9. SYNTHESIS

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Previous chapters reviewed various disciplinary perspectives to reconsider the stock structure of US Atlantic cod (*Gadus morhua*). In this synthesis chapter, the Atlantic Cod Stock Structure Working Group (ACSSWG) evaluates a plausible set of hypotheses representing biological stock structure of cod, and identifies the stock structure hypothesis with the greatest scientific support, one that is likely to be temporally stable and accurately captures the available data and assessment model frameworks. This synthesis chapter also summarizes recommendations for additional work, as developed by both the ACSSWG and by the external peer-review panel.

The following reference criteria, typically assumed in stock assessments, were used for evaluating plausible biological stock structures of cod:

1. Defining a unit stock as reproductively isolated, where the source of recruitment is from within the stock boundary, with little or no immigration and emigration of individuals across the stock boundary,
2. Considering a dynamic pool of individuals within a stock, where classes of age, length, or sex have homogeneous vital rates (e.g., growth, mortality, maturity, fecundity),
3. Abundance estimates, or aspects of demographics, are based on samples from a well-mixed population.

Stocks identified by these criteria may or may not be spatially distinct. When spatial overlap occurs, mixed-stock fisheries result.

We begin by defining the current management units, before we identify mismatches between these units and the biological evidence, and evaluate alternative stock hypotheses.

The current management unit framework

As outlined in the Introduction (McBride and Smedbol 2021; Chapter 1), aligning cod management units to reflect biological stock structure occurred over several decades and used an interdisciplinary set of research. The current management units conform largely to NAFO Divisions, which are composed of statistical areas used for reporting fishery catch (Cournane et al. 2021; Chapter 2). Cod distributed in Division 5, with statistical areas in the 500s, are considered in US waters, with the exceptions outlined in Figure 9.1.

The NAFO statistical area framework is foundational for aggregating fishery monitoring data. The ACSSWG accepts this and presents their conclusions in terms of these statistical areas, with the intent for their proposal to be more readily adopted by monitoring, assessment, and management actions. Also considered as an alternative spatial framework was 10’ squares of latitude-longitude, but this scale is not supported by all fishery monitoring data and many regions of Division 5 do not have data relevant for stock identity at that spatial scale, so this finer scale was judged as less likely to be adopted by end users.

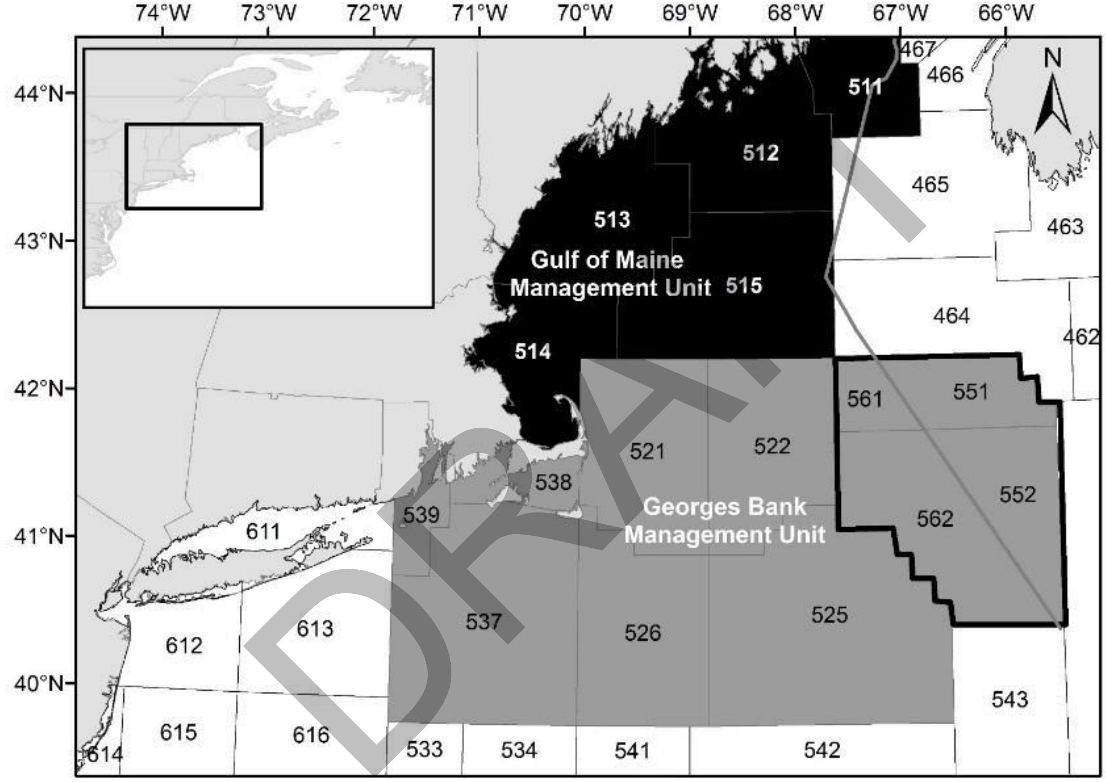


Figure 9.1. Current boundaries for the two US Atlantic cod (*Gadus morhua*) management units – Gulf of Maine (black polygons) and Georges Bank (gray polygons) – both within the Northwest Atlantic Fisheries Organization (NAFO) Division 5. The individual polygons are ‘statistical areas,’ used to aggregate fishery catch data. Statistical areas designated in the 500s and 600s (NAFO Divisions 5 and 6, respectively) are in US waters, and those in the 400s (NAFO Division 4X) are in Canadian waters. Note, however: 1) cod catches attributed to NAFO Division 6 are assigned to the Georges Bank US management unit; 2) areas 551-2 are in Canadian waters, and together with US areas 561-2, these four areas (outlined in black) are assessed and managed jointly between the United States and Canada under the auspices of the Transboundary Resources Assessment Committee (TRAC); and 3) the gray line running from area 511 and south through the TRAC area is the Hague line, the US-Canadian maritime border. Catches on the US side of the Hague line in

areas 464, 465, and 511 are assigned to the Gulf of Maine unit, whereas catches on the Canadian side of the Hague line in these areas are assigned to Canada.

Mismatches between current management units and biological stock structure

We outline below, several observations about cod trait heterogeneity, genetic variation, movements, spawning locations and seasons, and dispersal of larvae—all of which lead the ACSSWG to reject the current management units as an accurate representation of cod biological stock structure within the region.

1. Atlantic cod in US waters exhibit extensive phenotypic heterogeneity that is inconsistent with the current management units. As an example that cod are not well mixed within each management unit, cod traits in the eastern part of the Georges Bank management unit vary markedly compared to cod traits in the western part of the Georges Bank management unit, including different spawning seasons (Dean et al. 2021, DeCelles and Ames 2021; Chapters 3 and 8), growth rates (McBride et al. 2021a; Chapter 5), and morphometrics (Kerr et al. 2021; Chapter 6). As an example that cod mix between current management units, cod in the Great South Channel part of the Georges Bank Management Unit are more likely to share characteristics with cod in the southwestern Gulf of Maine and southern New England, such as similar spawning seasons (Chapters 3 and 8) and growth rates (Chapter 5). As an example of mixed stocks overlapping within a management unit, cod natural markers (otolith chemistry, structure and morphometrics; Fig. 9.2) indicate winter and spring spawners as unique groups within the Gulf of Maine management unit (Chapter 6).

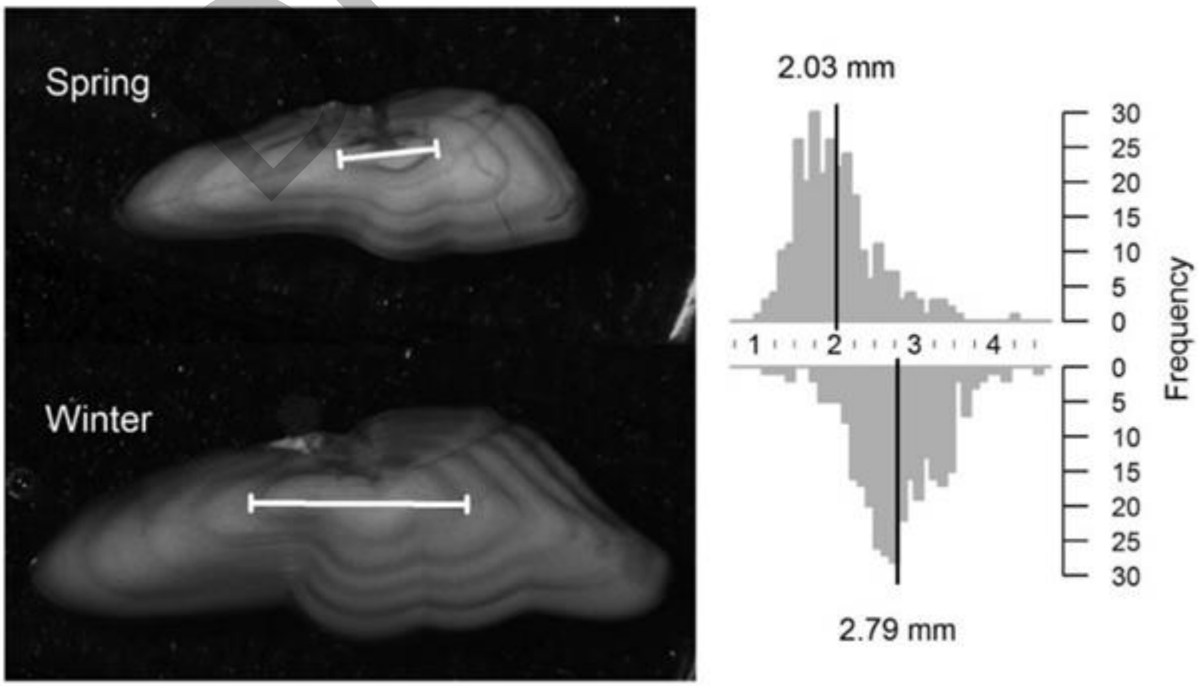


Figure 9.2 Winter and spring spawning cod (*Gadus morhua*), from the same management unit [Gulf of Maine], have different mean diameter measures of the first annulus. [Left] Otolith cross-sections from two age-4 cod, both captured in spawning condition. The one at top was captured in May, while the one at bottom was captured in December. The diameter of the first (A1) annulus is identified. [Right] Histograms of otolith A1 diameter (mm) from the training dataset, for spawning cod captured in spring (top, n = 278) and winter (bottom, n = 301); mean values are identified by the dark vertical line (Dean et al. 2019).

2. Atlantic cod in US waters also exhibit extensive genetic connectivity between as well as heterogeneity within the current management units (Kovach et al. 2021; Chapter 4). For example, cod in the eastern part of the Georges Bank Management Unit (Georges Bank) are genetically distinct from cod in the western part of that Management Unit (Great South Channel, Nantucket Shoals, and southern New England), and cod in the Cape Cod area (area 521, currently in the Georges Bank Management Unit) are more genetically similar to winter-spawning cod in the Gulf of Maine than to cod on Georges Bank or southern New England (Fig. 9.3). Mixed stocks overlap in one area, the western part of the Gulf of Maine Management Unit, where cod are comprised of two genetically distinct populations with different reproductive phenologies (i.e., winter vs. spring spawners). The genetic differences between winter and spring spawners include regions of the genome that contain adaptive variation, including genes that may underlie a genetic basis for spawning time (Chapter 4). This evidence for sympatric spawning groups in this area is well supported by other disciplines such as the early life history (Chapter 3), natural markers such as the width of otolith annuli (Chapter 6), electronic tagging (Cadrin et al. 2021; Chapter 7), and fisherman's ecological knowledge (Chapter 8). Spatial overlap of genetically distinct populations within the Gulf of Maine management unit has broad implications because it disrupts the spatial delineation of stock structure with mixed-stock fisheries at a fine scale (i.e., within single statistical areas, such as 514).

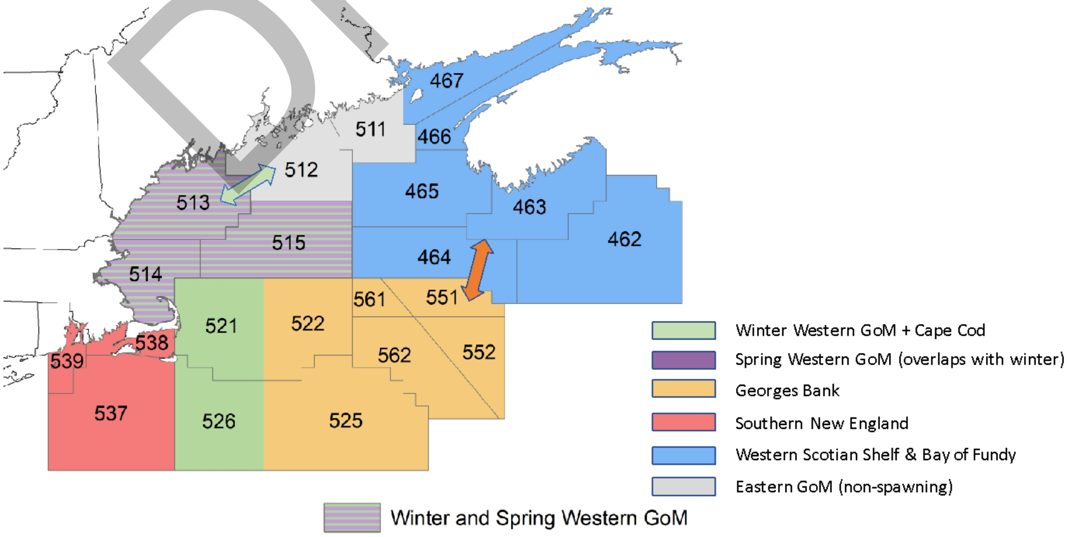


Figure 9.3. Population genetic structure of Atlantic cod (*Gadus morhua*) in NAFO divisions 5 and 4X, based on synthesis of all available data. Five US genetic populations and 1 Canadian genetic population are depicted, including two US populations that overlap, where the hatched polygons

(areas 513, 514 and 515) denote sympatric winter and spring spawning populations. Data are for fish in spawning condition, except for non-spawning cod in area 512, where a green arrow suggests connectivity between there and the western GoM winter spawning population. In addition, some level of connectivity exists between the western Scotian Shelf and Georges Bank via Browns Bank (indicated by orange arrow).

3. Adult cod in some areas are relatively sedentary, whereas adults in other areas exhibit extensive movements, including swimming between current US-US and US-Canada management units (Figure 9.4, Chapter 7). Adult cod that spawn in the southwestern Gulf of Maine are largely sedentary, with some movement to the Great South Channel, whereas cod in northeastern Gulf of Maine (e.g., 511) have, at least historically, moved across the US-Canadian boundary into various statistical areas of Division 4X (Chapter 7). Adult cod exhibit significant transboundary movements between the US side of Georges Bank and the Canadian Browns Bank. Adult cod in southern New England historically had extensive seasonal migrations between Nantucket Shoals and the Mid-Atlantic Bight, but recent tagging data indicates that they are now primarily residential within southern New England with some movement with Nantucket Shoals and Great South Channel. Some major movement patterns have persisted since the earliest tagging studies, and inferences of movement are similar from all tagging studies since the 1970s.

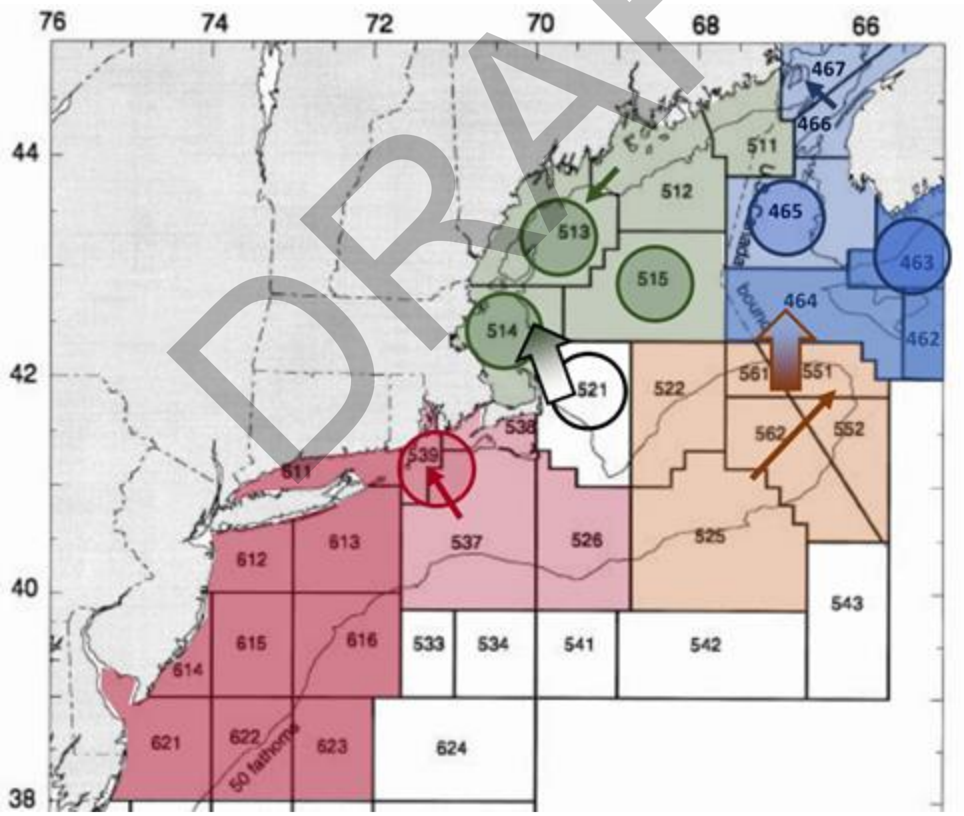


Figure 9.4. Major patterns of Atlantic cod (*Gadus morhua*) movements among regions (multicolor arrows: >10% movement), movement within regions (solid colored arrows: >50% movement from statistical area), and residence within statistical areas (circles: >50% residence in statistical area) from combined tagging studies.

4. Fidelity to spawning grounds/seasons is evident for each major spawning group, but the spatial extent of movement away from spawning grounds during non-spawning seasons varies (Chapter 7). Analysis of residence and dispersal of distinct spawning groups among fishing grounds suggest high residence and fidelity to spawning areas in the western Gulf of Maine and the Bay of Fundy, dispersal of Cape Cod spawners into both US management units, and dispersal of eastern Georges Bank spawners on both sides of the Hague line. Major movement patterns are consistent among studies and across recent decades of tagging studies, but the frequency of residence and movement vary.

   Although winter and spring spawning groups in the western Gulf of Maine show a high degree of residency, there is some evidence that these groups have different spatial ecology and movements while remaining resident within this area (Chapter 6), in addition to being offset in the timing of their seasonal inshore-offshore migration patterns.

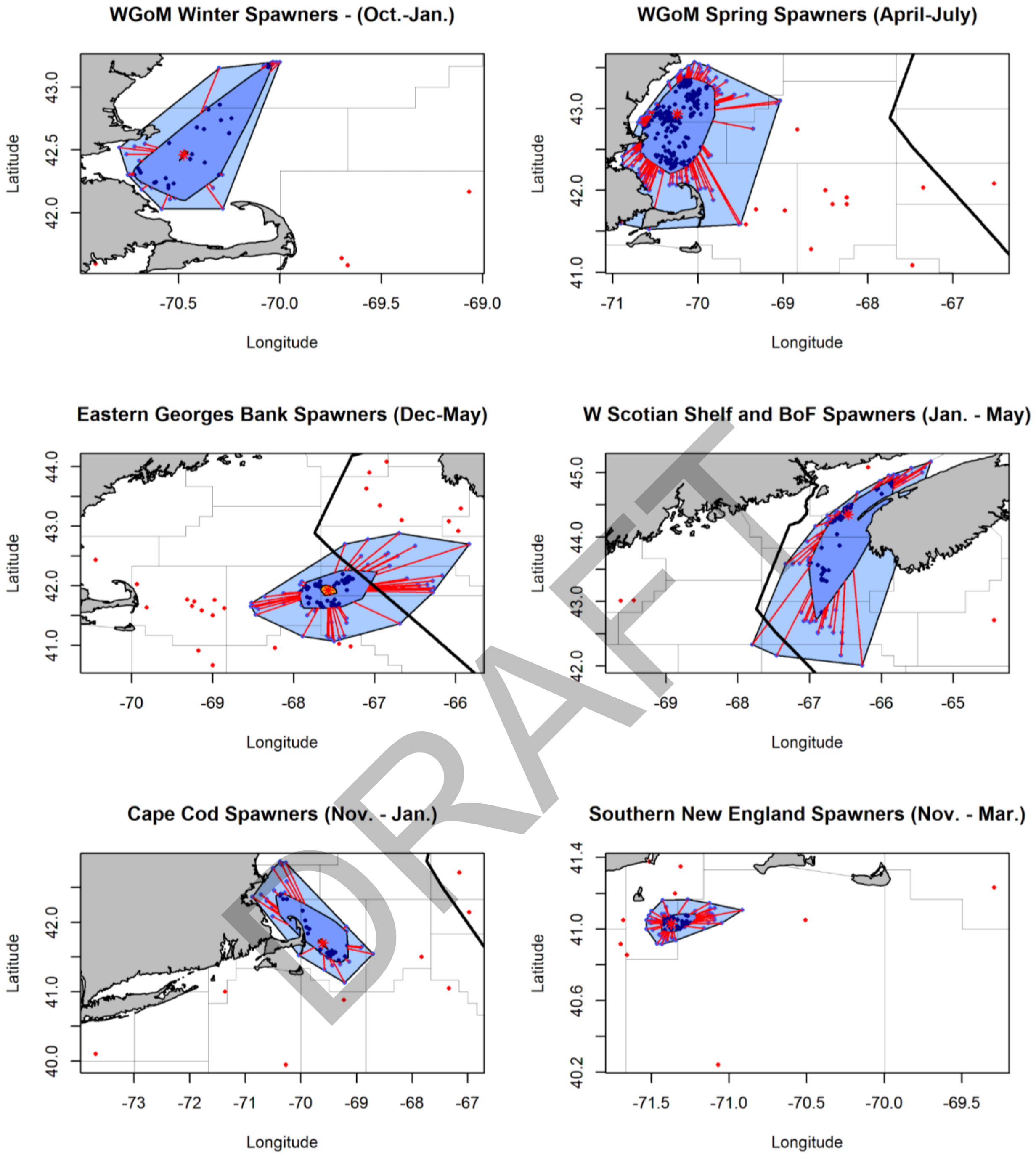
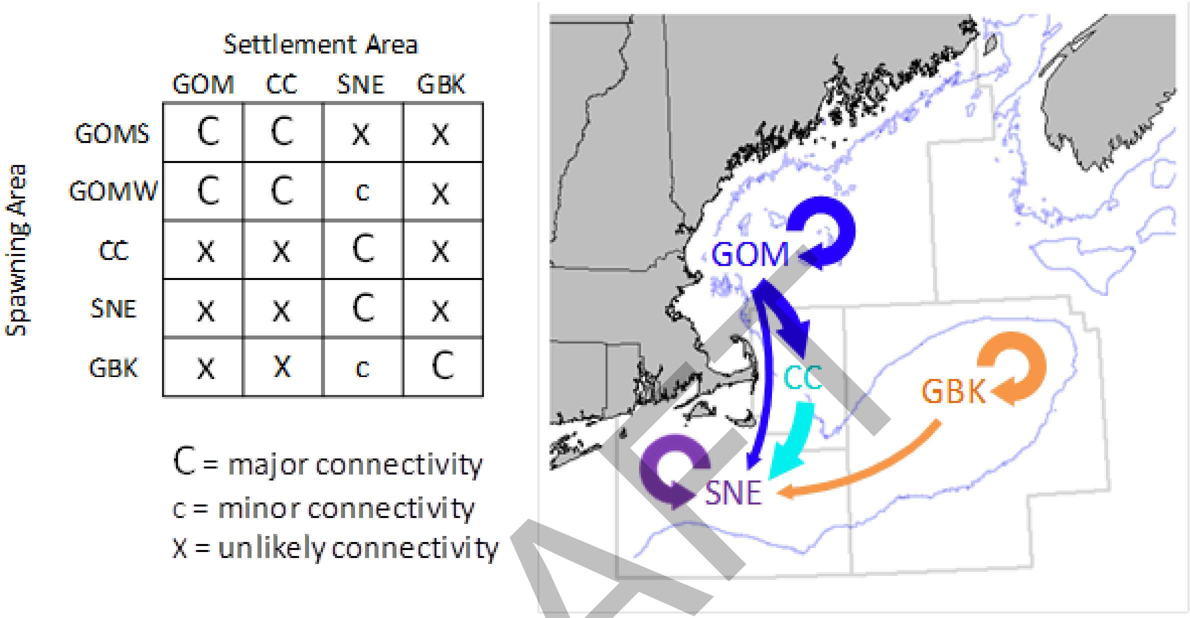


Figure 9.5. Bagplots depicting the location of Atlantic cod (*Gadus morhua*) recaptures for each of the major spawning groups during their respective spawning seasons. The bagplots only include cod that were at large for >4 months, and are intended to depict site fidelity, and straying behavior, during the spawning season. Some spawning groups (e.g., Southern New England) exhibit high rates of site fidelity, while others (e.g., Eastern Georges Bank) are more dispersive. The bagplot depicts the median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue) and outliers (red dots). Abbreviations used: WGoM (western Gulf of Maine), W Scotian Shelf and BoF (Western Scotian Shelf and Bay of Fundy).

5. Spring- and winter-spawned cod larvae are dispersed around Cape Cod from the western part of the Gulf of Maine management unit to the western part of the Georges Bank management unit (Fig. 9.6, Chapter 3). Larvae from the winter spawning season are dispersed further into southern New England than larvae from the spring spawning.



Settlement Area

Spawning Area	GOM	CC	SNE	GBK
GOMS	C	C	x	x
GOMW	C	C	c	x
CC	x	x	C	x
SNE	x	x	C	x
GBK	x	X	c	C

C = major connectivity
c = minor connectivity
X = unlikely connectivity

Figure 9.6. [left] Summary of the early life connectivity between spawning groups and settlement areas for Atlantic cod (*Gadus morhua*) in US waters. An uppercase "C" indicates *major* connectivity; a lowercase "c" indicates *minor* connectivity; an "X" indicates *unlikely* connectivity. The Gulf of Maine (GOM) stratum is defined by statistical areas 511-515, and includes two spawning groups (Spring, Winter); the Cape Cod (CC) stratum includes a single statistical area 521; the Georges Bank (GBK) stratum includes statistical areas 551, 552, 561, 562, 522, 525; and the Southern New England (SNE) stratum includes statistical areas 526, 537-539. [right] a map of the strata with arrows indicating connectivity pathways between spawning areas and settlement areas. Thicker arrows indicate *major* connectivity; thinner arrows indicate *minor* connectivity.

6. The status of some regions is still poorly known, especially the eastern Gulf of Maine. Eastern Maine cod have been depleted for decades making it difficult to sample spawning cod to clarify this region's position in terms of biological stock structure (Chapters 1, 4, 8). However, historical records indicate that both winter and spring spawning cod were present along coastal Maine in the 1940s (Ames 1997). The limited tagging data available from this region suggests greater connectivity between eastern Maine (area 511) and the Scotian Shelf than with the rest of the Gulf of Maine (Chapter 7). Genetic data from non-spawning cod in area 512 suggest contemporary movement between this area and area 513.

In summary, the current spatial boundaries of management units fail to account for considerable phenotypic and genetic heterogeneity from the western to eastern ends of the Georges Bank management unit, and additional heterogeneity within the Gulf of Maine management unit. Nor does it account for the considerable connectivity of larvae and movements by adults between these management units around Cape Cod, and the existence of two genetically distinct sympatric populations.

Evaluation of alternative hypotheses

Having rejected the current management units as the most accurate representation of cod biological structure, we consider alternatives that add biological complexity.

As proposed by Zemeckis et al. (2014), an alternative, yet still simple two-stock model splits the US range of cod into inshore and offshore management units, rather than north-south management units. This choice arises from the many traits of cod in the eastern part of the Georges Bank management unit (George Bank) that differ from cod in other areas, such as discrete spawning areas (Chapters 3, 8), genetic differentiation (Chapter 4), differences in growth and maturity (Chapter 5), etc. Elsewhere in the Atlantic there are examples of inshore versus offshore stock delineations of cod, including off Newfoundland (Smedbol and Stephenson 2001), off Iceland (Pampoulie et al., 2006), and the Norwegian coast (Northeast Arctic cod and Norwegian coastal cod, Berg et al. 2016).

Recognition of inshore-offshore biological stock structure has not always led to two management units. For example, in Canada, the northern cod (2J3KL) has inshore and offshore spawning components, with complex annual spawning and feeding migrations, and genetic differences; however, it is assessed and managed as one stock (DFO 2018). Nonetheless, the eastern part of the Georges Bank Management Unit is already treated separately from the US inshore cod, as part of the US-Canadian Transboundary Resource Assessment Committee, at least partly because of the movements of cod across the US-Canadian boundary (Fig. 9.4).

A specific boundary to delineate western and eastern portion of the Georges Bank Management Unit has been subject of historical debate. The hydrodynamics in this region isolate Georges Bank as a self-contained, anti-cyclonic gyre east of the Great South Channel, which serves as a mechanism to keep inshore and offshore cod separated (Fig. 9.7a). Wise (1963) proposed a boundary at 68^{o}W, but this would split statistical fishing areas 522 and 525, which would introduce its own uncertainty, something the ACSSWG has avoided in this process. Fishermen have also proposed various boundaries, such as at 68^{o}W, 69^{o}W, or the Great South Channel (Chapter 8). As recently as a few years ago, Zemeckis et al. (2014) stated: additional research is needed ‘to determine the natal origin of cod caught in the central portions of Georges Bank.’ That additional research is still needed. For example, recent analyses of genetic and natural marker data support a boundary in this vicinity but small sample sizes have been unable to identify a specific geographic break (Chapters 4, 6). Connectivity of early life stages do not suggest dispersal of larvae between inshore and offshore areas (Fig. 9.6) and fish tagged in the central portion of the bank tended to move east and only rarely crossed the Great South Channel to the west (Fig. 9.7b).

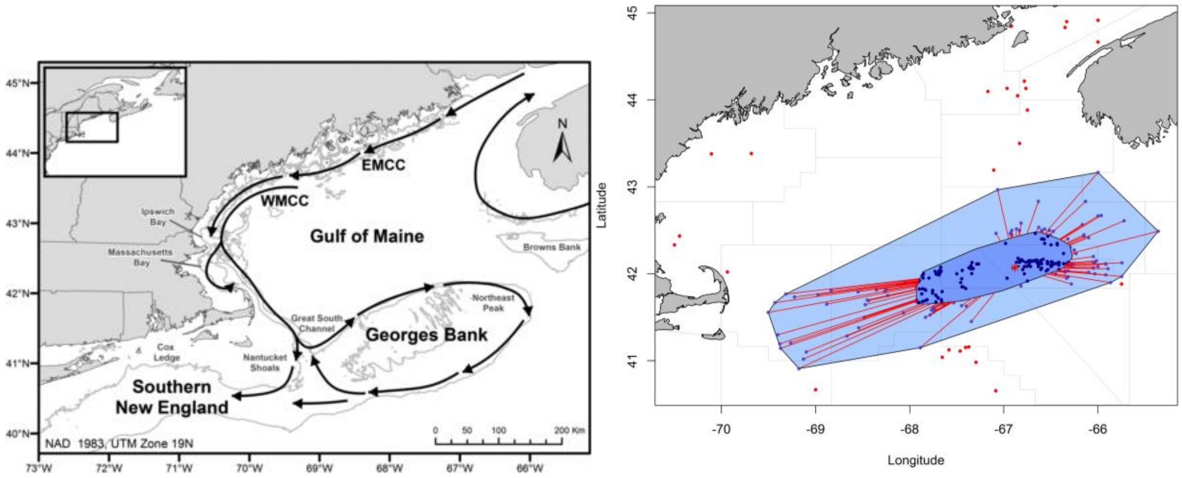


Figure 9.7. (a) Oceanographic delineation of Georges Bank as an anticyclonic gyre from the Great South Channel to the Northeast Peak (From Zemeckis et al. 2014); (b) A bagplot of 311 Atlantic cod (*Gadus morhua*) recaptures from fish released in stat area 522 and 525 from 2001 to 2006 in the months of December, February, March, April, and May (data source: Northeast Regional Cod Tagging Program, G. DeCelles). The bagplot depicts the median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue) and outliers (red dots).

Splitting cod in the Georges Bank management unit into two units, in an inshore-offshore manner, accounts for some but not all of the biological differences evident. The western portion of the Georges Bank management unit, statistical areas 537-9, is genetically distinct from the rest of this unit (Chapter 4, Fig. 9.3). In addition, in the central part of this management unit, there is considerable evidence that cod in area 521 are more aligned with the Gulf of Maine winter spawners than with cod offshore of southern New England or on Georges Bank (Chapters 3, 4, 5, Fig. 9.6). Recognizing all this evidence leads to splitting the current Georges Bank management unit into three biological stocks: eastern Georges Bank, southern New England, and areas 521 and 526, the latter of which are also aligned with Gulf of Maine winter spawners (Fig. 9.8).

In the current Gulf of Maine management unit, additional biological structure is evident inshore, where spring and winter spawning groups overlap in areas 513-514. This results in sympatric spawning groups that are caught by the fishery as mixed compositions in these areas, including 515 (Dean et al. 2019).

The stock identity of cod from the northern Gulf of Maine statistical areas, for which there is little information to evaluate directly, is still uncertain. Historical evidence exists for latitudinal trends in natural markers among inshore areas (e.g., Sherman and Wise 1961, Chapter 6) and limited movements of tagged fish in the northern Gulf of Maine (Chapter 7). These reports suggest that these fish were reproductively isolated from fish elsewhere in the Gulf of Maine. This has become a stubborn problem to resolve genetically because there are no spawning fish in recent decades, but Ames (1997) notes that both winter and spring spawning occurred there in the past.

Consensus structure

The ACSSWG proposes a biological stock structure that includes both an inshore-offshore separation, as well as multiple inshore stocks, including a mixed-stock composition of spring and winter spawners in multiple statistical areas (Fig. 9.8).

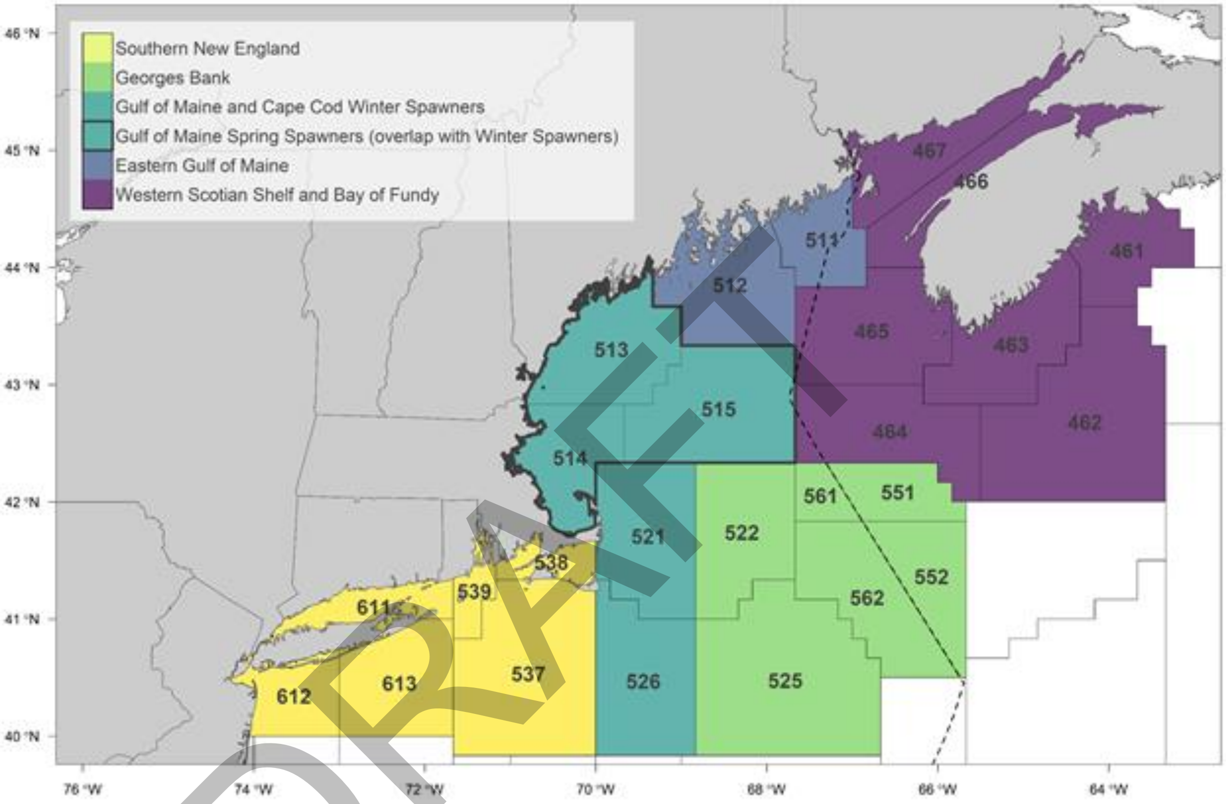


Figure 9.8. Proposed biological stock structure of Atlantic cod (*Gadus morhua*) in NAFO division 5 and adjacent division 4X.

1. A Georges Bank stock. This unit – an aggregate of areas 522, 525, 551, 552, 561, and 562 – includes what is already recognized and assessed by the Transboundary Resource Assessment Committee (i.e., 551, 552, 561, and 562) and areas 522 and 525. Oceanographic circulation creates a mechanism to retain cod larvae, and tagged fish rarely moved west, towards the Great South Channel, let alone the Southern New England parts of this management unit. Genetic markers confirm strong genetic differentiation. Discussed above is uncertainty about this offshore boundary, between 69^{o} and 68^{o} W, but the available evidence supports fully including both 522 and 525 in this stock unit, which sets this boundary in accordance with existing fishing statistical areas.

2. A southern New England stock. This unit – an aggregate of areas 537-9 in tandem with the 600s – is recognized from genetic data showing differentiation in both neutral and adaptive markers, including genes associated with thermal tolerance. The genetic evidence is at present from a small sample size for only one spawning area (Cox Ledge), but in total, supportive evidence for a separate stock is found in localized movements of tagged fish and simulations suggesting that settlement would be localized. Tag returns dating to the early 1900s indicated extensive seasonal connectivity between Nantucket Shoals (521) and part of the middle Atlantic seaboard, while tag returns since the 1980s suggest much less connectivity of 537-9 with 521; paired together, these findings support aggregating cod catches from statistical areas numbered in the 600s with catches in this stock area.

3. A western Gulf of Maine and Cape Cod winter spawner stock. This unit – an aggregate of areas 513-5, 521, and 526 – is recognized by considerable evidence of spawning in the western Gulf of Maine, historical spawning on Nantucket Shoals and in the Great South Channel, as well as connectivity between these areas by dispersal of winter-spawned eggs and larvae, genetic similarity, and localized movements by adults. The evidence is strongest in areas 513-15, but reduced data density creates more uncertainty about the stock alliance of area 521, and especially are 526, where there is potential for mixing with the newly re-defined Georges Bank stock (#1) and the newly defined southern New England stock (#2). It is clear, however, that this stock mixes with stock #4 in the western Gulf of Maine.

4. A western Gulf of Maine, spring spawner stock. This unit – an aggregate of areas 513-515 – is recognized by considerable evidence of spawning in the western Gulf of Maine, as well as localized tagging movements**.** This stock mixes with stock #3. It predominates in the southern part of 513 and western 514, while spawning north of those areas is rare. In terms of adaptive genetic differentiation, this stock is the most distinct from other genetically-defined stocks. Cod spawning in area 515 is not common, but cod in 515 are aligned with this stock by proximity.

5. An eastern Gulf of Maine stock. The stock affiliation of this area – an aggregate of areas 511-2 (e.g., Downeast Maine) – is the least certain of stocks proposed here but likely an additional biological stock. Ames (1997) suggested that both winter and spring spawning occurred here, but genetic analyses have been unable to resolve the affinity of these cod because of a lack of spawning adults in either historical or recent collections. The lack of spawning adults and the depleted state of cod along Downeast Maine stands in stark contrast to the southwestern Gulf (areas 513-4), where cod are both abundant and exhibit complex winter and spring-spawning (stocks #3, #4). Even when Downeast Maine spawning was evident in the past, Ames (2004) suggested that these cod were

reproductively isolated from the southwestern Gulf group. Larval modeling suggest self-replenishment is possible in 511-512, and outside sources less likely, which hints at the source-sink dynamics between the eastern Gulf cod and neighboring regions. Historic tagging data, when abundance was higher, showed limited movements in or out of Downeast Maine, and of those movements, greater movements towards Canada, on the western Scotian Shelf, than towards the southwestern Gulf of Maine (Chapter 7).

6. Canadian stocks of 4X. This unit is assessed and managed by Canada and includes the Bay of Fundy and western Scotian Shelf regions (areas 461-67). Discreteness and connectivity of US and Canadian cod are supported largely by genetic data. Also, tagging data identify important routes of adult movement between Bay of Fundy and western Scotian Shelf component with a mixing area in Browns Bank, a strong connection between Browns Bank and Eastern Georges Bank, and some connectivity with eastern Gulf of Maine.

Using the reference criteria defined at the beginning of this chapter, we reject the existing management units, and some modest variations on this, as accurately reflecting the biological stock structure of cod. Major issues were:

1. numerous instances of both phenotypic and genetic variability indicating that cod are not well mixed within each management unit,
2. adult cod in some areas exhibiting extensive movements, including swimming between current US-US and US-Canada management units,
3. dispersal of cod larvae around Cape Cod from the western part of the Gulf of Maine management unit to the central-western part of the Georges Bank management unit, and
4. recognition of mix-stock fisheries arising from interdisciplinary evidence of sympatric winter- and spring-spawning cod in the southwestern Gulf of Maine and around Cape Cod.

This led to our consensus proposal that expands the number of biological cod stocks from two to five in US waters (NAFO Division 5). Inferences by the ACSSWG are, however, based on a diminished biological resource, in terms of the historical biomass and productivity of cod. A review with a similar breadth of information, using different stock conditions, may have reached different conclusions about stock structure. As such, the working group recommends continued evaluations, for example, if extirpated spawning grounds become recolonized in downeast Maine or Nantucket Shoals, or if there are broadly-based changes in productivity to the region that affect cod.

Recommendations for additional work

Recommendations for additional work is presented in two parts. First, the ACSSWG tabulated 1-2 recommendations per discipline to convey a concise, prioritized list for further attention.

Second, the peer-review panel for the ACSSWG's findings developed an independent list of recommendations that were organized by putative cod stock.

Recommendations from the ACSSWG

The following tabulation of data collection and research recommendations was developed and prioritized by the Working Group for consideration by the 2020 peer-review panel to consider in their own recommendations.

High priority or short term recommendations

- Simulation testing the performance of alternative management procedures for meeting fishery management objectives, in which the operating model(s) reflect the most likely scenario(s) of population structure and alternative management procedures include the current stock boundaries, alternative stock boundaries, and intermediate approaches (e.g., spawning closures, stock composition monitoring). This will ideally occur before the 2023 research track assessment of cod.

- Additional research to clarify the genetic stock structure in eastern Gulf of Maine where there are no spawning cod. Avenues for such research include analysis of historical otolith samples (some research ongoing), and mixed-stock analyses of juveniles and adults. The eastern Gulf has been understudied and it is difficult to obtain relevant samples from this area because of the depletion of its historical spawning grounds. Its assignment as a separate stock is the least certain.

Medium priority or medium term recommendations

- The source of cod larvae and juveniles in the Great South Channel and Southern New England, as well as the fate of spawning in these areas. These spawning locations and settlement areas have not yet been the subject of dispersal modeling studies, and would provide valuable early life history information for these areas of uncertainty with respect to stock structure.

- More samples and studies to clarify the connectivity between Cape Cod and the western Georges Bank (the area east of the Great South Channel) in order to determine the boundary between these regions. It is currently unclear if this boundary is exact, and if so, where it occurs in vicinity of 68^{o}W or 69^{o}W.

- Develop tools for rapid assessment of spring and winter spawners in the western Gulf of Maine. The ACSSWG recognizes promising tools related to otolith morphology, a natural marker, and genomics, a genetic marker. The priority of this task could be higher depending on whether mixed-stock discrimination for managing the fishery catch in the southwest Gulf of Maine is required.

Lower priority or longer term recommendations

- Continue biological monitoring of growth and maturity dynamics, because there are interesting long-term trends evident in both management units. Life history samples are monitored as part of the assessment process, so at this time, no special effort is needed to continue this, assuming stable resources. Analysis of surveys other than the NOAA's bottom trawl survey is also warranted, especially in areas identified here as having small sample sizes (e.g., southern New England, downeast Maine).

- Interview those with local ecological knowledge regarding cod spawning and movement in southern New England. Although categorized as a low priority, this is a low-cost research approach in an area with small samples from fishery-independent sources, and therefore a good value.

- Additional use of natural markers is promising because of previously successful applications in documenting spatial variation, and these may be low-cost if done cooperatively with the fishing fleets.

- More electronic tagging of spawning groups (e.g., as done in Massachusetts Bay) to understand spawning dynamics.

- Integrated analysis of genetics and electronic tagging data to investigate different behavior and seasonal movement patterns among genotypes.

A summary of recommendations from the review panel

The following summarizes recommendations, and offers some commentary, of the peer-review panel's response to Term of Reference 3 ("Identify any major information gaps in the existing research with respect to cod stock structure. Develop an initial list of research recommendations to address these gaps."). The panel's response is posted in full as part of the New England Fishery Management Council's collections of June 2020 meeting notes about cod stock structure. The panel organized their recommendations by putative stock areas, focusing on the two areas of greatest uncertainty: eastern Gulf of Maine and southern New England.

Eastern Gulf of Maine

Although cod in the eastern Gulf of Maine are in a depleted state, a number of surveys exist in the area, such as a state trawl survey, a sentinel fishing survey, and other fishery-dependent sampling programs. These deserved continued attention and perhaps modifications for a variety of goals: to monitor abundance trends and hopefully document re-activation of spawning grounds; investigate natural markers, especially genetic markers, for stock identification and possibly use for mixed stock analysis; and look for feeding signals (e.g., recovery of anadromous prey) that could drive cod recovery in this area. Additional interviews with lobster fishermen in this area could also reveal ecological knowledge that could help define and predict the status of cod stock structure in this area.

Southern New England

There are also existing programs in southern New England that could be leveraged for further investigation of cod stock structure. The University of Rhode Island has collected cod larvae and built oceanographic models that could be interrogated for information about potential for self-recruitment or connectivity of larvae from elsewhere. The youngest fish life stages could be a source of genetic information to assign stock identity. Additional interviews with recreational fishing participants – an important regional fleet that includes private anglers, charter boats, and party boats – could reveal ecological knowledge that could help define and predict the status of cod stock structure. Sampling may be able to leverage NOAA's Marine Recreational Information Program, but likely has limited potential because that survey does not operate from January-February in southern New England.

More broadly, in U.S. Waters

Although the temporal and spatial coverage of genomics data available for this review is very high, relative to other marine species, the panel recognized a continued need to build the temporal scope and resolution, particularly to discern the temporal stability of the patterns observed. The evidence of mixed-stock fisheries, also necessitate additional studies with natural markers in areas with high catches/abundance of non spawning adult cod to determine the degree of mixing from adjacent stock units at these locations.

The panel also identified a number of fishery-independent surveys conducted in nearshore waters by state agencies and other entities that appeared underused by the ACSSWG. In discussions between the ACSSWG and the panel, it became evident that some of these surveys were considered but rejected for specific reasons, such as small sample sizes, differences in sampling design, etc., and in revision of this Technical Memorandum, more details were added to the disciplinary chapters in this regard. Regardless, the value of each and every relevant survey depends on the questions being asked.

Finally, the panel recognized that many disciplines were able to address evidence for historic stability of these putative cod stocks but that the ACSSWG's findings did not predict the stability of the number of stocks or their boundaries. A specific recommendation was to apply the Climate Vulnerability Assessment methodology (Hare et al. 2016) to the five cod stocks proposed by the ACSSWG. More quantitative approaches for predicting biogeographic range shifts are also available (e.g., McHenry et al. 2019).

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Appendix A, Working Group

Atlantic Cod Stock Structure Working Group, members and affiliations

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Appendix B, Terms of Reference

Atlantic Cod Stock Structure Working Group, Terms of Reference (May 14, 2018)

1. Inventory and summarize all relevant peer-review information about stock structure of Atlantic cod in NAFO Divs. 5 and 6 and interactions with 4X. Evaluate the relative importance of the information with respect to developing a holistic understanding of Atlantic cod stock structure.

2. Identify and evaluate any new or existing data or information about the stock structure of Atlantic cod in NAFO Divs. 5 and 6 and interactions with 4X, and subject to a peer-review by the working group. Integrate any additional information into the inventory developed in TOR 1.

3. Using a holistic approach, synthesize all available information (TOR 1 and 2) and develop sets of possible biological stock structures and consider scientific support for each alternative. In developing alternative stock structures, consider the temporal stability of stock structure and how the available information can inform the knowledge of stock structure over time.

4. Evaluate the historical and contemporary fisheries-dependent and -independent data collection programs and evaluate current modeling techniques relative to the alternatives developed in ToR3. Summarize the practical limitations for each alternative.

5. Broadly consider potential management procedures to meet management objectives including but not limited to maintaining status quo, altering stock boundaries, spatial and temporal restrictions, and stock composition analyses

6. Identify any major information gaps in the existing research with respect to cod stock structure. Develop a prioritized list of research recommendations to address these gaps. Comment on the feasibility and time horizon (e.g., short-term, long-term) of the proposed research recommendations.

7. Identify any major data collection and modeling gaps that limit the use of stock structure alternatives.

This document only addresses TORs 1-3; TORs 4-7 will be addressed as a separate process.

Appendix C, Objectives

Atlantic Cod Stock Structure Work Group, Objectives (May 14, 2018)

Determine the most appropriate representation of Atlantic Cod stock structure for use in regional stock assessments (NAFO Divisions 5 and 6 and interactions with 4X) based on currently available information. “Most appropriate” means having the greatest scientific support and accurately capturing the available data and assessment model frameworks. This determination will not include the running of assessment models.

Identify high priority research that would contribute significantly to the issue of cod stock structure.

Broadly consider potential management actions to meet management objectives including but not limited to maintaining status quo, altering stock boundaries, spatial and temporal restrictions, and stock composition analyses.

The following are explicitly not part of this Working Group: New benchmark assessment, reference determination, and quota setting.

Follow a transparent process by including stakeholders in public meetings and through regular updates.

Appendix D, Glossary, Acronyms, and Abbreviations

A_{50}, Median age at maturity. A specific point for age at maturity, the point where a fish at that age has a 50% probability of being immature or mature.

L_{50}, Median length at maturity. See A_{50}.

ACSSWG: Atlantic Cod Stock Structure Working Group

Adaptive genetic variation: Variation that is associated with functional genes, the expression of which influences characteristics or traits that affect the fitness of the organism.

Allozymes: variant forms of an enzyme (protein) that differ structurally but not functionally and these differences have underlying allelic differences. These were the first genetic markers used in population studies.

Assignment test: Assignment of individuals of unknown origin to a population of origin using reference samples that represent candidate progenitors.

Annulus: Fish otoliths and other hard parts that form An annual growth increment (plural: annuli) observable in a mineralized part of a marine organism, such as the ear stone (otolith). Acts as a natural mark of time to age an individual fish, similar to rings in the trunk of a tree.

Anticyclonic: An anticyclonic flow is clockwise in the northern hemisphere, as driven by the Coriolis effect. There is an anticyclonic circulation around Georges Bank.

Applied marker: Tags attached to marine animals to investigate behavior and life history (e.g., growth, survival), including conventional and advanced electronic tags.

Benthic: Of or in the bottom sediments of the ocean or other body of water.

Biological population: A self-sustaining group of individuals, from a single species, whose dynamics are primarily determined by birth and death processes (Cadrin et al. 2014).

Biocomplexity: The variation in biology, considered here among identifiable stocks of fish, regarding features as spawning habitat, spawning seasonality, planktonic larval duration, genetic variation, growth rate, morphology, maturation schedules, ecological and functional diversity, etc. This diversity is thought to provide resilience, adaptive capacity and evolutionary potential.

Candidate gene: a gene whose chromosomal location is associated with a particular phenotype or function.

Chromosomal inversion: A chromosomal rearrangement, in which. a segment of the chromosome is reversed end to end. Recombination is greatly reduced within these inversions due to incompatibility while pairing during meiosis.

Connectivity: The degree of movement of organisms among defined areas or populations (or components of a population).

Cyclonic: A cyclonic flow is counter-clockwise in the northern hemisphere, as driven by the Coriolis effect.

DFO: Canadian Department of Fisheries and Oceans

Early life history: Referring to the first year of a fish's life, including spawning (egg release), the planktonic stages (eggs, larvae) and early 'settlement' of cod juveniles to a benthic existence.

Ecotype: A distinct group of individuals that are genetically adapted to specific environmental conditions.

Electronic tag: Devices used to track the behavior and migrations of marine animals based on recorded oceanographic data (e.g., archival tags) or using tracking technologies (e.g., acoustic transmitters)

Extirpation: The disappearance of a species from a given area (e.g., a local extinction).

F_{ST}, fixation index: A measure of population differentiation. Ranges from 0 (undifferentiated) to 1 (unrelated).

Fishermen's Ecological Knowledge: Knowledge of local fishermen that can contribute to evaluation of living marine resources.

Fishing Statistical Area: See Statistical Area.

Genetic marker: A specific type of natural marker that is comprised of observable, heritable, genetic variation in a specific location on a chromosome. This variation is useful for identifying individuals or populations. .

Gene flow: The transfer of genetic material from one population to another.

Genetic drift: Changes in gene frequencies within a population due to random chance.

Genome: All of an individual's genetic material (RNA and DNA, coding and non-coding).

Genotype: An individual's genetic makeup at one or more genetic markers; its DNA, whether expressed by its phenotype or not.

Hague line: The North Atlantic Ocean boundary between U.S. and Canada fishing waters.

Interdisciplinary (holistic) approach: Collection, review, and synthesis of data from multiple disciplines (e.g., life history, natural markers, fishermen's ecological knowledge, etc.), each of which contribute different scales and types of inferences, with the intent that the conclusion will be more scientifically supported than if based on one discipline alone.

Jordan's Rule: An ecogeographical rule that describes the inverse relationship between water temperature and meristic characteristics in various species of fish. The most commonly observed relationship is that fin ray, vertebrae, or scale numbers increase with decreasing temperature.

Life history: Treated here as the distribution and abundance of cod as well as selected traits regarding growth and maturity.

Linkage disequilibrium: Non-random association of alleles at two locations in the genome. This can occur, for example, by physical linkage (close proximity of genes within a chromosome) or by nonrandom mating or evolutionary processes of genetic drift or selection.

Linkage group: A region of the genome in which there is little or no recombination, and thereby linkage. Genetic sequences in this region are inherited as a group.

Locus (plural, loci): A fixed position on a chromosome where a particular genetic sequence is located.

Local adaptation: A population becomes well suited to the particular environmental features of its location, through evolution and the associated gene frequency changes. For local adaptation to occur, different populations experience different selective pressures due to environmental differences. .

Low Coverage Genome Sequencing: DNA Sequencing of the genome at a low depth of coverage, meaning that each region is sequenced with very few unique reads (often 1X is targeted). With less read depth, typically statistical imputation is used to predict genotypes at unmeasured positions.

Management Unit: A geographically delineated fishery resource that is based on practical or jurisdictional boundaries for operational stock assessment and fishery management, which may or may not reflect biological population structure (Cadrin et al. 2014).

MARMAP: Marine Resources Monitoring, Assessment, and Prediction

Meristics: countable structures of fishes such as fin spines and rays, gill rakers, lateral line scales, and vertebrae.

Metapopulation: A system of interacting biological population units, termed subpopulations, that exhibit a degree of independence in local population dynamics as well as connectivity among subpopulations (Cadrin et al. 2014).

MA MFI: Massachusetts Marine Fisheries Institute.

Microsatellite markers: Tandem repeats or motifs of DNA consisting of 2-10 nucleotides. These short segments of DNA, which can span 5-50 repeats, typically have a relatively high mutation rate, making them a useful genetic marker.

Mitochondrial DNA: Small circular chromosome that is found inside of the mitochondrial organelle and is maternally inherited. It codes for proteins needed in the pathways of cellular respiration. As a genetic marker in population studies, it is useful for characterizing broad-scale differences among deep evolutionary lineages and less useful for fine-scale population differences.

Mixed stock: A management unit containing individuals with different genetic origins.

Mixture analysis: Discriminating the composition of a mixed stock.

Natal homing: A return migration of sexually mature individuals to spawn upon the grounds where they were spawned (Cadrin et al. 2014).

Natural marker: Markers that occur naturally with the fish, either intrinsic such as its color, shape, or chemical composition, or extrinsic, such as parasite types. Genetic markers, which is a type of natural marker, are treated as a separate chapter.

Natural selection: The nonrandom process by which phenotypic frequencies change in a population as a result of heritable variation in their fitness (Cadrin et al. 2014).

NAFO: North Atlantic Fisheries Organization

NAFO Divisions: The Northwest Atlantic Fisheries Organization divides the North Atlantic Ocean—offshore of western Greenland, eastern Canada, and the northeast United States—into management areas called Divisions. Cod in US waters are primarily distributed in Division 5, which includes the Gulf of Maine (5Y), Georges Bank (5Ze), and southern New England (5Zw). They are also distributed in Division 6, as seasonal migrants, from waters offshore of Long Island, New York, and further south, being recorded at least historically to the US Carolinas. Canadian waters are delineated as Division 4, particularly 4X, which encompasses the Bay of Fundy, the Scotian shelf, and offshore banks such as Browns Bank.

NEFMC: New England Fishery Management Council

NERCTP: Northeast Regional Cod Tagging Program.

Neutral genetic variation: Genetic variation not subject to the influence of natural selection, *i.e.*, genetic variants that do not have a direct bearing on an organism's fitness.

Outlier loci: Nucleotides or segments of DNA that have pronounced, elevated frequency differences between two groups of individuals. These are often described as having statistically higher differentiation than expected under neutrality and are diagnostic of adaptation.

Panmixia: Random mating. All individuals within a population are potential sexual partners and there are no restrictions to genetic recombination. Panmictic populations are well connected and therefore genetically homogenous.

Phenotype: An individual's actual observed properties, such as its size or shape, rate of growth, behavior, etc.

Planktonic: Pertaining to the small and microscopic organisms drifting or floating in the sea, in the case of cod, their early life stages (eggs, larvae).

Population: (see biological population).

RAD sequencing, Restriction-site-associated DNA sequencing: The most commonly used type of reduced representation sequencing to generate SNP markers for population genetic studies. Enzymes are used to target and digest DNA into smaller fragments at particular locations, or restriction sites, defined by designated short sequences of nucleotides. This is sometimes done using two enzymes that target different combinations of nucleotides; a process called double digest RAD sequencing, or ddRAD. This type of sequencing targets a fraction (typically <1%) of the whole genome.

Recombination: Exchange of genetic material between individuals leading to the production of offspring with different combinations of traits than their parents. Also refers to exchange of genetic material among regions of the genome, *i.e.*, the process in opposition to linkage.

Recruitment: The number or the life history process of young fish surviving to enter a fishery (for example, to be selected by a specific fishing gear).

SCCZ: (Spring Cod Conservation Zone).

Sequencing Coverage: The number of times a given nucleotide is recognized, or read, during sequencing. With higher coverage comes higher confidence in the exact nucleotide sequence.

Serological: Pertaining to serum (blood) or other body fluids.

Settlement: The transition of juveniles from the water column (a planktonic phase) to the bottom (the benthic phase).

SNPs, Single nucleotide polymorphisms (SNP): Single base differences at any position in the genome, occurring as the result of point mutations; one type ofs a genetic marker.

Spawning component (group, aggregation): Although individual cod spawn in pairs, spawning fish aggregate during a specific time in a specific area (ground). A biological population may comprise a single or a number of different spawning components. (Cadrin et al. 2014)

Spawning ground: A geographic location to which fish return on a regular basis in order to spawn.

Spawning seasons: Cod spawn nearly year round in US waters but in narrower periods of time in specific areas such as: Gulf of Maine (winter: November-December; spring: May-June), Cape Cod (November-December), southern New England (December-February), and Georges Bank (January-April).

SSC: Scientific and Statistical Committee

Stock: An exploited fishery unit. A stock may be a single spawning component, a biological population, a metapopulation, or comprise portions of these units. For management purposes stocks are considered discrete units, and each stock can be exploited independently or catches can be assigned to the stock of origin. (Cadrin et al. 2014)

Subpopulation (component of a metapopulation): A single, mostly self-sustaining unit within a metapopulation. (Cadrin et al. 2014)

Statistical Area: Spatial area to which fishery effort and landings are aggregated for compiling and reporting catch data. Statistical areas are a subset of NAFO Divisions.

Sympatric: Biological populations that overlap geographically.

TRAC: Transboundary Resources Assessment Committee

TMGC: Transboundary Management Guidance Committee

Transboundary: Atlantic cod is a transboundary fishery resource that is managed by treaty between the United States and Canada. Specifically, the eastern end of Georges Bank is east of the Hague line, in Canadian waters, and cod have been documented to move across this international boundary, requiring that management efforts are directed from a common understanding of the fishery resource status.

Whole genome sequencing: Sequencing DNA of the entire genome.

References to Appendix D.

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