Fidelity within and connectivity among spawning components of Atlantic cod

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Abstract - The Gulf of Maine stock of Atlantic cod is rebuilding after decades of overfishing. Many historic coastal spawning components have been depleted, causing reductions in spawning diversity, recruitment, and productivity. We used acoustic telemetry to study the movements of a coastal spawning component in the western Gulf of Maine. Fine-scale (<100m), multi-year spawning site fidelity with adjusted homing rates of 70% were documented. Individual cod remained on the spawning site for approximately three to eight weeks, exhibiting infrequent movements away from the spawning site. Movement data gathered from acoustic telemetry and tag recaptures identifies connectivity among coastal spawning sites up to 59km apart, which corroborates recent genetics studies. The extent of spawning site fidelity and connectivity among spawning components suggests complex population structure within the Gulf of Maine stock, which may be best described as a metapopulation. Stock assessments and management plans that recognize the complex population structure within the Gulf of Maine cod stock will help prevent continued declines in spawning diversity and promote rebuilding.

Keywords: Atlantic cod, Gulf of Maine, population structure, acoustic telemetry

Introduction:

The population structure of many Atlantic cod stocks (*Gadus morhua*) is more complex and occurs on a much finer-scale than the homogeneous units which are typically assumed for assessment and management (Hauser and Carvalho 2008; Heath et al. 2008; Stephenson 1999). Decades of overfishing have resulted in the loss of historic spawning components and subsequent collapses of population structure (Ames 2004; Cardinale and Svedäng 2004; Smedbol and Wroblewski 2002; Svedäng et al. 2010). Declining spawning diversity is significant because contributions to recruitment vary annually and may come from only a small or a different fraction of the spawning population each year (Berkeley et al. 2004). Maintaining the full suite of natural spawning components is expected to reduce the risk of widespread recruitment failure by decreasing the likelihood of a mismatch with positive environmental conditions (Begg and Marteinsdottir 2000; Cushing 1990; Mertz and Myers 1994; Sinclair 1988). Consequently, maintaining a high level of spawning diversity will enhance stock productivity and stability (Kerr et al. 2010) and promote fisheries sustainability (Hilborn et al. 2003).

The objective of this study was to examine the fine-scale population structure within the Gulf of Maine stock of Atlantic cod. Many historic coastal spawning components in the Gulf of Maine stock have been depleted (Ames 2004), causing reductions in spawning diversity and biocomplexity (Alexander et al. 2009). These reductions have become increasingly apparent since abandoned spawning sites have not been recolonized (Ames 1997) and the stock has faced continued difficulties in rebuilding (Northeast Fisheries Science Center 2011). In order to meet our objective, we studied the movements of individual fish from a coastal spawning component using acoustic telemetry and conventional tagging. We investigated the extent of spawning site fidelity, residency on the spawning site, and the connectivity among genetically-related coastal spawning components (Kovach et al. 2010). Our goal is to help determine the appropriate management scales for Gulf of Maine cod, and to identify potential rebuilding mechanisms.

Methods:

The study area focused on a seasonal spawning closure within Massachusetts Bay in the western Gulf of Maine, known as the Spring Cod Conservation Zone (SCCZ) (Figure 1). The SCCZ has been closed annually since 2009 during the spring spawning season (April 16^{th} - July

21st). Cod were captured from the spawning aggregation with rod and reel fishing gear using jigs and teasers. In 2010, spawning fish that were in excellent condition were selected for tagging with acoustic transmitters (Vemco V16P-6H coded transmitters; expected battery life >4 years), which were surgically implanted into the peritoneal cavity. These fish also received an externally attached archival data storage tag (Star-ODDI milli-L) (Figure 2) for future studies employing tidal-based geolocation. Fish which were not selected for electronic tagging received conventional t-bar anchor tags.

In 2010 and 2011, a 28-receiver Vemco VR2W Positioning System (VPS) (detection area = 9.5 km^2) (Figure 3) was deployed in the SCCZ to track the movements of acoustically tagged cod. The receivers were rigged individually or on short trawls with 400m spacing between each receiver to permit overlap in their detection radii. Acoustic telemetry data from 2010 was used to estimate the minimum residence times of cod in the SCCZ using the difference between the tag date and the date the fish was last detected in the SCCZ. The residency of cod within the array was measured by calculating a 'wander rate' for each fish to quantify the percent of time each fish was unobserved, similar to the methods of Robichaud and Rose (2003). The time period during which a fish was considered a resident was divided into day/night time intervals and each interval was assigned a value of '1' if the fish was observed or a value of '0' if unobserved. The wander rate for each fish was calculated as the total number of time intervals designated as a '0' divided by the total time intervals the fish was considered a resident.

Acoustic telemetry data collected in 2011 was used to investigate spawning site fidelity. Acoustically tagged cod which were tagged in 2010 and detected in the array in 2011 were determined to have exhibited spawning site fidelity. Rates of spawning site fidelity and homing behavior were calculated similar to Robichaud and Rose (2001), including adjustments for the natural mortality rate (M), fishing mortality rate (F), and tag-under reporting rate (u) using the following equations:

$$F = \frac{(\#\, returned)(1+u)}{(\#\, tagged)} \qquad \text{Equation 1}$$

$$Homing\ Rate = \frac{(\#\, observed)}{(\#\, tagged)\,(1-M\ -F)} \qquad \text{Equation 2}$$

where "# returned" represents the number of cod that were recaptured in the fishery between the 2010 and 2011 spawning seasons, the “# tagged” is the number of cod tagged in 2010, and the “# observed” represents the number of acoustically tagged cod which returned to the spawning site in 2011. For fish which exhibited spawning site fidelity, their actual residence times in the array were calculated based upon their dates of arrival and departure during the 2011 spawning season. Actual residence times are a more accurate representation of a fish's residence within the SCCZ than minimum residence times calculated for the 2010 season, which were based upon the date the fish was tagged as opposed to the actual date the fish arrived in the SCCZ. Wander rates were also calculated for fish which returned to the SCCZ in 2011.

In 2012, the number of receivers in the VPS array was reduced to 25, but the spacing between each receiver was expanded to 800m to increase the overall detection area of the array (15.89 km^2) (Figure 4). Acoustic telemetry data collected in 2012 was analyzed for the return of fish that were tagged in 2010 and therefore exhibited spawning site fidelity. Based upon information gathered from conventional tag recaptures (Figure 5) and data collected from sampling the commercial catch from coastal waters (B. Hoffman, unpublished data), an apparent connection was found between the SCCZ and other spawning sites in Massachusetts Bay and Ipswich Bay. As a result, four acoustic receivers were deployed on “Eagle Ridge”, a putative spawning site approximately 14 km south of the SCCZ in Massachusetts Bay, and eight receivers were deployed on the "Whaleback" spawning site, approximately 45 km north of the SCCZ in Ipswich Bay (Siceloff and Howell, in press) (Figure 6). Our goal was to detect cod moving between spawning sites and document connectivity. A small number of acoustic transmitters were also deployed in the SCCZ in 2011 and 2012, which were incorporated into the investigation of connectivity among spawning sites using the 2012 acoustic telemetry data.

Results:

A total of 52 cod were tagged with acoustic transmitters in 2010 (24 males : 28 females) (Figure 7). The length of acoustically tagged males ranged from 65 - 99cm (mean = 80cm), while females ranged from 68 - 125cm (mean = 93cm). Minimum residence times ranged from 1 – 54 days, with a mean of 23.5 days for males and 16.5 days for females. While being considered a resident, acoustically tagged cod exhibited infrequent movements out of the VPS array in 2010. The combined wander rate of all tagged males (8.2%) was higher than the wander rate of females

(4.2%), with the males being unobserved more often at night (10.1%) than during the day (6.3%) (Females: 4.7% night, 3.7% day) (Table 1).

A total of 15 of the 52 cod tagged in 2010 were detected in the VPS array in the SCCZ in 2011, and were therefore considered to have exhibited spawning site fidelity (unadjusted homing rate = 29%). There were 13 acoustically tagged cod returned from fishery recaptures between the 2010 and 2011 spawning seasons (return rate = 25%). When corrected for a tag under-reporting rate of 55% as estimated by a conventional tagging study (Miller and Tallack 2007), the fishing morality rate (F) estimated for this group of fish was 39% using Equation 1. This fishing mortality rate was then combined with the assumed natural mortality rate from the most recent stock assessment (M = 0.2) (Northeast Fisheries Science Center 2011) to estimate an adjusted homing rate of 70% for acoustically tagged cod, using Equation 2. Actual residence times calculated for fish which exhibited spawning site fidelity in 2011 ranged from 4 - 106 days, with a mean of 39 days for males (n=8) and 35 days for females (n=7) (Table 2). The wander rates of both males and females were greater in 2011 than in 2010, with males (21.6% combined, 13.5% day, 29.7% night) being unobserved more often than females (8.2% combined, 8.6% day, 7.7% night) (Table 1). A total of four additional cod were tagged with acoustic transmitters in 2011 (116cm male, 118cm male, 97cm female, 110cm male).

Five cod which were tagged in 2010 were detected in the SCCZ during 2012. All five of these cod were also detected in the SCCZ during 2011, signifying multi-year homing to the spawning site. The actual residence times for these fish ranged from 2 - 86+ days (two fish remained in the array during the most recent data download before preparing this manuscript) (Table 2). During the 2012 spawning season, a total of 14 additional cod were tagged with acoustic transmitters, including seven males (range= 63-108cm, mean= 78cm) and seven females (range= 63-99cm, mean= 80cm).

In addition to the 56 cod that were double-tagged with an acoustic transmitter and a data storage tag in 2010 and 2011, a total of 188 additional cod were tagged with just an archival data storage tag and 1,728 were tagged with conventional t-bar anchor tags. As of May 2012, there were 128 cod recaptured that were tagged in 2010 and 2011 (all tag types combined) and had sufficient information to permit analysis of movement patterns. Of particular interest with respect to connectivity among spawning components are the recaptures of cod tagged in the

SCCZ that were later caught during the spring spawning season on the Whaleback spawning site in Ipswich Bay and the Eagle Ridge spawning site in Massachusetts Bay (Figure 5).

The acoustic arrays deployed on the Whaleback and Eagle Ridge spawning sites in 2012 (Figure 6) detected a total of eight cod which were tagged with acoustic transmitters in the SCCZ. Only one cod was detected on Whaleback, Fish ID# 25, which was a 109 cm female when tagged in the SCCZ on May 11, 2010. In 2012, Fish ID# 25 was first detected in the SCCZ on April 4th. She was then detected on Whaleback on April 8th before returning to the SCCZ for April 10th. She was next detected at Eagle Ridge on April 11th, before again returning to the SCCZ from April 16th through May 20th. Another interesting detection history was Fish ID# 32, which was a 77cm female tagged in the SCCZ on June 8, 2010, and had a minimum residence time of 31 days in 2010. She was only present in the SCCZ for 4 days (May 31st - June 3rd) in 2011, and 2 days in 2012 (June 12th - June 13th). However, in 2012 she was detected at Eagle Ridge periodically from May 21st through June 11th before being arriving in the SCCZ. She then returned to Eagle Ridge on June 28th and remained there for 2 days.

In addition, two other cod were detected at Eagle Ridge for 1 day and 9 days before settling into the SCCZ for 11 days and 67 days, respectively. Also, Fish ID# 65 (97cm F, tagged June 10, 2011) was detected in the SCCZ only on May 30, 2012, later being detected periodically from June 1st through June 17th at Eagle Ridge. Fish ID# 74 was a 65cm ripe and running male tagged June 7, 2012 in the SCCZ and was only detected in the SCCZ for one day. However, he was detected at Eagle Ridge from June 10th through June 20th and from June 30th through July 8th. Fish ID# 71 was another ripe and running male of 67cm that was released in the SCCZ on May 31, 2012, and was detected there until June 3rd, before being detected again on June 14th at Eagle Ridge. Finally, Fish ID# 80 was a 94 cm spent female tagged in the SCCZ on June 7, 2012 where she remained for only one day before being detected at Eagle Ridge on June 10th. Therefore, the acoustic telemetry data collected in 2012 documents cod movements between spawning sites that are up to 59 km apart, and suggests connectivity among coastal spawning components in the Gulf of Maine.

Discussion:

The evidence of spawning site fidelity collected in this study represents fine-scale (<100m), multi-year homing to a coastal spawning site in the western Gulf of Maine. Similar studies have also documented fine-scale homing behavior in cod off Newfoundland (Robichaud and Rose 2001) and Norway (Skjaeraasen et al. 2011), but the adjusted homing rate of 70% reported here is greater than in earlier studies. Also, our results document spawning site fidelity on a finer spatial scale than suggested by previous studies in the Gulf of Maine using conventional tagging (~20 km) (e.g., Howell et al. 2008; Perkins et al. 1997). The residence times and wander rates calculated for cod in the SCCZ demonstrate that most fish spawn in a given location over a period of approximately three to eight weeks, while exhibiting infrequent movements away from the spawning site. Our findings are similar to those of Siceloff and Howell (in press), who investigated cod on the Whaleback spawning site during the spring of 2006, and reported residence times of 8-54+ days and individual home ranges of approximately 17-57 km^2. The high degree of residency observed while spawning serves as a likely isolation mechanism between spawning components. Additional mechanisms which contribute to the fine-scale and complex population structure in the Gulf of Maine include spawning site fidelity, restricted dispersal during the early life stages (Churchill et al. 2011; Huret et al. 2007), and temporal variation in spawning (Kovach et al. 2010).

The complex population structure in the Gulf of Maine is indicative of a metapopulation, which is comprised of many semi-discrete spawning components (GMRI 2012). As a consequence, the stock is particularly vulnerable to overexploitation, and the sequential depletion of semi-isolated spawning components has led to the collapse of population structure (Ames 2004). It is evident that the biological processes that determine population structure operate on a much finer-scale than the large spatial units used for assessment and management. Failure of management strategies to account for this complex stock structure is expected to lead to continued declines in diversity, which can go undetected and be exacerbated by large-scale, system-wide assessments that are unlikely to adequately represent the true stock status because they lack information on both the spatial and temporal variations in abundance (Ames 2004; Frank and Brickman 2000; Smedbol and Stephenson 2001; Svedäng an d Bardon 2003). Therefore, treating the complex structuring of Gulf of Maine cod as a single stock is expected to result in biased estimates of spawning stock biomass, annual yield, and recruitment, while simultaneously masking steady declines in these variables as spawning aggregations become depleted (Reich and DeAlteris 2009). In order to be effective, management strategies must acknowledge the complex population structure of cod to better account for natural biological processes (Kovach et al. 2010). In fact, the failure of past management strategies may be partly attributable to a lack of understanding of basic ecology and evolution (Rowe and Hutchings 2003).

The scales at which cod stocks would be most appropriately assessed and managed depends on factors such as the size and number of subpopulations and spawning components, the level of exchange among them, and their degree of relative isolation (Smedbol and Stephenson 2001). Documentation of prevalent and accurate fine-scale spawning site fidelity indicates that there is a relatively large degree of isolation among spawning components in the Gulf of Maine. However, we have also gathered significant evidence to suggest that coastal spawning sites in the western Gulf of Maine have some degree of connectivity. Evidence for connectivity among spawning components exists in the adjusted homing rate being <100%, which suggests straying and potentially cod spawning at different locations in subsequent years. Perhaps a life history balance exists between homing and straying that maintains population stability, but allows for the colonization of new or inactive spawning sites (Robichaud and Rose 2001). However, recolonization rates are expected to be low given the prevalent and accurate homing behavior. Additional evidence of connectivity exists in the residence time data collected in the SCCZ. For example, fish that were only detected in the SCCZ for periods less than two weeks may have then moved on to spawn at another location.

Further evidence of connectivity exists in the recapture of cod tagged in the SCCZ on the Whaleback and Eagle Ridge spawning sites during the spawning season (Figure 4), as well as the 2012 acoustic telemetry data which documents movements between these spawning sites. These findings were interpreted to indicate movements between spawning sites in search of a mate and spawning activity. Other evidence exists in the Massachusetts Division of Marine Fisheries at-sea sampling of the commercial catch from Massachusetts state waters (Bill Hoffman, unpublished data). These data demonstrate that a high percentage of the catch taken from state waters in May and June is in spawning condition. When interpreted in light of our tagging data, this may represent cod being intercepted by the fishery as they move between coastal spawning sites. The observed connectivity among spawning components corroborates findings from recent genetic studies, which also identify connectivity and reproductive overlap among spring spawning components in the western Gulf of Maine (Kovach et al. 2010).

Critical features of a metapopulation include the existence of local populations that experience partially independent dynamics with some degree of connectivity (Kritzer and Sale 2004). Therefore, the prevalent homing behavior and the connectivity observed among spawning components provides additional support for the application of metapopulation theory to cod in the Gulf of Maine. Fortunately, metapopulation structure is expected to aid in the recolonization process by increasing the potential for range expansion of individual spawning components and improving the likelihood of recolonization on shorter timescales than would be expected within a more isolated stock (Rose et al. 2011; Stephenson 1999). Future research efforts should focus on gaining a better understanding of the movements and connectivity between spawning components to evaluate potential mechanisms for recolonization, including the impacts of environmental influences and recruitment processes (Rose et al. 2000). This is particularly important because recruitment will become increasingly reliant upon the few remaining spawning sites (Cardinale and Svedäng 2004).

Our findings will help determine the appropriate scales for management of cod in the Gulf of Maine. The documentation of prevalent and accurate homing behavior, combined with the findings of genetic studies, indicates that each spawning component is a semi-independent and partially self-reproducing group. Therefore, in order to promote recovery and prevent further collapse of population structure, it is essential to identify spawning areas and to protect them from overexploitation during the spawning season (Heath et al. 2008). The connectivity observed between spawning components suggests that restricted fishing within coastal waters during the spawning season may be warranted to protect spawning aggregations from overexploitation and to prevent interruption of their spawning activity (e.g., Dean et al. 2012; Morgan et al. 1997). However, management of Gulf of Maine cod will be complicated by the existence of many genetically distinct spawning components (Kovach et al. 2010) whose distributions overlap outside of the spawning season (Tallack 2012).

The implementation of complex and dynamic population structures into novel and less static management procedures has been considered a primary goal for future fisheries management approaches (Reiss et al. 2009). This is particularly important since the response time of the full science-management process has often been too slow to prevent major stock declines (Rice 2006). Moving forward, decision-making that builds on more detailed ecological knowledge is required because spatially separate stocks demand individual, spatially sensitive management plans with more local decision-making (Hutchings 2000; Sterner 2007). Future stock assessments and management plans must account for the complex structure of cod populations and begin to acknowledge biologically meaningful populations by managing fish complexes on finer-scales than previously considered to preserve stock complexity and promote stock rebuilding (Stephenson 1999).

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Figure 1: Location of the Spring Cod Conservation Zone (SCCZ) within Massachusetts Bay in the western Gulf of Maine, an area which is closed annually from April 16th - July 21st to protect spawning cod that aggregate there each spring (From Dean et al. 2012, Figure 1).

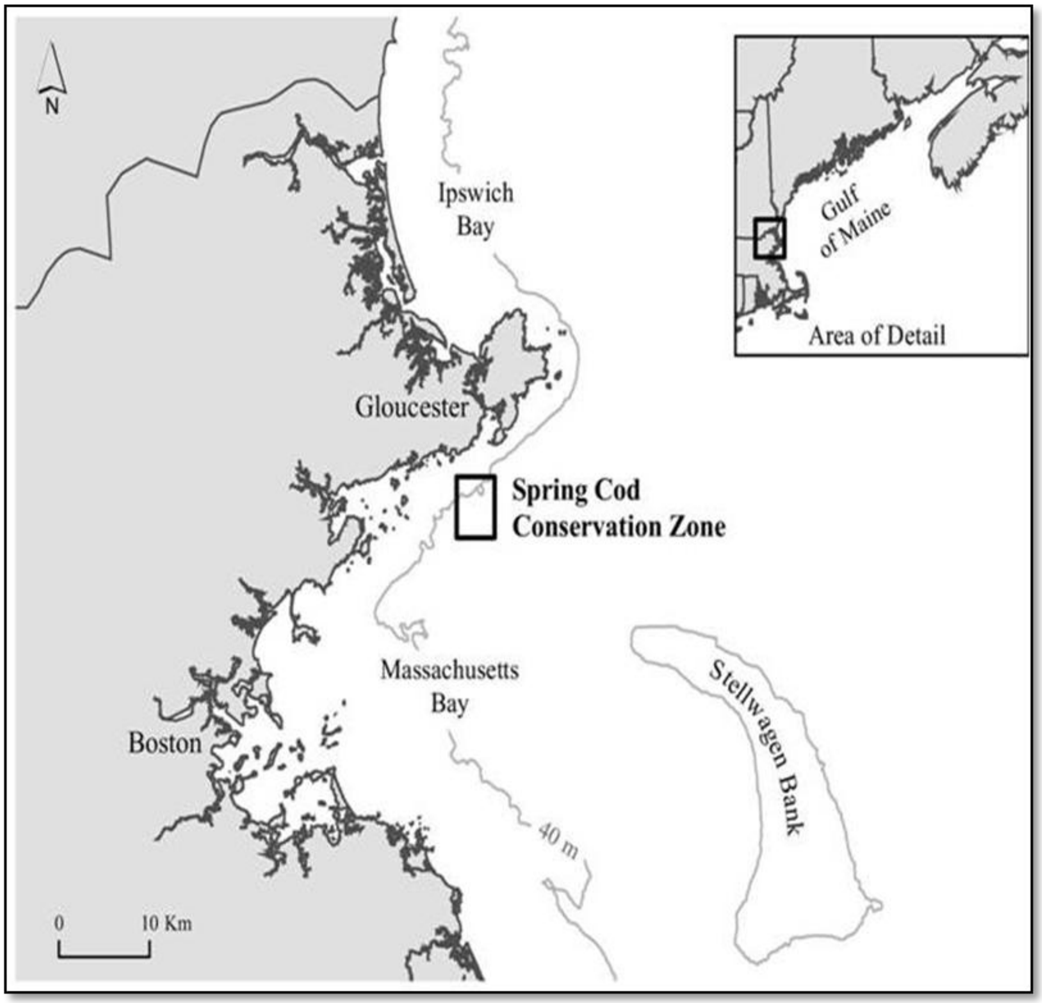

Figure 2: Image of a cod tagged with a surgically implanted acoustic transmitter (Vemco V16P-6H) and an externally attached archival data storage tag (Star-ODDI milli-L) below the first dorsal fin.

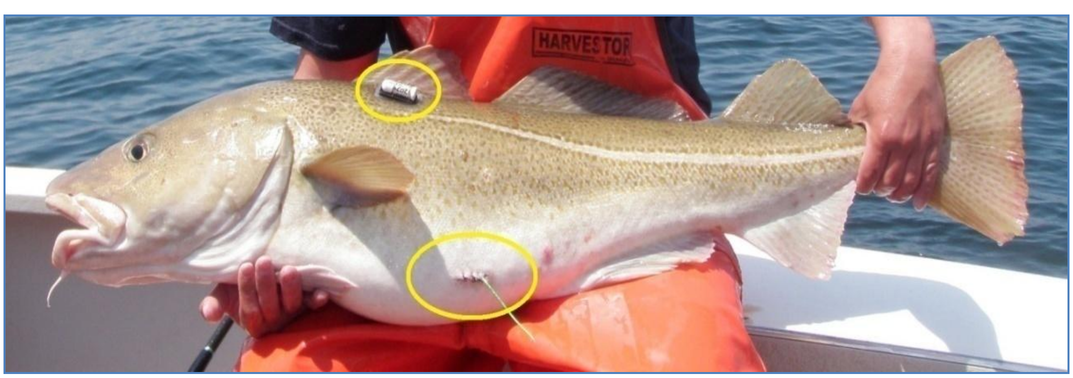

Figure 3: Schematic of the 28-receiver Vemco VR2W Positioning System (VPS) that was deployed in the Spring Cod Conservation Zone (SCCZ) in 2010 and 2011 to track cod movements within the spawning closure. Each receiver is spaced 400m apart and the array has a total detection range of 9.5 km^2.

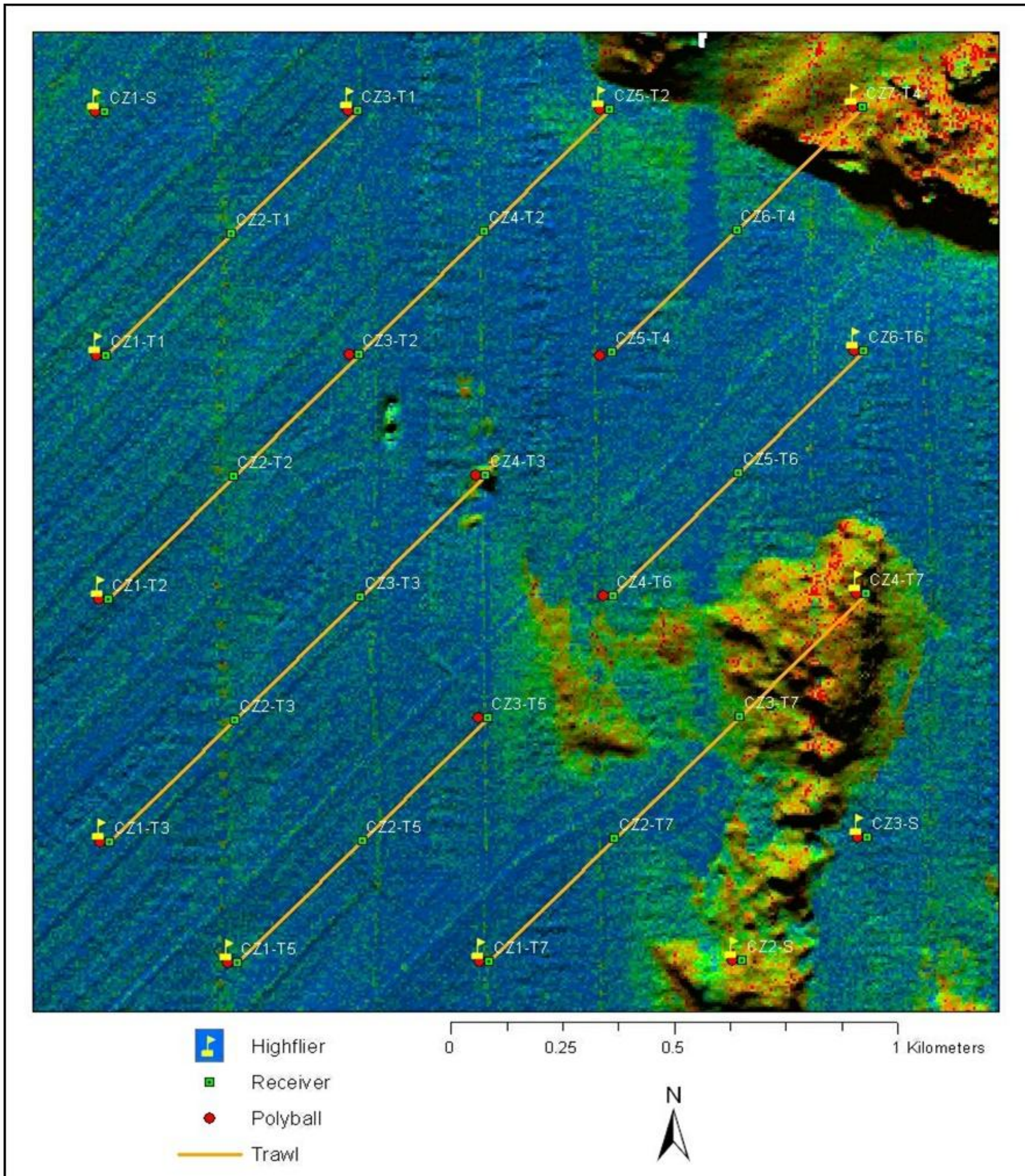

Figure 4: Schematic of the 2012 Vemco VR2W Positioning System (VPS) that was deployed in the Spring Cod Conservation Zone (SCCZ). The 2012 VPS array consisted of 25 receivers spaced 800m apart to provide a detection area of 15.89 km^2.

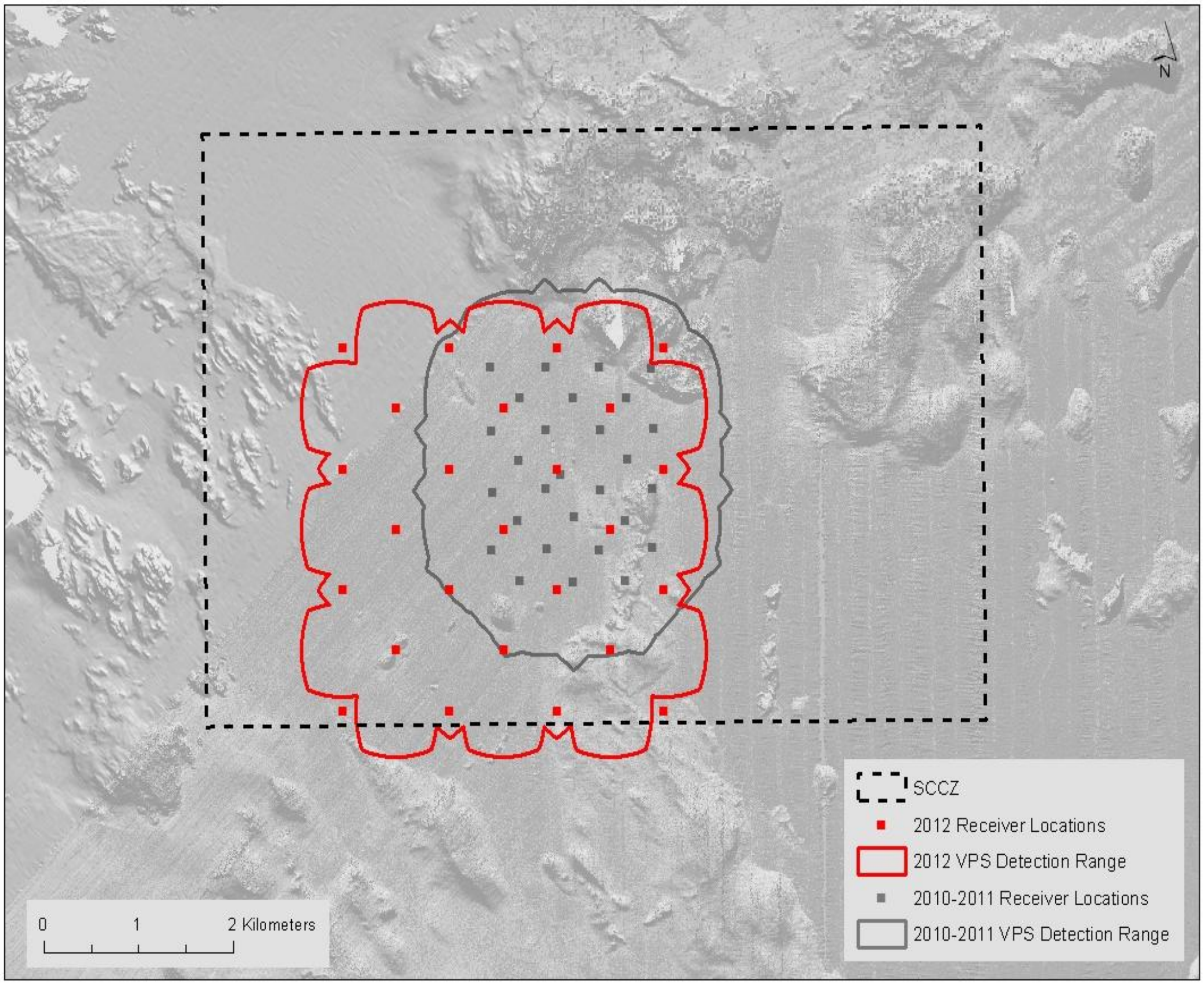

Figure 5: Plot of the recapture locations of cod that were tagged in the SCCZ during the 2010 and 2011 spawning seasons and were reported by fishermen as of May 2012 (n = 128). Tag recaptures which came during the spawning season from the Whaleback spawning site in Ipswich Bay and the region of Eagle Ridge in Massachusetts Bay are circled since they present evidence of connectivity among cod spawning components in the western Gulf of Maine.

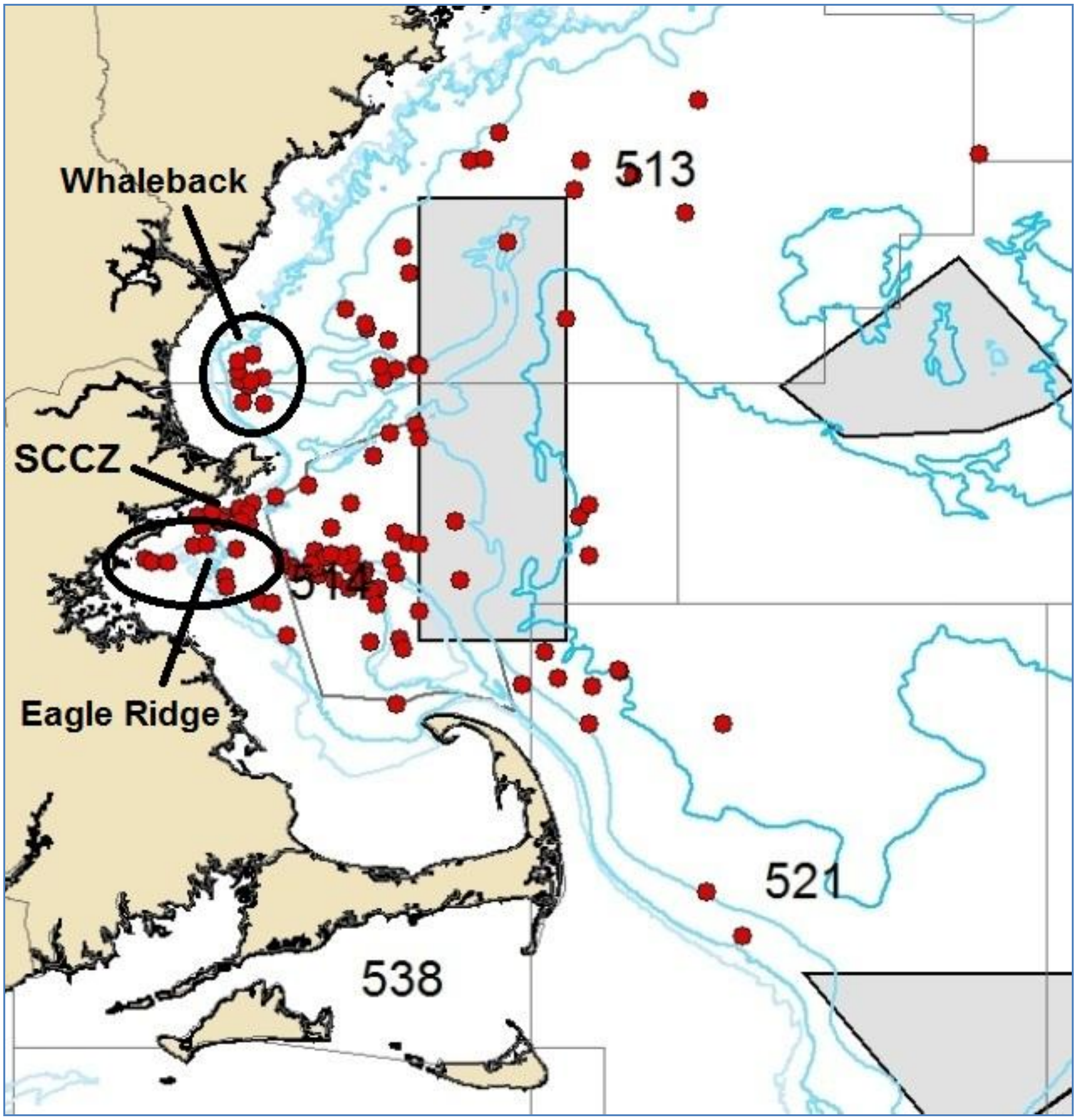

Figure 6: Map of the acoustic receivers deployed during the spring of 2012. In addition to the 25-receiver VPS array deployed in the SCCZ, there were eight receivers deployed on the Whaleback spawning site in Ipswich Bay (~45km north of the SCCZ) and four receivers were set on the Eagle Ridge spawning site in Massachusetts Bay (~14km south of the SCCZ).

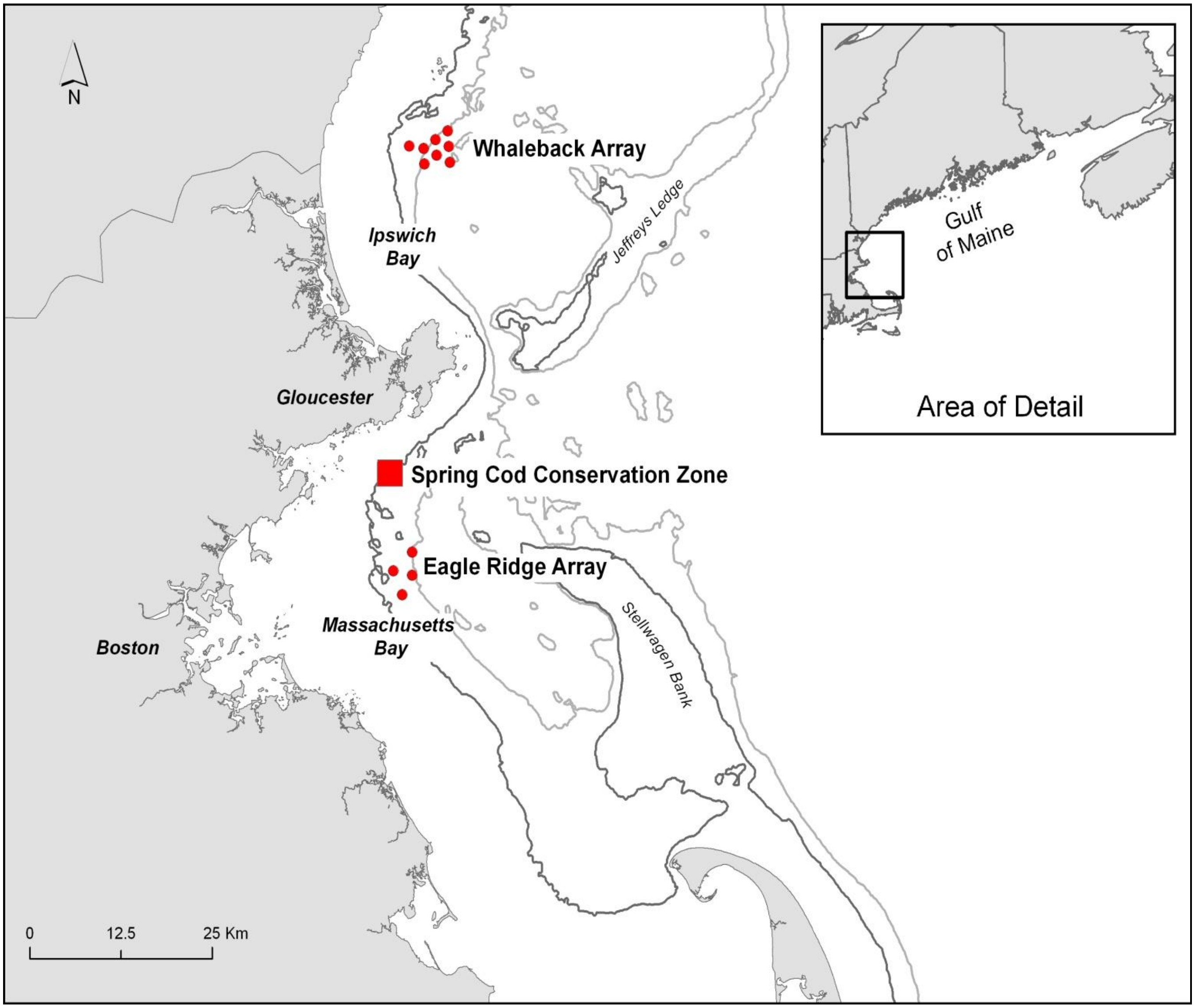

Figure 7: Length distribution of the 52 cod that were tagged with acoustic transmitters in 2010 (24 males : 28 females).

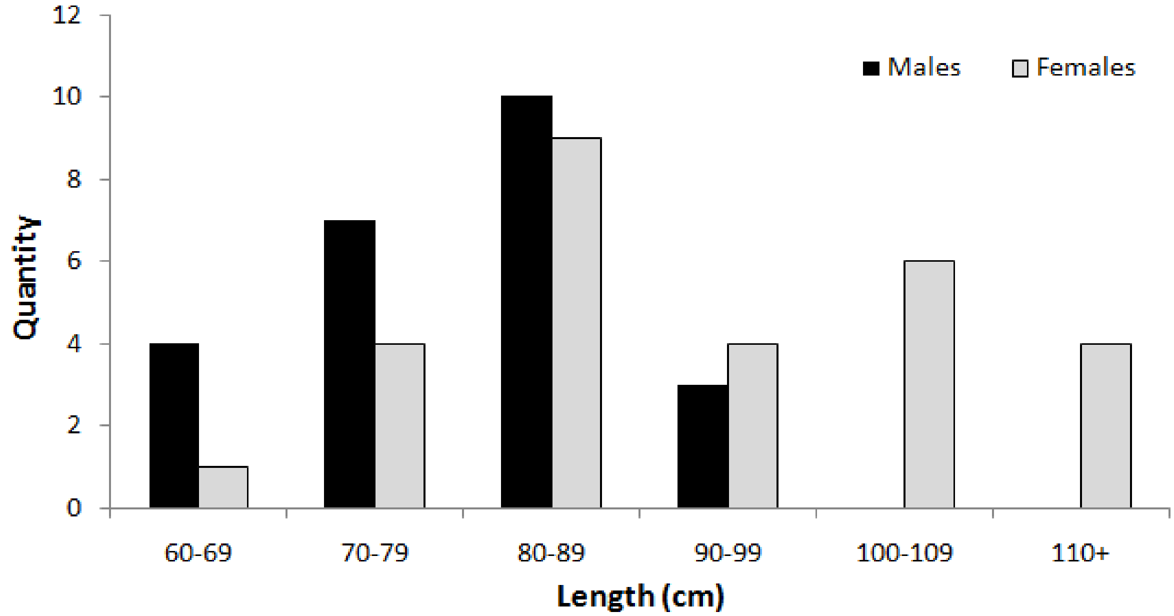

Table 1: Wander rates calculated from 2010 and 2011 acoustic telemetry data for cod that were tagged in 2010. Data is divided between males and females, and between day and night time intervals.

	Wander Rate		Day		Night	
	Males	Females	Males	Females	Males	Females
2010	8.2%	4.2%	6.3%	3.7%	10.1%	4.7%
2011	21.6%	8.2%	13.5%	8.6%	29.7%	7.7%

Table 2: Residence time data for fish that were tagged in 2010 and returned to the SCCZ in 2011, thus exhibiting spawning site fidelity. Included are estimates of 2010 minimum residence times, actual residence times from 2011, and 2012 actual residence times for fish that returned to the SCCZ for a third consecutive year. Tag lengths (cm) are reported as recorded when tagged in 2010.

				Residence Time		
Fish #	Date Tagged	Tag Length	Sex	2010	2011	2012
32	6/8/2010	77	F	31	4	2
41	6/18/2010	81	F	16	19	11
42	6/18/2010	99	F	11	20	-
62	7/20/2010	112	F	15	20	-
26	5/11/2010	69	M	14	27	-
25	5/11/2010	109	F	22	28	47
16	5/7/2010	77	M	28	30	-
29	5/11/2010	84	M	51	33	-
61	7/16/2010	99	M	2	34	-
39	6/8/2010	82	M	11	37	-
17	5/7/2010	80	M	32	46	67+
35	6/8/2010	104	F	4	51	86+
28	5/11/2010	74	M	12	52	-
44	6/18/2010	69	M	54	53	-
52	7/2/2010	118	F	40	106	-