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Using Fishermen's Ecological Knowledge to map Atlantic cod spawning grounds on Georges Bank

Gregory R. DeCelles[1,2]*, David Martins[1,2], Douglas R. Zemeckis[1,‡], and Steven X. Cadrin[1]

[1]*School for Marine Science and Technology, University of Massachusetts Dartmouth, 706 South Rodney French Blvd, New Bedford, MA 02740, USA*

[2]*Massachusetts Division of Marine Fisheries, 1213 Purchase Street, New Bedford, MA 02740, USA*

**Corresponding author: tel: +1 508 990 2860; fax: + 1 508 990 0449; e-mail: gregory.decelles@state.ma.us*

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The spawning dynamics of Atlantic cod (*Gadus morhua*) on Georges Bank and Nantucket Shoals are not well understood. To address this uncertainty, we combined Fishermen's Ecological Knowledge (FEK) with traditional scientific data to develop a more holistic understanding of cod spawning on Georges Bank. Data from historical reports, trawl surveys, fisheries observers, and ichthyoplankton surveys were used to describe the spatial and temporal distribution of cod spawning activity. We also collected FEK regarding cod spawning dynamics through semi-structured interviews ($n = 40$). The fishermen had detailed knowledge of the spatial and temporal distribution of cod spawning, and identified persistent fine-scale (i.e. $<50\,km^2$) spawning grounds that were often associated with specific habitat features, including spawning grounds that were previously unreported in the scientific literature. The spawning seasons and locations identified by fishermen generally agreed with information from traditional scientific data, but it was evident that seasonal scientific surveys lack the spatial and temporal resolution needed to fully characterize the distribution of cod spawning activity. Our results will help inform management measures designed to promote the rebuilding of Georges Bank cod, and also provide a basis for further investigations of cod spawning dynamics and stock structure.

Keywords: Atlantic cod, Fishermen's Ecological Knowledge, *Gadus morhua*, Georges Bank, spawning grounds, stock structure.

Introduction

Fishermen and scientists observe the marine environment from different perspectives. Scientists use standardized data collection methods, such as trawl surveys, to collect random samples representative of the population of inference. Although surveys may occur over the course of days or weeks, observations collected at a single station only provide snapshots of these complex ecosystems (Murray *et al.*, 2008a; Macdonald *et al.*, 2014). Surveys are typically conducted across large spatial scales and the data are aggregated over relatively coarse temporal scales (e.g. seasonal or annual) to construct time series of information on the abundance, distribution, and demographics of fishery resources. Modern stock assessment methods have been designed to use these standardized time series of abundance data to estimate population size, evaluate stock status, and provide a basis for management advice.

On the other hand, the objective of fishermen is to catch fish, and their observations are not random. A fisherman's decision about when and where to fish is dictated by a variety of factors, including their expectation of catch per unit effort, weather, fishery regulations, fuel prices, and market demands. As a result, fishermen's observations are not standardized, making it difficult to integrate this information with traditional scientific knowledge (Neis *et al.*, 1999a; Anuchiracheeva *et al.*, 2003). In turn, fishermen's observations are frequently dismissed as "anecdotal", and their perspectives are often overlooked by scientists and policy

[‡]Present address: Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, NJ 08901, USA.

makers (Pederson and Hall-Arber, 1999; Ames, 2003; Hind, 2015). However, involving fishermen more directly in stock assessment and management can improve fishery science and increase the credibility of management decisions (Bergmann *et al.*, 2004; Yates, 2014; Stephenson *et al.*, 2016).

Fishermen typically keep detailed records of their fishing activity and catch, and this information is often shared in real time and passed down over multiple generations (Neis *et al.*, 1999a; Bergmann *et al.*, 2004). The transmission of knowledge among fishermen allows them to "scale up" their observations across time and space, enabling fishermen to acquire unique perspectives encompassing a range of spatial and temporal scales (Murray *et al.*, 2008a). For example, fishermen commonly have a thorough understanding of how fish move seasonally over a wide geographic range to feed or spawn, as well as how small-scale bathymetric features (e.g. specific boulder piles, convex sand humps) may each influence fish behaviour or abundance. Whereas fishermen are keenly aware of these fine-scale habitats, our scientific data collection methods often lack the spatial resolution to examine abundance and distribution at such a small scale. Following years of observation, fishermen are also cognizant of long-term trends in fish abundance and changes in size structure (Pederson and Hall-Arber, 1999; Macdonald *et al.*, 2014). In addition, fishermen also understand how the distribution and abundance of target species can change across tidal, diel, lunar, and seasonal scales (Neis *et al.*, 1999a; Johannes *et al.*, 2000).

Many authors have asserted that Fishermen's Ecological Knowledge (FEK) is part of the best available science, and as such, it should play a larger role in fishery management (e.g. Johannes *et al.*, 2000; Hutchings and Ferguson, 2000a; Stephenson *et al.*, 2016). FEK has proved to be a valuable and cost-effective supplement to existing institutional data, and incorporating FEK into the scientific process has led to more robust management decisions (e.g. Bergmann *et al.*, 2004; Scholz *et al.*, 2004). For example, FEK has been used to offer insights into long-term trends in the abundance and distribution of fish populations such as megrim (*Lepidorhombus whiffiagonis*) in the North Sea (Macdonald *et al.*, 2014) and cod (*Gadus morhua*) in Greenland (Hedeholm *et al.*, 2016). Bergmann *et al.* (2004) used the knowledge of fishermen to identify Essential Fish Habitat for cod, haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) in the Irish Sea. FEK is informative for investigating changes in the harvesting dynamics of fish populations, as Hutchings and Ferguson (2000a, b) demonstrated for cod in Newfoundland. FEK can also provide valuable information for stock identification research, because fishermen often have a detailed understanding of the migratory patterns, morphological characteristics, and feeding habits of their target species (Neis, 1998; Hedeholm *et al.*, 2016). For example, FEK has offered insight into the stock structure of cod in the Gulf of St Lawrence (Murray *et al.*, 2008b) and Newfoundland (Neis, 1998). Fishermen often know where and when spawning activity occurs, and FEK has been used to identify spawning grounds for many species, including cod in the Gulf of Maine (Ames, 1997) and Newfoundland (Neis, 1999b), bonefish (*Albula glossodonta*) in Tarawa, Kiribati (Johannes *et al.*, 2000), and coastal fishes in Brazil (Silvano *et al.*, 2006). FEK has also led to the discovery of cod spawning grounds previously unknown to scientists in Newfoundland (Neis, 1998) and along the coast of Norway (Maurstad, 2002). Furthermore, FEK has been used to identify

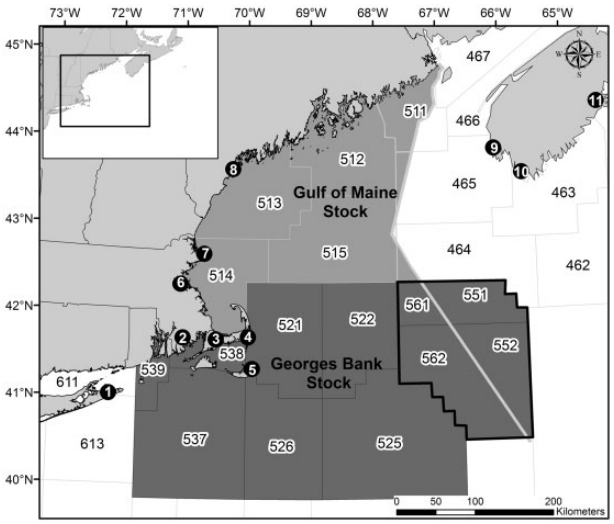

Figure 1. Management boundaries for cod in U.S. waters, including the Gulf of Maine and Georges Bank stocks. Cod on eastern Georges Bank (outlined in bold) are managed as a transboundary resource by the United States and Canada. The black numbered circles depict the ports where we interviewed fishermen: 1 = Montauk, NY, 2 = New Bedford, MA, 3 = Hyannis, MA, 4 = Chatham, MA, 5 = Nantucket, MA, 6 = Boston, MA, 7 = Gloucester, MA, 8 = Portland, ME, 9 = Yarmouth, Nova Scotia, 10 = Pubnico, Nova Scotia, and 11 = Lunenburg, Nova Scotia.

cod spawning grounds that have been extirpated in the Gulf of Maine (Pederson and Hall-Arber, 1999; Ames, 2004), and in Newfoundland (Neis, 1998), which can be critical for understanding long-term changes in stock productivity and recruitment.

In this study, we sought to gather FEK related to the spatial and temporal distribution of Atlantic cod (*G. morhua*) spawning activity on Georges Bank and Nantucket Shoals. For many centuries, cod have supported major commercial and recreational fisheries throughout the North Atlantic (e.g. Rose, 2007), including off the coast of New England (Serchuk and Wigley, 1992; Rosenberg *et al.*, 2005). However, in recent decades, cod stocks off New England have decreased in abundance, and recent catches are a small fraction of historical landings and estimates of Maximum Sustainable Yield (NEFSC, 2013; NEFSC, 2015; Wang *et al.*, 2015). From 1972 onwards, cod have been managed in U.S. waters as two units: the Georges Bank and Gulf of Maine stocks (Serchuk and Wigley, 1992) (Figure 1). Cod on the eastern portion of Georges Bank are assessed and managed jointly between the United States and Canada by the Transboundary Resources Assessment Committee (Wang *et al.*, 2015). Despite continuously evolving fishery management strategies (NEFMC, 2009; NEFSC, 2013), persistent difficulties remain with respect to ending overfishing (Rothschild *et al.*, 2014) and managing the rebuilding of cod (NEFSC, 2013, 2015; Wang *et al.*, 2015). Some of the factors contributing to the lack of rebuilding include poor recruitment, low weights at age, age truncation, and high natural mortality rates (Wang *et al.*, 2015). Therefore, additional research is required to improve our understanding of cod population and spawning dynamics on Georges Bank to inform future fishery management decisions intended to support rebuilding.

Understanding where and when cod spawn can aid in stock identification, because the variability in spawning location and

timing often function as mechanisms that contribute to the development of metapopulations by limiting the reproductive connectivity among subpopulations (Grabowski *et al.*, 2011; Zemeckis *et al.*, 2014a). Cod spawning components will be the most geographically discrete and exhibit minimal mixing whilst spawning (Cushing, 1981). Therefore, studying the spatial and temporal distribution of cod spawning can provide insights into cod population structure. Cod spawning activity also presents important implications for fishery management (Zemeckis *et al.*, 2014b). Cod spawn over an extended period of time at locations that are often predictable and close to shore (Siceloff and Howell, 2013; Dean *et al.*, 2014), and fishing activity can disrupt cod spawning behaviour (Dean *et al.*, 2012). In addition, given that cod spawning components are semi-discrete and there is often limited connectivity among them (Smedbol and Stephenson, 2001), there is a great deal of risk with respect to the extirpation of these population segments. In fact, declines in spawning diversity have been well documented in many cod stocks, including in the Gulf of Maine (Ames, 2004) and the North Sea (Svedäng et al., 2010). The failure of past management plans to achieve rebuilding targets in the Gulf of Maine has been considered to be in part due to their lack of consideration of the complex metapopulation structure (Ames, 2004; Kovach *et al.*, 2010; Armstrong *et al.*, 2013). However, relatively little is currently known about the spawning dynamics of cod on Georges Bank, and it is uncertain whether declines in spawning diversity have influenced stock productivity.

By soliciting FEK and analysing historical reports, Ames (1997, 2004) created detailed maps of the spawning grounds and migratory patterns of Atlantic cod in the Gulf of Maine. His results provided valuable insight into cod stock structure and population dynamics, and helped inform future research investigating cod spawning dynamics in the Gulf of Maine (Armstrong *et al.*, 2013; Gurshin *et al.*, 2013; Siceloff and Howell, 2013; Dean *et al.*, 2014; Zemeckis *et al.*, 2014a). However, similar fine-scale information on cod spawning grounds is not available for Georges Bank, including the Great South Channel and Nantucket Shoals regions. Given the depleted status of Georges Bank cod and the low stock productivity (NEFSC, 2013), additional directed research is needed to improve our understanding of cod spawning activity and population dynamics on Georges Bank, which can help inform future management decisions intended to promote rebuilding. In this study we sought to combine FEK with traditional scientific data to improve our understanding of cod spawning on Georges Bank, and compare historical and contemporary data to investigate potential shifts in spawning activity.

Methods

Analysis of scientific data

We analysed several scientific datasets and published reports to gather information related to cod spawning activity on Georges Bank to provide context and comparison to FEK. Historical reports of cod fishing and spawning grounds on Georges Bank were reviewed (Goode, 1884; Rich, 1929; Bigelow and Schroeder, 1953), along with information from historical tagging studies (Smith, 1902; Schroeder, 1930; Wise 1963).

The abundance and distribution of cod were investigated using the NOAA Northeast Fisheries Science Center's (NEFSC) spring and fall bottom trawl survey data. Our analysis was limited to tows completed from 1970 to 2014, and in NEFSC offshore strata 9–25 to match the strata included in the Georges Bank cod stock assessment (NEFSC, 2013). Burnett *et al.* (1989) provide details on maturity staging guidelines and report that the NEFSC began collecting spawning stage information for cod in 1970. The timing of NEFSC surveys varied from year to year, but all spring trawl survey tows were conducted in March, April, May, and June, with most of the tows completed in April (70.9%) and March (22.9%). The fall trawl survey tows occurred in September, October, November, and December, and most tows were completed in October (80.1%) and November (10.1%). Similarly, the abundance and distribution of cod observed from 1987 to 2015 during the Canadian Department of Fisheries and Oceans (DFO) annual trawl survey during February and March were examined. Morrison (1990) described the maturity staging guidelines that are used on the DFO trawl survey. For both surveys, the abundance of spawning cod (defined here as maturity stages; ripe, ripe and running, or spent) observed at each survey station was aggregated over ten year time periods (e.g. 1970–1979) and plotted to identify areas where spawning cod were sampled, and to investigate potential changes in the distribution of spawning activity over time. For both the NEFSC spring trawl survey and the DFO trawl survey, we performed a G* hotspot analysis (Getis and Ord, 1992) to identify survey tow locations where the number of spawning cod was significantly greater than average ($p < 0.05$) and were surrounded by other tows with above average catches of spawning cod, following the methods outlined by the Closed Area Technical Team (NEFMC, 2013). For both surveys, the number of hotspots within a 100 km^2 grid was summarized to identify spatial clusters of spawning activity.

Ichthyoplankton sampling datasets from the United States and Canada were investigated to describe the temporal and spatial distribution of cod eggs on Georges Bank. We obtained data on the distribution and abundance of cod eggs observed during the United States Global Ocean Ecosystems Dynamics (GLOBEC) program, which sampled on Georges Bank from February to July in 1995, and from January to June from 1996 to 1999 (Sibunka *et al.*, 2006). Cod eggs were classified to three stages, and stage-one eggs represented the period from "spawned to just before blastopore closure" (Sibunka *et al.*, 2006). The monthly distribution and abundance of stage-one cod eggs that were observed from 1995 to 1999 were plotted. We chose to examine the distribution of stage-one eggs, because these eggs had been adrift for the shortest period of time and would presumably be closer to the spawning grounds than later stage eggs. We also reviewed published reports from the Marine Resource Monitoring Assessment and Prediction (MARMAP) program, which collected monthly bongo net samples of fish eggs and larvae in the Northwest Atlantic from 1977 to 1987 (Page *et al.*, 1998; Berrien and Sibunka, 1999), and Hanke *et al.* (2000), which summarized the results of three ichthyoplankton sampling programs completed by the Canadian DFO on Georges Bank and the Scotian Shelf from 1975 to 1997.

Data collected by the Canadian Fisheries Observer Program between 1983 and 2015 were used to investigate the timing and location of cod spawning on eastern Georges Bank. Canadian fishery observers sampled the maturity stages of cod using the same classification scheme employed on the DFO trawl survey. Cod were often subsampled for maturity when the catches were large. The spatial and temporal distribution of observations reflect patterns of fishing effort on eastern Georges Bank by the trawl fleet, which is constrained by factors such as the Canadian

jurisdiction and seasonal fishery regulations. For example, trawling is typically prohibited on eastern Georges Bank from early February to May to protect spawning cod (Wang *et al.*, 2015), which limited the ability of observers to collect cod maturity data during certain times of the year.

Interviews with fishermen

We used a semi-structured interview approach to gather FEK regarding their understanding of cod spawning dynamics on Georges Bank, with a focus on the spatial and temporal distribution of spawning activity. The semi-structured interview format allowed us to collect information that could be compared and standardized across interviews. In this flexible format, the interview was guided by a common set of questions, but the fisherman had latitude to discuss their observations and perspectives. Two or more scientists were present for almost every interview, with one scientist leading the discussion, and the other scientist(s) recording answers and marking spatial information by hand on paper nautical charts of Georges Bank. An audio recording was also captured for each interview. Current and retired captains ($n = 40$) with experience fishing for cod on Georges Bank were interviewed. We started by interviewing experienced captains known from previous collaborative research projects, and used a snowball sampling process (Babbie, 1989) to generate additional interviews by asking captains to refer other fishermen who also targeted cod on Georges Bank. One interviewer is fluent in Portuguese, which enabled us to interview Portuguese speaking fishermen in New Bedford, MA, USA, where many of the captains in the trawl fishery are of Portuguese descent.

The interviews were done at times and locations that were convenient for fishermen, and were typically conducted aboard their vessels whilst in port, in cafes, their homes, or in our office. Participation was voluntary, and fishermen were not required to share any information they did not want to. Participating fishermen were compensated for their time with a $50USD gift card, although most fishermen were not aware of the compensation until after the interview had been completed. Each fisherman was required to read and sign an interview consent form, which had the approval of the University of Massachusetts Dartmouth Office of Institutional Compliance and Ethics. The duration of interviews ranged from 45 min to 3 h, depending upon each fisherman's knowledge and their willingness to provide information. We interviewed fishermen from throughout New England and Nova Scotia, in order to gain the perspectives of a diverse group of fishermen with experience fishing across all regions of Georges Bank. A conscious effort was made to interview fishermen without the presence of other fishermen, so that participants could answer survey questions freely and to the best of their knowledge without influence from others. However, in one instance, three fishermen were interviewed together on Cape Cod due to unavoidable logistical reasons.

Each interview began with a series of demographic questions designed to gauge the fishermen's experience fishing for groundfish, including specifically targeting cod on Georges Bank (Table 1). Next, fishermen were asked to recall times and locations where they had observed spawning cod. Fishermen were asked to identify and delineate these locations on NOAA nautical chart 13 200 (http://www.charts.noaa.gov/OnLineViewer/13200.shtml, last accessed 9 January 2017.) which encompasses the area from southern New England to eastern Georges Bank. Many fishermen also provided information from their own charts, logbooks, and plotters, and used this information to precisely identify the locations and time of year where they captured spawning cod. For each spawning ground that fishermen identified, we asked them a series of questions to classify the timing of spawning at that location and to collect information on the biological characteristics and habitat associated with that spawning ground (Table 1). Fishermen were asked to specify the criteria they used to determine that area was a cod spawning ground. Fishermen were also shown pictures of male and female cod at different maturity stages, and were asked to identify which maturity stages they observed at that location. Having the photos of the gonads of spawning cod helped to distinguish cod feeding grounds from spawning grounds. The cod maturity stage guide was obtained from the NOAA NEFSC (Richard McBride, pers. comm.) and is the same guide used during trawl surveys (Burnett *et al.*, 1989). Finally, as time allowed, we asked the fishermen questions related to the biology and stock structure of cod on Georges Bank (Table 1).

After each interview, the spawning grounds identified by the fishermen were digitally mapped in ArcGIS. By relying on the nautical charts and the GIS mapping, we were able to standardize the spatial information provided by the fishermen. A unique shapefile was created for each spawning ground, and a layer file containing all of the spawning grounds identified by each fisherman was created. The spawning grounds were also grouped in space and time for visualization purposes. For example, layer files were created which contained all of the spawning grounds that were identified in each month. Spawning grounds were classified according to different regions of Georges Bank (Figure 2), and layer files were created to display all of the spawning grounds identified in each region. We used geoprocessing tools in ArcGIS to quantify the amount of overlap between spawning grounds (i.e. shapefiles) and to quantify the number of fishermen that identified spawning activity at a given location. We identified "consensus spawning grounds" which were locations where spawning activity was reported by three or more fishermen.

Results

Analysis of scientific data

Goode (1884) and Rich (1929) described the "Winter Fishing Grounds", an area on eastern Georges Bank between the parallels of 41°30′N and 42°N and 66°38′W and 67°30′W with rocky bottom and depths ranging from 55 to 73 m. The Winter Fishing Ground was reported to serve as a major cod spawning ground in February, March, and April, when dense aggregations of spawning cod would predictably form every year (Goode, 1884). Bigelow and Schroeder (1953) described major cod spawning activity that occurred on Georges Bank in February, March and April, and defined the grounds as occurring in depths of ∼64 m from about 41°21′N to 41°31′N and from 66°50′W to 67°W.

Nantucket Shoals has long been known to serve as a cod spawning and feeding ground (Bigelow and Schroeder, 1953), and Goode (1884) described a number of important cod fishing grounds on Nantucket Shoals and east of Cape Cod, including Outer Crab Ledge, Pollock Rip, Great Rip, Fishing, Rip, and Phelps Bank. Smith (1902) collected mature cod from Nantucket Shoals, held them in a laboratory, and observed that spawning occurred from the middle of November until the end of January. On the basis of tag returns, Schroeder (1930) concluded that cod spawn on Nantucket Shoals from November to April, with peak

Table 1. Questions that we asked fishermen during the interviews.

Part 1: Demograhic questions
1) What is your year of birth?
2) How many total years of experience do you have commercial fishing?
2) How many years of experience do you have commercial fishing for groundfish on Georges Bank and Nantucket Shoals?
3) How many years of experience do you have fishing specifically for cod on Georges Bank and Nantucket Shoals?
4) Of the total years you have spent fishing for groundfish on Georges Bank and Nantucket Shoals, how many years were you a deckhand, a mate, and a captain?
5) What gear types did you use when fishing for cod?
Part 2: Questions specific to each spawning ground
1) What was the name of the spawning ground?
2) What months did spawning occur here?
3) How were you able to determine this area was a cod spawning ground?
4) What maturity stages did you see at this spawning ground?
5) Were there more males or females in the catch?
6) What depths did you find spawning cod at this location?
7) How would you describe the magnitude of cod spawning at this site?
8) What was the predictability or consistency of this spawning ground from year to year?
9) What size were the majority of cod you encountered at this spawning ground?
10) How would you describe the habitat at this spawning ground?
11) Is this spawning ground still active?
11a) If the spawning ground is still active, what is the magnitude of spawning now, compared with past levels?
11b) If the spawning ground is no longer active, what year did it cease to be active, and why do you think spawning stopped at this location?
Part 3: Secondary questions that were asked as time allowed
1) Did cod feed during the spawning season? Were cod also feeding at the spawning ground?
2) Was cod spawning activity related to time of day?
3) Is there connectivity between the spawning sites you identified within the larger spawning ground?
4) Did you notice a change in the size of the cod over the course of the year?
5) Was there anything unique about the shape of the cod at any of the spawning grounds?
6) Was there anything unique about the colour of the cod at any of the spawning grounds?
7) Do you think there is a boundary between Georges Bank cod and inshore cod?

spawning activity occurring in December and January. Schroeder (1930) also mapped cod spawning grounds on Nantucket Shoals that appear to correspond to areas that are currently known as the Fingers, Old Man Shoal, Old South Shoal, and Davis Bank. Tagging studies documented two migratory behavioural patterns of cod on Nantucket Shoals, with a group of fish that would remain resident on Nantucket Shoals throughout the year, and a second group of cod that would migrate in the fall to spawning grounds at several locations in southern New England and the mid-Atlantic (Smith, 1902; Schroeder, 1930; Wise, 1963).

From 1970 to 2014, 22 402 cod were sampled for maturity on the NEFSC spring trawl survey, of which 415 (1.9%) were ripe, 160 (0.7%) were ripe and running, and 2837 (12.7%) were spent. These observations suggest that most of the cod spawning activity had ended by the time the survey sampled on Georges Bank (i.e. 70.9% of tows in April). The G* hotspot analysis indicated that cod spawning hotspots were present on the northern and eastern portions of Georges Bank from 41°40′N to 42°12′N and between 66°W and 68°W, with the greatest concentrations of hotspots located on the Northeast Peak (Figure 3).

A total of 16 234 cod were sampled for maturity during the NEFSC fall survey, 305 (1.9%) cod were ripe, nine (0.06%) were ripe and running, and 221 (1.4%) were spent. In addition, 3031 cod (18.7%) were noted to be developing, suggesting that the fall survey, which primarily samples Georges Bank in October (80.1% of tows), occurs before most cod spawning activity.

Of the 16 668 cod that were sampled for maturity on the DFO trawl survey, 2359 (14.2%) were ripe, 2412 (14.5%) were ripe and running, and 2467 (14.8%) were spent. The greatest concentrations of spawning cod were observed in Canadian waters on eastern Georges Bank, primarily in depths between 50 and 100 m. Spawning cod were occasionally sampled across the Southwest Part of Georges Bank in depths <100 m, but were not observed in any tows completed in waters >100 m on the Southwest Part. The G* hotspot analysis demonstrated that the majority of cod spawning hotspots was located in Canadian waters on eastern Georges Bank, between 66°5′W and 66°50′W and 41°35′N and 42°5′N, although some spawning hotspots were also present in Closed Area II (Figure 4).

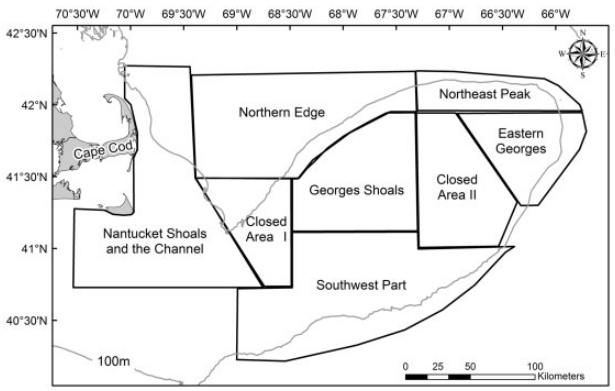

Figure 2. Eight geographic regions that were used to classify the location and timing of cod spawning on Georges Bank.

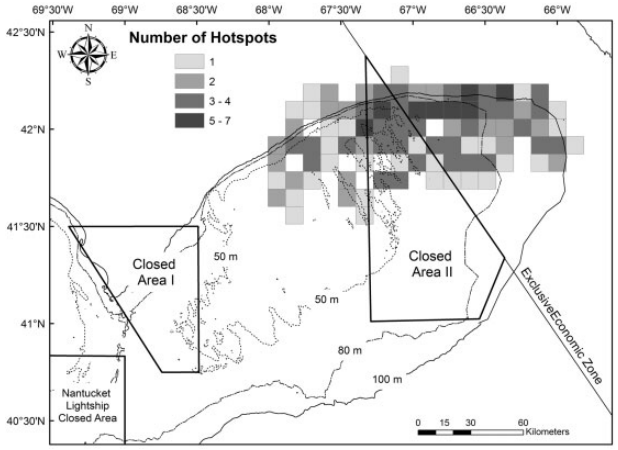

Figure 3. Distribution of cod spawning hotspots observed during the NEFSC spring trawl survey from 1970 to 2014. The number of hotspots within a 100 km^2 grid was summarized to identify spatial clusters of spawning activity. Cod fishing has been prohibited in the Closed Areas since 1994, with some exceptions. The Exclusive Economic Zone marks the boundary between the United States and Canadian portions of Georges Bank.

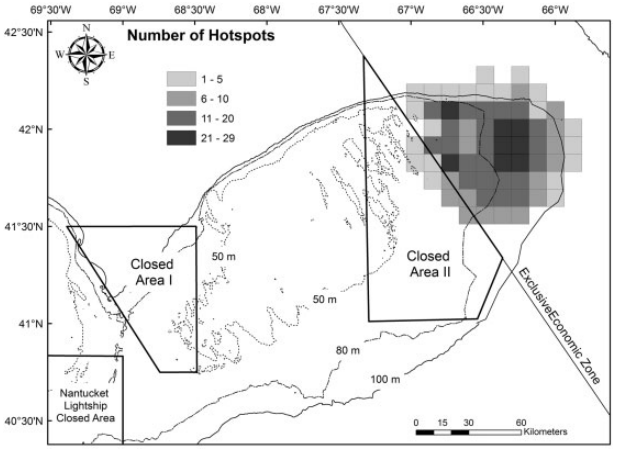

Figure 4. Distribution of cod spawning hotspots observed during the DFO trawl survey from 1987 to 2015. The number of hotspots within a 100 km^2 grid was summarized to identify spatial clusters of spawning activity.

Whereas cod eggs have been collected across a wide range of depths on Georges Bank, the highest concentrations of eggs were typically observed in depths < 100 m (Berrien and Sibunka, 1999; Hanke *et al.*, 2000). Cod eggs collected during the MARMAP program indicated that 60% of cod spawning occurs on Georges Bank between February 23rd and April 6th, with 90% of the spawning activity occurring between mid-November and mid-May (Page *et al.*, 1998). Cod eggs were observed on both eastern and western Georges Bank, with the highest concentration of eggs observed on the Northeast Peak (Page *et al.*, 1998; Berrien and Sibunka, 1999). Hanke *et al.* (2000) reported that cod eggs were not collected on Georges Bank in July and August, and that cod spawning on Georges Bank began in September and October, and continued with increasing intensity in November and December. Hanke *et al.* (2000) noted that cod eggs were abundant on Georges Bank in March and April, and that the spawning season ended in May or June.

During the GLOBEC ichthyoplankton sampling program, stage one cod eggs were present in the majority of tows completed from January to March, which suggests that cod spawning activity is widespread across Georges Bank during these months, and the greatest concentration of stage one cod eggs were observed in February and March (Table 2). In January, stage one eggs were rarely observed on the Southwest Part and on the Northern Edge, but were abundant on the Northeast Peak, Eastern Georges, and Closed Area II. In February stage one cod eggs were observed to be abundant on the Northeast Peak, Eastern Georges, and Closed Area II, with lower concentrations on Georges Shoals, the Southwest Part, and the Northern Edge. The distribution of stage one eggs was similar in March, although they were less commonly observed on the Northern Edge and Georges Shoals. Stage one cod eggs were observed in 35% of the samples collected in April, although the concentrations were substantially reduced from prior months. Stage one cod eggs were rarely observed in May and June, and no cod eggs were present in the 38 samples collected in July of 1995.

Of the 18 804 cod that were sampled by the Canadian Fisheries Observer Program, 7713 (41%) were in spawning condition, including 1780 (9.5%) that were ripe and running. Spawning activity appeared to increase from November to January, before peaking in February and March, which was when the highest proportion of spawning fish were observed (Table 3). A clear understanding of monthly trends is confounded to some extent by the paucity of fishery observations in March and April, but samples collected on the DFO bottom trawl survey indicate that cod are still actively spawning on eastern Georges Bank in early spring. The lowest proportions of ripe and ripe and running cod were observed from May to October. In May and June, a relatively large proportion of cod were spent or recovering, indicating that most spawning activity had ended.

Interviews with fishermen

Of the 52 fishermen we contacted for the project, 40 agreed to complete an interview. The fishermen we interviewed were captains, and 39 of the 40 had been captains for the majority of their careers. These fishermen collectively had 1566 total years of fishing experience, including 1373 years fishing specifically for cod on Georges Bank. On average, each fishermen had 34 years of experience targeting Georges Bank cod (range = 12–52 years). Eight of the 40 fishermen used multiple gear types to target Georges Bank cod. The majority of fishermen ($n = 35$) used an otter trawl, whereas others used gillnets ($n = 8$), longline ($n = 7$), and rod and reel ($n = 2$). The captains we interviewed fished from New Bedford, MA, USA ($n = 21$), Chatham, MA, USA ($n = 7$), Hyannis, MA, USA ($n = 1$), Gloucester, MA, USA ($n = 1$), Nantucket, MA, USA ($n = 1$), Boston, MA, USA ($n = 1$), Montauk, NY, USA ($n = 1$), Portland, ME, USA ($n = 1$), Pubnico, Nova Scotia, Canada ($n = 3$), Yarmouth, Nova Scotia, Canada ($n = 2$), and Lunenburg, Nova Scotia, Canada ($n = 1$) (Figure 1).

The captains were attentive to the reproductive condition of the cod they had caught, and could frequently recall in great detail the spawning condition of the fish in their catches. U.S. fishermen dressed their cod catch at sea, and often described seeing eggs and milt spilling out of the fish as an indication the cod were

Table 2. Monthly sampling intensity and concentration of cod eggs observed during the GLOBEC ichthyoplankton sampling program from 1995 to 1999.

Month	# of tows	# of tows with cod eggs (all stages)	# of tows with stage one cod eggs	Mean concentration stage one cod eggs (number/10 m^2)
Jan.	229	148 (65%)	115 (50%)	49.1
Feb.	338	260 (77%)	212 (63%)	173.1
Mar.	342	223 (65%)	171 (50%)	157.9
Apr.	334	179 (54%)	118 (35%)	17.9
May	374	55 (15%)	34 (9%)	11.9
Jun.	200	7 (4%)	3 (2%)	2.2
Jul.	38	0 (0%)	0 (0%)	0

The data were provided by Jon Hare at the NOAA Northeast Fisheries Science Center, and are described in Sibunka et al. (2006).

Table 3. Cod maturity stages observed each month by the Canadian Fisheries Observer Program on eastern Georges Bank from 1983 to 2015.

Month	Number of tows sampled	Number of cod sampled	Immature	Developing 1	Developing 2	Ripe	Ripe and running	Spent	Recovering	Resting
Jan.	852	9 537	3%	14%	29%	38%	9%	3%	3%	2%
Feb.	240	3 983	2%	8%	20%	31%	20%	7%	9%	3%
Mar.	6	28	0%	4%	4%	39%	50%	4%	0%	0%
Apr.	0	0								
May	18	362	2%	36%	2%	1%	0%	17%	25%	16%
Jun.	47	496	10%	22%	9%	3%	2%	23%	22%	8%
Jul.	85	1 089	11%	20%	7%	2%	0%	4%	15%	40%
Aug.	132	1 466	8%	20%	6%	1%	0%	5%	11%	48%
Sep.	86	721	8%	35%	13%	5%	1%	0%	5%	34%
Oct.	30	366	3%	32%	17%	3%	0%	4%	10%	30%
Nov.	29	372	5%	33%	30%	8%	5%	2%	4%	12%
Dec.	41	384	3%	20%	34%	22%	5%	2%	3%	12%

The data were provided by Irene Andruschenko at the Canadian Department of Fisheries and Oceans.

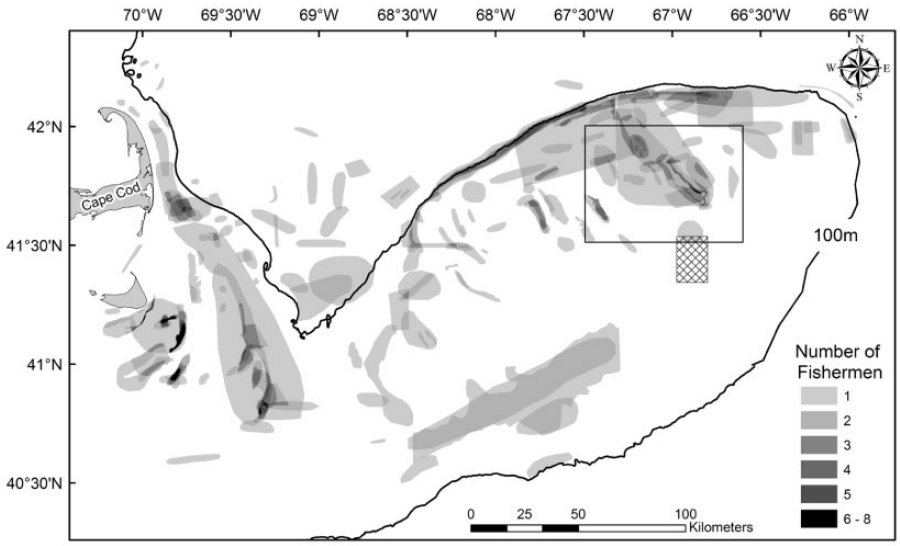

Figure 5. Cod spawning grounds that were identified by fishermen. Each polygon represents a spawning ground that was identified by a single fisherman. The shading is used to identify areas where there is overlap in the spawning locations reported by multiple fishermen. The rectangle outlined in black depicts the "Winter Fishing Grounds" that were described by Goode (1884) and Rich (1929). The hashed rectangle represents the cod spawning grounds that were reported by Bigelow and Schroeder (1953).

Table 4. Number of cod spawning and feeding grounds that were identified in each region of Georges Bank during interviews with fishermen.

Region	Number of fishermen that identified spawning grounds	Number of spawning grounds identified
Nantucket Shoals and Channel	27	84
Closed Area I	7	7
Northern Edge	18	28
Georges Shoals	20	41
Southwest Part	8	9
Closed Area II	12	21
Northeast Peak	12	13
Eastern Georges	4	7

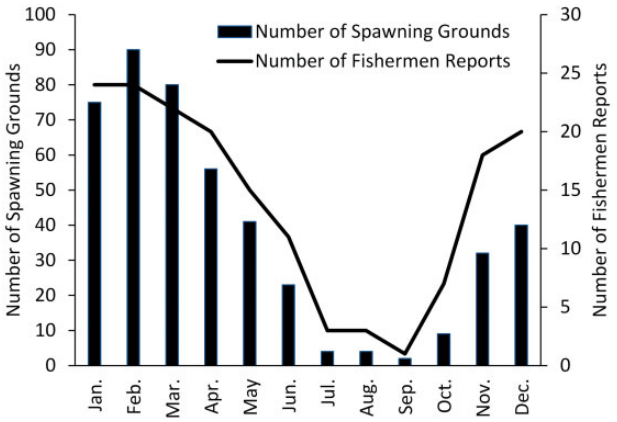

Figure 7. The number of fishermen who reported spawning activity in each month, and the number of spawning sites identified in each month throughout the entire study area.

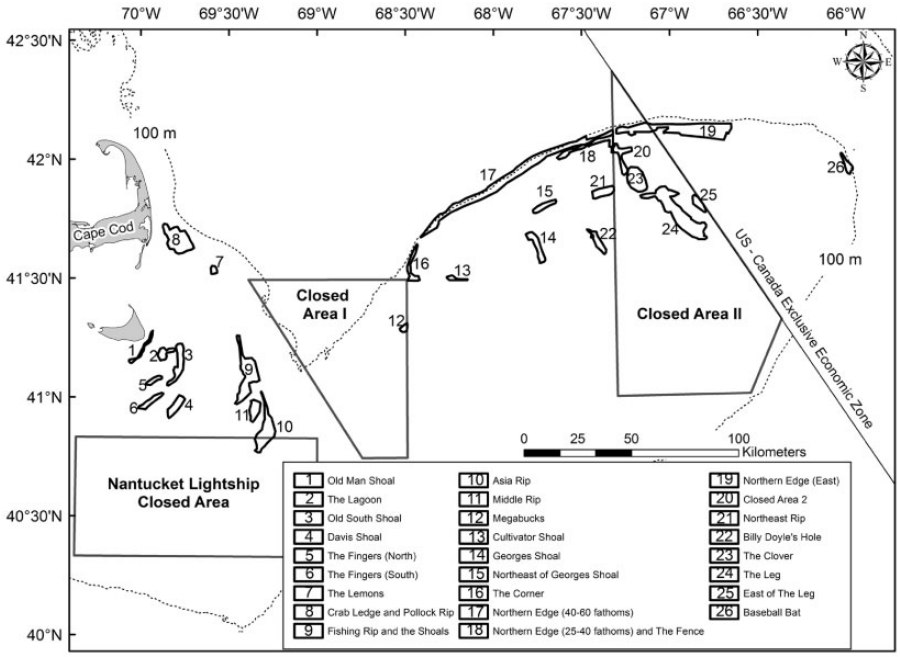

Figure 6. Consensus cod spawning grounds that were identified by at least three fishermen during the interviews.

spawning. During the interviews, we provided the fishermen with pictures of cod at different maturity stages, and they could readily identify ripe, and ripe and running cod in the pictures. Some U.S. fishermen also described eating the roe of the female cod, and indicated that they preferred to eat the roe of developing females. Some fishermen also reported that they could use their sounders to differentiate between feeding and spawning aggregations of cod.

The fishermen identified 210 cod spawning grounds on Georges Bank and Nantucket Shoals, but the same spawning grounds were often identified independently by multiple fishermen (Figure 5). On average, each fisherman identified five cod spawning grounds (range = 2–25 spawning grounds). The region around "Nantucket Shoals and the Channel" was most commonly identified as having cod spawning grounds (Table 4). Georges Shoal and the Northern Edge were also identified as important regions for cod spawning, whereas relatively few spawning grounds were reported on the Southwest and Eastern Parts on Georges Bank (Table 4).

Twenty six consensus spawning grounds (areas independently identified by three or more fishermen) were identified during the interviews (Figure 6). These spawning grounds were widespread throughout the Georges Bank stock area. Many of the spawning grounds are discrete, and associated with specific bathymetric features such as channels between shoals, edge habitats adjacent to shoals, complex rocky bottom, or areas with steep bathymetric contours. These consensus spawning grounds were familiar to most of the fishermen that we interviewed, and had common names that fishermen used to identify each location. Nine of these spawning grounds were located on Nantucket Shoals and two were located in relatively shallow water just east of Cape Cod. Consensus spawning grounds were also identified on Georges

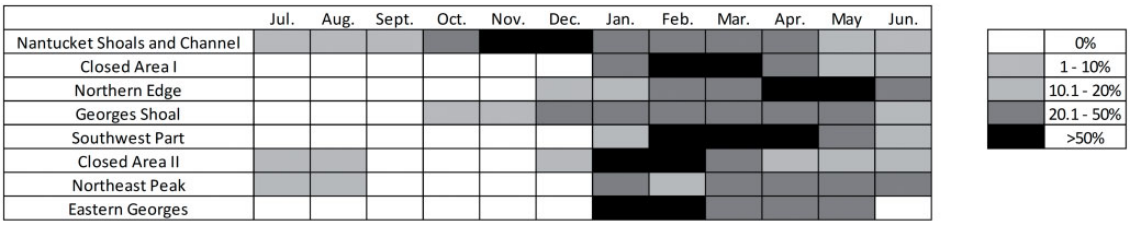

Figure 8. Proportion of fishermen who reported spawning activity each month in the different geographic regions of Georges Bank.

Table 5. Fishermen reported habitat characteristics associated with cod spawning grounds.

Abiotic habitat attributes		Biotic habitat attributes	
Sand or sand lumps	105	Shellfish	50
Rocks and "hard" bottom	67	Herring	9
Gravel	36	Sand lance	8
Pebble and cobble	11	Macroalgae	5
Mud	9	Mackerel	3
Strong tides and currents	9	Sea stars	3
Shipwrecks	7	Worms	2
"Broken" bottom	3	Squid	1
		Silver hake	1
		Sponges	1
		Small haddock	1
		Crabs	1

The table shows the frequency with which each habitat characteristic was reported.

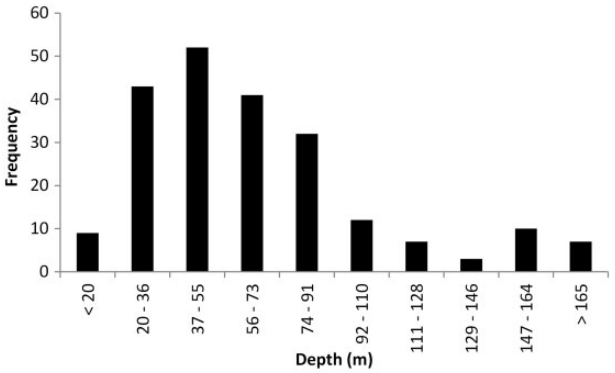

Figure 9. Depth range (m) of cod spawning grounds reported by fishermen.

Shoals, the Northern Edge of Georges Bank, and in Closed Area II. Only two consensus spawning grounds were identified in Canadian waters on the Northeast Peak, and none was identified on the Southwest Part of Georges Bank.

The captains had detailed knowledge about the timing of cod spawning, and the seasonal availability of cod on the fishing grounds. Fishermen reported few observations of spawning cod between July and September, and observed that spawning activity increases from October to December (Figure 7). Over half of the participating fishermen reported active spawning grounds in January, February, and March. Fishermen noted that cod spawning declined from relatively high levels in April to lesser amounts in May and June.

Fishermen reported that the timing of spawning varied between regions of Georges Bank. Although at least one fisherman described spawning activity on Nantucket Shoals and the Channel in each month, most fishermen identified the spawning period in this region occurred from October to April, with peak spawning in November and December, which is earlier than regions further east (Figure 8). On Georges Shoal, the spawning season was described as lasting from October to June, with the majority of spawning taking place between December and May (Figure 8). Peak spawning in the relatively deep waters of the Northern Edge was reported in April and May, which is later than peak spawning reported in other regions.

Fishermen typically identified abiotic or biotic habitat characteristics associated with each spawning ground. Cod spawning grounds were most commonly characterized as occurring in areas with sandy substrates, and fishermen often described sand "lumps" as the preferred spawning habitat (Table 5). Rocky, hard bottom habitats and areas with gravel substrate were also identified as important for cod spawning activity. The fishermen observed that cod spawning grounds were often in areas with complex bathymetric features such as ridges, valleys, and deep holes. Fishing in these complex habitats is often difficult and dangerous, particularly with mobile gear, and requires *a priori* knowledge that the fishermen acquire through direct experience and information sharing among captains. The persistence of mobile gear fishermen to pursue cod in these dangerous habitats reflects the importance of these areas as locations where cod would densely aggregate to spawn. The fishermen also reported that cod spawning grounds were frequently in areas with high concentrations of shellfish, including surf clams (*Spisula solidissima*), quahogs (*Mercenaria* spp.), and mussels (*Mytilus edulis*) (Table 5). Cod spawning aggregations were also often associated with areas that held high concentrations of forage fish, such as herring (*Clupea harengus*), mackerel (*Scomber scombrus*), or sand lance (*Ammodytes* spp.).

Fishermen reported that cod spawning occurs across a wide range of depths on Georges Bank and Nantucket Shoals (Figure 9). Although the bulk of spawning activity was reported to occur in depths ranging from 20 to 91 meters, fishermen also reported that cod also spawn in shoal habitats ($\leq$20 m) and in deep water ($\geq$150 m) off the Northern Edge of Georges Bank. On the western portion of Nantucket Shoals, the fishermen commonly observed that cod aggregate to spawn in narrow channels where depths typically ranged from 19 to 38 m, and these channels were often surrounded by shoals ($<$18 m) where cod were far less abundant. Fishermen reported a similar distributional pattern on eastern Nantucket Shoals and on Georges Shoals, where cod appeared to be most abundant on the edges of the shoals in depths that ranged from 19 to 55 m, whereas spawning cod were not present in the shallower water ($<$18 m) on top of the shoals.

Fishermen's observations also provided some insight into the consistency and predictability of the cod spawning grounds that were identified on Georges Bank. For the majority of spawning grounds (73%), fishermen remarked that they consistently caught spawning cod at that location every year. Fishermen noted that some spawning grounds (12%) were more variable, and they caught spawning cod at these locations in some, but not all years. Fishermen also identified a small number of spawning grounds (4%) where spawning cod were only captured in a single year, or during a single trip. In some cases (13%), the fisherman was unsure of the predictability or consistency of the spawning ground. Of the 210 cod spawning grounds that were identified in this study, fishermen reported 28 locations that they thought were no longer active. However, in many cases, the fishermen observed that cod stopped spawning at a location years ago (e.g. in the 1980s), and they subsequently shifted their fishing effort to other locations. The fishermen also identified 60 spawning grounds that they thought were still active. However, in the majority of cases (122 of 210 spawning grounds), fishermen were unsure if the spawning ground they identified was still active.

Many fishermen participating in this study expressed concern that the current management units for cod in U.S. waters do not match the biological population structure of the resource. Fifteen of the sixteen fishermen who had experience fishing on both eastern and western Georges Bank remarked that cod on eastern Georges Bank were distinct from those on Nantucket Shoals and western Georges Bank, whereas one fisherman felt that cod move widely throughout Georges Bank in search of food and optimal temperatures. In particular, the 15 fishermen noted that cod on eastern Georges Bank often attained larger sizes than those taken inshore. Fishermen also consistently described differences in the colour and shape of cod between eastern and western Georges Bank, and observed that cod from eastern Georges Bank were firmer and higher quality than cod from Nantucket Shoals. Many fishermen identified a longitudinal divide that they believe separate the two groups of cod on eastern and western Georges Bank, and most suggested a boundary line of either 68°W or 69°W. Furthermore, ten fishermen perceived that there is connectivity between cod in the Gulf of Maine and Nantucket Shoals, and observed that cod make seasonal migrations from the western Gulf of Maine to Nantucket Shoals in search of food.

Discussion

Fishermen's reported timing and location of cod spawning activity generally agreed with the scientific literature, but FEK improved the resolution of information available to investigate cod spawning dynamics on Georges Bank. Many of the spawning grounds identified by fishermen were documented on broad spatial scales from prior scientific research (e.g. ICES, 2005), but the reports from fishermen suggest that spawning activity can occur on much finer spatial scales, and that spawning grounds are often associated with specific habitat features. Cod spawning dynamics were not well represented by only examining data from seasonal trawl surveys, which do not routinely sample many of the consensus spawning grounds, particularly those on Nantucket Shoals or Georges Shoals.

Across all of Georges Bank and Nantucket Shoals, the timing of spawning reported by the fishermen (Figure 7) was in close agreement with results from the MARMAP and GLOBEC ichthyoplankton sampling programs (Berrien and Sibunka, 1999; Table 2). The fishermen typically reported that spawning activity would persist for months at a given location, and that aggregations would consist of cod in ripe, and ripe and running condition. Cod exhibit protracted spawning (Pinsent and Methven, 1997; ICES, 2005) with female cod releasing several batches of eggs at regular intervals over a period of 50–60 days (Kjesbu, 1989; 1990), during which time an individual cod will alternative between ripe and ripe running stages. It takes several months for cod to progress from the developing stage to the beginning of spawning (Kjesbu, 1994; Burton *et al.*, 1997), and developing cod were commonly observed during the NEFSC fall trawl survey, which primarily samples Georges Bank in October, whereas ripe and ripe and running cod were relatively rare. Similarly, the fishermen reported relatively little cod spawning activity on Georges Bank in October, and observed that cod spawning activity increases in November and December (Figure 7). Fishermen observed peak spawning activity from January to March (Figure 7), which matches closely with data collected by the DFO trawl survey and the Canadian Fisheries Observer program (Table 3). Fishermen reported that cod spawning activity continues into April and May, and this observation is corroborated by the GLOBEC program, which sampled stage one cod eggs during these months (Table 2). The NEFSC spring trawl survey also observed cod in spawning condition during April and May, although a higher proportion of the cod were spent.

Although fishermen reported that the spawning season on Nantucket Shoals is protracted, they identified November and December as the peak spawning season (Figure 8). This timing aligns well with the scientific information. Sampling conducted during the MARMAP program observed a relatively high density of cod eggs in the waters around Nantucket Shoals in November and December, which may indicate spawning activity in the region (Berrien and Sibunka, 1999). Schroeder (1930) documented spawning on Nantucket Shoals from November to April, with peak spawning in December and January, whereas Smith (1902) reported that spawning lasted from November until January.

The four spawning grounds on Nantucket Shoals described by Schroeder (1930) were identified by three or more fishermen during the interviews, as were a number of other spawning grounds in the region. The NEFSC trawl survey occasionally samples the consensus spawning grounds that were identified on eastern Nantucket Shoals ("Asia Rip", "Middle Rip", and "Fishing Rip"), and small catches of spawning cod have been observed near these spawning grounds during both the NEFSC fall and spring surveys. However, consensus spawning grounds on western Nantucket Shoals (e.g. "The Lagoon", "The Fingers") are not routinely sampled during the NEFSC trawl survey, possibly due to the complex, shallow bathymetry and strong tidal currents which make it dangerous to trawl in this area.

Fishermen reported widespread spawning activity on Georges Shoals from December to April, and identified several spawning grounds in this region (Figures 5 and 8). Interestingly, Georges Shoals had not been indicated as a cod spawning ground in prior scientific reports. Cod eggs were sampled on Georges Shoals during the MARMAP program, primarily from November to April, although the egg stages were not reported (Berrien and Sibunka, 1999). However, stage one cod eggs were not commonly observed on Georges Shoals during the GLOBEC program. The consensus spawning grounds identified on Georges Shoals are not routinely sampled during the NEFSC trawl survey, potentially due to their small size and the complex bathymetry in this region. However, relatively small catches of spawning cod were observed in close

proximity to the "Northeast of Georges Shoal" and "Northeast Rip" consensus spawning grounds during NEFSC spring trawl survey tows.

Goode (1884) and Rich (1929) described large cod spawning aggregations on the "Winter Fishing Grounds" that occurred predictably every year in February, March, and April. A number of the consensus spawning grounds identified in the present study are within the "Winter Fishing Grounds" including "The Leg", "Billy Doyle's Hole", "The Clover", "East of the Leg", "Northeast Rip", and "Closed Area II" (Figures 5 and 6). The timing of spawning reported by Goode (1884) and Rich (1929) matches closely with the contemporary reports we received from the fishermen who indicated that most of the cod spawning activity occurs at "The Leg" and "Billy Doyle's Hole" from January to March. Spawning cod were routinely caught in this region during the NEFSC spring trawl survey, and many of the cod spawning hotspots from the NEFSC spring survey were located in the "Winter Fishing Grounds" (Figure 3). Spawning cod were also observed in the "Winter Fishing Ground" during DFO trawl surveys (Figure 4), and stage one cod eggs were sampled in this area from January to April during the GLOBEC program.

The fishermen reported cod spawning activity on the Northern Edge from December to June, with a peak in April and May (Figure 8). Cod spawning on the Northern Edge was reported to occur across a wide range of depths (45–200 m), and on a variety of substrates including mud, sand, gravel, and rocks. Spawning cod were rarely observed on the Northern Edge during the NEFSC fall survey, which matches the fishermen's reports that cod do not spawn on the Northern Edge in October and November. During the NEFSC spring survey, spawning cod were commonly observed on the Northern Edge in depths ranging from 40 to 140 m, and were occasionally sampled in waters up to ~200 m, which is well aligned with fishermen's reports in this region. During the GLOBEC program, stage one cod eggs were sampled on the Northern Edge from January to May, with the greatest concentrations observed in February.

Fishermen reported that the cod spawning season on the Northeast Peak was protracted, extending from January to August (Figure 8), and identified two consensus spawning grounds in this region (Figure 6). The greatest concentrations of spawning cod observed during both the NEFSC spring and DFO trawl surveys were on the Northeast Peak of Georges Bank, and many of the cod spawning hotspots identified by the DFO trawl survey were on the Northeast Peak (Figure 4). Spawning cod were routinely sampled in this area from January to March by the Canadian Fisheries Observer Program. Cod eggs were also abundant on the Northeast Peak during the MARMAP and GLOBEC sampling programs, with peak spawning noted in February and March (Berrien and Sibunka, 1999; Sibunka *et al*., 2006). The Northeast Peak has long been known to serve as a cod spawning ground (Rich, 1929), and spawning cod sampled on the Northeast Peak were genetically distinct from those sampled on Nantucket Shoals (Ruzzante *et al*., 1998; Lage *et al*., 2004; Wirgin *et al*., 2007; Kovach et al, 2010). Although there is ample scientific evidence of cod spawning on eastern Georges Bank, relatively few fishermen identified spawning grounds in this region, and no consensus spawning grounds were identified on eastern Georges Bank.

Few fishermen identified cod spawning activity on the Southwest Part (Figure 5), and no consensus spawning grounds were observed in this region. Relatively small catches of spawning cod were observed on the Southwest Part during both the NEFSC spring and DFO trawl surveys. Cod eggs were routinely sampled on the Southwest Part during the MARMAP and GLOBEC ichthyoplankton surveys (Berrien and Sibunka, 1999; Sibunka et al, 2006), although it is unclear if these eggs were spawned on the Southwest Part or advected from other spawning locations.

The geographic distribution of the cod spawning grounds that were identified by the 40 fishermen in this study is reflective of the distribution of their fishing effort over the course of their careers and is considered to be generally representative of the trawl effort on Georges Bank, which was widely distributed across the Bank before the establishment of closed areas and seasons (e.g. NRC 2002). The cod spawning grounds identified in this study may not represent an exhaustive depiction of spawning activity across all of Georges Bank. For example, many fishermen identified cod spawning grounds on Nantucket Shoals. Nantucket Shoals is relatively close to New Bedford, MA, and the New Bedford trawl fleet commonly targeted cod on Nantucket Shoals in the 1970s and 1980s. We interviewed 21 fishermen from New Bedford, so it is not surprising that numerous spawning grounds were identified on Nantucket Shoals. Similarly, consensus spawning grounds were also identified east of Cape Cod, primarily by fishermen from Chatham, MA, who formerly targeted cod in this region. It is likely that we could have identified additional spawning grounds if we had interviewed more fishermen. Furthermore, although we made an effort to interview fishermen from throughout New England and Nova Scotia, most of the fishermen we interviewed fished from Massachusetts. If we had interviewed more fishermen from other regions (e.g. Maine, Nova Scotia), the FEK may have represented a more geographically diverse set of fishing effort and observations, which may have allowed us to identify additional spawning grounds across other regions of Georges Bank.

One objective of this study was to use FEK to examine long-term shifts in the distribution of cod spawning activity on Georges Bank and Nantucket Shoals. However, meeting this objective proved to be difficult. Many of the fishermen we interviewed were retired, and nearly all of the fishermen that are still active reported that they no longer target cod because of the low quotas in recent years. The majority of fishermen noted that they no longer fish in areas where cod are abundant in order to target stocks with higher allocations and to avoid exceeding their cod quota. Closed areas that were implemented in U.S. waters to reduce fishing mortality (e.g. Closed Areas I and II) or protect habitat (e.g. Nantucket Shoals habitat closure) have prohibited fishing in many of the areas where the U.S. fleet used to target spawning cod, and U.S. fishermen have been banned from fishing on eastern Georges Bank since the Hague Line was established in 1984. On the Canadian portion of eastern Georges Bank, the trawl fleet is required to use selective fishing gear (e.g. haddock separator trawl) which is designed to reduce cod bycatch, and fishing is typically prohibited from early February to May to protect spawning cod (Wang *et al*., 2015). These regulations, and resulting shifts in fishing behaviour, make it difficult to assess the current productivity of cod spawning on Georges Bank. For example, fishermen identified 28 cod spawning grounds that they thought were no longer active, but given the current low quotas for cod, there is little incentive for fishermen to fish in these areas to see if the spawning cod have returned. These regulations could also help to explain why so few fishermen were able to identify cod spawning grounds on eastern Georges Bank, despite the ample scientific

evidence which indicates that major spawning activity occurs in this region.

Fishermen observed that cod spawning grounds were often associated with habitats that had high concentrations of shellfish, particularly on Nantucket Shoals and Georges Shoals. Many fishermen reported that shellfish were an important prey item for cod, and their observations are in close agreement with Bigelow and Schroeder (1953), who noted that mollusks were a primary food source for cod. Some fishermen surmised that cod spawn in close proximity to shellfish beds to ensure that they have a readily available food source to exploit immediately after spawning.

Fifteen fishermen believed that cod on eastern Georges Bank are separate from those on western Georges Bank and Nantucket Shoals, based on their observations of disparate migratory patterns and persistent morphological differences between the two groups. Their perceptions are consistent with the available scientific information (Zemeckis *et al.*, 2014c) and have important implications for the assessment and management of the resource. Fishermen's observations of distinct groups of cod on eastern and western Georges Bank, with a suggested longitudinal boundary near 68°W, is also consistent with the boundary that Wise (1963) suggested from tagging observations. Tallack (2011) and Loehrke (2013) also observed that few cod moved between Georges Bank and southern New England, and Schroeder (1930) reported that cod tagged on Nantucket Shoals were rarely recaptured on Georges Bank east of 68°W. Additionally, genetic differences have been observed between cod on eastern Georges Bank and those on Nantucket Shoals (Lage *et al.*, 2004; Wirgin *et al.*, 2007; Kovach *et al.*, 2010).

Fishermen also described connectivity between cod on Nantucket Shoals, the Great South Channel, and the western Gulf of Maine. These observations agree with a genetic study completed by Kovach *et al.* (2010), which identified a "southern complex" of winter spawning cod in the Gulf of Maine and locations south of Cape Cod, Massachusetts. On the basis of conventional tag returns, Tallack (2011) observed considerable movement of cod between Cape Cod and the inshore Gulf of Maine, although some sub-legal cod were also reported to migrate from Cape Cod to Georges Bank. We suggest that FEK should be routinely collected as part of interdisciplinary stock identification studies along with traditional stock identification techniques such as genetics, analysis of life history traits, and applied marks.

The FEK collected in this study can serve as a valuable guide for future research efforts to better understand the stock dynamics and productivity of cod. For example, a directed trawl survey could be initiated to sample at the spawning locations that were identified by fishermen and assess which spawning grounds remain active. In addition, the location and timing of cod spawning grounds that were identified by fishermen could be used to inform the initial conditions for Individual Based Modelling experiments designed to examine the transport and survival of cod eggs and larvae. Finally, these putative spawning areas could be used to guide the design of future tagging studies to investigate stock identity and connectivity of spawning cod.

There are several reasons why FEK was informative for investigating the spawning dynamics of cod on Georges Bank and Nantucket Shoals. Cod is an important target species that has been heavily exploited for decades (NEFSC, 2013), over which time the fishermen developed an intimate understanding of their migratory patterns and spawning locations. Second, cod fisheries on Georges Bank have been primarily prosecuted by medium to large vessels (12–30 m) that fish using mobile gear (e.g. trawl and gillnets), which gave fishermen the ability to target cod over a wide geographic area. In addition, we interviewed retired captains who had experience targeting cod prior to the implementation of closed areas and restrictive quotas, so we were able to gather FEK related to cod spawning in areas that are currently closed to fishing. For our case study, FEK provided much greater spatio-temporal resolution and more comprehensive perspectives than scientific surveys. FEK may have less utility when the geographic distribution of fishing effort is limited to a relatively small portion of the species spatial distribution. Furthermore, the value of FEK may be limited for species that are primarily taken as bycatch, or for species without a long exploitation history.

The high participation rates, and the quality and reliability of the information provided by the fishermen in this study were likely the result of several factors. First, through prior cooperative research projects we had a pre-existing relationship with many of these fishermen, enabling us to gain their trust. Second, we conducted the interviews at times and locations that were convenient to the fishermen, which didn't cause them to lose fishing opportunities, and showed them that we valued their perspectives. Many fishermen were thankful that we solicited their knowledge and expertise, and they appreciated the opportunity to contribute to scientific research. One interviewer is fluent in Portuguese, which allowed us to interview eight fishermen that have extensive experience fishing for Georges Bank cod, but often do not participate in fishery management because of a language barrier. Many of the fishermen who we interviewed were retired, and may have been more willing to share their information because they would not be affected by any resultant management measures. Finally, given the depleted status of Georges Bank cod, some fishermen were motivated to participate out of a desire to share knowledge that could potentially help contribute to cod rebuilding.

In conclusion, FEK has improved our understanding of cod spawning activity on Georges Bank. There was substantial agreement between the available scientific information and the information reported by the fishermen about the spatial and temporal distribution of cod spawning on Georges Bank, which suggests that the reports provided by the fishermen were reliable. Although the major spawning grounds reported by fishermen were also identified in the scientific literature (e.g. the Northeast Peak and Nantucket Shoals), the fishermen we interviewed had extensive knowledge related to the timing and location of cod spawning, and identified some cod spawning grounds that were not previously described in scientific reports. Multiple fishermen who were interviewed independently identified several fine-scale geographic regions (often $< 50\,km^2$) where cod spawning occurs, and they had detailed knowledge about the habitat characteristics of these fine-scale locations. This level of spatial resolution could not typically be obtained using traditional scientific data collection approaches. The information gathered in this study can serve as a valuable guide for future research, and can help inform future management actions.

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