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Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach

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Mismatches between biological population structure and management unit boundaries often violate the unit-stock assumption, which can reduce the accuracy and relevance of stock assessment results and lead to ineffective fishery management. Since 1972, Atlantic cod (*Gadus morhua*) have been managed in US waters as two units: the Gulf of Maine and the Georges Bank stocks, both of which have experienced recent difficulties in rebuilding. An interdisciplinary review of available biological information was conducted to investigate cod population structure in US waters and to evaluate the biological appropriateness of the current two-stock model. Our review demonstrates that spawning components in the Great South Channel, Nantucket Shoals, southern New England, and Middle Atlantic are more connected with spawning components in the Gulf of Maine than on eastern Georges Bank, with which they are currently managed. Therefore, a modification of current stock boundaries is recommended to provide a more accurate representation of biological population structure. Proposed alternatives divide inshore and offshore spawning components into separate management units, thereby separating the current Georges Bank stock longitudinally. Continued research, including stock composition analysis, is required to evaluate uncertainties, delineate biological stocks, and develop sustainable management practices that account for intrastock diversity (e.g. winter and spring-spawning components that overlap spatially).

Keywords: Atlantic cod, fishery management, Georges Bank, Gulf of Maine, stock identification.

Introduction

Stock boundaries are often an oversimplification of complex populations and do not always accurately represent biological population structure (Stephenson, 1999; Reiss *et al.*, 2009). Ideally, stock boundaries encompass groups of randomly mating individuals that are reproductively isolated from other conspecific groups with spatial or temporal integrity (Ihssen *et al.*, 1981) and similar life-history characteristics (Cadrin *et al.*, 2014). Stock assessment models commonly assume the population is a “unit-stock”, or a closed population with negligible immigration and emigration from the stock area (Hilborn and Walters, 1992). Violating this assumption for complex population structures can compromise the accuracy and reliability of model results (Begg *et al.*, 1999a).

Stock identification methods are used to evaluate the validity of the unit-stock assumption by identifying self-sustaining components

within natural populations (Cadrin *et al.*, 2014). Stock identification, therefore, serves as an essential partner to stock assessment, because demographics and fate of unit-stocks cannot be assessed unless stock boundaries are accurately defined (Waldman, 2005a). Despite the importance of stock identification, few stock assessments consider new information from stock identification methods or explore alternative population structures (Begg *et al.*, 1999a; Cadrin *et al.*, 2014). Typically, traditional stock definitions are maintained despite continuous advances in understanding of fish populations (Begg and Waldman, 1999; Begg *et al.*, 1999a).

A thorough understanding of population structure is crucial when delineating stock boundaries and developing appropriate management regulations (Kutkuhn, 1981; Grimes *et al.*, 1987). This is particularly important when populations consist of multiple, fine-scale subpopulations, and management efforts need to

be distributed among them (Altukhov, 1981). Accounting for population structure is also important when subpopulations have varying levels of productivity and are differentially exploited (Ricker, 1981). For example, less productive subpopulations may be harvested at a rate that could threaten their long-term stability, whereas more productive subpopulations may be underharvested and result in foregone yield (Ricker, 1958; Hunt and Neilson, 1993).

Since 1972, Atlantic cod (*Gadus morhua*) have been managed in US waters as two units: the Gulf of Maine and the Georges Bank stocks (Serchuk and Wigley, 1992; NEFSC, 2013; Figure 1). As part of a sharing agreement and for consistent management, cod on the eastern portion of Georges Bank are managed jointly between the United States and Canada. Joint assessments and management recommendations are prepared by the Transboundary Resources Assessment Committee (TRAC; Wang et al., 2011). Recent assessments of the Gulf of Maine stock have resulted in a substantial shift in perception. Mayo et al. (2009) concluded that the stock was not overfished in 2007 (mature biomass = 33 877 t), but overfishing was occurring [fishing mortality (F) = 0.46], and

the stock was projected to be rebuilt by the target date of 2014. However, results from a subsequent benchmark stock assessment determined that the stock was overfished in 2010 (mature biomass = 12 270 t), overfishing was occurring (F = 1.14), and the stock would be unable to rebuild by the target date (NEFSC, 2012). Given the major shift in perception, an updated stock assessment was performed and determined that the stock remained overfished in 2011 (mature biomass = 9903 t) and overfishing was still occurring (F = 0.86; NEFSC, 2013). Similarly, the most recent stock assessment determined that the Georges Bank stock was overfished in 2011 (mature biomass = 13 216 t) and overfishing was occurring (F = 0.43; NEFSC, 2013), which also represented a negative shift in perception with respect to an earlier assessment (mature biomass = 17 672 t, F = 0.30 in 2007; NEFSC, 2008). Based on the results of two separate models, the eastern Georges Bank stock had the second lowest biomass in the time-series and an F greater than the target in 2010 (“Split M 0.20 model”: mature biomass = 3288 t, F = 0.41; “Split M 0.5 model”: mature biomass = 5088 t, F = 0.25; Wang et al., 2011).

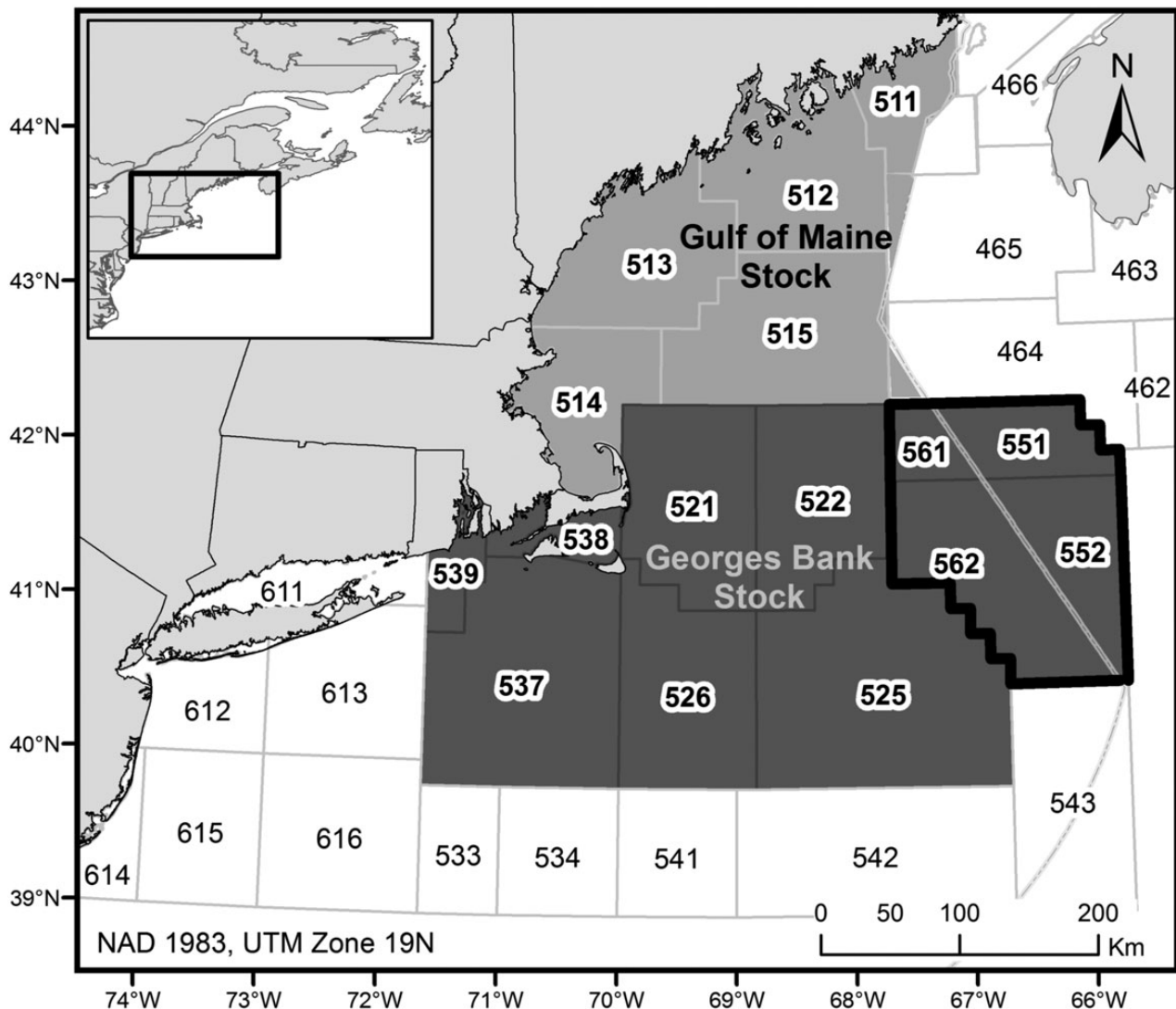


Figure 1. Current management units applied to Atlantic cod in US waters, including a Gulf of Maine and a Georges Bank stock. The eastern portion of Georges Bank (outlined in bold) is managed jointly between the United States and Canada as a transboundary resource.

Despite continuously evolving management strategies (Serchuk and Wood, 1979; Serchuk and Wigley, 1992; O'Brien *et al.*, 2006; NEFMC, 2009), cod in the Gulf of Maine and on Georges Bank have experienced persistent overfishing and difficulty in rebuilding due to interactions between scientific uncertainty (i.e. changes in perception from one assessment to the next) and environmental influences (e.g. Rothschild, 2007; Fogarty *et al.*, 2008). The New England Fishery Management Council's Scientific and Statistical Committee identified the lack of understanding of cod population structure as an area of scientific uncertainty that is contributing to delays in rebuilding and recommended that future research include "a comprehensive evaluation of scientific information on cod population structure and its management implications, including the possibility of revising management units" (SSC, 2012). In response to this recommendation, a three-phase process for re-evaluating, and possibly revising, the spatial basis for assessment and management of Atlantic cod in the Gulf of Maine region was developed. As part of the first phase in this process, a workshop on "Stock Structure of Atlantic cod in the Gulf of Maine Region" was held to review information relevant to stock structure and make recommendations regarding the most likely biological stock structure in the region, including recommendations for future research and advice on the alignment (or misalignment) of current management units (Annala, 2012). However, these objectives were not fulfilled during the workshop. As a result, our objective was to review the contemporary research on Atlantic cod in US waters in the context of historical information and to draw conclusions about the biological population structure of cod in US waters. Our conclusions were based on the consensus of an interdisciplinary literature review and were used to evaluate the biological appropriateness of the current stock boundaries, including discussion of alternative scenarios.

Basis for current management units

The current two-unit model was based on traditional fishing areas (Halliday and Pinhorn, 1990) and results from early studies on movement (Smith, 1902; Schroeder, 1930; NACFI, 1932, 1935; Wise, 1963), parasite infestation rates (Sherman and Wise, 1961), growth rate analyses (Penttila and Gifford, 1976; Serchuk and Wood, 1979), and differences in spawning times (Colton *et al.*, 1979). The results of these studies were interpreted to indicate minimal exchange between cod in the Gulf of Maine and Georges Bank, but extensive mixing between cod on Georges Bank and in the southern New England/Middle Atlantic region (Serchuk and Wood, 1979).

Wise (1963) analysed historical tagging data collected since 1897. Cod in southern New England were the most mobile, with many fish moving west and south into the Middle Atlantic. Very few recaptures of fish tagged in the Great South Channel or on Nantucket Shoals were caught on Georges Bank, whereas a greater number of recaptures came from within the Gulf of Maine (Schroeder, 1930; Wise, 1963). Fish tagged on Georges Bank were most often caught on Georges Bank, but frequent movement in a northeasterly direction to Browns Bank was observed. Few fish tagged on eastern Georges Bank were recaptured in the Great South Channel or on Nantucket Shoals. Cod tagged on Browns Bank generally stayed on Browns Bank or moved eastward onto the Scotian Shelf, rarely moving into US waters. Fish tagged off Maine near Mt. Desert Island were relatively stationary and exhibited little mixing with cod from other regions (NACFI, 1932). Wise (1963) identified four distinct groups of cod in the New England area: (i) cod of the offshore banks (Georges and Browns) that are closely related to

fish off the southwest coast of Nova Scotia, (ii) cod of the Gulf of Maine, probably divided into many subgroups and receiving considerable recruitment from the south, (iii) cod of southern New England and the Great South Channel, and (iv) the New Jersey coastal cod, which spend part of the year mingled to a greater or lesser degree with southern New England fish. Wise (1963) suggested that the western shoals of Georges Bank around 68°W represent a division between inshore and offshore groups. Therefore, apparent inconsistencies exist between historical movement data and the stock boundaries that were subsequently created using this information (e.g. grouping of Georges Bank, Great South Channel, Nantucket Shoals, and New Jersey cod into a single stock despite being identified here as separate groups).

Penttila and Gifford (1976) studied the growth and mortality of cod in the Gulf of Maine and on Georges Bank. Some analyses of the Georges Bank region were further divided into a "Georges Bank" and a "South and Nauset" section that included the Great South Channel and southern New England. An analysis of variance showed a significant difference in the mean lengths at age for all three areas, with Gulf of Maine cod being consistently smaller than the other areas. Southern New England samples of age 1 and age 2 cod collected during spring and autumn surveys, as well as age 3 samples from autumn surveys, were significantly smaller than samples from eastern Georges Bank. Their results also demonstrated that cod from Georges Bank ($k = 0.120$, $L_{\infty} = 148.1$ cm) had faster growth rates than cod from the Gulf of Maine ($k = 0.116$, $L_{\infty} = 146.5$ cm), but growth rates were not individually reported for each of the Georges Bank divisions. Total mortality rates were calculated from declines in the numbers of cod caught per tow, and Gulf of Maine cod were subjected to a greater mortality rate than cod on Georges Bank. Comparisons of growth rate information from Penttila and Gifford (1976) and Schroeder (1930) suggest differences in growth between cod in southern New England ($k = 0.177$, $L_{\infty} = 123.1$ cm) and on Georges Bank ($k = 0.120$, $L_{\infty} = 148.1$ cm), but these differences were dismissed by Penttila and Gifford (1976) due to the age distribution of samples and the use of scales for ageing by Schroeder (1930). Despite some evidence of differences in life history between cod in southern New England and on eastern Georges Bank, the results from Penttila and Gifford (1976) were used to support their grouping into a single Georges Bank management unit.

Sherman and Wise (1961) investigated the differential infestation of cod by the copepod parasite *Lernaecocera branchialis* in New England waters. Infestation rates decreased from north to south, with the greatest infestation rates in colder waters off Maine (8.7–29.2%) and in the northern Bay of Fundy (32.5%). The lowest infestation rates were found off Rhode Island (0%) and in the Great South Channel (0.8–1.0%). Infestation rates also decreased from inshore to offshore regions, with fish taken within 20 miles of shore having a higher infestation rate (8.3%) than those taken farther offshore (3.0%). The inshore–offshore pattern was believed to parallel the distribution of the intermediate host, the lumpfish (*Cyclopterus lumpus*), which is predominantly found in inshore areas in the Gulf of Maine and rarely found on offshore banks (Bigelow and Schroeder, 1953). Results from infestation rates suggested the existence of three groups of cod. Moderate infestation in the central Gulf of Maine and heavy infestation of the northern coastal region suggested that mixing between those groups regularly occurred. The low infestation rates found on Georges Bank and in the Great South Channel was interpreted to indicate mixing between these groups, but little mixing with groups to the north and south. The lack of infestation in samples collected

in the Middle Atlantic and on Nantucket Shoals suggested that cod in these regions are separate from those to the east and north. Therefore, the conclusions of Sherman and Wise (1961) are somewhat inconsistent with the stock boundaries for which their findings serve the basis, particularly the apparent lack of connectivity between the Middle Atlantic and Nantucket Shoals with Georges Bank.

Based on survey results and commercial catch data, Serchuk and Wood (1979) inferred a close correspondence between cod in the southern New England/Middle Atlantic and Georges Bank regions. This connection was inferred based partly on the determination that cod in the southern New England/Middle Atlantic region cannot be self-sustaining, given the near absence of juvenile cod in survey tows from Block Island to Cape Hatteras. Similar trends in year-class strength were also observed between regions. The growth rate, as derived from mean lengths at age for southern New England/Middle Atlantic cod, exhibited little change between years and was perceived to correspond closely to that of cod on Georges Bank. Only “minor non-systematic” differences in lengths for age groups 0–6 were interpreted to exist between regions, and comparison between older age groups was difficult due to small sample sizes. The maximum length differed between regions, with southern New England/Middle Atlantic cod ($L_{\infty} = 113$ cm) being smaller than fish caught in the Gulf of Maine ($L_{\infty} = 146$ cm) and on Georges Bank ($L_{\infty} = 149$ cm). The relative market category composition of the commercial catches was also similar for almost all years between southern New England/Middle Atlantic (Serchuk and Wood, 1979) and Georges Bank (Serchuk *et al.*, 1979). As a result of similar growth patterns, yield-per-recruit curves were similar between regions (Serchuk *et al.*, 1979; Serchuk and Wood, 1979). These similarities suggested that management decisions would result in nearly identical yield responses between regions and supported their grouping into a single Georges Bank stock. However, as demonstrated by Hart (2001), heterogeneous spatial patterns in a fishery or a resource can result in misinterpretations of yield-per-recruit from traditional theories that assume homogeneity, which, in this case, can occur in response to variability in fishing mortality, life history, and behaviour among semi-discrete spawning components.

Recent research on cod in US waters

Many historical spawning components of cod in the Gulf of Maine region have been depleted (Ames, 2004), which has been coincident with reductions in age and length at maturity (Hunt, 1996; O'Brien, 1999; Barot *et al.*, 2004) and considerable shifts in fishery dynamics (Alexander *et al.*, 2009). These changes occurred during a period of varying management regimes (O'Brien *et al.*, 2006; NEFMC, 2009; NEFSC, 2012) and changing environmental conditions that likely affect cod productivity patterns (e.g. Rose, 2005; Fogarty *et al.*, 2008; Drinkwater, 2009). Current stock boundaries were delineated in the 1970s before recent research that employed more thorough field sampling, modern laboratory techniques, and advanced analytical methods. The following sections will examine recent investigations of cod in US waters, with emphasis on studies that test for geographic variation by including samples from multiple regions, which is imperative for application to stock identification.

Population structure

Metapopulation theory (Kritzer and Sale, 2004) has been used to describe cod populations (Smedbol and Wroblewski, 2002; Wright *et al.*, 2006; Rose *et al.*, 2011) that consist of multiple subpopulations (semi-independent, self-reproducing groups of individuals within a larger population that undergo some measurable, but limited,

exchange of individuals with other areas within a population) and many finer-scale spawning components (segments of a population that do not differ in genetics or growth, but occupy discrete spawning areas interannually; Smedbol and Stephenson, 2001). There is growing support for the application of the metapopulation theory to cod populations in US waters (Perkins *et al.*, 1997; Ames, 2004; Kovach *et al.*, 2010; Armstrong *et al.*, 2013; Zemeckis *et al.*, 2014a). Several studies indicate that cod exhibit spawning-site fidelity and return to the same sites to spawn each season (Green and Wroblewski, 2000; Robichaud and Rose, 2001; Skjæraasen *et al.*, 2011; Zemeckis *et al.*, 2014a). Therefore, examination of cod population structure is anticipated to be most accurate when investigating the differences and connectivity among spawning components, because population segments will be the most geographically discrete and exhibit minimal mixing while spawning (Cushing, 1981).

Cod are distributed off the northeast coast of the United States from the eastern Gulf of Maine through the Middle Atlantic (Figure 2). Within this region, cod spawn in a variety of locations and seasons (Table 1). The major spawning components that remain active include spring and winter spawners in Ipswich Bay (Howell *et al.*, 2008; Gurshin *et al.*, 2013; Siceloff and Howell, 2013), spring and winter spawners in Massachusetts Bay (Armstrong *et al.*, 2013), winter and early spring spawners on Stellwagen Bank and Jeffreys Ledge in the Gulf of Maine (Kovach *et al.*, 2010; Runge *et al.*, 2010), autumn/winter spawners in the Great South Channel and Nantucket Shoals (Weiss *et al.*, 2005; Kovach *et al.*, 2010), winter/early spring spawners on the Northeast Peak of Georges Bank (Page *et al.*, 1999; Lough *et al.*, 2006), and winter spawners off Block Island/Cox Ledge in southern New England (Kovach *et al.*, 2010), which have undergone a resurgence in recent years.

Historical information documents reductions in biocomplexity (Alexander *et al.*, 2009) and extensive depletion of spawning components along coastal Maine by the late 1940s (Maine Department of Sea and Shore Fisheries, 1949), which occurred in response to overexploitation, habitat degradation, and declines in forage species (Ames, 2004). Historical winter spawning sites in Massachusetts Bay off Plymouth and in Ipswich Bay were once regarded as the most important inshore grounds off New England (Fish, 1928; Rich, 1929). However, present spawning sites off Plymouth appear to have substantially reduced spawning activity (W. Hoffman, pers. comm.). Further research is required to investigate the spawning components on Jeffreys Ledge and Stellwagen Bank, because the spatio-temporal extent of spawning in these areas has not been well documented.

The Northeast Peak of Georges Bank is a major cod spawning ground (Goode, 1884; Rich, 1929), but this area resides primarily in Canadian waters. The remaining offshore fishing grounds of the Gulf of Maine and Georges Bank are not documented as spawning grounds in historical references (Goode, 1884; Rich, 1929; Ames, 2004), suggesting that they were primarily feeding grounds. Ames' (2004) inferences of cod movements suggest that the offshore fishing grounds of the Gulf of Maine were inhabited by cod that migrate offshore after spawning along the coast, likely moving in pursuit of prey (Ames and Lichter, 2013). If these inferences are accurate, the depletion of the coastal spawning components might explain the low abundance of cod on offshore grounds in the Gulf of Maine (Ames, 2004).

Spawning sites in the Great South Channel and on the Nantucket Shoals (Weiss *et al.*, 2005; Kovach *et al.*, 2010) have shown signs of substantial reductions in abundance in recent years (NEFSC,

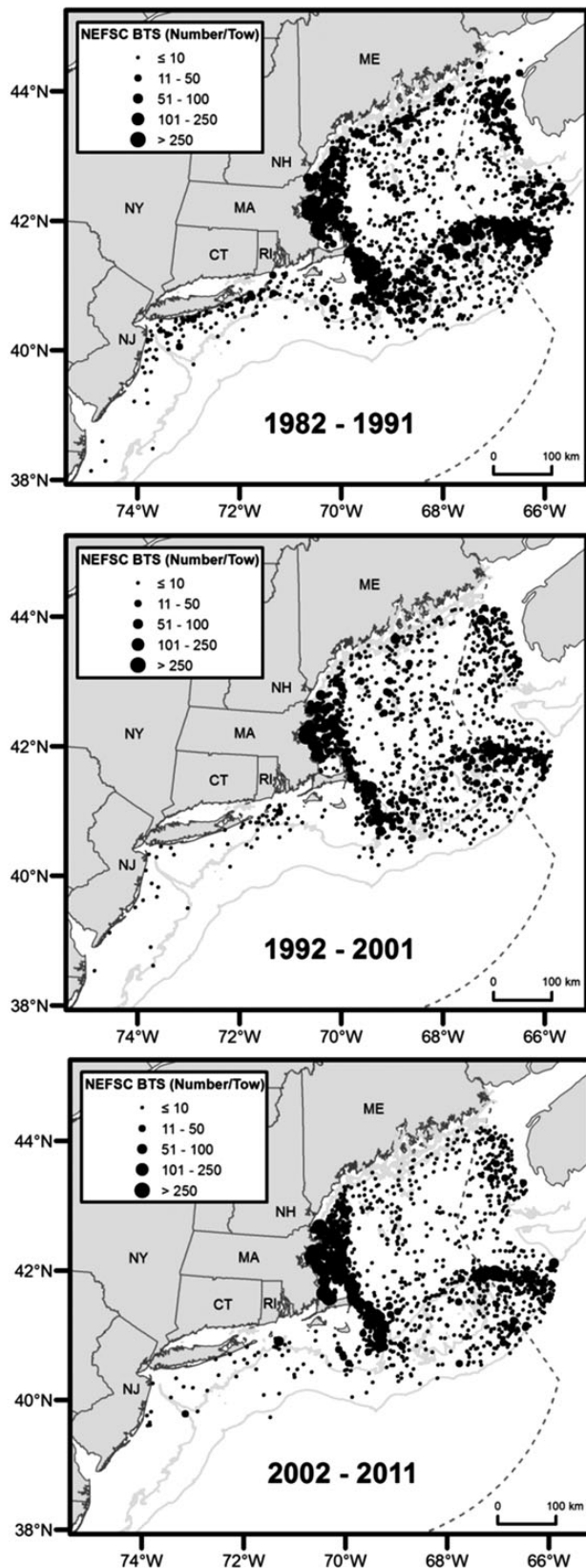


Figure 2. Distribution of Atlantic cod from the NOAA Northeast Fisheries Science Center (NEFSC) spring and autumn bottom trawl surveys (BTS) (1982–2011).

2013). Historically, the movement of cod from the Nantucket Shoals region into the Middle Atlantic was thought to be a spawning migration to waters off New Jersey (Wise, 1958). Therefore, the presence of spawning activity in southern New England and the Middle Atlantic suggest that these regions are at least partially self-sustaining and are not as dependent on receiving recruits from Georges Bank as previously concluded (Serchuk and Wood, 1979). Unfortunately, only samples from non-spawning fish in the Middle Atlantic were available for inclusion in recent genetic studies (e.g. Wirgin *et al.*, 2007; Kovach *et al.*, 2010). The continued presence of cod off New Jersey suggests that some spawning may still be occurring in these regions, and future work should investigate this possibility.

Once a spawning site has lost its resident population, it may remain barren even when spawning cod are present on neighboring grounds (Ames, 1997). Reductions in spawning diversity increase the risk of widespread recruitment failure (Sinclair, 1988; Begg and Marteinsdottir, 2000) and reduce stock productivity and stability (Kerr *et al.*, 2010), when compared with a more heterogeneous stock. Consequently, intrastock diversity and complex population structuring are important for consideration in stock assessment and fishery management. Continued tagging on spawning grounds, including depleted spawning components, would help to quantify movement rates and to understand connectivity patterns and spawning dynamics, which will provide further insights into the complex population structure of cod in the Gulf of Maine region.

Genetic variation

Molecular genetic techniques serve as robust tools in conservation biology for identifying reproductive isolation between stocks, permitting delineation of management units, and allowing assessment of conservation priorities from an evolutionary perspective (Begg *et al.*, 1999a). Genetic approaches have shifted the paradigm of marine ecology by contributing to the discovery of extensive genetic population structuring, greater biocomplexity, and more complex recruitment dynamics than previously assumed (Hauser and Carvalho, 2008). Despite the substantial increase in using genetic markers for exploring population structure, published data are often not considered in cod management plans (Reiss *et al.*, 2009). The level of divergence among populations can justify their separate management (Waples *et al.*, 2008). Bentzen (1998) proposed that populations should be considered demographically independent and managed separately if a significant and reproducible genetic differentiation can be detected. This is applicable to cod, because even low levels of differentiation can be biologically meaningful due to the presence of temporally persistent, local populations (Knutsen *et al.*, 2011).

Several studies have investigated genetic variation among cod subpopulations in US waters, and their results have proven valuable for examining population structure. Ruzzante *et al.* (1998) reported genetic variation in microsatellite DNA among 14 cod populations throughout the Northwest Atlantic. Cod from eastern Georges Bank and the Bay of Fundy were found to be genetically distinct from all other populations and were marginally distinct from each other. Lage *et al.* (2004) discovered significant genetic variation in microsatellite loci between cod on Nantucket Shoals and eastern Georges Bank and also between cod on Nantucket Shoals and Browns Bank. However, significant differentiation was not observed between Georges Bank and Browns Bank. The lack of heterogeneity between the two banks does not agree with results from Ruzzante

Table 1. Locations and timing of spawning for Atlantic cod (*Gadus morhua*) in US waters.

Spawning location	Timing	References
Coastal Maine	April–July October–December	Perkins <i>et al.</i> (1997), Berrien and Sibunka (1999), and Ames (2004)
Ipswich Bay	April–July November–March	Fish (1928), Howell <i>et al.</i> (2008), and Siceloff and Howell (2013)
Massachusetts Bay	April–July November–February	Fish (1928), Rich (1929), Dean <i>et al.</i> (2012), and Armstrong <i>et al.</i> (2013)
Jeffreys Ledge	December–February	Berrien and Sibunka (1999) and Kovach <i>et al.</i> (2010)
Stellwagen Bank	January–May	Berrien and Sibunka (1999), Kovach <i>et al.</i> (2010), and Wirgin <i>et al.</i> (2007)
Great South Channel/Nantucket Shoals	October–March	Berrien and Sibunka (1999), Kovach <i>et al.</i> (2010), and Weiss <i>et al.</i> (2005)
Georges Bank—Northeast Peak	December–May	Berrien and Sibunka (1999), Lough <i>et al.</i> (2006), and Weiss <i>et al.</i> (2005)
Southern New England—Cox Ledge	December–April	Berrien and Sibunka (1999) and Kovach <i>et al.</i> (2010)
Middle Atlantic	December–April	Berrien and Sibunka (1999) and Wise (1958)

et al. (1998), which is possibly a result of the use of different loci or the small sample sizes included in each study. Lage *et al.* (2004) suggested that cod on Nantucket Shoals may be genetically distinct from other samples because of the isolation of eggs and larvae that results from the clockwise gyre on Georges Bank, or possibly due to limited movement of adults between regions and differences in thermal tolerance due to the warmer waters on Nantucket Shoals. Therefore, based on their genetic differentiation, Lage *et al.* (2004) concluded that managers should include cod on Nantucket Shoals in a separate stock from cod on Georges Bank and Browns Bank.

Weiss *et al.* (2005) sought to determine if the temporal spawning difference between cod on eastern Georges Bank (winter/early spring) and western Georges Bank (late autumn/early winter) (Table 1) constitutes two genetically distinct subpopulations. By using DNA microsatellite markers, spawning cod sampled on western Georges Bank in locations west of the Great South Channel were found to be genetically distinct from spawning cod on eastern Georges Bank. Larvae collected on Nantucket Shoals were determined to have most likely originated from the western Georges Bank population, whereas the results for the juveniles were less conclusive, but suggested that they represented a mixture of adult populations or an unsampled population. However, it is difficult to draw definitive conclusions from these genetic assignments because of small sample sizes and the relatively small genetic differences that exist among subpopulations.

Wirgin *et al.* (2007) investigated the contemporary genetic population structure of cod in US waters using samples from 2 years. In the first year, they sampled juveniles and non-spawning adults and found no significant difference in allelic frequencies between a composite sample of adults and juveniles from the Gulf of Maine and Georges Bank nor between the Great South Channel and any other site. However, juveniles from Massachusetts Bay were determined to be significantly different from the Georges Bank collection and juveniles from Maine. Samples of spawning adults from the second year revealed highly significant differences in allelic frequencies between cod from the Gulf of Maine and Georges Bank, contrary to their findings from the first year's samples that included non-spawning fish. Furthermore, spring-spawning samples collected in Ipswich Bay were significantly different from all other sites, including the winter spawning Ipswich Bay collection, thus identifying genetic differentiation between seasonally divergent spawning components from the same location. Samples collected from non-spawning cod off Long Island were genetically distinct from the Georges Bank and the spring Ipswich Bay samples, but not from other locations.

Results from Breton (2008) and Kovach *et al.* (2010) provided a more comprehensive, fine-scale characterization of the population structure of spatially and temporally segregated spawning components in US waters, including the spawning component on the Northeast Peak of Georges Bank, which spawns primarily in Canadian waters, but the spatial distribution of which spans the international boundary. Using ten microsatellite loci, the *PanI* locus, and five single-nucleotide polymorphism markers to characterize cod genetic structure, Kovach *et al.* (2010) identified three primary genetic groupings: (i) a “Northern Spring Coastal Complex” which spawns in coastal Gulf of Maine waters from Massachusetts Bay to Bigelow Bight in spring; (ii) a “Southern Complex”, which spawns within the inshore Gulf of Maine in winter (Massachusetts Bay and Ipswich Bay) and at different offshore locations and seasons within the Gulf of Maine (Jeffreys Ledge and Stellwagen Bank) and south of Cape Cod (Nantucket Shoals and Cox Ledge); and (iii) a population on the Northeast Peak of Georges Bank which spawns in late winter/early spring (Figure 3). Non-spawning samples collected off Long Island in the Middle Atlantic clustered within the “Southern Complex”. Fine-scale population structuring was also observed within these major complexes, including weak differentiation between samples from southern New England and samples collected on Stellwagen Bank and Jeffreys Ledge in the Gulf of Maine. Weak differentiation was also observed between cod on Cox Ledge in southern New England and Nantucket Shoals. Evidence for stable, fine-scale genetic differentiation was, therefore, found among spatially and seasonally divergent subpopulations.

One of the most important findings of recent genetics studies is that genetic differentiation exists among seasonally separated subpopulations that overlap spatially (e.g. winter vs. spring subpopulations; Wirgin *et al.*, 2007; Breton, 2008; Kovach *et al.*, 2010), which provides evidence of the complex population structure that exists in the Gulf of Maine. Results also demonstrate that cod in southern New England and the Middle Atlantic are genetically distinct from cod on eastern Georges Bank (Wirgin *et al.*, 2007; Kovach *et al.*, 2010), suggesting that the connectivity previously inferred between these regions based on phenotypic traits (Serchuk and Wood, 1979) may be a phenotypic response to similar environmental conditions, rather than a reproductive connection (e.g. Rothschild, 2007).

Genetic samples collected off eastern Maine would help to understand connectivity among adjacent spawning components. The lack of spawning activity in this region and the persistent spawning aggregations in Ipswich Bay and Massachusetts Bay suggests that cod off eastern Maine may be demographically independent

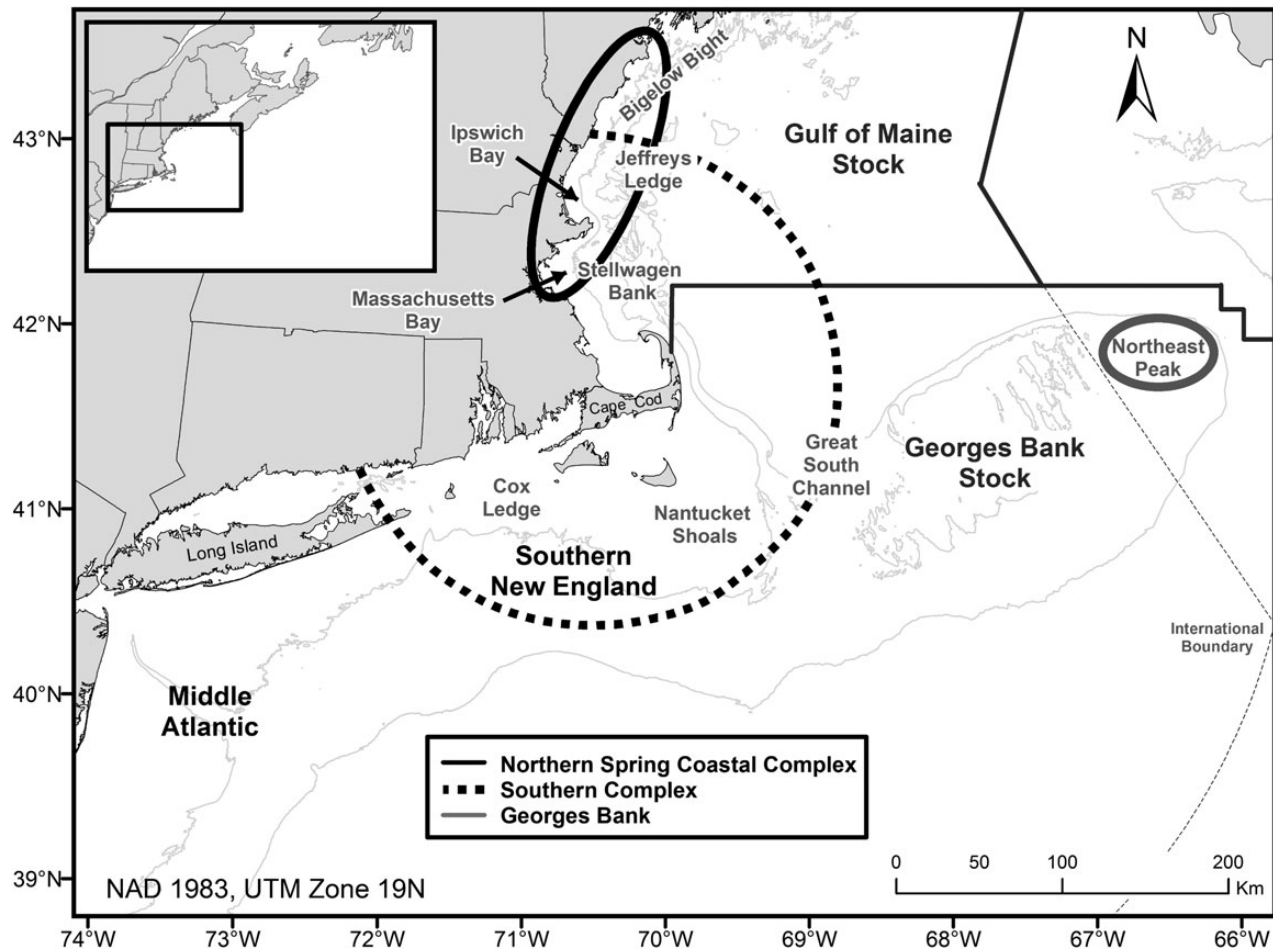


Figure 3. Genetic groupings of Atlantic cod spawning sites based on the results of Breton (2008) and Kovach *et al.* (2010). The three primary genetic groupings include the “Northern Spring Coastal Complex”, the “Southern Complex”, and the Northeast Peak of Georges Bank, where spawning primarily occurs in Canadian waters, but the spatial distribution of this spawning component spans the international boundary.

(Kovach *et al.*, 2010). Tagging data (e.g. NACFI, 1932; Howell *et al.*, 2008; Clark and Emberley, 2010; Tallack, 2011) and the delineations of coastal subpopulations (Ames, 2004) offer additional evidence of a separation between spawning components in the eastern and western portions of the Gulf of Maine. Further research, including stock composition analysis using a suite of stock identification methods, would help refine biological stock boundaries and identify seasons, areas, and fisheries with mixed biological stocks to advise fishery management decisions.

Phenotypic variation

Phenotypic variation is due to both environmental and genetic components (Swain and Foote, 1999), and distinguishing between them is the basic difficulty that must be addressed when using these characters to investigate population structure (Begg *et al.*, 1999a). Phenotypic traits are typically most useful when multiple traits are investigated to study short-term, environmentally induced variation (Begg *et al.*, 1999a). Phenotypic plasticity can occur in fish that appear to represent distinct stocks, but instead share a common genotype, presenting another issue to consider when applying these traits for stock identification (Swain and Foote, 1999), thus supporting the interdisciplinary approach applied in this review.

Life-history parameters

Life-history parameters are the manifestation of the adaptive strategies to which fish stocks have evolved (Begg, 2005), and they assist in the recognition and delineation of geographical areas representative of stocks (Pawson and Jennings, 1996) by providing evidence that populations are reproductively isolated to some degree (Ihssen *et al.*, 1981) and have distinct vital rates that are important for population dynamics (Cadrin and Secor, 2009). The utility of life-history parameters for stock identification decreases with stock complexity and exploitation history, but their applicability is increased by examining multiple parameters (Begg *et al.*, 1999a). Fortunately, many life-history parameters are already investigated for use in stock assessment and can be easily applied to stock identification (Begg and Cadrin, 2009).

Begg *et al.* (1999b) demonstrated that the spatial distribution of cod has decreased since the 1960s, and they noted an apparent division between cod on eastern and western Georges Bank based on distribution patterns (Figure 2). Growth rates were found to be consistently greater for cod on Georges Bank compared to cod in the Gulf of Maine. Intra-stock variability in growth rates was observed, with cod on western Georges Bank growing slower than cod on eastern Georges Bank in many years sampled (see Table 1 and Figure 4 in Begg *et al.*, 1999b). Considerable variability was also recorded in the maximum length of cod within the eastern and

western Georges Bank samples. Mortality rates generally did not differ between cod on Georges Bank and in the Gulf of Maine. Cod from Georges Bank matured at younger ages and greater lengths than Gulf of Maine cod. Typically, there were no differences in maturity rates between eastern and western Georges Bank, except between 1975–1979 and 1980–1984.

Tallack (2009a) confirmed the persistence of complex patterns in cod growth through analysis of tag recapture data from the Northeast Regional Cod Tagging Program (Tallack, 2009b). In contrast to previous findings of Penttila and Gifford (1976), cod were significantly larger in the Gulf of Maine ($L_{\text{mean}} = 67.1$ cm, $L_{\text{max}} = 124$ cm) than on Georges Bank ($L_{\text{mean}} = 55.5$ cm, $L_{\text{max}} = 90$ cm). The largest cod were sampled in the inshore Gulf of Maine ($L_{\text{mean}} = 65.9$ cm, $L_{\text{max}} = 124$ cm), whereas the smallest cod were found in Cape Cod waters ($L_{\text{mean}} = 52.1$ cm, $L_{\text{max}} = 83$ cm), which were significantly smaller than cod on offshore Georges Bank ($L_{\text{mean}} = 64.9$ cm, $L_{\text{max}} = 85$ cm). Results using a modified von Bertalanffy growth curve found Gulf of Maine cod to exhibit slower growth rates and a larger asymptotic size ($k = 0.13$, $L_{\infty} = 151.3$ cm) than cod on Georges Bank ($k = 0.31$, $L_{\infty} = 105.7$ cm). Fish sampled just east of Cape Cod had considerably slower growth ($k = 0.13$) and greater maximum length ($L_{\infty} = 173.5$ cm) compared with cod released and recaptured on offshore Georges Bank ($k = 0.26$, $L_{\infty} = 104.1$ cm). However, growth rates of cod around Cape Cod were similar to cod in the Gulf of Maine. Consequently, it appears that the Georges Bank stock is represented by two different size structures, including the larger, faster-growing cod of offshore Georges Bank, and the smaller, slower-growing cod of nearshore Cape Cod, which includes areas such as the Great South Channel and Nantucket Shoals (Tallack, 2009a).

Cod in the Gulf of Maine and on Georges Bank have experienced a reduction in age and length at maturity in recent decades (Hunt, 1996; O'Brien, 1999; Barot *et al.*, 2004). O'Brien (1999) analysed maturation data from 1970 to 1998 and reported that median maturity at age for Georges Bank females ($A_{50} = 2.1$ years) was earlier than for Gulf of Maine females ($A_{50} = 2.9$ years), whereas the average median length at maturity was similar for Georges Bank ($L_{50} = 45.2$ cm) and the Gulf of Maine ($L_{50} = 42.0$ cm). The age at 100% maturity declined between 1970 and 1998 from ages 5 and 6 to ages 4 and 5 for Georges Bank cod, and from ages 6 and 7 to ages 5 and 6 in the Gulf of Maine. The proportion mature at ages 2–4 increased significantly for both sexes on Georges Bank from 1970 to 1998, whereas it has also increased significantly for Gulf of Maine males for ages 2–4 and females ages 3–5. Investigations of large-scale maturation trends were performed at the stock level based on current stock boundaries, but results were only reported for current management units and did not explore patterns of geographic variation on a scale fine enough for stock identification.

Otolith analyses have also indicated variable growth rates between Georges Bank, southern New England, and the Gulf of Maine (Penttila, 1988). However, data are only reported on the scale of current management units, preventing further investigation of fine-scale geographic variation among and within stocks. Analysing samples over finer scales would be more informative for stock identification. Additional research should also include comparative analysis of fish condition to help understand the variability in productivity among spawning components and to develop sustainable management practices, because fish populations with low-energy reserves are generally more susceptible to reduced recruitment at low spawning–stock biomass, whereas stocks in

good condition can typically withstand greater exploitation rates (Ratz and Lloret, 2003).

Early life stages: larval dispersal

The distribution of early life stages, including eggs, larvae, and juveniles, provides an indication of the spatial and temporal distribution of spawning activity (Hare, 2005). Retention mechanisms for larvae are commonly identified in association with genetic differences (Hare, 2005) and are expected to have an important influence on population structure (e.g. Espeland *et al.*, 2007).

Berrien and Sibunka (1999) presented information on the distribution of fish eggs collected from broadscale ichthyoplankton surveys conducted off the northeastern US coast during 1977–1987. The distribution of cod eggs was used to investigate interannual and interseasonal trends in spawning intensity. Cod eggs were found from Nova Scotia southward to almost Cape Hatteras. Egg abundance was greatest in the western Gulf of Maine, Georges Bank, and in southern New England regions, primarily in waters <100 m depth. Spawning increased during autumn and winter throughout the region. Maximum average abundance peaked in March, but a large part of the Gulf of Maine was not sampled in this month, and the highest densities occurred on Georges Bank. Spawning decreased throughout spring and early summer, but areas of intense spawning persisted during this time in Massachusetts Bay and Ipswich Bay. Egg abundance decreased throughout the region over the study period, which might be an indication of continued depletion of spawning components. Additional ichthyoplankton surveys in conjunction with genetic investigations (e.g. Bui *et al.*, 2011) should be performed to identify the locations and timing of spawning events that remain active, which would improve our understanding of contemporary population structure and productivity patterns among subpopulations.

The transport of eggs and larvae from coastal spawning sites in the western Gulf of Maine has been intensively investigated. Local windforcing and spawning site location with respect to the Western Maine Coastal Current (Figure 4) strongly influence transport success (Huret *et al.*, 2007). Downwelling conditions, which are more common in spring, retain recently spawned eggs and larvae west of the coastal current. The coastal spawning sites are connected to juvenile nursery areas downstream (Huret *et al.*, 2007), and retention west of the coastal current promotes settlement within coastal embayments that serve as critical habitat for juveniles (Howe *et al.*, 2002). In contrast, upwelling conditions, more common in winter, transport recently spawned eggs and larvae offshore, where they are more likely to be entrained in the coastal current and advected a greater distance (Churchill and Runge, 2009). Simulations indicate a low likelihood of retention of winter-spawned larvae in the western Gulf of Maine (Churchill *et al.*, 2011), and transport to the Great South Channel, Nantucket Shoals, and the southern New England shelf is possible (Huret *et al.*, 2007).

As a result, spring- and winter-spawning components in the Gulf of Maine appear to serve different functions in sustaining cod populations in US waters (Churchill *et al.*, 2011). Spring-spawning components in Massachusetts Bay and Ipswich Bay appear to have limited reproductive connectivity with other regional components, whereas winter-spawning components in Massachusetts Bay, Ipswich Bay, and offshore on Stellwagen Bank and Jeffreys Ledge appear to be connected with spawning components outside of the Gulf of Maine over a larger geographic scale, including those in the region of the Great South Channel, Nantucket Shoals, and southern New England. These findings are supported by the genetic population structure identified by Breton (2008) and

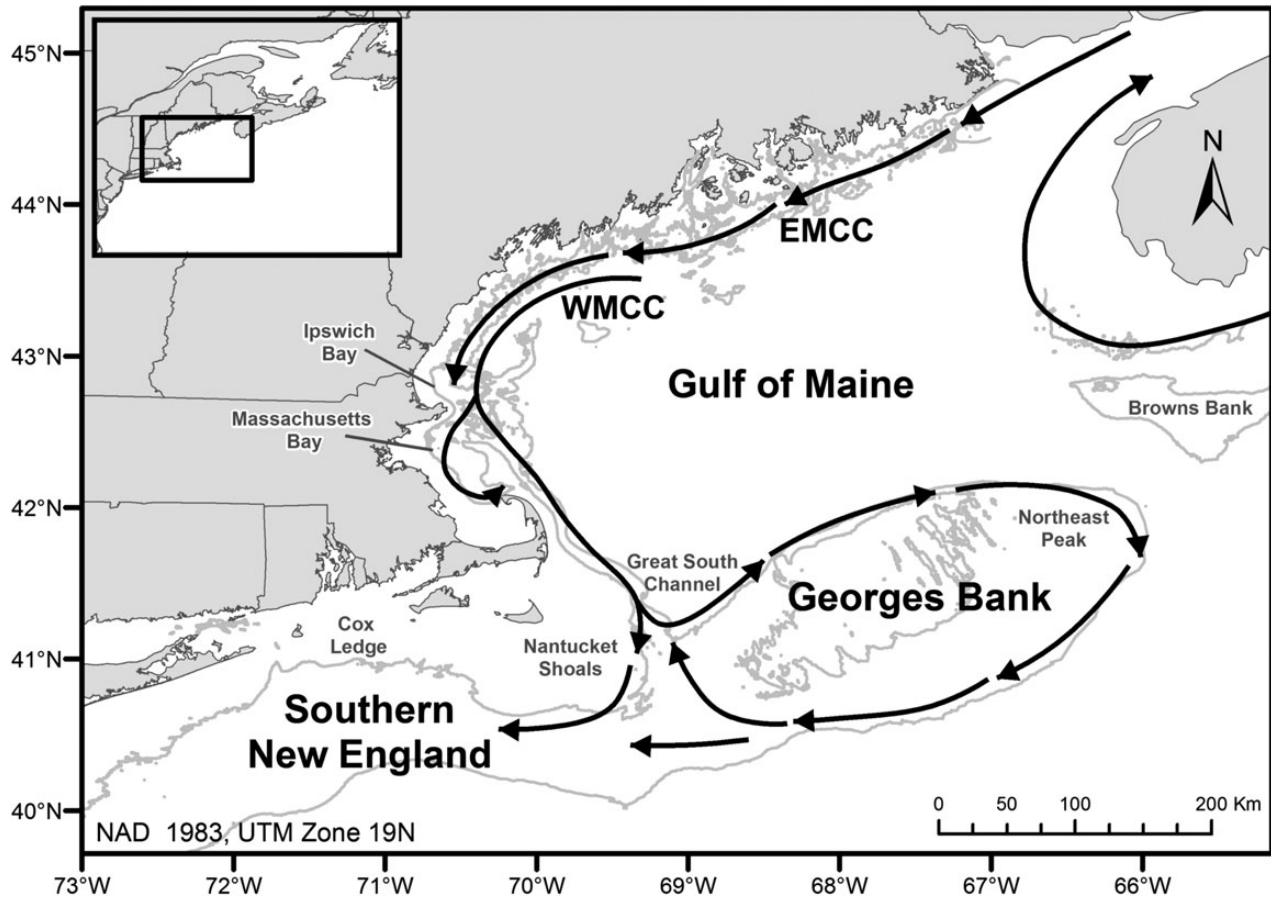


Figure 4. General near-surface circulation in the Gulf of Maine and Georges Bank, reproduced from previous studies (Keafer *et al.*, 2005; Lough *et al.*, 2005; Huret *et al.*, 2007; Churchill *et al.*, 2011). Included in the Gulf of Maine are the Western Maine Coastal Current (WMCC) and the Eastern Maine Coastal Current (EMCC). Also included is the clockwise gyre of Georges Bank.

Kovach *et al.* (2010). Therefore, the western Gulf of Maine cod population may currently be more sustained by larvae produced from spring-spawning components than winter-spawning components (Churchill *et al.*, 2011). Natal homing of larvae transported out of the Gulf of Maine has not been determined, but such evidence would improve our understanding of population dynamics. Perhaps, the movement of juvenile cod from the Great South Channel and Nantucket Shoals into the Gulf of Maine (Tallack, 2011) is indicative of such behaviour.

The primary spawning ground for cod on Georges Bank is the Northeast Peak (Colton and Temple, 1961; Page *et al.*, 1999). Eggs and larvae generally drift south and west from the Northeast Peak along the southern flank of Georges Bank. A large portion of the cohort can be retained on the shoals of Georges Bank by recirculation on the western end near the Great South Channel and the clockwise gyre around Georges Bank (Lough *et al.*, 2006; Figure 4). In most years, a portion of larvae are advected across the Great South Channel to Nantucket Shoals (Lough *et al.*, 2006). A large portion of the eggs and larvae can also be transported off the southern edge of Georges Bank to deep water (>300 m) and are presumably lost, but some eggs and larvae are retained on the bank under unusual hydrographic conditions, and these experience higher rates of survival (Colton and Temple, 1961). Therefore, the larvae spawned on the Northeast Peak of Georges Bank remain generally isolated from the larvae of the Gulf of Maine, with some chance of mixing on the Nantucket Shoals due to annual variability in hydrographic conditions.

Investigating the connectivity among spawning sites during the early life stages (e.g. Knutsen *et al.*, 2004) would help to understand population processes and productivity patterns among spawning components. The effects of location and timing of spawning on recruitment (e.g. Bradbury *et al.*, 2000), as well as how advective effects interact with retention and dispersal (e.g. Bradbury *et al.*, 2001, 2008), also warrant examination to understand factors influencing productivity. Furthermore, the dispersal of eggs and larvae from spawning events in southern New England has not yet been examined and should be a topic of future research to investigate connectivity with other spawning components and for comparison with results from previous work that applied other stock identification methods (e.g. tagging and genetics).

Applied marks: tagging studies

Most stock assessment models are based on the assumption that fish are distributed homogeneously or freely mix across the region being assessed. Any local patterns in density, age structure, or mortality are assumed to be ephemeral (Punt and Methot, 2004). Tagging studies can help test the closed population assumption of stock assessment models by providing information on population structure (Lear, 1984), migration, spawning areas, and the temporal and spatial degree of overlap with other stocks (Jacobsen and Hansen, 2005).

Hunt *et al.* (1999) investigated the movements of cod tagged in the Gulf of Maine area from 1979 to 1997. Over 22 000 cod were

tagged with standard t-bar tags, mostly during the winter spawning season, and >2400 recaptures were available to interpret movement patterns. NAFO Division 5Yb spans the international boundary between the United States and Canada (Statistical Area 511 in Figure 1). Tagging occurred on the Grand Manan Banks in the Canadian portion of 5Yb. Very few recaptures (1.4%) of cod tagged in 5Yb moved west into other subdivisions included in the US Gulf of Maine cod stock, whereas a greater percentage (10.4%) were caught within 5Yb (not specified whether in US or Canadian waters) or moved into the Canadian 4X stock (includes the Southern Scotian Shelf and Bay of Fundy; 86.4%). Few recaptures of cod tagged in 4X came from within the US Gulf of Maine cod stock (see Table 3 in Hunt *et al.*, 1999), which is consistent with the low mixing between these stocks described in Clark and Emberley (2010). Hunt *et al.* (1999) found an exchange rate of ~15% between the waters off Nova Scotia (4X) and Georges Bank (5Z), with a net loss from Georges Bank to Browns Bank. Few recaptures of cod tagged on eastern Georges Bank (5Zj and 5Zm) moved west and were recaptured near the Great South Channel or Nantucket Shoals (5Zg and 5Zo), and even fewer moved northwest and were recaptured in the US Gulf of Maine cod stock. The results of Hunt *et al.* (1999) are consistent with other tagging studies (e.g. Wise, 1963; Clark and Emberley, 2010), indicating that mixing primarily occurs between eastern Georges Bank and the Scotian Shelf, but a review of tagging data concluded that these areas could be managed and assessed separately (Wang *et al.*, 2009).

The Northeast Regional Cod Tagging Program provided a region-wide, international snapshot of cod movements across the region (Tallack, 2009b). In all, 114 473 cod were tagged in the Gulf of Maine, on Georges Bank, and the Scotian Shelf during 2003–2005. More than 6500 tags were recaptured to interpret movement patterns applicable to stock identification (Tallack, 2011). Dominant migration routes were identified based on information gathered from tag returns. Small fish were found to move to Georges Bank from Cape Cod waters, with most adult fish remaining offshore on Georges Bank. Seasonal northward movements were observed from Georges Bank into the Bay of Fundy during spring and summer, but recaptures also suggest that fish then returned south to Georges Bank for autumn and winter. Cod in the Bay of Fundy remained confined to that area during spring and summer, but some then moved south to Georges Basin and Georges Bank in autumn. Little exchange was observed between the Bay of Fundy and the Gulf of Maine stock, which is similar to findings of Hunt *et al.* (1999). Few cod tagged in the inshore Gulf of Maine were recaptured outside this area, whereas small fish from the Great South Channel often moved north into the Gulf of Maine (Tallack, 2011). Estimated mixing rates between management units ranged from 0.03 to 0.23 per year (Miller and Tallack, 2007), with the least mixing occurring between the Gulf of Maine and Scotian Shelf, and the most mixing between Georges Bank and the Scotian Shelf (Tallack, 2009b). Loehrke (2013) analysed movements of cod spawning groups off New England and found distinct patterns of dispersal, with inshore spawners dispersing much less than cod on eastern Georges Bank, which was consistent with movement patterns described in other papers.

The inshore spawning components of the western Gulf of Maine appear to be major contributors to the Gulf of Maine stock. Perkins *et al.* (1997) conducted a tagging study of the spring-spawning component in Sheepscoot Bay off Maine (Statistical Area 513, Figure 1). Their results demonstrated a high affinity for coastal areas and a pattern of concentration indicating pre- and post-spawning

aggregations offshore from the spawning site. Cod that spawn in Sheepscoot Bay appeared to be distinct from cod in the Bay of Fundy investigated by Hunt and Neilson (1993). Individual cod were found to return to Sheepscoot Bay each season to spawn, thus providing evidence that Gulf of Maine cod exhibit spawning-site fidelity and that the stock consists of multiple, semi-discrete spawning components. As a result, the authors concluded that the Gulf of Maine stock should be considered a “stock complex” rather than a unit-stock (Perkins *et al.*, 1997).

Howell *et al.* (2008) conducted a mark–recapture study to investigate seasonal movements of cod in the western Gulf of Maine. Their results indicate that cod in the western Gulf of Maine near Ipswich Bay are resident in the area and relatively sedentary. They also found evidence for two subpopulations in Ipswich Bay: a winter subpopulation that spawns in November–January, and a spring subpopulation that spawns in April–July. The spring-spawning subpopulation displayed signs of spawning-site fidelity, with cod returning to the same spawning ground during the same period each year. The expression of spawning-site fidelity (Perkins *et al.*, 1997; Howell *et al.*, 2008) provides evidence of meta-population structuring with extensive intrastock diversity, where genetically distinct subpopulations (Kovach *et al.*, 2010) may be reproductively isolated and at least partially self-sustaining (e.g. Espeland *et al.*, 2007).

Electronic data-storage tags that archive data on environmental parameters, such as temperature, salinity, or pressure (depth), allow researchers to reconstruct the movements of free-ranging demersal fish based on the calculation of fishery-independent movement parameters that could not be gathered by traditional mark–recapture experiments (Bolle *et al.*, 2005). For example, Gröger *et al.* (2007) utilized tidal models to geolocate cod tagged in Massachusetts Bay. They found that the Great South Channel served as a migration corridor between Massachusetts Bay and the Nantucket Shoals regions, signifying movement across current management unit boundaries. Additional electronic tagging studies would improve our understanding of cod movements in US waters and provide further insights into behaviour patterns, including the overlap among spawning components. Also, tagging studies in the western Gulf of Maine and on western Georges Bank would help to quantify movements across current stock boundaries. Furthermore, tagging of cod in the offshore regions of the Gulf of Maine would help to test the general inshore–offshore movement pattern postulated by Ames (2004) for cod along coastal Maine.

Additional stock identification methods for future research

Otoliths: elemental composition and shape analysis

Elemental composition of otoliths can be used to discriminate between fish that have resided in different environments (Campana, 2005). Despite their utility, studies employing otolith analyses are generally lacking for cod in US waters. Campana *et al.* (1994) found significant differences in the elemental fingerprints of otoliths collected from spawning grounds throughout the Northwest Atlantic. However, future studies should include samples collected from multiple spawning sites in US waters to permit investigation on finer scales than the management unit. Townsend *et al.* (1995) found that Sr:Ca ratios in larval cod otoliths are useful for hindcasting larval distributions in relation to water mass distributions on Georges Bank. Analysis of otolith samples collected from other spawning areas would help to interpret larval

transport patterns of different regions and to investigate the juvenile source of spawning cod (e.g. Thorisson *et al.*, 2011), which will provide insight into the connectivity among spawning components. Studies of otolith-shape analysis could also help to identify spawning areas and discriminate between subpopulations (e.g. Jónsdóttir *et al.*, 2006; Petursdóttir *et al.*, 2006). For example, Galley *et al.* (2006) successfully used otolith shape to classify cod from different spawning components in the North Sea. Furthermore, significant age-specific differences in otolith shape have been documented for haddock (*Melanogrammus aeglefinus*) between eastern and western Georges Bank (Begg and Brown, 2000). Testing for similar variation among cod spawning components in US waters can compliment information acquired from other stock identification methods for application in stock composition analyses and to help investigate the movements and distribution of spawning components (i.e. natural tags).

Morphological analyses

Morphological characters such as body shape or meristic counts reflect phenotypic variation and have long been used to delineate stocks (Swain and Foote, 1999; Cadrin, 2005). Similarly, meristics serve as another useful tool for stock identification (Waldman, 2005b). Sherwood and Grabowski (2010) identified significant life-history variation among colour types of cod in the Gulf of Maine. Future studies should include samples from additional locations to investigate geographic variability as well as include genetic analyses from the same individuals to determine whether colour types are reproductively isolated, because varying colour types are often captured together on the same spawning site. Fishers have identified “groups” of cod based on their morphological differences (Goode, 1884). Applying this information would expand our understanding of spawning components acquired from fishers (Ames, 2004), and acknowledge fishers’ ecological knowledge (FEK), which can provide critical information to researchers and managers (Johannes *et al.*, 2000). Future studies could further investigate variation in body shape (e.g. Marcil *et al.*, 2006), colouration (e.g. Goose and Wroblewski, 2004; Wroblewski *et al.*, 2005), and vertebral number (e.g. Templeman, 1981; Swain *et al.*, 2001), which would have great utility for investigation of behavioural patterns and for incorporation into stock composition analyses.

Discussion

An interdisciplinary review of available biological information demonstrates that the spawning components in the Gulf of Maine have limited connectivity with spawning components on eastern Georges Bank. Supporting evidence includes genetic differentiation between regions (Wirgin *et al.*, 2007; Kovach *et al.*, 2010), differences in growth rates (Penttila and Gifford, 1976; Begg *et al.*, 1999b; Tallack, 2009a), larval dispersal dynamics (Lough *et al.*, 2006; Huret *et al.*, 2007; Churchill *et al.*, 2011), and movement patterns (Wise, 1963; Perkins *et al.*, 1997; Hunt *et al.*, 1999; Howell *et al.*, 2008; Tallack, 2011). Available biological information indicates that spawning components on eastern Georges Bank are also reproductively isolated from those in the western portion of the current Georges Bank management unit, including the Great South Channel, Nantucket Shoals, southern New England, and Middle Atlantic regions. Supporting evidence for a separation between spawning components in the eastern and western portions of the current Georges Bank management unit includes genetic variation between regions (Lage *et al.*, 2004; Weiss *et al.*, 2005; Breton, 2008; Kovach *et al.*, 2010), resource distribution patterns (Begg *et al.*,

1999b), life-history data (Penttila and Gifford, 1976; Begg *et al.*, 1999b; Tallack, 2009a), and movement patterns (Wise, 1963; Hunt *et al.*, 1999; Tallack, 2011; Loehrke, 2013).

Available biological information indicates that the inshore spawning components in the Great South Channel, Nantucket Shoals, southern New England, and Middle Atlantic regions are more connected with the inshore spawning components in the Gulf of Maine than the offshore spawning components on eastern Georges Bank (Figure 5). This presents a new paradigm with respect to cod population structure in US waters by identifying a division between inshore and offshore spawning components, compared with the previous paradigm of a north–south division based on current management units. Evidence for reproductive connectivity among inshore spawning components includes larval dispersal models (Huret *et al.*, 2007; Churchill *et al.*, 2011) and genetic studies (Lage *et al.*, 2004; Wirgin *et al.*, 2007; Kovach *et al.*, 2010), which suggest that this connection is largely influenced by larval transport dynamics along the coast and out of the western Gulf of Maine. The weak genetic differentiations observed by Kovach *et al.* (2010) suggest that such transport events to southern New England might occur episodically, and these spawning components are at least partially self-sustaining through self-recruitment, representing a recent ancestor–descendent relationship (Wirgin *et al.*, 2007). Data on life-history parameters (Tallack, 2009a) and movement patterns (Wise, 1963; Gröger *et al.*, 2007; Tallack, 2011) also support the connection among inshore spawning components. Consequently, the Great South Channel and Nantucket Shoals regions appear to serve as a mixing zone between inshore and offshore spawning components. The spatial gap between eastern Georges Bank and the Great South Channel is due to available information on spawning locations (Figure 5), which are limited to the eastern and western portions of Georges Bank. Future research is required to investigate the mixing between inshore and offshore spawning components and to determine the natal origin of cod caught in the central portions of Georges Bank.

Our interdisciplinary review indicates that current stock boundaries do not provide an accurate representation of the biological population structure of cod in US waters. The misalignment of stock boundaries can cause misperceptions of the magnitude and distribution of productivity (Kerr *et al.*, 2014) and has potentially contributed to rebuilding difficulties and the depletion of spawning components. For example, daily trip limits in the Georges Bank stock have historically been greater (O’Brien *et al.*, 2006; NEFSC, 2012) than those in the Gulf of Maine (Mayo *et al.*, 2009), due largely to their faster growth and earlier maturation. Also, the majority of US cod landings are from the western portion of the current Georges Bank management unit (NEFSC, 2013), including regions such as the Great South Channel and Nantucket Shoals. This level of fishing pressure may have been unsustainable for these spawning components, which would be more appropriately grouped with the slower-growing cod in the Gulf of Maine, and they may not have experienced recent declines if properly managed. As a result, we recommend a modification of the two-stock model that is currently acknowledged in stock assessments and fishery management to more appropriately manage cod based on their biological population structure.

Genetic investigations support the division of cod subpopulations into three genotypic stocks (Figure 3), which is consistent with the connectivity observed among inshore spawning components. However, the spatial overlap of spawning components in the “Northern Spring Coastal Complex” and the “Southern Complex” makes it difficult to manage them separately. As a result, an initial

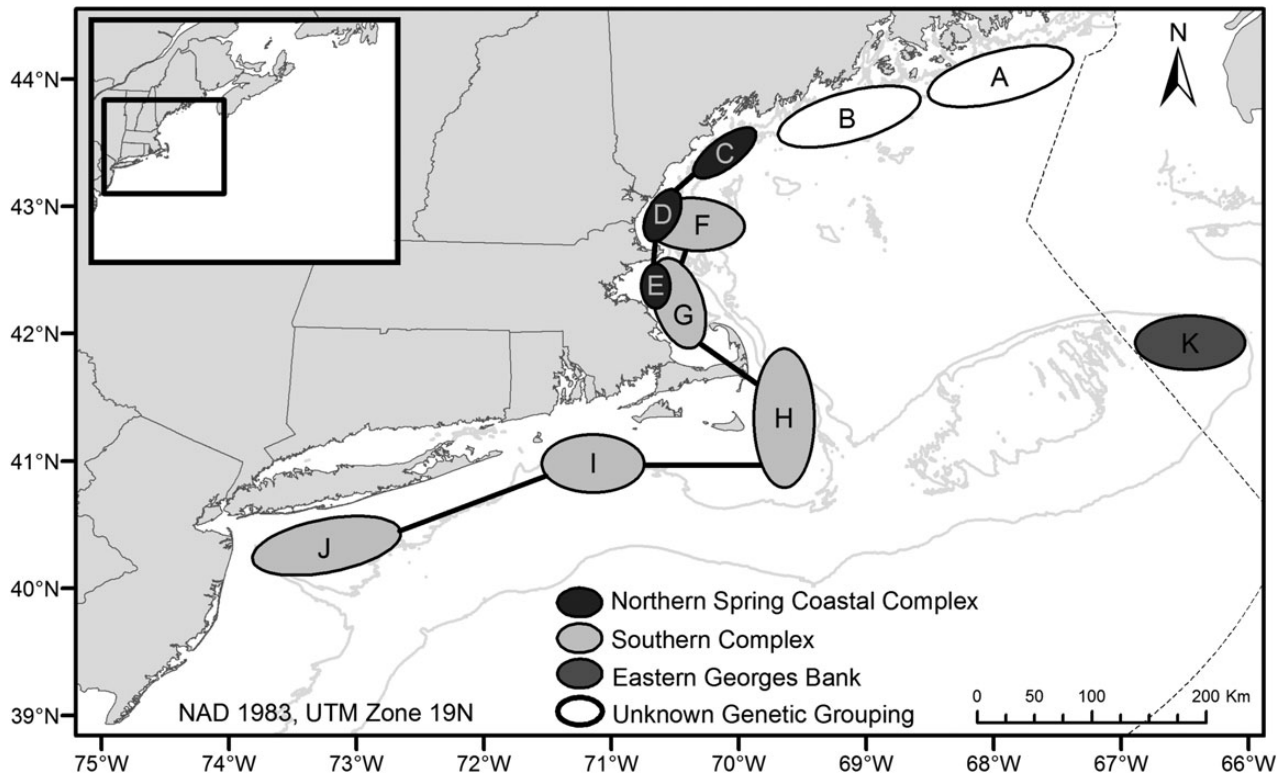


Figure 5. Metapopulation schematic depicting the new paradigm of cod population structure in US waters demonstrating that spawning components in the Great South Channel, Nantucket Shoals, southern New England, and Middle Atlantic are more connected with spawning components in the Gulf of Maine than on eastern Georges Bank. Each spawning component from Table 1 is included (ellipses roughly represent spawning grounds); where data are available, they are colour-coded based on their genetic grouping as assigned by Breton (2008) and Kovach *et al.* (2010). Lines connecting spawning components represent reproductive connectivity. (a and b) Mid-coast and eastern subpopulations as outlined by Ames (2004); (c) spring spawners in Bigelow Bight; (d) spring spawners in Ipswich Bay; (e) spring spawners in Massachusetts Bay; (f) winter spawners in Ipswich Bay and on Jeffreys Ledge; (g) winter and early-spring spawners in Massachusetts Bay and on Stellwagen Bank; (h) winter spawners on Nantucket Shoals and in the Great South Channel; (i) winter spawners in southern New England; (j) winter spawners in the Middle Atlantic; and (k) winter/early-spring spawners on the Northeast Peak of Georges Bank.

redefinition of management units could include an inshore management unit consisting of spawning components in the Gulf of Maine, Great South Channel, Nantucket Shoals, southern New England, and the Middle Atlantic based on the connectivity among these regions until stock composition information is available. A second management unit would then include spawning components on eastern Georges Bank, similar to the existing transboundary management unit. This alternative management scenario creates a division between eastern and western Georges Bank, which was suggested in earlier studies (Wise and Jensen, 1960; Wise, 1963) and is consistent with Canadian management strategies (CAFSAC, 1989; Halliday and Pinhorn, 1990; Wang *et al.*, 2011). Also, the alternative stock boundaries recognize a division between inshore and offshore spawning components, which is similar to the cod population structure observed in other regions (e.g. Newfoundland—Ruzzante *et al.*, 1996; Greenland—Pampoulie *et al.*, 2011; northeast Atlantic—Sarvas and Fevolden, 2005).

Another refinement could be to separate the remnant spawning components off eastern Maine from other inshore spawning components. For example, it has been hypothesized that subpopulations along coastal Maine are reproductively isolated from those in the western Gulf of Maine (Ames, 2004; Wirgin *et al.*, 2007; Kovach *et al.*, 2010). If this hypothesis can be confirmed, their grouping with cod in the western Gulf of Maine will need to be re-evaluated

to allow for maximum rebuilding potential. Identifying reproductive isolation between these regions would also have important implications regarding perceptions of stock productivity and status. For example, many spawning components along coastal Maine were critically depleted by the 1940s (Maine Department of Sea and Shore Fisheries, 1949), and the region continues to have low cod abundance (Figure 2). In contrast, spawning components in the western Gulf of Maine remain productive (e.g. Ipswich Bay and Massachusetts Bay), suggesting that, for many decades, the stock has been largely sustained by recruitment from spawning components in this region. Also, the majority of cod biomass in the Gulf of Maine stock is currently restricted to the western portion (Figure 2). Consequently, if future research confirms that subpopulations in the western Gulf of Maine are reproductively isolated from those along coastal Maine, including these regions in separate stock assessments would likely result in a substantial shift in perception regarding stock productivity and status.

Additional research is required to develop sustainable management strategies that account for the genetically differentiated spawning components that overlap spatially (e.g. the “Northern Spring Coastal Complex” and the “Southern Complex”). Future studies should investigate differences in vital rates (e.g. maturation schedules and growth rates) and year-class strength among subpopulations, which would provide insights into patterns of

stock productivity. Furthermore, samples collected from fishery-independent and fishery-dependent surveys should be used in multidisciplinary stock composition analyses (e.g. Higgins *et al.*, 2010) to quantify the relative contribution of each subpopulation to overall stock biomass and fishery landings, including changes over time and potential environmental influences on productivity. Preliminary investigations using otolith microchemistry and growth differences (M. Dean, pers. comm.) demonstrate that such stock composition analyses can be successful in distinguishing between individuals from different subpopulations. Results from these studies could inform the development of future stock assessment models and fishery management plans that account for the observed metapopulation structure, including the overlapping spring and winter subpopulations. This information will also be useful for investigating the mixing zone around the Great South Channel and Nantucket Shoals to identify the most appropriate boundary between inshore and offshore spawning components.

Connectivity has been identified between cod populations in US and Canadian waters, most notably mixing of cod on eastern Georges Bank with cod on Browns Bank and the Scotian Shelf (Ruzzante *et al.*, 1998; Hunt *et al.*, 1999; Lage *et al.*, 2004; Tallack, 2011). Some mixing has also been observed between the Bay of Fundy and eastern Georges Bank (Ruzzante *et al.*, 1998; Tallack, 2011). Relatively little mixing was observed between the Gulf of Maine stock and the Canadian 4X stock, which includes the Southern Scotian Shelf and Bay of Fundy (Hunt *et al.*, 1999; Clark and Emberley, 2010). Future research should continue to investigate connectivity across the international boundary, given its importance in determining quotas for transboundary resources, as is true for eastern Georges Bank. For example, future studies employing stock identification methods (e.g. tagging, genetics, morphometrics, otolith microchemistry) and/or stock composition analyses should include samples from spawning sites in both US and Canadian waters whenever possible.

Biocomplexity is important for both successful recruitment (Sinclair, 1988; Begg and Marteinsdottir, 2000) and resiliency to environmental changes (Hilborn *et al.*, 2003). As a result, the intrastock diversity identified for cod in US waters is important for consideration in stock assessment and fishery management decisions. Reductions in spawning diversity are likely delaying recovery (Ames, 2004), and continued collapse of population structure can occur without detection by system-wide assessments, because they fail to acknowledge the fine scales at which cod population processes operate (Kovach *et al.*, 2010), which can bias perceptions of stock status (Reich and DeAlteris, 2009). The implementation of small-scale fishery closures to prevent the extirpation of spawning components in the Gulf of Maine (e.g. Armstrong *et al.*, 2013) represents management practices that are beginning to acknowledge biologically meaningful populations, which is critical for maintaining intrastock diversity and achieving fishery management objectives (Zemeckis *et al.*, 2014b). Implementation of additional management strategies that account for the fine-scale population structure is particularly important under the current sector-based management regime, which has shifted from daily trip limits to a quota-based approach (NEFMC, 2009). As a result of this shift in management, both spawning and feeding aggregations may be more vulnerable to overexploitation because of the intense fishing pressure that can be directed on them in a relatively short period, which may have been less likely when daily trip limits were in place.

The proposed modifications to current stock boundaries are expected to be robust to future changes in climate. Cod frequently

follow the same migration patterns during consecutive years (e.g. Robichaud and Rose, 2001; Tamdrari *et al.*, 2012; Thorsteinsson *et al.*, 2012), and broadscale movement patterns in US waters have remained consistent for many decades (Wise, 1963; Hunt *et al.*, 1999; Tallack, 2011). The consistency of behavioural patterns suggests that population processes have been stable despite considerable changes in climate and exploitation over the last century. Cod are predicted to experience a loss of thermal habitat on Georges Bank under future climate change scenarios, including substantial losses in southern New England and the Middle Atlantic (Fogarty *et al.*, 2008). Increasing temperatures are predicted to also cause reductions in recruitment and biomass for both the Gulf of Maine and Georges Bank stocks (Drinkwater, 2005). We hypothesize that spawning components in US waters will experience fluctuations in their relative productivity with future changes in climate, but population processes would remain relatively constant as subpopulations continue to repeat learned migration patterns (e.g. fidelity to spawning and feeding grounds). Therefore, seasonally separated subpopulations are expected to respond differently to climate change, but matching management units with biological stocks should improve the responsiveness of fishery management to climatic effects.

In conclusion, our interdisciplinary review of available biological information demonstrates that current stock boundaries applied to cod in US waters do not provide an accurate representation of biological population structure. Spawning components in the Great South Channel, Nantucket Shoals, southern New England, and Middle Atlantic are more connected with spawning components in the Gulf of Maine than on eastern Georges Bank, with which they are currently managed. Therefore, stock boundaries warrant restructuring to provide a more accurate representation of biological population structure, which has the potential to improve the accuracy of stock assessment models and the effectiveness of fishery management. Recognition of this mismatch is the first step towards mapping new management units, including evaluation of the trade-offs and limitations associated with adopting new spatial configurations. As a result, our conclusions should be considered in subsequent phases of the process outlined by the New England Fishery Management Council's Scientific and Statistical Committee to re-evaluate, and possibly revise, the spatial basis for assessment and management of Atlantic cod in US waters. Continued research focusing on the areas of uncertainty highlighted in this paper will contribute to the next phases of this process by helping to design alternative management units and develop effective fishery management plans.

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