture, Suppl. 3: 101–107.

Reich, D. A., and DeAlteris, J. T. 2009. A simulation study of the effects of spatially complex population structure for Gulf of Maine cod. North American Journal of Fisheries Management, 29: 116–126.

Rideout, R. M., and Rose, G. A. 2006. Suppression of reproduction in Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, 320: 267–277.

Robichaud, D., and Rose, G. A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Sciences, 58: 2325–2329.

Robichaud, D., and Rose, G. A. 2002. The return of cod transplanted from a spawning ground in southern Newfoundland. ICES Journal of Marine Science, 59: 1285–1293.

Robichaud, D., and Rose, G. A. 2003. Sex differences in cod residency on a spawning ground. Fisheries Research, 60: 33–43.

Robichaud, D., and Rose, G. A. 2004. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish and Fisheries, 5: 185–214.

Rose, G. A. 1993. Cod spawning on a migration highway in the northwest Atlantic. Nature, 366: 458–461.

Rose, G. A., Nelson, R. J., and Mello, L. G. S. 2011. Isolation or metapopulation: whence and whither the Smith Sound cod? Canadian Journal of Fisheries and Aquatic Sciences, 68: 152–169.

Rothschild, B. J. 2007. Coherence of Atlantic cod stock dynamics in the northwest Atlantic Ocean. Transactions of the American Fisheries Society, 136: 858–874.

Rothschild, B. J., Keiley, E. F., and Jiao, Y. 2014. Failure to eliminate overfishing and attain optimum yield in the New England groundfish fishery. ICES Journal of Marine Science, 71: 226–233.

Scientific and Statistical Committee (SSC). 2012a. Groundfish ABC for FY2013–2015. Report to New England Fishery Management Council.

Scientific and Statistical Committee (SSC). 2012b. Gulf of Maine cod. Report to the New England Fishery Management Council.

Serchuk, F. M., and Wigley, S. E. 1992. Assessment and management of the Georges Bank cod fishery: An historical review and evaluation. Journal of Northwest Atlantic Fishery Science, 13: 25–52.

Siceloff, L., and Howell, W. H. 2013. Fine-scale temporal and spatial distributions of Atlantic cod (*Gadus morhua*) on a western Gulf of Maine spawning ground. Fisheries Research, 141: 31–43.

Skjæraasen, J. E., Meager, J. J., Karlsen, O., Hutchings, J. A., and Fernöö, A. 2011. Extreme spawning-site fidelity in Atlantic cod. ICES Journal of Marine Science, 68: 1472–1477.

Skjæraasen, J. E., Nash, R. D. M., Korsbrekke, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K. H., *et al.* 2012. Frequent skipped spawning in the world's largest cod population. Proceedings of the National Academy of Sciences of the USA, 109: 8995–8999.

Sokal, R. R., and Rohlf, F. J. 2012. Biometry, 4th edn. W.H. Freeman and Co., New York. 937p.

Stephenson, R. L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fisheries Research, 43: 247–249.

Svedäng, H., André, C., Jonsson, P., Elfman, M., and Limburg, K. E. 2010. Migratory behaviour and otolith chemistry suggest fine-scale sub-population structure within a genetically homogeneous Atlantic Cod population. Environmental Biology of Fishes, 89: 383–397.

Svedäng, H., Righton, D., and Jonsson, P. 2007. Migratory behaviour of Atlantic cod *Gadus morhua*: natal homing is the prime stock-separating mechanism. Marine Ecology Progress Series, 345: 1–12.

Tallack, S. M. L. 2009. Regional growth estimates of Atlantic cod, *Gadus morhua*: Applications of the maximum likelihood GROTAG model to tagging data in the Gulf of Maine (USA/Canada) region. Fisheries Research, 99: 137–150.

Tallack, S. M. L. 2011. Stock identification applications of conventional tagging data for Atlantic cod in the Gulf of Maine. *In* Proceedings from the 2nd International Symposium on Advances in Fish Tagging and Marking Techniques, pp. 1–15. Ed. by J. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. Mesa, and Q. Phelps. American Fisheries Society, Auckland, NZ.

Windle, M. J. S., and Rose, G. A. 2005. Migration familiarity and homing of transplanted Atlantic cod (*Gadus morhua*). Fisheries Research, 75: 193–199.

Wirgin, I., Kovach, A. I., Maceda, L., Roy, N. K., Waldman, J., and Berlinsky, D. L. 2007. Stock identification of Atlantic cod in U.S. waters using microsatellite and single nucleotide polymorphism DNA analyses. Transactions of the American Fisheries Society, 136: 375–391.

Wright, P. J., Galley, E., Gibb, I. M., and Neat, F. C. 2006. Fidelity of adult cod to spawning grounds in Scottish waters. Fisheries Research, 77: 148–158.

Wroblewski, J., Neis, B., and Gosse, K. 2005. Inshore stocks of Atlantic cod are important for rebuilding the east coast fishery. Coastal Management, 33: 411–432.

Zemeckis, D. R., Dean, M. J., and Cadrin, S. X. 2014b. Spawning dynamics and associated management implications for Atlantic cod (*Gadus morhua*). North American Journal of Fisheries Management, 34: 424–442.

Zemeckis, D. R., Martins, D., Kerr, L. A., and Cadrin, S. X. 2014a. Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. ICES Journal of Marine Science, 71: 1490–1506.

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