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An Interdisciplinary Review of Atlantic Cod (*Gadus morhua*) Stock Structure in the Western North Atlantic Ocean

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An Interdisciplinary Review of Atlantic Cod (*Gadus morhua*) Stock Structure in the Western North Atlantic Ocean

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Editorial Notes

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EXECUTIVE SUMMARY

An Atlantic Cod Stock Structure Working Group (ACSSWG) was formed in early 2018 to inventory and summarize all relevant peer-review information about stock structure of Atlantic cod in US and adjacent waters (i.e., NAFO management divisions 5 and 6 and interactions with 4X). In addition, new data or information could be internally reviewed by the ACSSWG for inclusion in this report. Additional feedback was gained from 3 engagement sessions, 2 sponsored by New England Fishery Management Council and New Hampshire Sea Grant and 1 sponsored by the Maine Fishermen's Forum, each of which added local ecological knowledge into the ACSSWG deliberations.

The ACSSWG followed an interdisciplinary, peer-review approach, forming 6 topical subgroups: early life history, genetic markers, life history, natural markers, applied markers, and fishermen's ecological knowledge. All this was synthesized to evaluate the scientific support for alternative biological stock structure scenarios of Atlantic cod. The material in this Technical Memorandum received internal review by the entire working group, meeting together twice, and the New England Fishery Management Council conducted an external peer review in 2020.

Since 1972, Atlantic cod have been managed in US waters as 2 units: the Gulf of Maine and the Georges Bank management units. In their synthesis, the ACSSWG identified a number of mismatches between the current management units and biological stock structure. First, numerous instances of both phenotypic and genetic heterogeneity indicate that Atlantic cod are not well mixed within each management unit. Second, adult Atlantic cod in some areas exhibit extensive movements, including swimming between current US-US and US-Canada management units. Third, Atlantic 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. Additionally, there is interdisciplinary evidence of mix-stock fisheries arising from sympatric winter- and spring-spawning Atlantic cod in the southwestern Gulf of Maine and around Cape Cod.

In response, 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 winter and spring spawners in multiple statistical areas. Specifically, the proposal is for 5 biological stocks in US waters: (1) a Georges Bank stock (fishing statistical areas 522, 525, 551, 552, 561, and 562), (2) a southern New England stock (areas 537-9), (3) a western Gulf of Maine and Cape Cod winter spawner stock (areas 513-5, 521, and 526), (4) a western Gulf of Maine spring spawner stock (overlap spatially with stock #3 in areas 513-5), and (5) an eastern Gulf of Maine stock (areas 511-2).

The ACSSWG believes that improved recognition of population structure may help prevent further loss of spawning components, better guide adjustments of allowable catch to balance fishing mortality across populations, facilitate recovery of currently depleted stocks, and strengthen the resiliency of the populations that exist within fishing areas.

1. INTRODUCTION

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This document reviews the available data and information pertaining to stock identity of Atlantic cod (*Gadus morhua*) in US and adjacent waters, and evaluates plausible alternative models of its stock structure. The spatial coverage considers the southern distribution of Atlantic cod in the western Atlantic Ocean, which extends as far south as along the Mid-Atlantic seaboard between Cape Cod, MA, and Cape Hatteras, NC. This review typically focuses on the US portions of in the Gulf of Maine and Georges Bank regions, where Atlantic cod are concentrated in US waters, as well as their transboundary interactions with Canadian waters (i.e., Northwest Atlantic Fisheries Organization [NAFO] management divisions 5 and 6 in US waters and interactions with the western portion of division 4 in Canadian waters, Fig. 1.1).

Defining the number of stocks of an exploited species, including stock boundaries and other components of its biocomplexity, is fundamental for efficient monitoring, predictive assessment, and successful management (Cadrin et al. 2005, 2014). For example, estimates of abundance and vital rates assume samples come from a unit stock: well-mixed within the stock boundaries, but reproductively isolated and without significant immigration or emigration in relation to other stock units. Atlantic cod exhibits relatively high population richness for a marine fish (Smedbol and Stephenson 2001), making this a challenging species to determine its stock structure across its extensive range in the North Atlantic Ocean.

Atlantic cod in US waters are overfished and subject to overfishing (NEFSC 2022), and among plausible mechanisms impeding its recovery are concerns that Atlantic cod's biological population structure is not properly aligned with the current assessment and management units (Annala 2012; Zemeckis et al. 2014). Since 1972, Atlantic cod have been managed in US waters as 2 units: the Gulf of Maine and the Georges Bank management units (Serchuk and Wigley 1992; NEFSC 2013; Fig. 1.1). This management paradigm is also part of an international boundary decision, identifying separate Atlantic cod stocks in the Gulf of Maine, on Georges Bank, on Browns Bank, and on the Scotian Shelf (US 1984). In 1998, the United States and Canada established the Transboundary Resources Assessment Committee, which led to shared assessment and allocation of Atlantic cod on the eastern portion of Georges Bank since 2004, under the auspices of the Transboundary Management Guidance Committee (TMGC) (Wang et al. 2009).

In 2018, the Atlantic Cod Stock Structure Working Group (ACSSWG) was formed to produce this interdisciplinary review of Atlantic cod stock structure in US and adjacent Canadian waters. In this introductory material, a brief history of the spatial framework for monitoring, assessment, and management is outlined, along with short descriptions of the ACSSWG and the organization of this document.

A Brief History

Arising from the need to collect fishery catch data for research and management, a framework for delineating and naming fishing areas of the North Atlantic Ocean became established over 100 years ago (Rounsefell 1948; Halliday and Pinhorn 1990). By the 1930s, this framework had evolved from descriptive names of fishing grounds recognized by the fishery (Rich 1929; Alexander et al. 2009) to statistical areas nested into larger management divisions (e.g., NAFO management divisions 4 5, 6 which correspond to the statistical areas labeled in the 400s [i.e., 462-467], 500s, and 600s in Fig. 1.1). At that time, there was little biological information for the many species that were landed, but these delineations were "designed to correspond as far as possible with natural divisions of the fish populations or with barriers to fish migrations" Halliday and Pinhorn (1990). This history set the initial framework for management units in existence today.

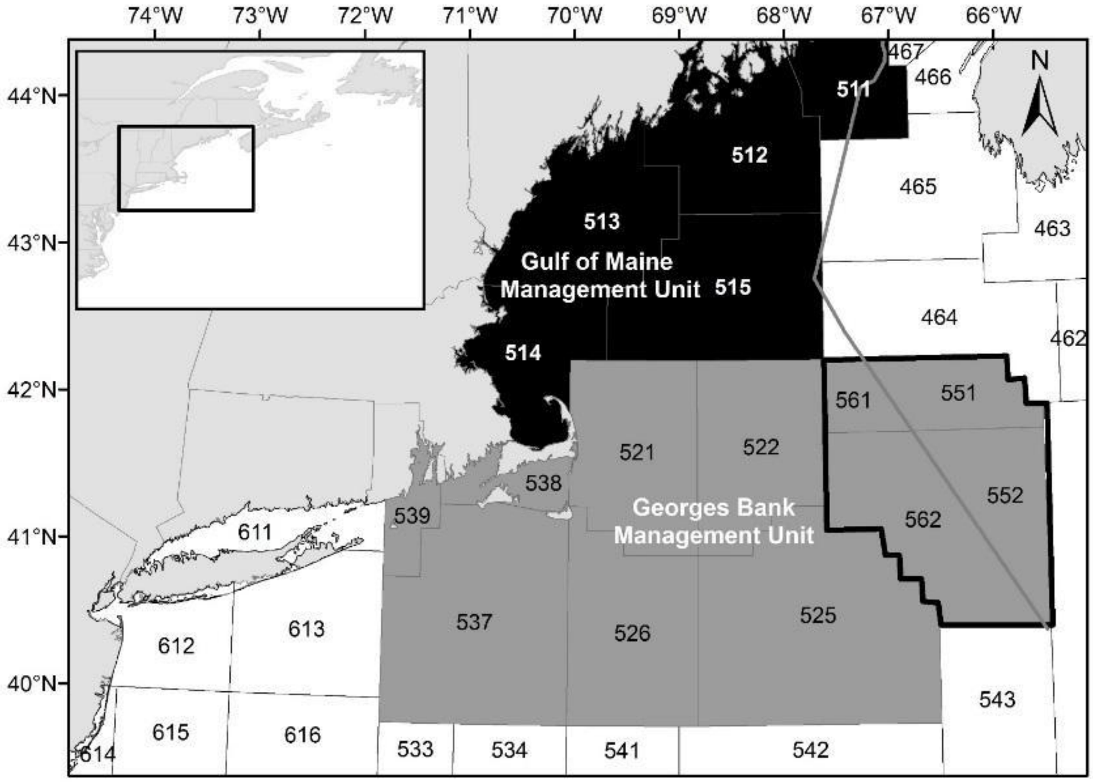

Figure 1.1. Current boundaries for the 2 US Atlantic cod (*Gadus morhua*) management units – Gulf of Maine (black polygons) and Georges Bank (gray polygons) – both within the Northwest Atlantic Fisheries Organization (NAFO) management division 5 (https://www.nafo.int/About-us/Maps). The individual polygons are "statistical areas," used to aggregate fishery catch data. Statistical areas designated in the 500s and 600s (NAFO divisions 5 and 6, respectively) are US waters, and those in the 462-466 (NAFO management division 4X) are Canadian waters. Note, however: (1) Atlantic cod catches attributed to NAFO management division 6 are assigned to the Georges Bank US management unit; (2) Canadian areas 551-2, together with US areas 561-2 (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.

As more information accumulated, it became evident that this existing statistical grid system was better suited for some species than others (e.g., Grosslein 1973). Further spatial alignment of fish populations with this statistical reporting structure was an explicit goal of the regional governing bodies that followed: first with the North American Council on Fishery Investigations (1930s-1950s), then the International Commission for the Northwest Atlantic Fisheries (1950s-1970s), and finally, since 1970, the Northwest Atlantic Fisheries Organization (NAFO) (Halliday and Pinhorn 1990). Nonetheless, administrative and co-management realities have kept this grid system in place, primarily because changing the boundaries would disrupt the historical allocation of catch to areas. Therefore, the aggregation, evaluation, and synthesis of data and information in this document repeatedly reference this framework of statistical areas nested in NAFO management divisions.

By the 1960s, sufficient information about Atlantic cod existed for an interdisciplinary review on its biological population structure. Templeman's (1962) proposal for Atlantic cod stock structure was based on meristics (vertebral numbers), parasites, distributional and migratory patterns, growth, year-class strength, and spawning times and locations. This and subsequent information supported the broad patterns of biological stock structure that roughly corresponded to both latitudinal and inshore-offshore fishing divisions. For example, following Jordan's rule, Atlantic cod vertebral counts increased with increasing latitude across the North American range of the species (Jordan 1891; McDowall 2008). In US waters, the average count from Nantucket Shoals, the southernmost sample, was lower than averages from any other region (Templeman 1981). Parasite infestation rates suggested 2 groups of Atlantic cod in the Gulf of Maine separate from a Georges Bank and a southern New England population (Sherman and Wise 1961). Wise (1963) summarized decades of tagging Atlantic cod in New England's waters to define 4 geographic groups: Atlantic cod of the Gulf of Maine, Atlantic cod of the offshore banks (e.g., Georges and Brown Banks), Atlantic cod of southern New England and the Great South Channel, and New Jersey coastal Atlantic cod (see Chapter 2 for a map of most locations mentioned in the text). This information also supported notable connectivity among NAFO divisions. For example, tag returns showed intermingling of adults across NAFO management divisions 5Z and 4X, such as between the offshore Browns Bank and eastern Georges Bank, as well as seasonal migration between Nantucket Shoals and New Jersey, and as far southwest as North Carolina (NAFO management division 6) (McKenzie 1956; Wise and Jensen 1960; Wise 1963).

In the 1960s a standardized, fishery-independent groundfish survey began to collect life history samples that provided additional information types for stock identification of Atlantic cod. For example, the near absence of juvenile Atlantic cod in survey tows from Block Island, RI, to Cape Hatteras, NC, suggested that the Atlantic cod from that area were not self-sustaining (Serchuk and Wood 1979). Also, significant differences in the mean lengths-at-age of young Atlantic cod were noted in 3 areas: the Gulf of Maine, on Georges Bank, and off Cape Cod/southern New England. Differences in age at maturity were noted among Gulf of Maine, Georges Bank, and Browns Bank (Penttila and Giffords 1976; Livingstone and Dery 1976; Serchuk and Wood 1979). Other information arising in the 1970s included differences in body color, otolith shape and size, and genetic differences detected by serological or biochemical methods (Templeman 1978). In the decades since, stock identification of Atlantic cod has expanded further as an interdisciplinary field of study (Lough 2004; Cadrin et al. 2005, 2014; Annala 2012; Zemeckis et al. 2014; Dean et al. 2019).

Populations of Atlantic cod have declined despite substantially reduced fishery catch and a series of management actions over decades in US waters. This decline has led to concerns that existing Atlantic cod management units have not adequately captured Atlantic cod's biological stock structure, contributing to delays in rebuilding (Smedbol and Stephenson 2001; Annala 2012; Zemeckis et al. 2014). Fishery management systems ideally address a single, panmictic population within a management unit, but in this case, historic evidence demonstrates both uneven declines in abundance among aggregations of Atlantic cod within management units and even complete extirpation of spawning groups offshore of Maine, within the Gulf of Maine management unit (Ames 2004; Smedbol and Stephenson 2001). Such examples of heterogeneous levels of productivity or stability within management units may be tied to cryptic stock structure. Moreover, recent investigations have demonstrated sympatric but genetically distinct populations within the southwestern Gulf of Maine: winter- and spring-spawning subpopulations (Kovach et al. 2010; Siceloff and Howell 2013; Dean et al. 2014; Zemeckis et al. 2019) indicating a mixed stock fishery operates in this management unit (Dean et al. 2019). Finally, compilations of fisherman's ecological knowledge have identified fine-scale structure of spawning grounds around Cape Cod, including the Great South Channel and Nantucket Shoals, and on Georges Bank (DeCelles et al. 2017), as well as historically within the eastern and western Gulf of Maine (Ames 1997, 2004).

The Atlantic Cod Stock Structure Working Group (ACSSWG)

Although the data available for Atlantic cod are more detailed than those available for most species, persistent scientific uncertainty has been identified as a key factor contributing to difficulties in rebuilding of Atlantic cod in US waters (Annala 2012). Throughout their range, Atlantic cod are regarded as a population-rich species (Smedbol and Stephenson 2001; ICES 2020), making it all the more plausible that improved recognition of population structure may help prevent further loss of spawning components, better guide adjustments of allowable catch to balance fishing mortality across populations, facilitate recovery of currently declined stocks, and strengthen the resiliency of the populations that exist within fishing areas.

In response to these concerns and aspirations, the Atlantic Cod Stock Structure Working Group (ACSSWG; Appendix A) was formed in early 2018 to inventory and summarize all relevant peer-review information about stock structure of Atlantic cod in NAFO management divisions 5 and 6 and interactions with 4X. In addition, new data and information were also internally reviewed by the ACSSWG and included as appropriate. Additional feedback was gained from 3 engagement sessions with industry and other interested parties to create transparency and add local ecological knowledge into the ACSSWG deliberations (New Hampshire Sea Grant; Maine Fishermen's Forum).

The ACSSWG organized materials to review by discipline and evaluated them with a holistic or interdisciplinary approach, as espoused by Cadrin et al. (2014). The 6 topical or disciplinary subgroups were: early life history, genetic markers, life history, natural markers, applied markers, and fishermen's ecological knowledge (Chapters 3-8, this volume). Each subgroup reviewed the relevance of all published literature on the topic, as well as new data or information that could be peer-reviewed by the subgroup. The conclusions of each discipline's approach were presented by each subgroup to the entire working group in November 2018. Later, they were drafted into the chapters of this report and reviewed by coauthors and other experts both within and outside the ACSSWG in 2019.

To reach an interdisciplinary conclusion, no preferential weighting of evidence was assigned to any discipline. Instead, the ACSSWG agreed that each discipline's approach offered independent perspectives on population distribution and dispersal, and geographic variation of traits, each of which could be evaluated on their own merits. This approach explicitly recognizes that the different disciplines build lines of evidence at different spatial or temporal scales, particularly across different periods of a fish's life span or across generations (Fig. 1.2). The ACSSWG was open to looking at each discipline as complementary rather than competing, to build stronger, broader inference to test alternative stock hypotheses than any one discipline could do alone (Cadrin 2020). This challenge of an interdisciplinary synthesis by the ACSSWG led to a consensus proposal of biological stock structure (Chapter 9, this volume).

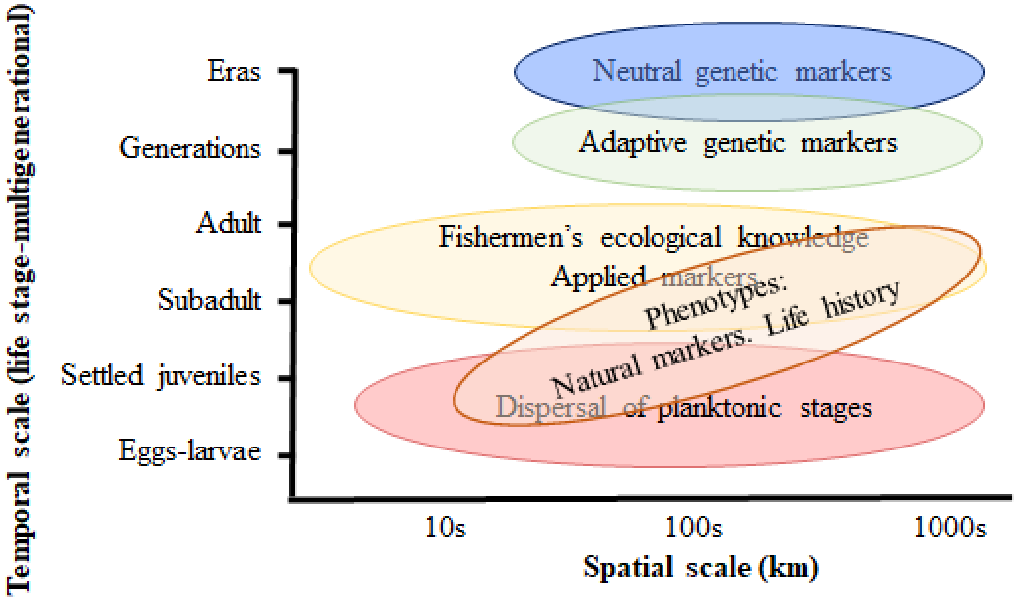

Figure 1.2. Spatial and temporal sensitivities of different disciplines to resolve emergent stock structure in fishes. Different disciplines apply to mildly differing ranges of physical space, as indicated on the abscissa. On the ordinate, periods refer to early life stages (i.e., egg-larvae, settled juveniles), older life stages (subadults, adults), generations (heritable traits across relatively few generations), and eras (multiple generations across geological time scales).

This Technical Memorandum assembles the findings of the ACSSWG with respect to these 3 terms of reference (TORs, Appendix B):

1. Inventory and summarize all relevant peer-review information about stock structure of Atlantic cod in NAFO management divisions5 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 management divisions 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. Use a holistic approach to synthesize all available information (TOR 1 and 2; Appendix B) 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.

A draft of this Technical Memorandum received external peer review on May 18-29, 2020, and summaries of the ACSSWG and the peer-review panel were the subject of the June 2020, meeting of the New England Fishery Management Council. This document responds to specific concerns of the peer-review report in its final revision.

The application of this report's conclusions is still evolving. From June to September, 2021, a series of workshops were held to inform and discuss the different perspectives on how the findings of the ACSSWG could affect the monitoring, assessment, and management options of Atlantic cod in US waters. In October 2021, a new Working Group was formed to evaluate new datasets that can either inform or be used in new or existing stock assessment models for the 2023 Atlantic Cod Research Track Assessment.

Outline of This Report

Following this introductory material is a section providing a fishery management context, which includes reference maps, locations named in the text, and an outline of management by the United States and transboundary agreements with Canada (Chapter 2). Chapters that cover the individual disciplines reviewed by the ACSSWG follow:

- Early life history (Chapter 3)
- Genetic markers (Chapter 4),
- Life history (Chapter 5),
- Natural markers (Chapter 6),
- Applied markers (Chapter 7),
- Fishermen's ecological knowledge (Chapter 8).

A synthesis chapter, Chapter 9, develops a set of plausible biological stock structures and evaluates the scientific evidence for each to determine the most accurate representation of Atlantic Cod stock structure. As the ultimate purpose of this determination is for use in regional stock assessment and management, thresholds for scientific support are that the proposed biological stock structure should be temporally stable and accurately capture the available data and assessment model frameworks. The synthesis chapter also summarizes recommendations for additional work, as developed by both the ACSSWG and by the external peer-review panel.

The report ends with a complete list of the working group members (Appendix A); TORs (Appendix B); objectives (Appendix C); and a glossary of terms, acronyms, and abbreviations (Appendix D).

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2. OVERVIEW OF ATLANTIC COD MANAGEMENT

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Abstract

This chapter gives a broad overview of the US management of Atlantic cod (*Gadus morhua*). It introduces the relevant Northeast Multispecies (Groundfish) Fishery Management Plan and explains the governance structure for management between the New England Fisheries Management Council and National Marine Fisheries Service under the authority of the Magnuson-Stevens Fishery Conservation and Management Act. It briefly summarizes the management measures for commercial and recreational fishing components and describes the current stock structure used for management and the recent status determination of these stocks. The conclusion identifies several special considerations related to cod management, including co-management of cod with Canada on the northeast tip of Georges Bank (Fig. 2.1).

Introduction

This chapter puts in place an overview of the Fishery Management Plan and its governance related to Atlantic cod in US waters. It also includes a map that identifies locations used throughout the Technical Memorandum. Finally, it includes details of the current stock structure used for management, the recent status determination of these stocks, and special area considerations related to cod management.

Fishery Management Plan

A fishery management plan (FMP) is used to describe a fishery and how it is managed. Atlantic cod is one of the 13 groundfish species in the Northeast Multispecies (Groundfish) FMP. These groundfish include the following 10 targeted species off New England and Mid-Atlantic coasts: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limanda ferruginea*), pollock (*Pollachius virens*), American plaice (*Hippoglossoides platessoides*), witch flounder (*Glyptocephalus cynoglossus*), white hake (*Urophycis tenuis*), winter flounder (*Pseudopleuronectes americanus*), Acadian redfish (*Sebastes fasciatus*) and Atlantic halibut (*Hippoglossus hippoglossus*). The FMP also includes 3 nontarget species: windowpane flounder (*Scophthalmus aquosus*), ocean pout (*Zoarces americanus*), and Atlantic wolffish (*Anarhichas lupus*). Some of these species (cod, haddock, yellowtail flounder, winter flounder, and windowpane flounder) are further subdivided into stocks attributed to different geographic areas. Two stocks, Georges Bank (GB) cod and GB haddock, also have transboundary management units on eastern Georges Bank (EGB) (Figs 2.2-2.4), with an additional stock, GB yellowtail flounder, managed as a transboundary stock as a single unit. The FMP therefore consists of 20 stocks and 2 management units, with both commercial and recreational fisheries catching these species.

An FMP is dynamic. As new information becomes available, the New England Fishery Management Council (NEFMC) proposes changes for the Northeast Multispecies (Groundfish) FMP to the National Marine Fisheries Service (NMFS). The NEFMC updates the FMP through a series of amendments and framework adjustments. In 2010 Amendment 16 adopted a broad suite of management measures to achieve the fishing mortality targets necessary to rebuild overfished stocks and meet other requirements of the Magnuson-Stevens Fishery Conservation and Management Act (MSA), the federal law that governs marine fisheries in the United States. Amendment 16 greatly expanded the sector management program, which identifies which commercial fishermen are in the fishery, and adopted a process for setting annual catch limits (ACLs) that requires catch levels to be set in biennial specifications. In 2011 Amendment 17 allowed for NOAA-sponsored, state-operated, permit banks (i.e., organizations that purchase fishing quota) to function within the structure of Amendment 16. In 2017 Amendment 18 addressed fishing fleet diversity and accumulation limits. Sixteen framework adjustments have updated the measures in Amendment 16, primarily based on the results of assessments of the fish stocks in the FMP. Currently, Amendment 23 is being prepared for submission to NMFS and is expected to improve monitoring in the commercial groundfish fishery.

Amendment 16 made major changes to the FMP by adopting a system of ACLs and accountability measures (AMs) that are designed to ensure catches remain below desired targets for each stock in the management complex. In addition to preventing ACLs from being exceeded, AMs are management controls that can correct or mitigate any overages of the ACL once they occur, whether annually or in-season. Ideally, the AMs address and minimize both the frequency and magnitude of overages, as well as provide an effective and timely solution to the problem causing the overage.

There is no requirement that AMs and ACLs be implemented as total allowable catches (TACs) or quotas, but these conservation and management measures must prevent the ACL from being exceeded, as well as mitigate the situation in cases where the ACL is exceeded (74 Federal Register 3184). Although many measures in the management program are intended to control fishing mortality and might be interpreted to be AMs, the term AM is usually applied to specific, automatic measures that are implemented either as an ACL is approached or after an ACL is exceeded.

Current Management Structure and Status

Atlantic cod has been managed as 2 independent stocks – Gulf of Maine (GOM) cod and GB cod – in US waters since 1972 (Serchuk and Wigley 1992). Stock boundaries were based on fishing grounds; tagging observations; and geographic variation in spawning times, growth, and parasites (Zemeckis et al. 2014; Chapter 1, this volume). GB cod is also divided into western and eastern management units, with the eastern management unit subject to a transboundary quota sharing agreement between the United States and Canada since 2001 (TMGC 2002). The GOM and GB cod fishery includes commercial and recreational catches in the United States and commercial catches in Canada. The commercial fishery in the United States is managed as 2 components: groups of fishermen identifying as sectors and other fishermen collectively in a common pool, as outlined in the sector management program. The recreational fishery (composed of private anglers and for-hire charter and party) is generally managed through seasons, bag limits, and minimum fish sizes.

The status of Atlantic cod is determined by separate assessments of the GOM cod and the GB cod management units. Recent assessments of these stocks examined fishery catch, a fishery-independent survey of fish abundance, and results of a quantitative model (NEFSC 2022). Such stock assessments occur every 2 years, while the EGB cod management unit is assessed annually. Based on recent assessments (NEFSC 2022), GOM cod are overfished and overfishing is occurring, while GB cod are overfished and the overfishing status was undetermined. Each stock is subject to rebuilding plans with rebuild by dates of 2024 and 2026, respectively. The stock status of cod in the EGB management unit is poor and subject to a rebuilding plan in Canada. In October, 2021, a Working Group was formed to review the data and assessment models suitable for the 2023 Atlantic Cod Research Track Assessment.

Special Management Considerations

In addition to management measures of quotas and accountability, as outlined above, there are specific considerations in certain areas, as described below.

Gulf of Maine Cod

GOM cod management includes a complex system of additional measures to reduce fishing mortality and protect spawning fish and habitat. For example, the commercial fishery is subject to seasonal rolling closures and gear-specific year-round closures. Both the commercial and recreational fisheries are subject to spawning closures.

Georges Bank Cod

Like GOM cod, additional measures are in place to reduce fishing mortality and to protect spawning fish and habitat. The GB commercial fishery is subject to seasonal rolling closures and year-round closures, based on fishing gear.

Eastern Georges Bank Cod

EGB cod is subject to a transboundary sharing management agreement between the United States and Canada. Quotas are set and allocated to the United States and Canada annually by the Transboundary Management Guidance Committee (TMGC) based on the catch advice from the Transboundary Resources Assessment Committee (TRAC). In the United States, the commercial fishery is also subject to year-round closures and gear restricted access areas. In Canada, the commercial fishery is managed with quotas, gear modification requirements, minimum fish sizes, bycatch restrictions, and seasonal closures.

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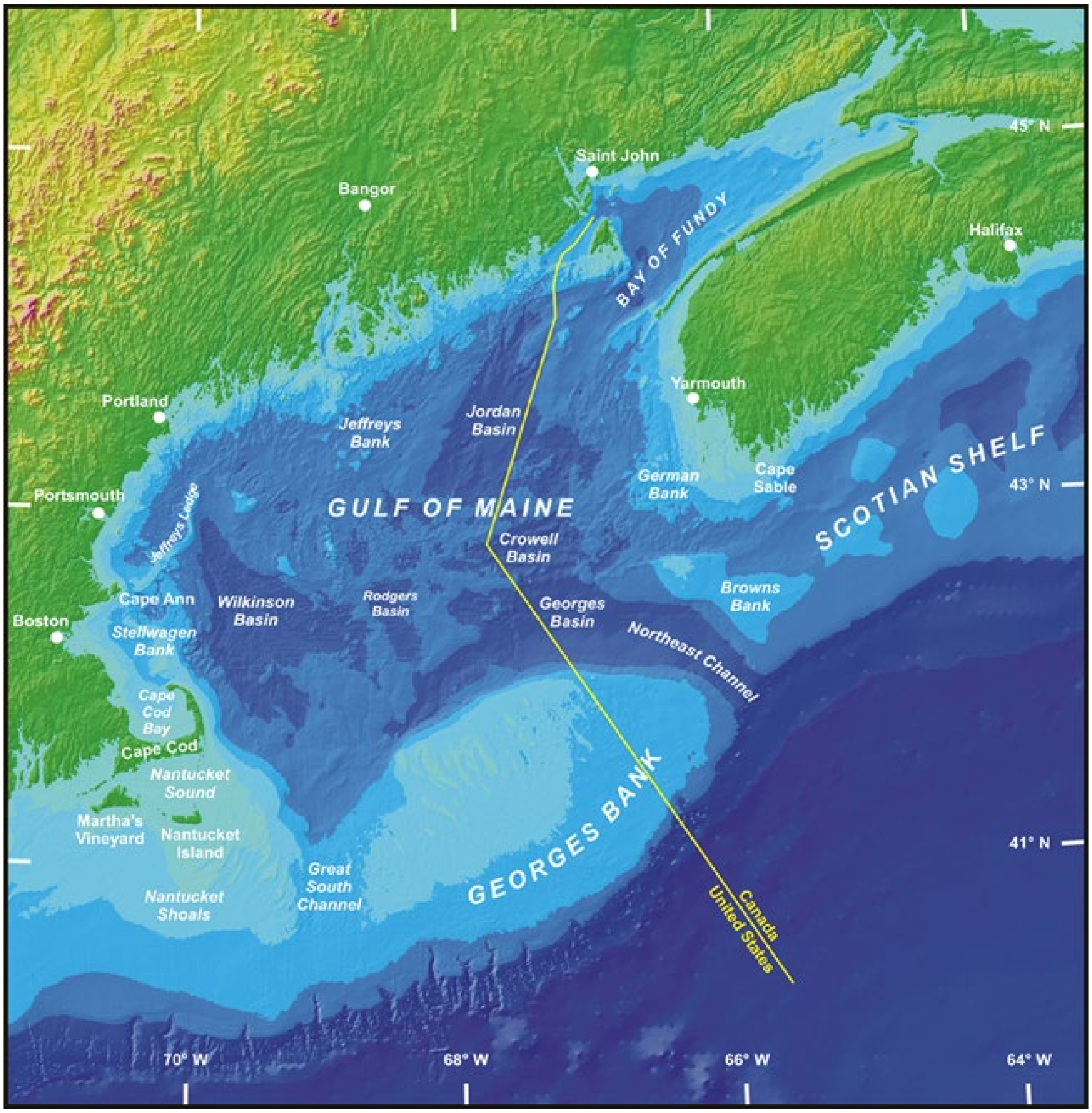

Figure 2.1 Map of the Gulf of Maine and Georges Bank depicting major submarine features and the transboundary line for management between the United States and Canada.

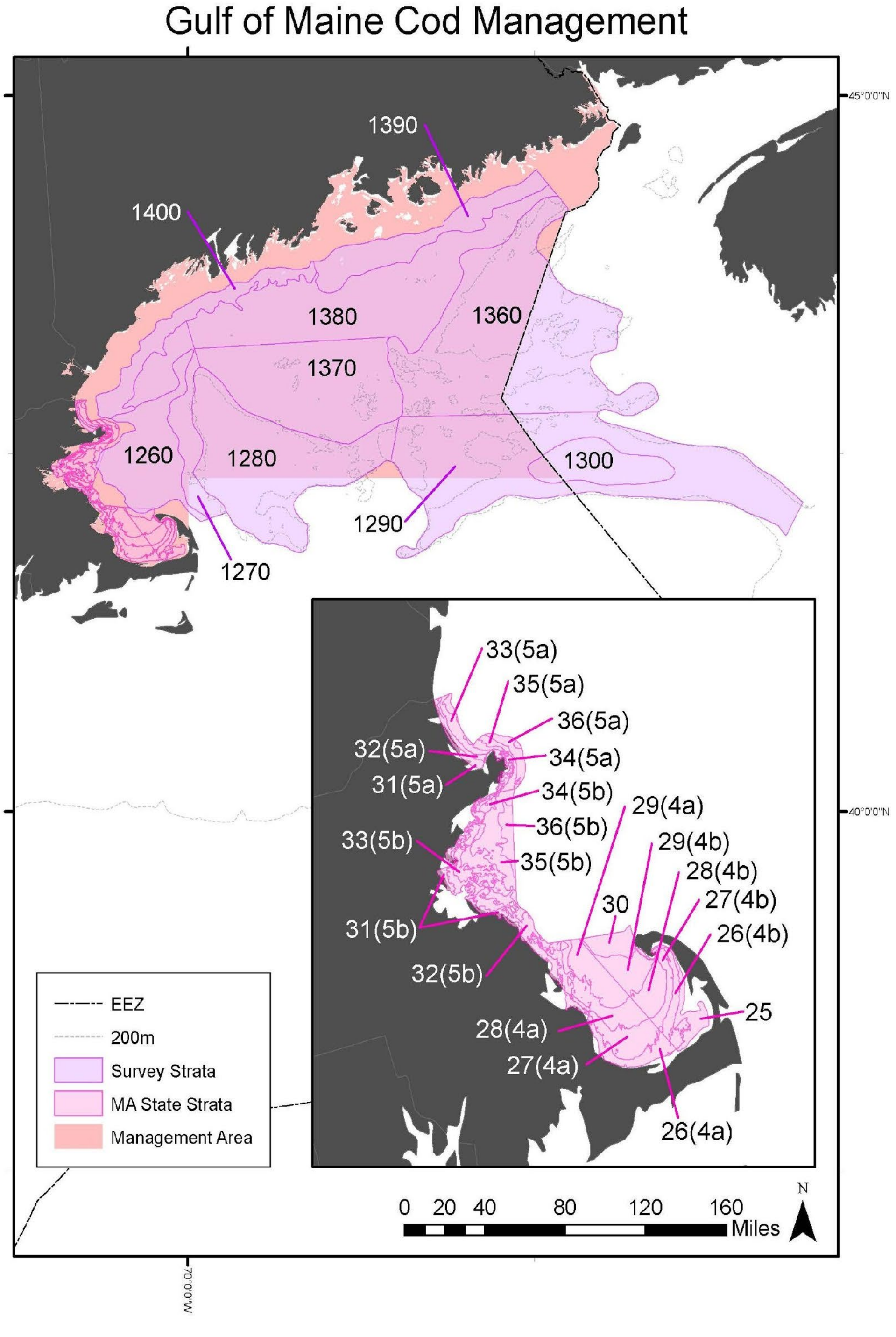

Figure 2.2 The overlap between the Gulf of Maine Atlantic cod (*Gadus morhua*) stock management area and survey strata of the National Marine Fisheries Service [whole] and the Massachusetts Division of Marine Fisheries [inset].

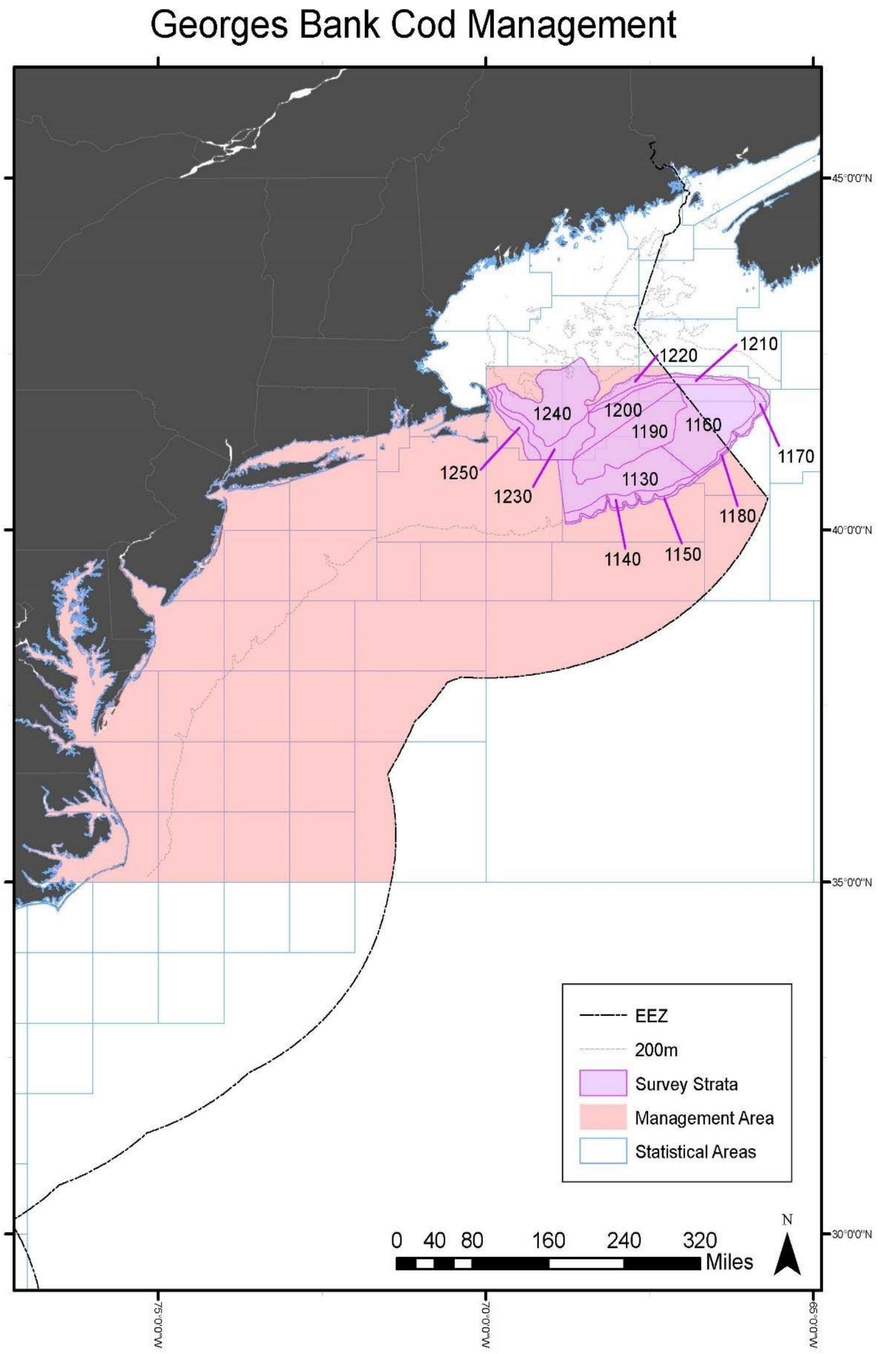

Figure 2.3 Georges Bank Atlantic cod (*Gadus morhua*) stock management area and stock assessment survey strata (National Marine Fisheries Service). EEZ = Exclusive Economic Zone.

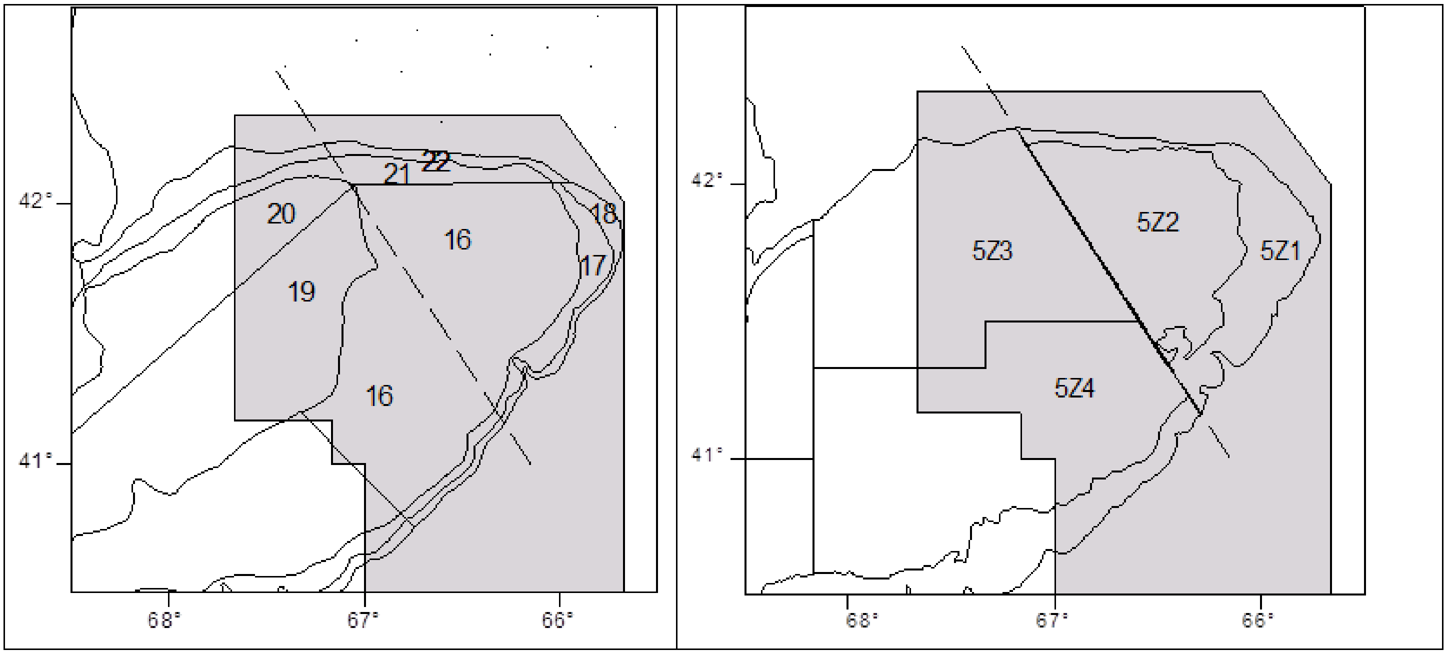

Figure 2.4 Eastern Georges Bank management unit area (gray) with National Marine Fisheries Service survey strata (left) and Department of Fisheries and Oceans (DFO) Canada survey strata (right). Source: 2020 Transboundary Resource Assessment Committee (TRAC). DFO survey strata of 5Z3-5Z4 are post-stratified for the eastern Georges Bank assessment and Canada and United States allocation shares to align with eastern Georges Bank management area.

3. EARLY LIFE HISTORY: SPAWNING TO SETTLEMENT

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Abstract

The period between spawning and juvenile settlement is a critical part of the life history of Atlantic cod (*Gadus morhua*). Dispersal from spawning grounds to nursery areas by pelagic early life stages creates connectivity links between regions that can shape the structure of a population. In this chapter, we review larval transport studies for cod within US waters, as well as examine bottom trawl and ichthyoplankton survey datasets for evidence of transport pathways. All available data were summarized and integrated to form conclusions on the connectivity between 4 regions known to host persistent spawning grounds: Gulf of Maine (GOM); Georges Bank (GBK); Cape Cod (CC); and southern New England (SNE). Both GOM and GBK appear to be zones of significant self-recruitment with little input from outside, supporting the continued use of at least 2 separate management units. Several lines of evidence suggest major connectivity pathways exist between GOM/CC, CC/SNE, and SNE/SNE; with minor pathways between GOM/SNE and GBK/SNE. From an early life history perspective, the GOM, CC, and SNE regions appear to be interconnected and are distinct from the GBK region.

Introduction

Early life history stages can help elucidate the population structure of a fish stock, particularly when considered in the context of a holistic approach that includes multiple lines of supporting evidence (Hare and Richardson 2014). Discrete spawning events and transport pathways lead to discontinuous egg and larval distributions that are commonly identified in association with genotypic and phenotypic differences (Hare 2005) and can have an important influence on the population structure of marine fishes (e.g., Espeland et al. 2007). Early life history stages have been used within a multidisciplinary framework to investigate the stock structure of several species including American lobster (*Homarus americanus*), Japanese eels (*Anguilla japonica*), Atlantic herring (*Clupea harengus*), and Atlantic bluefin tuna (*Thunnus thynnus*) (Hare 2005; Hare and Richardson 2014). The aim of this chapter is to provide a comprehensive review of the early life history of Atlantic cod (*Gadus morhua*) in US waters in order to provide a supporting line of evidence for the underlying structure of the population.

For the purpose of this chapter, we consider "early life history" to include all phases of life from egg release (i.e., spawning) through juvenile settlement. This portion of the Atlantic cod life cycle forms the critical link between reproductive potential and subsequent recruitment, and therefore it lays the foundation for stock dynamics (Hare and Richardson 2014). Given a high individual fecundity (May 1967) and a prolonged planktonic stage (Bolz and Lough 1988), cod have the potential for broad dispersal and mixing among spawning groups. Yet, despite this reproductive strategy, most cod stocks have fine-scale population structure that persists across many generations, as evidenced by high fidelity to persistent spawning sites (Robichaud and Rose 2001; Skjæraasen et al. 2011; Dean et al. 2014) and genetic structuring (e.g., Kovach et al. 2010; Hutchinson et al. 2001).

One consequence of a dispersive life history is high mortality during early life (Tian et al. 2007), with a variety of biotic and abiotic factors constraining the survival of young cod (Werner et al. 1996). The most important factors influencing the distribution of eggs and larvae are the timing and location of spawning (Hare and Richardson 2014). After egg release, a variety of physical oceanographic forces affect the pelagic transport of offspring, which can be modified by physical characteristics (e.g., buoyancy) and larval behavior (Huret et al. 2007). Spatio-temporal overlap with primary prey species determines the extent of losses from starvation (Lough et al. 2005; Friedland et al. 2013). In addition, specific habitat requirements determine which surviving larvae ultimately become settled benthic juveniles (Grabowski et al. 2018). Therefore, despite a high reproductive and dispersive capacity, only a small number of individuals overcome each life history hurdle and survive to recruit to the population. Understanding the sequence of these early life stages can help reveal the structure of the population and the mechanisms that maintain it.

Numerous particle simulation studies using hydrodynamic models have been conducted for the Gulf of Maine and Georges Bank to examine the probability of transport between specific spawning grounds and known juvenile settlement habitat (Huret et al. 2007; Churchill et al. 2011, 2017; Werner et al. 1993, 1996). These studies provide an overall picture of the potential early-life connectivity between areas within the range of cod in US waters. However, it is important to consider that larval transport potential does not necessarily indicate survival to the juvenile stage. Fortunately, there is also a wealth of empirical information on the spatial and seasonal distribution of early life stages of cod within the region, from spawning through settlement. When considered independently, each life stage offers only a limited perspective on population structure, with many possible interpretations; however, when examined collectively, we can reconstruct this adult-juvenile link to inform hypotheses about regional connectivity within and between stocks.

The primary objective of this chapter is to review previously published studies and survey datasets in order to evaluate the early-life connectivity between areas within the range of Atlantic cod in US waters. Specifically, we sought to answer the following questions: (1) is there evidence of major connectivity across the current 2-stock management boundary? and (2) is there an alternative set of boundaries that better aligns with regional patterns in reproductive ecology and early life history?

Methods and Materials

Study Area and Spatial Strata

Early-life connectivity was evaluated according to a set of 4 spatial strata that captures the broad-scale patterns in regional spawning activity. To augment the relevance and interpretation of results, strata were aligned to the NOAA "statistical areas" used for fishery-dependent reporting (Fig. 3.1): GOM (areas 511-515), CC (area 521), SNE (areas 526, 527, 538, 539), and GBK (areas 522, 525, 551, 552, 561, 562). The GOM stratum is equivalent to the current definition for the Gulf of Maine management unit, whereas the other 3 strata collectively make up the current definition for the Georges Bank management unit.

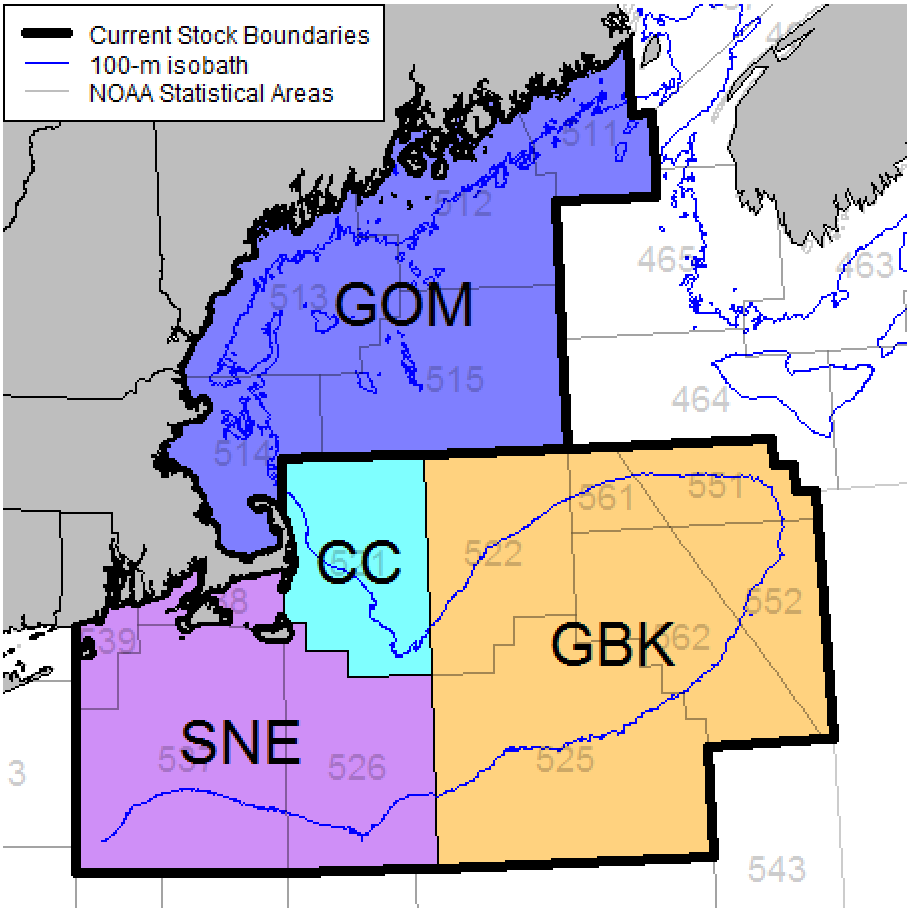


Figure 3.1. Spatial strata used for evaluating regional connectivity of Atlantic cod (*Gadus morhua*) stocks. The Gulf of Maine (GOM) stratum includes NOAA statistical reporting areas 511-515; Georges Bank (GBK) areas 522, 525, 551, 552, 561, 562; Cape Cod (CC) area 521; southern New England (SNE) areas 526, 537, 538, 539.

Survey Data Sources

Cod eggs and larvae have routinely been captured throughout the region via annual ichthyoplankton cruises since 1971. The program name and study design for these surveys has changed multiple times over the years: International Commission for the Northwest Atlantic Fisheries (ICNAF 1971-1977); Marine Resources Monitoring, Assessment, and Prediction (MARMAP 1977-1987); Atlantic Herring and Sand Lance (*Ammodytes*) surveys (H-SL 1988-1994); Georges Bank Global Ocean Ecosystems Dynamics (GLOBEC, 1995-1999); Ecosystem Monitoring Program (EcoMon, 1992-present). Despite these changes, each program sought to broadly sample in space and time the ichthyoplankton community across the continental shelf of the US Atlantic coast between North Carolina and Nova Scotia (Richardson et al. 2010). On each survey cruise, a 61-cm bongo net was used to sample the water column from the surface to within 5 m of the seafloor up to a maximum of 200 m. Prior to 1999, the mesh size of the net was 505 um, which was reduced to 333 um after 1999. The available data include the relative abundance of fish eggs and larvae (in units of #/m^2 and #/m^3), identified to lowest possible taxon, which is often to the species.

It is not possible to distinguish between the early-stage eggs of cod, haddock (*Melanogrammus aeglefinus*), and witch flounder (*Glyptocephalus cynoglossus*) through typical visual examination of physical attributes (Markle and Frost 1985; Lough et al. 1994). Regardless, researchers in some parts of the North Atlantic have used the relative abundance of eggs to identify the locations of cod spawning and early dispersal by making assumptions about the species mix based on the presence and reproductive phenology of cod, haddock, and witch flounder in those regions (e.g., Ouellet et al. 1997). Unfortunately, it is not reasonable to make such assumptions about cod-haddock-witch eggs within the range of cod in US waters. The multitude and diversity of spawning groups mean that cod eggs could be present in nearly every month, creating substantial overlap with the spawning seasons of haddock and witch flounder, both of which are relatively abundant in the Gulf of Maine and Georges Bank management units. Berrien and Sibunka (1999) attempted to circumvent this issue by determining the species mix of late stage eggs and then applying those proportions to the abundance of early stage eggs. Given the inherent uncertainty in this approach and that late stage cod-haddock-witch eggs have not been identified to species since the 1990s, we have concentrated on just the larval phase for spatial analysis. Furthermore, we have focused on the period 1977-2017, because these were the only years for which electronic data were available.

Although several bottom trawl surveys operate in the region, we have focused on 2 long-term surveys that routinely catch recently settled age-0 juvenile cod in appreciable numbers. The Northeast Fisheries Science Center (NEFSC) survey utilizes a small mesh net to make standard tows at randomly selected stations throughout the continental shelf from North Carolina to Nova Scotia. Each year, the NEFSC survey covers the entire study area in 2 seasonal cruises. The "spring cruise," which began in 1968, typically reaches the New England region in March-April and captures recently settled juveniles that were spawned during the late fall and early winter months. The "fall cruise" (September-October; beginning 1963) captures juveniles that were spawned in spring and early summer months. The Massachusetts Division of Marine Fisheries (MADMF) uses a similar stratified-random design concept and small mesh bottom trawl to operate spring (May) and fall (September) cruises that are restricted to just Massachusetts state waters. The MADMF survey has operated every year since 1978 and encompasses juvenile settlement areas within the GOM, CC, and SNE strata.

Other NEFSC bottom trawl survey cruises (summer, winter, shrimp) were initially examined but excluded from further analysis because of a lack of age-0 cod, a limited time series, or both. Likewise, the Northeast Area Monitoring and Assessment Program (NEAMAP, 2006-present) and Maine-New Hampshire (MENH, 2000-present) bottom trawl surveys were also not pursued because of a lack of age-0 cod catches and limited time series. Rhode Island Department of Environmental Management (RIDEM) operates the only other long-term seasonal bottom trawl survey that routinely encounters age-0 cod in US waters; unfortunately, these data were unavailable to us at the time of this analysis. Regardless, the observations of age-0 cod from MADMF and NEFSC surveys near Rhode Island waters corroborate the patterns found in the RIDEM dataset (Langan et al. 2020), and our conclusions would not have changed had these data been available and included in the spatial modeling.

Spatial Models

In order to better evaluate connectivity between spatial strata, observations of larval cod from ichthyoplankton surveys were summarized via geostatistical interpolation (i.e., kriging). Geostatistical approaches have been recommended for the analysis of early life history data, as they allow for more robust inferences regarding likely transport patterns and discreteness of spawning events (Hare and Richardson 2014). The overarching goal of this process was to disentangle the general spatial pattern from interannual variability and the waxing and waning of various spawning groups. For most of the years encompassed by the ichthyoplankton sampling programs, the relative abundance of cod larvae found in the GBK stratum was far greater than in the other 3 areas. As a result, the signal originating from Georges Bank spawning nearly overwhelms that of the Gulf of Maine or southern New England. Because the focus of this investigation is on connectivity between areas and is less concerned with relative abundance, only the occurrence of larvae was used to describe the spatial distribution of cod during their pelagic phase.

Empirical variograms were calculated by month and year (8 km lag bins, out to 200 km), and then an exponential variogram model was fit to the median values by month (Fig. 3.2). Monthly variogram models were then used to interpolate between survey observations to generate a predicted map for each year and month. Finally, these maps were then pixel-averaged across years to capture the general spatial pattern of the probability of larval occurrence.

The spatial pattern of settlement was summarized in a similar manner. For each bottom trawl survey dataset, there was a distinct length frequency mode, centered on 3-5 cm, representing the first observation of a cohort at age-0. In most cases, this group of fish could be isolated by selecting lengths shorter than 8 cm (Fig. 3.3). Because of the similarities in survey timing and gear, the NEFSC and MADMF datasets were pooled together by season, and the occurrence of recently settled juveniles < 8 cm was used as the input data for spatial analysis. Empirical variograms were calculated by year and season, and an exponential variogram model was fit to the median values by season (Fig. 3.4). Given an apparent finer-scale structure to the spatial relationship of observed settlement, substantially smaller lag bins were used (0.8 km bins, out to 20 km). Seasonal variogram models were applied to survey observations to generate a predicted map for each year and season, which were then pixel-averaged across years to create a general map of settlement probability.

Time Series Correlations

Given the variation in spatial coverage and seasonal timing caused by the programmatic changes to the ichthyoplankton surveys (Richardson et al. 2010), we did not attempt to create regional/seasonal time series of larval abundance. Although some changes have occurred over the course of the bottom trawl surveys, the spatial and seasonal coverage have been relatively consistent. Therefore, we focused on time series correlations of the abundance of recently settled juveniles. For both spring and fall cruises of the MADMF and NEFSC bottom trawl surveys, the mean occurrence (fraction of tows with 1 or more individuals) and mean abundance (numbers per tow) of cod < 8 cm were calculated by year and stratum. The Pearson correlation coefficient was then calculated for each possible pair of time series. A correlation was considered significant if the p-value was less than 0.05.

Evaluation of Connectivity

Each possible combination between spawning ground and settlement area was evaluated for evidence of early-life connectivity and assigned to 1 of 3 categories: unlikely, minor, or major. Although strict quantitative criteria were not given to these terms, "unlikely connectivity" is meant to represent an absence or negligible amount of connectivity between a spawning area (source) and a settlement area (sink). "Minor connectivity" suggests that a settlement area is significantly influenced by a spawning area, but that a minority of the source's production ends up in the sink and that a minority of the sink's settlement comes from that source. "Major connectivity" suggests that either a majority of the source's production settles in the sink, or a majority of the sink's settlement comes from the source.

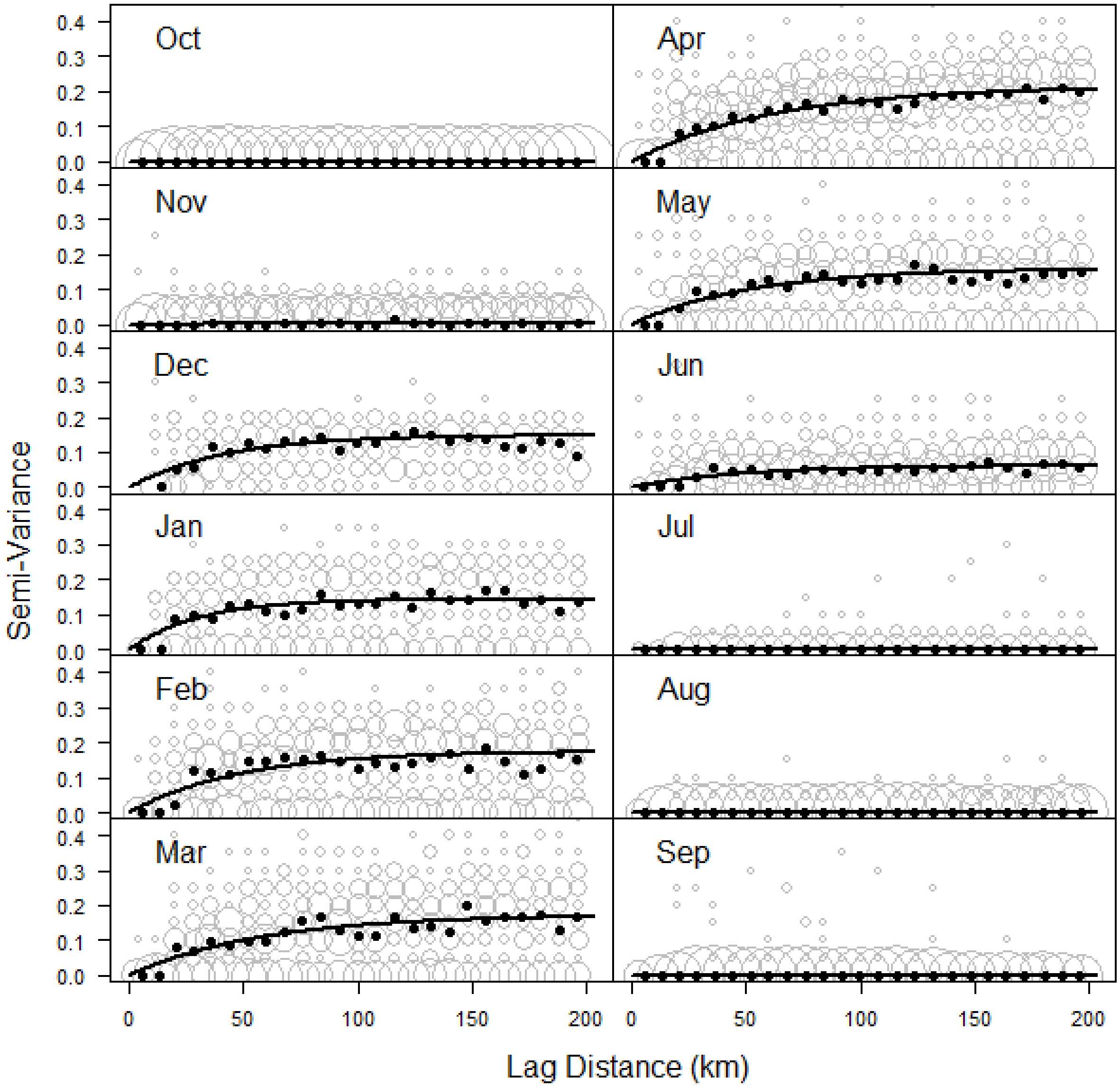


Figure 3.2. Variograms of larval Atlantic cod (*Gadus morhua*) occurrence used for geostatistical interpolation (i.e., kriging), by month. Hollow bubbles represent the distribution of annual empirical variogram values, where bubble size is proportional to the frequency at that level. Solid points represent the median semivariance value for each 8 km lag bin. Solid lines represent an exponential variogram model fit to the median values. Larval occurrence data come from ichthyoplankton surveys conducted between 1977-2017.

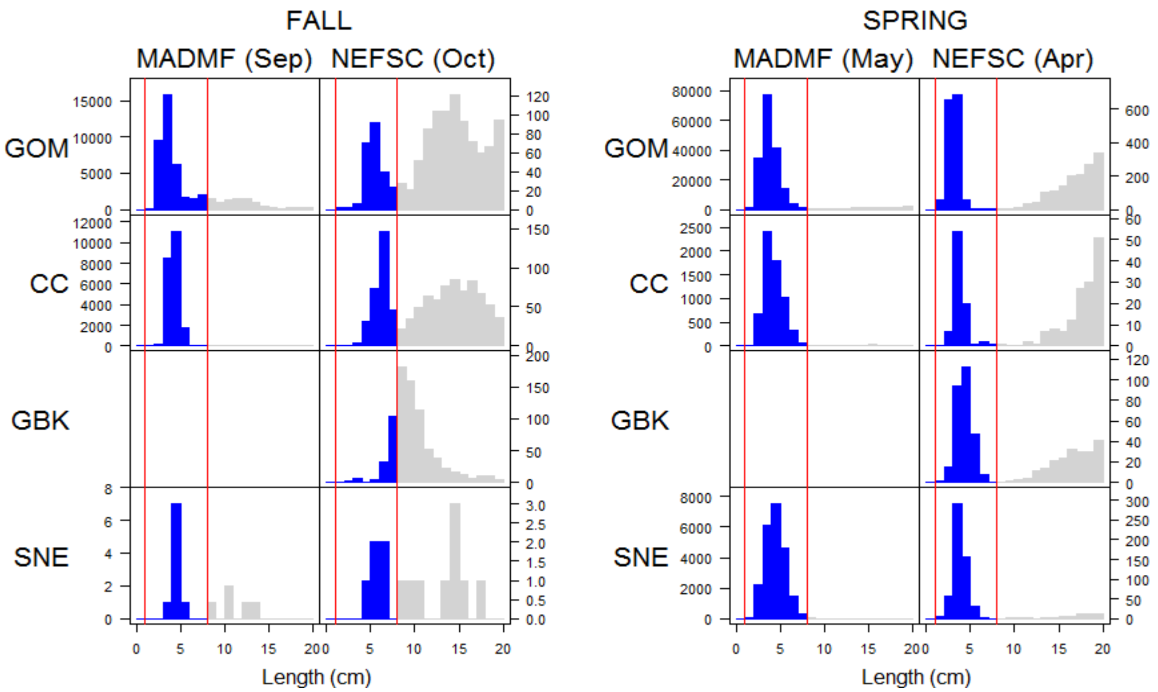


Figure 3.3. Frequency of juvenile Atlantic cod (*Gadus morhua*) measuring less than 20 cm. The cod were captured in Northeast Fisheries Science Center (NEFSC) and Massachusetts Division of Marine Fisheries (MADMF) bottom trawl surveys and assigned to the 4 strata defined in Figure 3.1 (MADMF survey does not sample Georges Bank [GBK]). The blue portion represents fish with total length less than 8 cm (red vertical line), which are considered recently settled juveniles.

Potential connectivity links were partly identified from a review of larval transport simulation studies. In addition, the spatial distributions of spawning, larvae, and juvenile settlement were consulted for further evidence of logical connectivity pathways. In some cases, a lack of connectivity was apparent because of a consistent, near-zero probability of larval occurrence separating a larval source and a juvenile settlement area. In other cases, multiple plumes of larval production extended over a single juvenile settlement area. To assist in determining the most plausible connectivity pathways, the size frequency information from both larval and juvenile surveys were examined for coherent developmental trajectories. Time series correlations were also consulted for further evidence that settlement in different strata could have originated from a common source.

Review of Cod Early Life History in US Waters

Spawning

Atlantic cod have a high potential fecundity, with individual females capable of producing several million eggs per year (Thorsen and Kjesbu 2001). Eggs are released in multiple batches over an extended period that may span 1-2 months (Kjesbu 1989). Spawning occurs within dense aggregations (Nordeide and Kjellsby 1999; Robichaud and Rose 2001), yet mating takes place in pairs, following a complex sequence of behaviors (Rowe et al. 2008; Brawn 1961). Spawning is typically associated with specific seafloor features (Siceloff and Howell 2013; Dean et al. 2014), yet it often involves some amount of vertical movements prior to egg release (Grabowski et al. 2012). Throughout their range, cod exhibit strong fidelity to spawning sites and seasons. This tendency has been demonstrated via multiyear observations of tagged individuals (Robichaud and

Rose 2001; Skjæraasen et al. 2011; Dean et al. 2014; Zemeckis et al. 2014a), as well as through persistent patterns in where and when spawning fish are caught (Morgan and Trippel 1996; Armstrong et al. 2004). However, there is ample variation across stocks with respect to the depth or time of year when spawning occurs (ICES 2005).

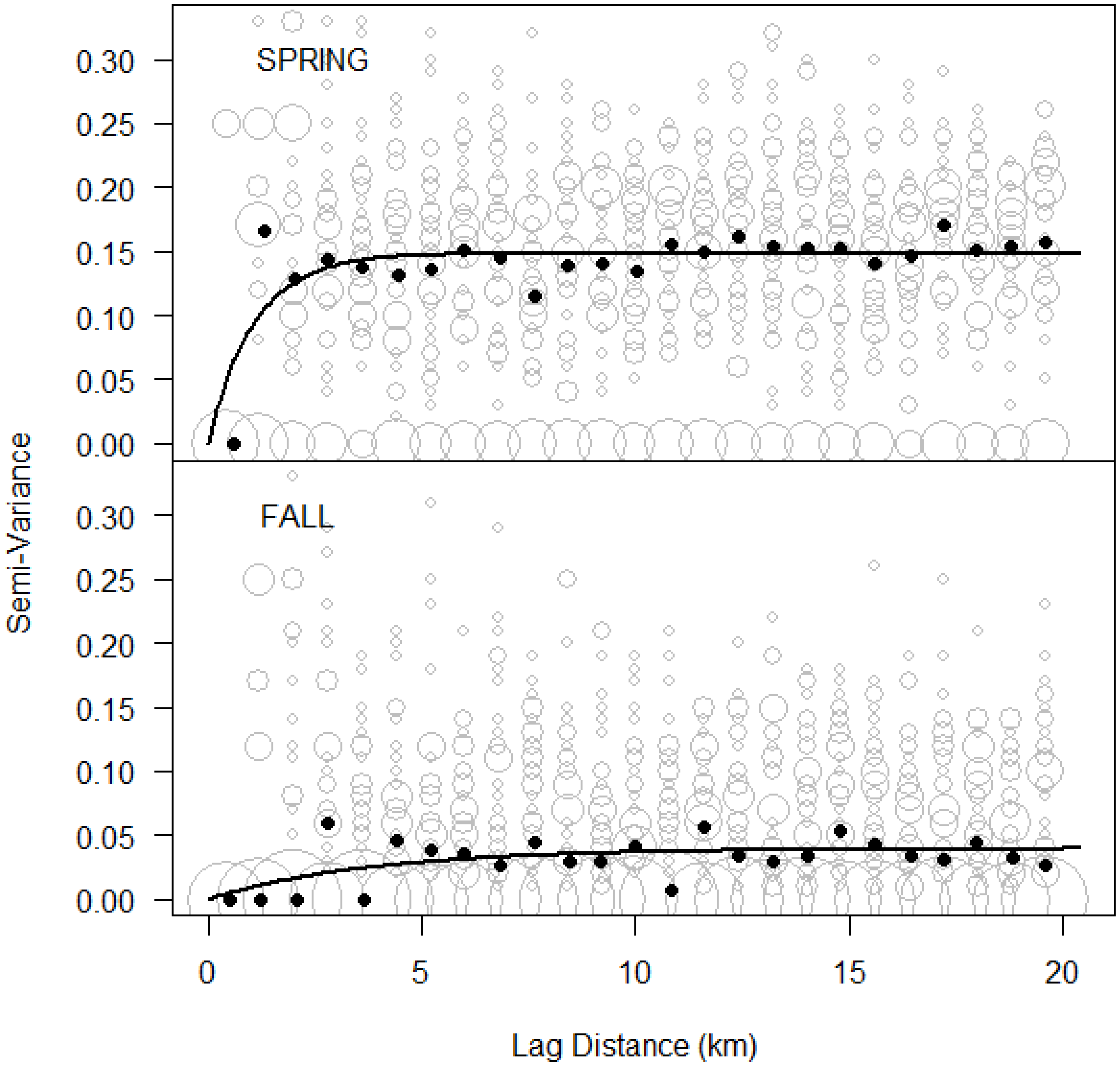


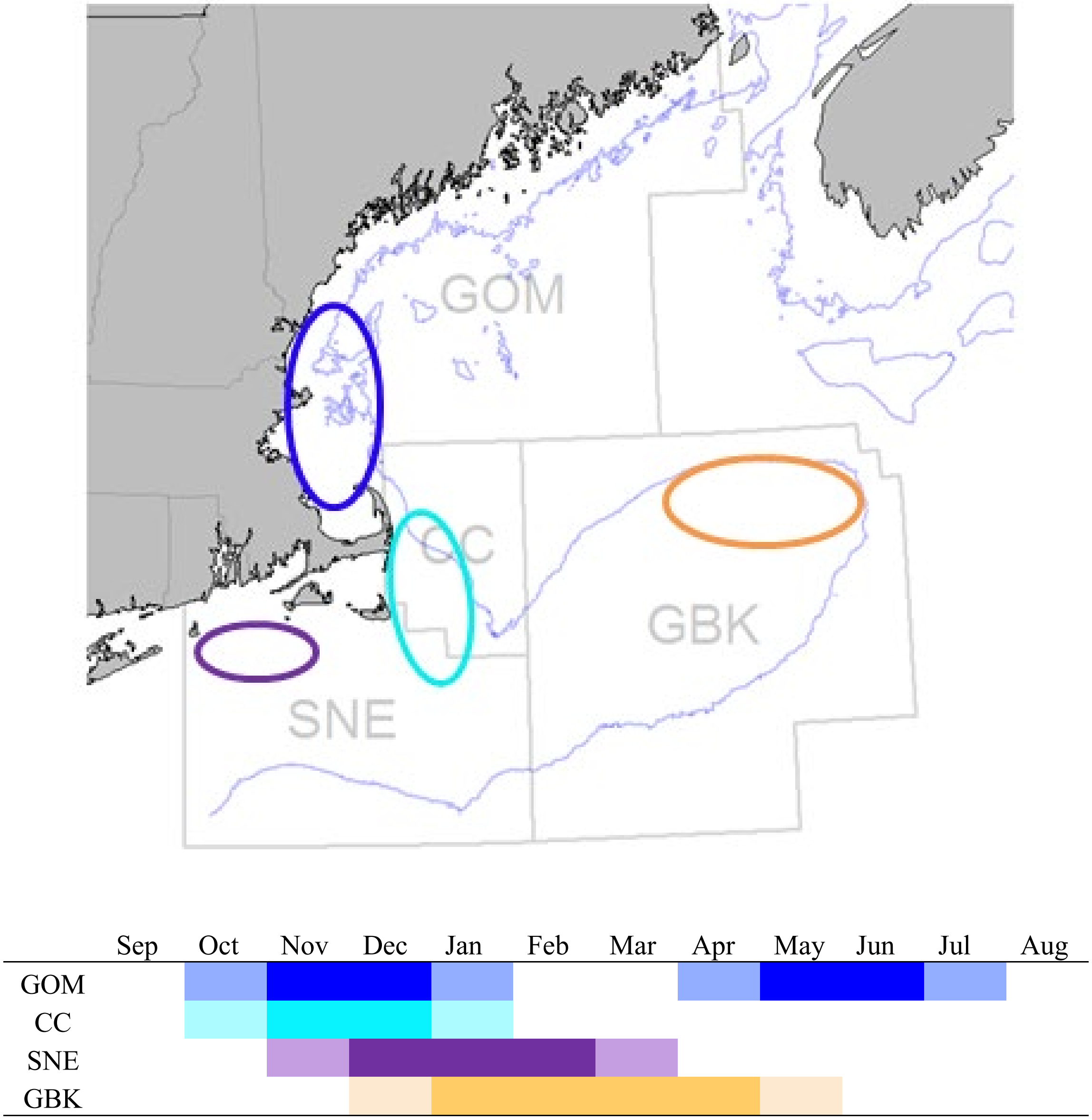
Figure 3.4. Variograms of Atlantic cod (*Gadus morhua*) settlement occurrence used for geostatistical interpolation (i.e., kriging), by season. Hollow bubbles represent the distribution of annual empirical variogram values, where bubble size is proportional to the frequency at that level. Solid points represent the median semivariance value for each 800 m lag bin. Solid lines represent an exponential variogram model fit to the median values. Locations of juvenile settlement were identified by trawl survey tows where cod <8 cm were caught from either the Northeast Fisheries Science Center (NEFSC) or the Massachusetts Division of Marine Fisheries (MADMF) bottom trawl surveys.

Several recent reviews offer a comprehensive description of the spatial/seasonal distribution of cod spawning in both the Gulf of Maine (Zemeckis et al. 2014b; Chapter 8, this volume; Ames 2004) and on Georges Bank (DeCelles et al. 2017). While substantial fine-scale variation exists within the defined strata, particularly when historical time periods are included, a clear overall seasonal pattern exists for each primary spawning ground. Within the Gulf of Maine, there are 2 distinct seasonal modes in spawning, each corresponding to a unique subpopulation: "winter" spawning peaks in November-December, while "spring" spawning peaks in May-June. Both subpopulations spawn near the 50 m isobath in the western Gulf of Maine, primarily along the Massachusetts and New Hampshire coasts (Fig. 3.5). On Georges Bank, several persistent spawning locations have been identified, yet the most productive area appears to be near the "northeast peak" of the Georges Bank, straddling the US-Canada border. Spawning on Georges Bank appears to be more protracted than for either subpopulation in the Gulf of Maine, and mainly occurs between 20 and 90 m and peaks in January-April. The cod spawning grounds west of the Great South Channel and on Nantucket Shoals (CC stratum) occur at somewhat shallower depths (20-55 m), and peak in activity occurs November-December, several months earlier than on Georges Bank.

There are far less data available to describe the cod spawning activity southwest of Cape Cod, and what little exists has yet to be summarized or reviewed. However, a persistent winter aggregation occurs on Cox Ledge (approximately halfway between Block Island and Martha's Vineyard) that supports a burgeoning recreational fishery. Between 2007 and 2011, the UMass Dartmouth's School for Marine Science and Technology (SMAST) collected maturity observations from nearly 2000 cod as part of a mark-recapture experiment in this area, representing the best contemporary scientific record of cod spawning in the SNE stratum. Most of the ripe cod observed under this effort were captured December-February (Fig. 3.6).

Eggs

The incubation time of cod eggs is directly related to temperature (Pepin et al. 1997; Geffen et al. 2006). Consequently, the time between spawning release and hatch will vary seasonally, but likely ranges between 1-3 weeks in US waters (Thompson and Riley 1981). While the specific gravity of cod eggs does vary among populations in the Northeast Atlantic Ocean (Nissling et al. 1994), it appears to be relatively homogeneous within US waters (Clapp et al. 2013; ICES 2005). However, because of the seasonal, geographic, and vertical variation in temperature and salinity, the density of water in which eggs are released can be quite different (Huret et al. 2007; Churchill et al. 2011). Cod eggs are buoyant under most conditions and are therefore subject to epipelagic drift prior to hatching. If spawning occurs at a time of year when the water column is stratified, the eggs may become entrained near the pycnocline. During times of year without stratification, the eggs remain near the surface layer and are therefore subject to additional wind forcing and Ekman transport, further amplifying their dispersal (Lough et al. 1994).



	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
GOM		░	▓	▓	░			░	▓	▓	░	
CC		░	▓	▓	░							
SNE			░	▓	▓	▓	░					
GBK				░	▓	▓	▓	▓	░			

Figure 3.5. Primary Atlantic cod (*Gadus morhua*) spawning areas (top) and seasons (bottom) in US waters. It is important to note that substantial fine-scale heterogeneity is ignored here and that this figure represents only the general pattern of contemporary cod spawning. Darker colors indicate months where spawning cod are most frequently encountered.

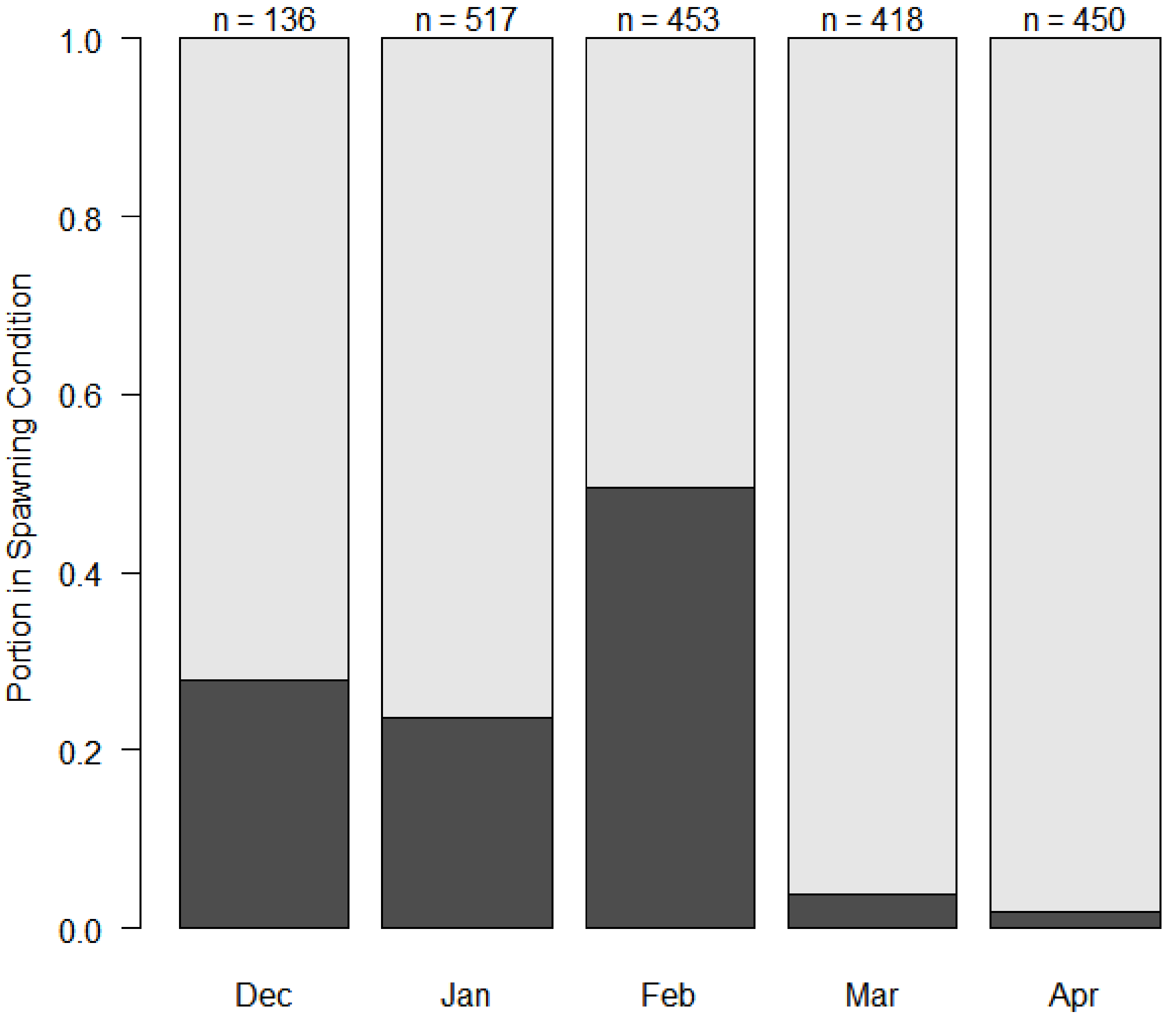


Figure 3.6. Proportion of Atlantic cod (*Gadus morhua*) in spawning condition by month captured under the UMass Dartmouth School for Marine Science and Technology (SMAST) tagging project off southern New England, 2007-2011. Dark bars represent the proportion of all cod captured (sample sizes listed above each bar) with either hydrated eggs or flowing sperm. Lighter regions above the dark bars represent the proportion not spawning, and includes both immature fish and adults with developing gonads.

Larvae

Upon hatching, cod larvae are approximately 4.5 mm in standard length (Bolz and Lough 1988; Pepin et al. 1997; Folkvord 2005), although size at hatch is positively correlated with temperature (Purchase and Brown 2000). Once exogenous feeding begins (~5.5 mm), their vertical distribution is most associated with prey availability (Grønkjaer and Wieland 1997), with their primary prey being calanoid copepods (Friedland et al. 2013). In a stratified water column, these smallest larvae (<9 mm) are most abundant near the thermocline, yet can easily be dispersed throughout by wind mixing (Lough and Potter 1993). Although individual larvae are swimming capable at first feeding (Gronkjaer and Wieland 1997), evidence of diel vertical migration (DVM) is not present until ~9 mm (Lough and Potter 1993). During the day, larvae are broadly distributed in the water column (Lough and Potter 1993; Grønkjaer and Wieland 1997); at night, their vertical distribution shifts upward. The mean depth of larvae moves closer to the seafloor as they develop

(Lough and Potter 1993), and once their vertical movements begin to intersect the seafloor, they transition from pelagic planktivory to a benthic diet. This switch to benthic life is referred to as "settlement" and typically occurs at 3-5 cm (Tupper and Boutilier 1995; Bastrikin et al. 2014). The duration of each larval phase is a function of the growth rate, which is dependent upon ambient water temperature (Otterlei et al. 1999; Folkvord 2005). Given the seasonal variation in temperature in the region, the time between spawning and settlement can vary substantially between spawning groups. For GOM spring spawners, approximately 90 days separate peak spawning (~June 1st) and when 3-5 cm juveniles are first observed (~September 1st). In contrast, the time between peak spawning (~December 1st) and first observed settlement (~May 1st) is approximately 150 days for GOM winter spawners.

The geostatistical summary of more than 4 decades (1977-2017) of ichthyoplankton survey data show several discrete areas of larval production that are consistent with the general description of spawning grounds provided here (Fig. 3.7). Cod larvae can be found at the western end of the GOM stratum in 2 separate waves: December-March and May-August. At their peak, both waves of larvae originating from the GOM extend into the CC stratum. Larvae in the SNE are present from December through May and occur most frequently toward the northern end of the stratum and near Nantucket Shoals. The single largest plume of larval production occurs on Georges Bank from January through May, with April having the highest abundance and broadest distribution. At its peak, the cloud of larvae originating from GBK extends into the southeastern corner of the CC stratum and the eastern end of the SNE stratum. Morse (1994) conducted an in-depth review of the regional distribution of cod larvae from MARMAP survey data (1977-1987) and found similar patterns to the summary provided here of the broader dataset, which includes these MARMAP data.

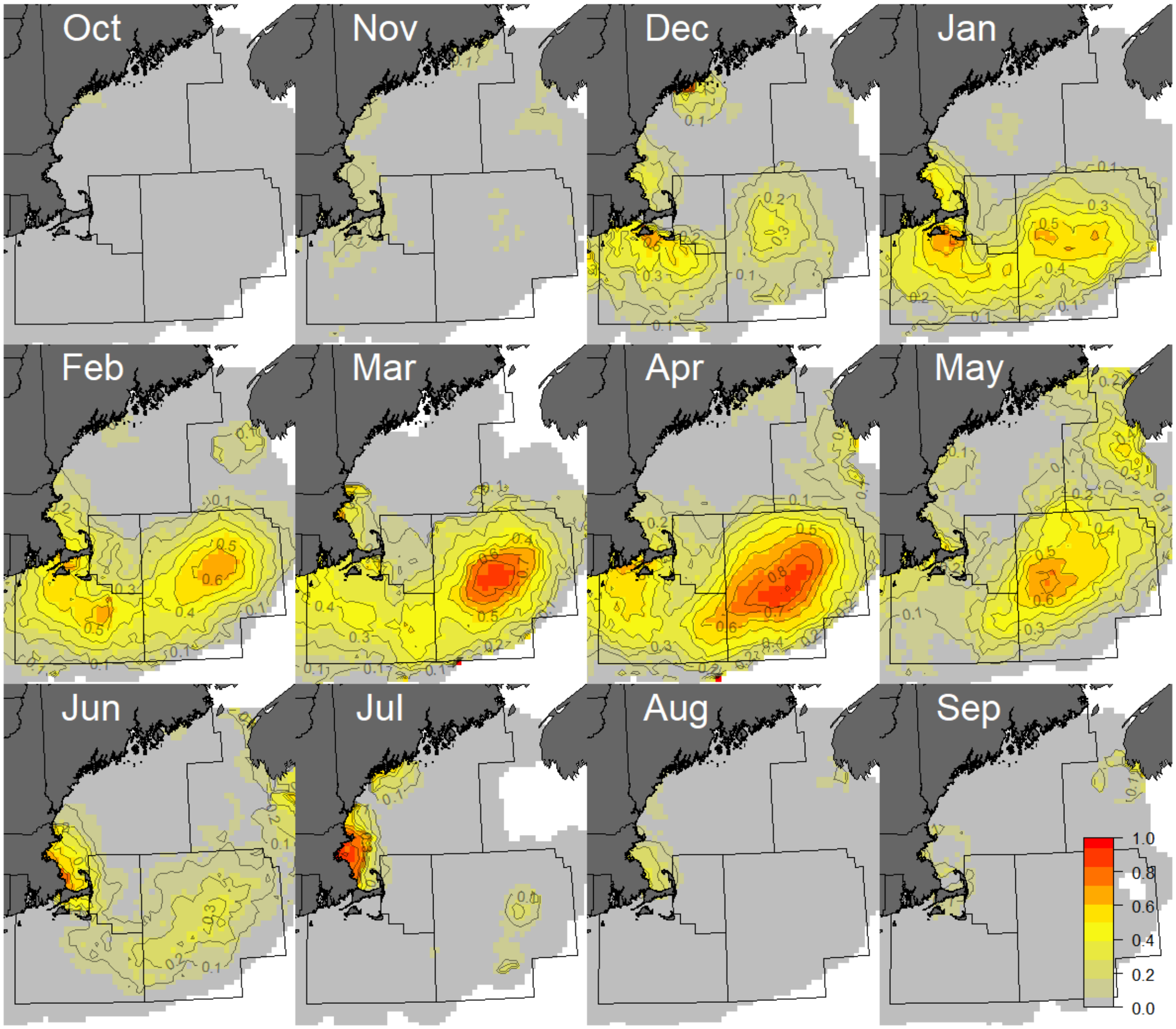


Figure 3.7. Mean probability of occurrence of Atlantic cod (*Gadus morhua*) larvae from ichthyoplankton survey data, 1977– 2017, as predicted by geostatistical interpolation (i.e., kriging). Dark red colors indicate the highest probability of occurrence, while gray regions represent the lowest probability of occurrence. White regions represent areas where no survey data were available.

Juvenile Settlement

Despite the broad dispersal of larvae, juvenile settlement occurs within a relatively narrow range of habitats. Recently settled juvenile cod are most abundant at depths <30 m and where bottom temperatures are <9°C (Grabowski et al. 2018). Both laboratory experiments and survey observations reveal a preference for more complex substrates (e.g., eelgrass, kelp, rock, gravel), particularly when predators are abundant (Gotceitas and Brown 1993; Linehan et al. 2001). Juvenile cod do not appear to make large horizontal movements at the beginning of their benthic life (Tupper and Boutlier 1995; Olsen et al. 2004), suggesting high mortality for those individuals that do not settle over suitable habitat. As juveniles develop beyond their first year of life, they are typically found in areas adjacent to and slightly deeper than age-0 settlement habitat (Howe et al. 2002; Grabowski et al. 2018).

During the spring bottom trawl surveys (April-May), there appears to be a continuous area of juvenile settlement along the coast from New Hampshire to Rhode Island, at depths shallower than 100 m (GOM, CC, and SNE strata – Fig. 3.8). A separate concurrent settlement zone occurs in spring over the central and western portion of Georges Bank, east of the Great South Channel (GBK stratum). These 3-5 cm fish found in both settlement areas are the product of spawning that occurs over the preceding fall-winter months (October-March). During the fall surveys (September-October), recently settled juveniles are found in similar habitat in the GOM and CC strata, but they are largely absent from coastal SNE and central GBK, where bottom temperatures typically exceed 16°C, an apparent upper threshold for thermal tolerance (Fig. 3.9). Some small juveniles are captured at the northeast peak of Georges Bank in fall, but these belong to the lower tail of a distribution of larger juveniles that likely represent the survivors of a single wave of GBK settlement, first observed in the spring survey (Fig. 3.3).

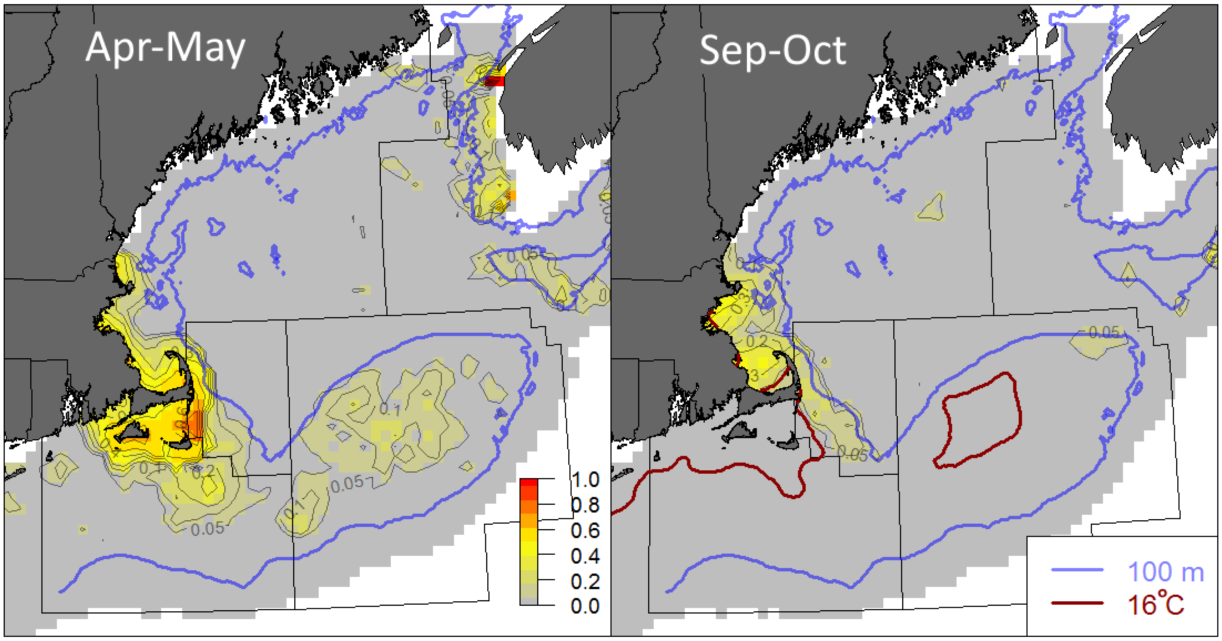


Figure 3.8. Predicted probability of occurrence of juvenile Atlantic cod (*Gadus morhua*) <8 cm from Northeast Fisheries Science Center (NEFSC) and Massachusetts Division of Marine Fisheries (MADMF) bottom trawl surveys, 1963-2017. The blue line represents the 100 meter isobath. The red line represents the 16°C isotherm, as predicted by the Northeast Coastal Ocean Forecast System (NECOFS) oceanographic model in recent years (2015-2018).

Conclusions on Regional Connectivity

In general, prevailing ocean currents within the region cause planktonic particles released in the GOM to move counter-clockwise along the coast (i.e., northward along the Nova Scotian coast, southward along the US coast) (Townsend et al. 2015). A clockwise gyre on Georges Bank serves to retain pelagic particles within the GBK stratum, yet a variable portion is exported off-bank each year (Werner et al. 1993). Both of these currents meet at the Great South Channel (CC stratum) and move southwest into SNE (Fig. 3.10). Given this general circulation pattern, it is improbable that connectivity occurs in the "upstream" direction during early pelagic life. Therefore, the following pathways were categorized as unlikely: SNE/GOM, SNE/GBK, SNE/CC, CC/GOM, GBK/GOM.

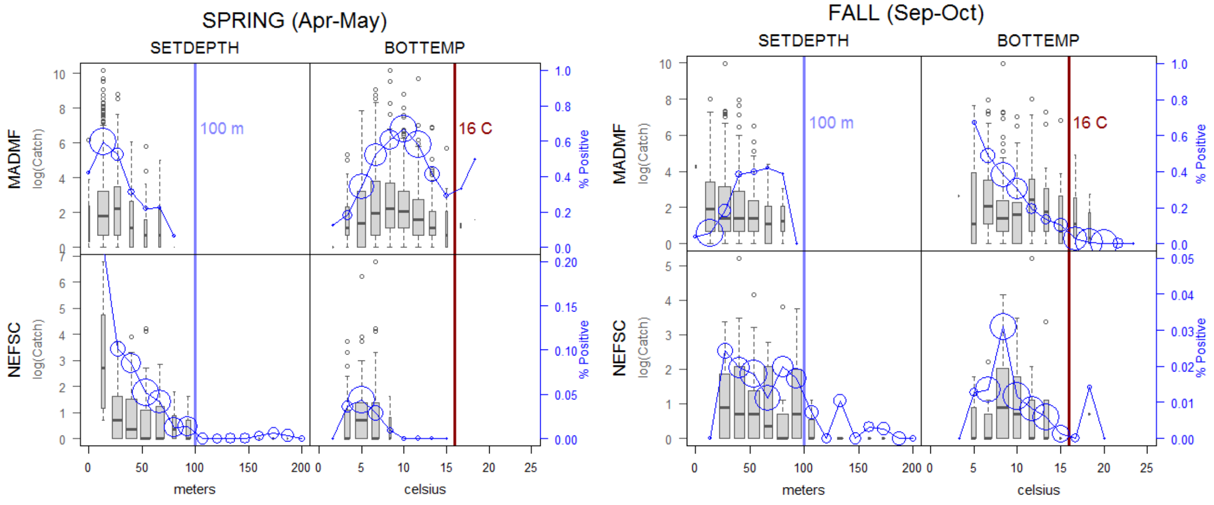


Figure 3.9. The relative abundance (gray box plots) and percent occurrence (blue lines) of recently settled juvenile Atlantic cod (*Gadus morhua*) <8 cm from the Massachusetts Division of Marine Fisheries (MADMF) and Northeast Fisheries Science Centers (NEFSC) bottom trawl surveys, as a function of depth and bottom temperature. The width of the boxes and size of bubbles are proportional to the number of observations at that level. The dark blue vertical line represents a depth of 100 m, below which there are few juvenile cod. Similarly, the dark red vertical line represents a bottom temperature of 16°C, which also appears to be a limit for where juvenile cod are observed.

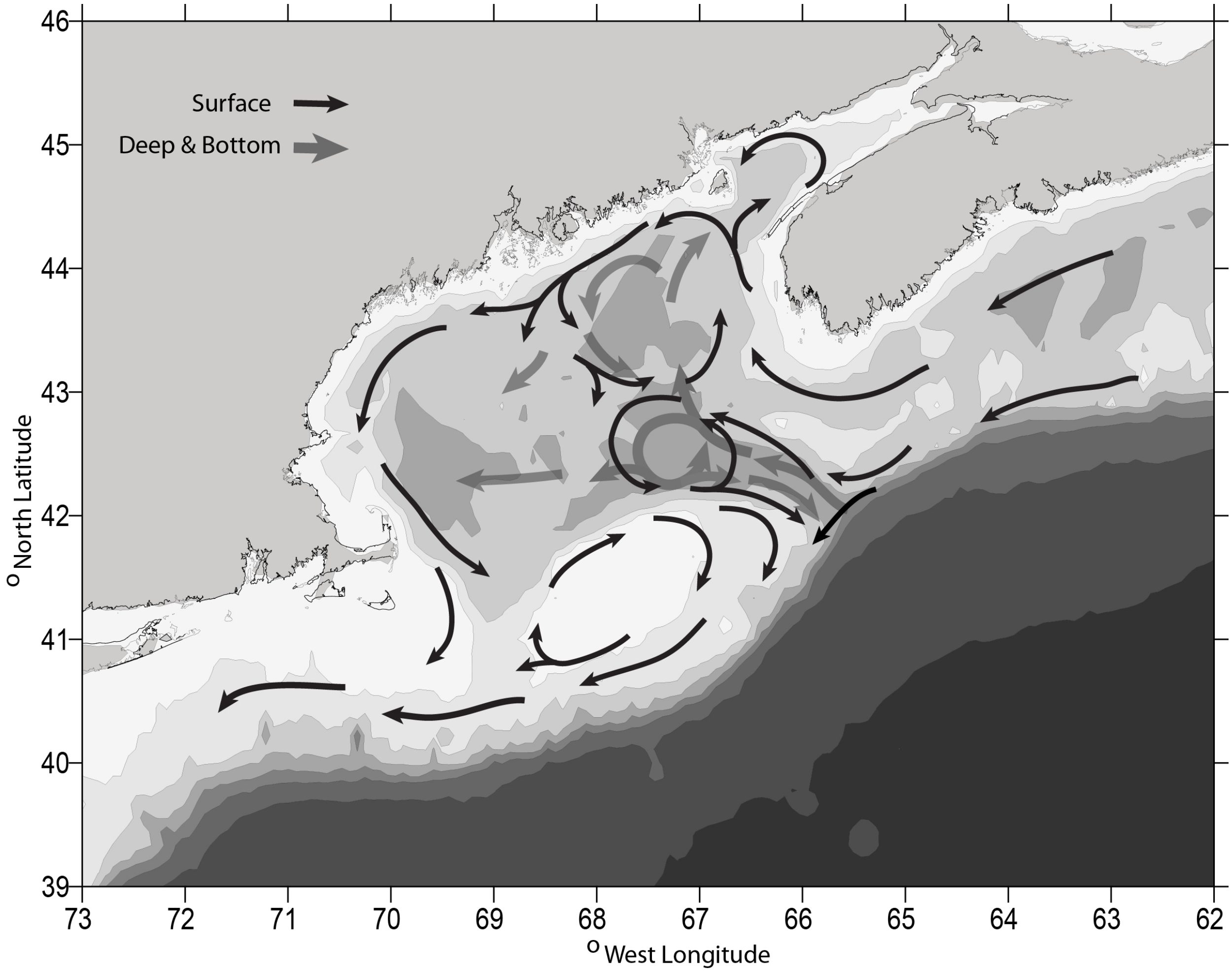


Figure 3.10. General circulation patterns in the Gulf of Maine and Georges Bank regions (reproduced with permission from Townsend et al. 2015).

GOM/GOM (major self-connectivity)

Given the regional circulation pattern, it is reasonable to assume that the recently settled juvenile cod captured north of Cape Cod originate solely from spawning events within the GOM stratum. Larval transport simulations for both spring (Churchill et al. 2011) and winter (Huret et al. 2007) spawning events suggest there is high potential for local retention, particularly within Massachusetts Bay and Cape Cod Bay. This local retention appears to be strongest in spring, when spawning occurs closer to shore and wind-driven, down-welling conditions prevail. Furthermore, patterns in the spatio-temporal distribution (Figs. 3.7 and 3.8), seasonal abundance (Fig. 3.11), and size frequency (Fig. 3.12) for both larvae and juveniles corroborate 2 separate waves of reproduction, resulting in local settlement.

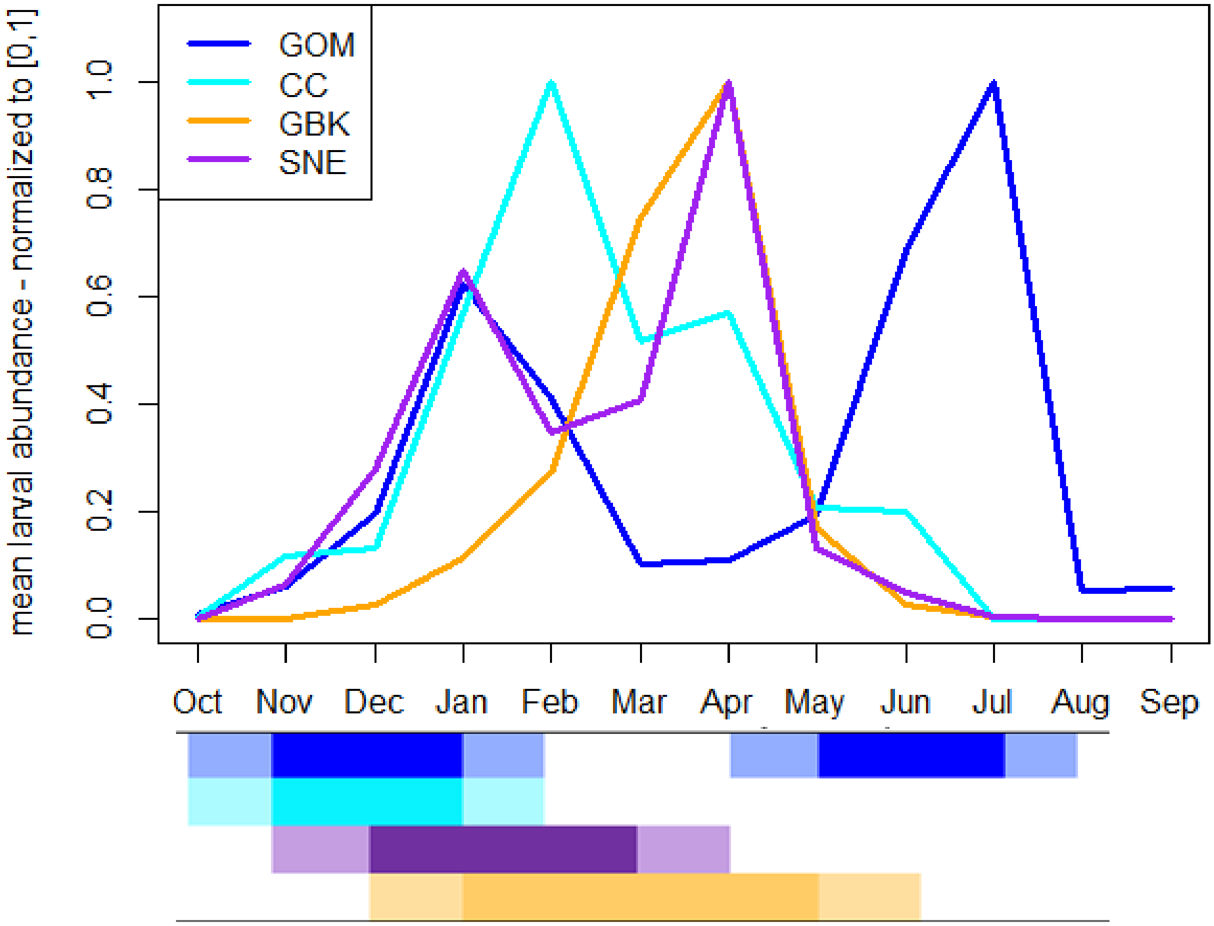


Figure 3.11. Seasonal abundance of Atlantic cod (*Gadus morhua*) larvae by strata from ichthyoplankton surveys (above), as compared to seasonal distribution of spawning (below; see Fig. 3.6 for details). Strata are formally defined in Fig. 3.1 and abbreviated here as: the Gulf of Maine (GOM), Georges Bank (GBK), Cape Cod (CC), southern New England (SNE).

GBK/GBK (major self-connectivity)

Several larval transport studies describe the process of local retention of juvenile cod within the GBK stratum, particularly resulting from spawning near the "northeast peak" of Georges Bank. Eggs and larvae become entrained in the clockwise gyre and eventually settle out across the shallow central portions of the bank. Werner et al. (1996) estimated that approximately 80% of larval production is retained within the GBK stratum, with the deeper and more northerly distributed larvae having a higher retention probability (Werner et al. 1993). Larval data suggest a single wave of protracted spawning from December-June, resulting in settlement that is first observed in the NEFSC spring bottom trawl survey (April-May). The age-0 cod captured on Georges Bank in the NEFSC fall bottom trawl survey (September-October) are significantly larger than those captured in the spring and likely represent survivors from this earlier wave. These larger juveniles are found primarily on the gravel-pebble habitat of the "northeast peak," which is consistent with the expected ontogenetic habitat shift from Grabowski et al. (2018).

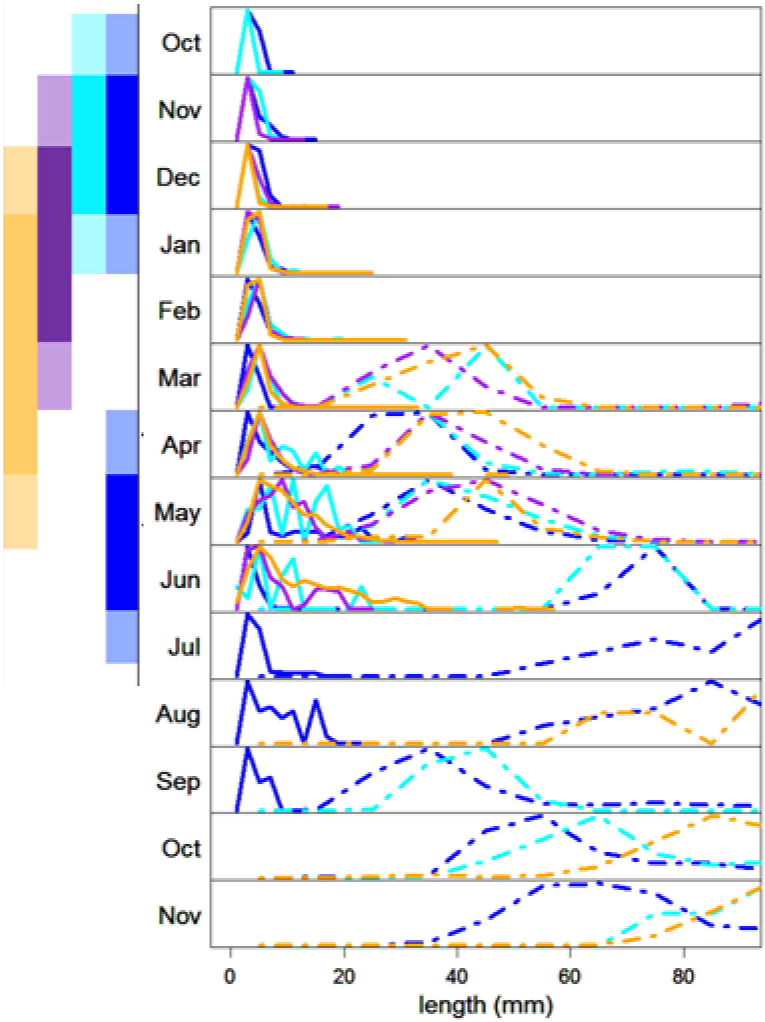


Figure 3.12. Size frequency distributions of Atlantic cod (*Gadus morhua*) larvae (solid lines) from ichthyoplankton surveys (1977 – 2017) and age-0 juveniles (dashed lines) from bottom trawl surveys (1963-2017), by strata. Each size frequency distribution was normalized to [0, 1] to account for seasonal and spatial differences in relative abundance, and colorized to associate with their source spawning season and region. The spawning season for each stratum, from Fig. 3.6, are shown at left for reference; see Fig. 3.5 for spawning locations of each season.

CC/CC (unlikely self-connectivity)

Given the relatively small size of this stratum, prevailing southward flow, and a 2-4 month pelagic phase, it is likely that very few if any larvae produced by CC spawning would result in local settlement. Nearly all of the known spawning grounds in the CC stratum are west of the Great South Channel and are located in the southern half of the area, all of which are more than 80 km farther downstream from the GOM spawning grounds (Chapter 8, this volume). Larval transport models suggest that a substantial fraction of larvae produced farther north (GOM stratum) pass through the entire CC stratum in under 2 months (Huret et al. 2007; Churchill et al. 2011), supporting our conclusion that larvae produced by CC spawning would not reach settlement size before being advected out of the CC stratum.

SNE/SNE (major self-connectivity)

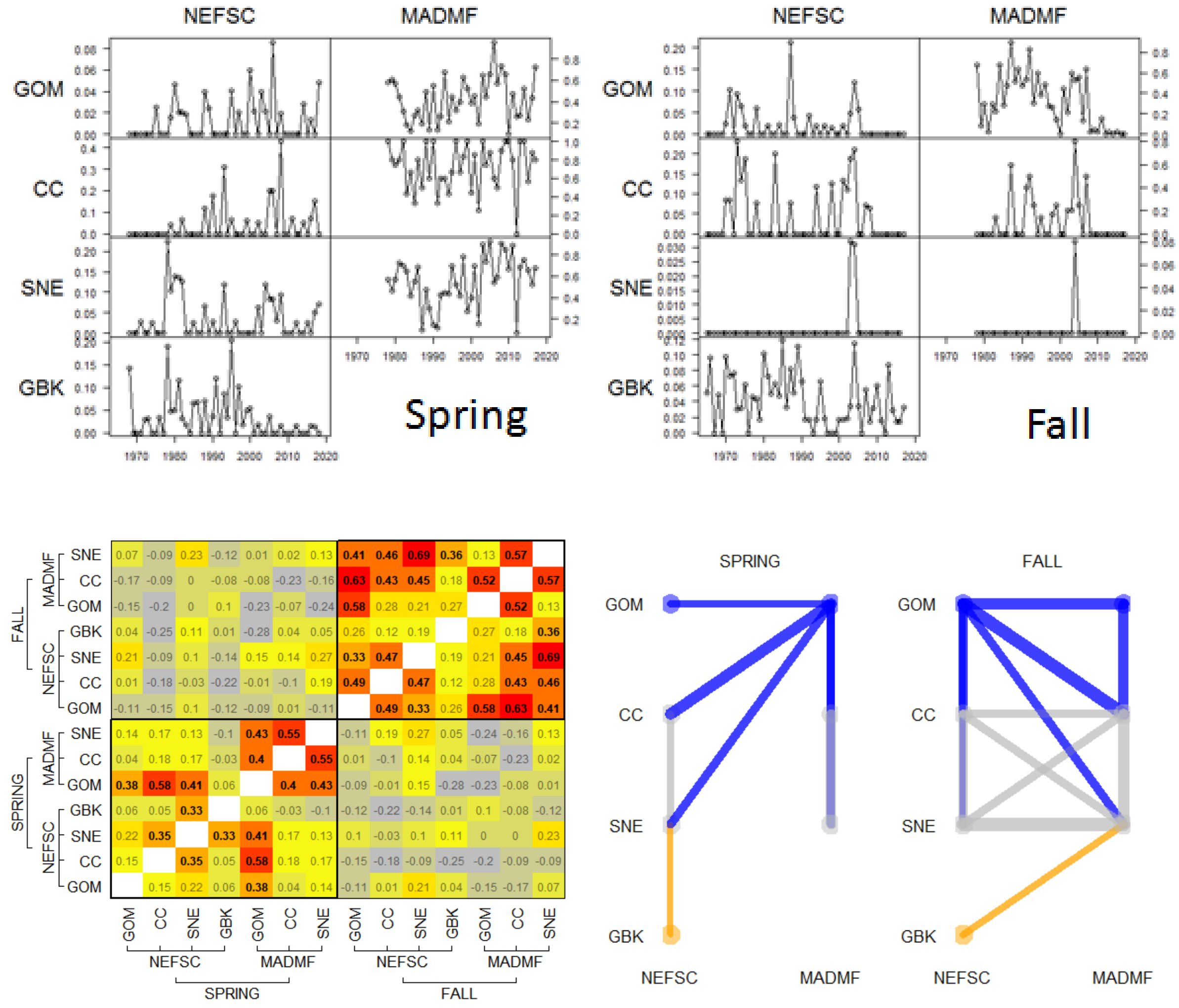
It is assumed that spawning in the SNE stratum does not result in GOM, GBK, nor CC settlement, as there are no plausible "downstream" connectivity pathways originating from this area. Instead, it is likely that SNE spawning results predominantly in local settlement within the SNE stratum. Periodic episodes have occurred where larvae and juvenile settlement were observed farther to the southwest, particularly along the southeastern shore of Long Island, NY (Morse 1994; Serchuk and Wood 1979). Although this area falls outside the established management domain for US cod stocks, these settlement events are rare and most likely result from spawning in SNE.

GOM/GBK (unlikely connectivity)

Larval transport simulations have shown that it may be possible for a small fraction of the larvae produced by winter or spring spawning cod in the GOM to be transported into the GBK stratum (Huret et al. 2007; Churchill et al. 2011). However, it seems far more likely that the juveniles captured on Georges Bank originate from spawning within the GBK stratum. In the fall, the size of age-0 juveniles captured on GBK is significantly larger than those captured in the GOM, suggesting they do not originate from the same source (Fig. 3.12). While in the spring, the size of age-0 juveniles captured on Georges Bank in the spring is similar to those in the Gulf of Maine. Ichthyoplankton data suggest there is a consistent near-zero probability of larval occurrence in the area between the GOM and GBK strata for all months (Fig. 3.7). There is also a discontinuity in settlement areas at the Great South Channel (Fig. 3.8). At the same time, there is a plume of larvae originating from Georges Bank from January through May that completely encompasses the settlement area on top of the bank. The age-0 benthic juveniles observed on GBK in April most likely result from the early portion of the protracted Georges Bank spawning season. Several GBK-focused larval transport studies further support the hypothesis of GBK self-recruitment (Werner et al. 1993, 1996; Lough et al. 2005), as does the lack of time series correlations between the GOM and GBK bottom trawl surveys (Figs. 3.13 and 3.14).

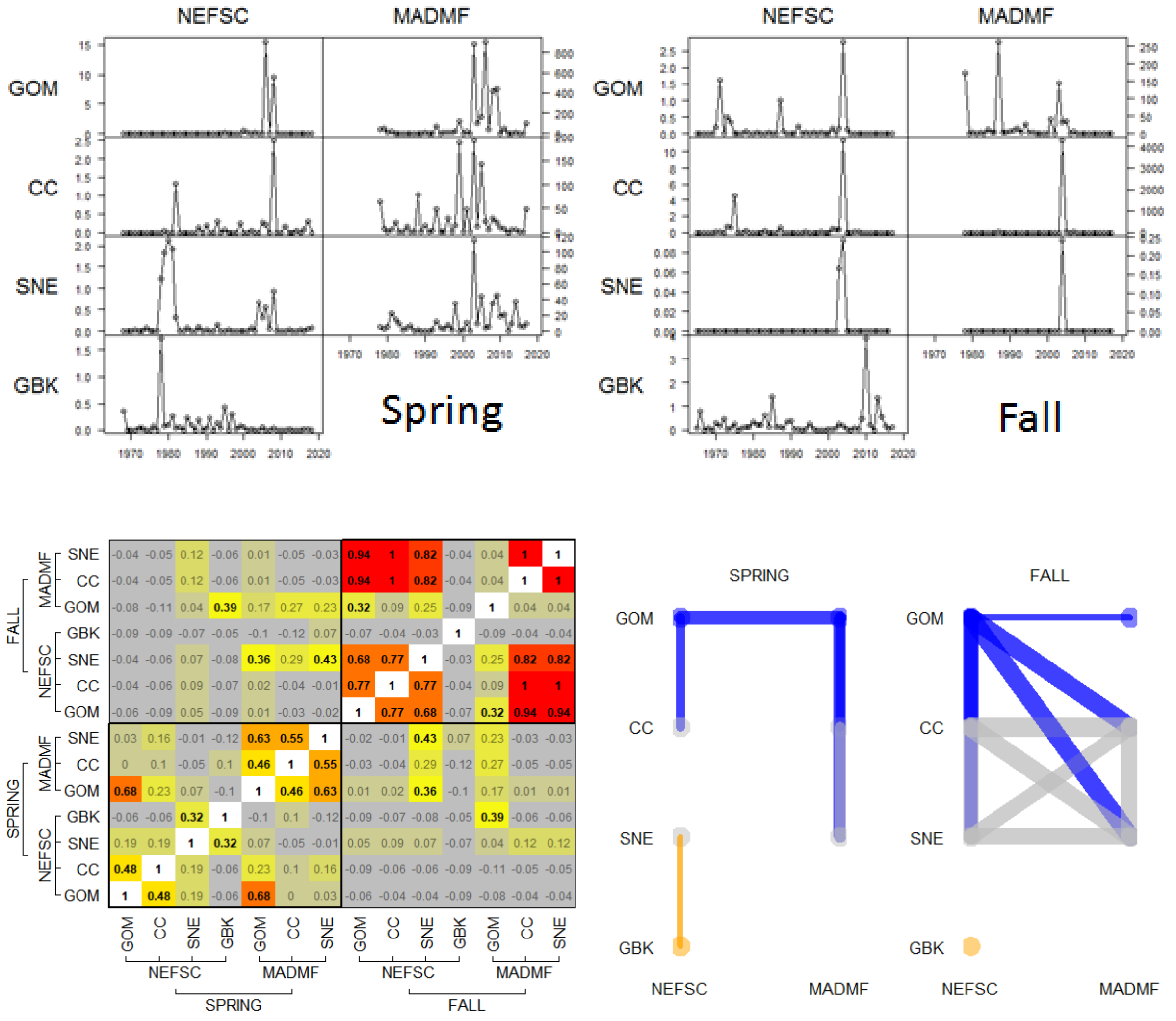
GOM/CC (major connectivity)

Within the CC stratum, cod larvae are present from November through June, several months beyond the local spawning period (October-January), suggesting that this area receives larval input from elsewhere. Larval transport studies indicate a high potential for connectivity between both spring and winter spawners in the GOM and CC (Huret et al. 2007; Churchill et al. 2011). In particular, some winter GOM spawning grounds may export more larvae to CC and beyond than are retained locally within the GOM. The characteristics of juvenile settlement in the CC stratum offer further evidence of a strong GOM-CC connectivity: recently settled CC juveniles are only found west of the Great South Channel, and their size distribution actually decreases between June and September, suggesting 2 waves of settlement, as in the GOM. Given the assumption of no CC self-connectivity discussed earlier, it is likely that nearly all observed settlement in this stratum originates from the GOM. Further supporting this hypothesis are several significant time series correlations between GOM and CC (Figs. 3.13 and 3.14).



			SPRING							FALL						
			NEFSC				MADMF			NEFSC				MADMF		
			GOM	CC	SNE	GBK	GOM	CC	SNE	GOM	CC	SNE	GBK	GOM	CC	SNE
FALL	MADMF	SNE	0.07	-0.09	0.23	-0.12	0.01	0.02	0.13	**0.41**	**0.46**	**0.69**	**0.36**	0.13	**0.57**	
		CC	-0.17	-0.09	0	-0.08	-0.08	-0.23	-0.16	**0.63**	**0.43**	**0.45**	0.18	**0.52**		**0.57**
		GOM	-0.15	-0.2	0	0.1	-0.23	-0.07	-0.24	**0.58**	0.28	0.21	0.27		**0.52**	0.13
	NEFSC	GBK	0.04	-0.25	0.11	0.01	-0.28	0.04	0.05	0.26	0.12	0.19		0.27	0.18	**0.36**
		SNE	0.21	-0.09	0.1	-0.14	0.15	0.14	0.27	**0.33**	**0.47**		0.19	0.21	**0.45**	**0.69**
		CC	0.01	-0.18	-0.03	-0.22	-0.01	-0.1	0.19	**0.49**		**0.47**	0.12	0.28	**0.43**	**0.46**
		GOM	-0.11	-0.15	0.1	-0.12	-0.09	0.01	-0.11		**0.49**	**0.33**	0.26	**0.58**	**0.63**	**0.41**
SPRING	MADMF	SNE	0.14	0.17	0.13	-0.1	**0.43**	**0.55**		-0.11	0.19	0.27	0.05	-0.24	-0.16	0.13
		CC	0.04	0.18	0.17	-0.03	**0.4**		**0.55**	0.01	-0.1	0.14	0.04	-0.07	-0.23	0.02
		GOM	**0.38**	**0.58**	**0.41**	0.06		**0.4**	**0.43**	-0.09	-0.01	0.15	-0.28	-0.23	-0.08	0.01
	NEFSC	GBK	0.06	0.05	**0.33**		0.06	-0.03	-0.1	-0.12	-0.22	-0.14	0.01	0.1	-0.08	-0.12
		SNE	0.22	**0.35**		**0.33**	**0.41**	0.17	0.13	0.1	-0.03	0.1	0.11	0	0	0.23
		CC	0.15		**0.35**	0.05	**0.58**	0.18	0.17	-0.15	-0.18	-0.09	-0.25	-0.2	-0.09	-0.09
		GOM		0.15	0.22	0.06	**0.38**	0.04	0.14	-0.11	0.01	0.21	0.04	-0.15	-0.17	0.07

Figure 3.13. [Top row] Indices of stratified mean occurrence of juvenile Atlantic cod (*Gadus morhua*) <8 cm from bottom trawl surveys, by season, survey, and stratum. MADMF = Massachusetts Division of Marine Fisheries Survey; NEFSC = Northeast Fisheries Science Center Survey; GOM = Gulf of Maine stratum; CC = Cape Cod stratum; SNE = Southern New England stratum; GBK = Georges Bank stratum. [Bottom left] Correlation matrix for the indices of occurrence. Warmer colors indicate a higher correlation and bold values indicate a significant correlation (α = 0.05). [Bottom right] Visual representation of the significant correlations between survey time series. The width of each line is proportional to the correlation value between a pair of time series. Correlations with the GOM are shown in blue, whereas those with GBK are shown in orange; all others are shown in gray.



			SPRING							FALL						
			NEFSC				MADMF			NEFSC				MADMF		
			GOM	CC	SNE	GBK	GOM	CC	SNE	GOM	CC	SNE	GBK	GOM	CC	SNE
FALL	MADMF	SNE	-0.04	-0.05	0.12	-0.06	0.01	-0.05	-0.03	**0.94**	**1**	**0.82**	-0.04	0.04	**1**	**1**
		CC	-0.04	-0.05	0.12	-0.06	0.01	-0.05	-0.03	**0.94**	**1**	**0.82**	-0.04	0.04	**1**	**1**
		GOM	-0.08	-0.11	0.04	**0.39**	0.17	0.27	0.23	**0.32**	0.09	0.25	-0.09	**1**	0.04	0.04
	NEFSC	GBK	-0.09	-0.09	-0.07	-0.05	-0.1	-0.12	0.07	-0.07	-0.04	-0.03	**1**	-0.09	-0.04	-0.04
		SNE	-0.04	-0.06	0.07	-0.08	**0.36**	0.29	**0.43**	**0.68**	**0.77**	**1**	-0.03	0.25	**0.82**	**0.82**
		CC	-0.04	-0.06	0.09	-0.07	0.02	-0.04	-0.01	**0.77**	**1**	**0.77**	-0.04	0.09	**1**	**1**
		GOM	-0.06	-0.09	0.05	-0.09	0.01	-0.03	-0.02	**1**	**0.77**	**0.68**	-0.07	**0.32**	**0.94**	**0.94**
SPRING	MADMF	SNE	0.03	0.16	-0.01	-0.12	**0.63**	**0.55**	**1**	-0.02	-0.01	**0.43**	0.07	0.23	-0.03	-0.03
		CC	0	0.1	-0.05	0.1	**0.46**	**1**	**0.55**	-0.03	-0.04	0.29	-0.12	0.27	-0.05	-0.05
		GOM	**0.68**	0.23	0.07	-0.1	**1**	**0.46**	**0.63**	0.01	0.02	**0.36**	-0.1	0.17	0.01	0.01
	NEFSC	GBK	-0.06	-0.06	**0.32**	**1**	-0.1	0.1	-0.12	-0.09	-0.07	-0.08	-0.05	**0.39**	-0.06	-0.06
		SNE	0.19	0.19	**1**	**0.32**	0.07	-0.05	-0.01	0.05	0.09	0.07	-0.07	0.04	0.12	0.12
		CC	**0.48**	**1**	0.19	-0.06	0.23	0.1	0.16	-0.09	-0.06	-0.06	-0.09	-0.11	-0.05	-0.05
		GOM	**1**	**0.48**	0.19	-0.06	**0.68**	0	0.03	-0.06	-0.04	-0.04	-0.09	-0.08	-0.04	-0.04

Figure 3.14. [Top row] Indices of stratified mean abundance of juvenile Atlantic cod (*Gadus morhua*) <8 cm from bottom trawl surveys, by season, survey, and stratum. (MADMF = Massachusetts Division of Marine Fisheries Survey; NEFSC = Northeast Fisheries Science Center Survey; GOM = Gulf of Maine stratum; CC = Cape Cod stratum; SNE = Southern New England stratum; GBK = Georges Bank stratum)[Bottom left] Correlation matrix for the indices of abundance. Warmer colors indicate a higher correlation and bold values indicate a significant correlation (α = 0.05). [Bottom right] Visual representation of the significant correlations between survey time series. The width of each line is proportional to the correlation value between a pair of time series. Correlations with the GOM are shown in blue, whereas those with GBK are shown in orange; all others are shown in gray.

GBK/CC (unlikely connectivity)

While GBK-focused transport simulations suggest high local retention on Georges Bank, a minority of larvae are exported off-bank each year; however, these exported larvae are most likely to occur at the southern fringe of the gyre (Werner et al. 1996), making GBK-CC connectivity less probable (i.e., GBK-SNE connectivity is more likely). Ichthyoplankton surveys show a broad plume of larvae originating from GBK that does extend into the southeastern corner of the CC stratum, particularly in March-May (Fig. 3.7). However, this larval source does not appear to extend over the CC settlement areas west of the Great South Channel (Figs. 2.1, 3.8). A lack of time series correlation between GBK and CC corroborates this hypothesis of unlikely connectivity.

GOM/SNE (minor connectivity)

As with the CC stratum, cod larvae are present in SNE well beyond the local spawning period; this occurrence implies that this area also receives larval input from external sources. Simulation studies suggest that larvae from GOM spring spawning could be transported into the SNE stratum (Churchill et al. 2011). However, it is clear from empirical observations of both larvae and juveniles that a spring-spawning GOM-SNE connectivity pathway is improbable: Larvae are nearly absent from this area June-September (Figs. 3.7 and 3.11), and age-0 juveniles are rarely caught south of Cape Cod during the fall bottom trawl surveys (Fig. 3.8). Significant fall settlement was observed in SNE only in 2004, which appeared to be an exceptionally high recruitment event for GOM spring spawning (time series high abundance for GOM, CC, and SNE).

In contrast, the longer pelagic phase of the GOM winter-spawned larvae and seasonal environmental conditions (increased wind; upwelling; cold, dense, unstratified water column) make broader dispersal more likely for this group. Transport potential to CC/SNE appears to be greater than local retention within the GOM for some winter spawning grounds (Huret et al. 2007). Additionally, there appears to be ample suitable habitat available in SNE (< 100 m and < 16°C) at the time of year when winter-spawned larvae become capable of settlement (Fig. 3.8). The juveniles and larvae observed in SNE in late winter and early spring are of a similar size to those captured in GOM at the same time (Fig. 3.3). Significant GOM-SNE time series correlations exist for both occurrence and abundance of settlement, further corroborating this connectivity pathway. However, there several reasons why GOM-SNE connectivity is probably of a lesser degree than the other "major" pathways: (1) There is no SNE settlement resulting from GOM spring spawning; (2) GOM winter-spawning also results in significant settlement in GOM and CC; and (3) SNE settlement also receives contributions from spawning in CC, GBK, and SNE strata.

CC/SNE (major connectivity)

Given that nearly all CC spawning areas are located west of the Great South Channel, it is unlikely that the larvae resulting from these spawning events were transported anywhere other than the SNE stratum. The Great South Channel is an area of high current velocity with a residual southward flow, and the long pelagic phase between spawning and settlement (2-4 months) suggests that cod eggs released at CC spawning grounds would not remain in the area long enough to contribute to local settlement. It seems equally as improbable that eggs/larvae of CC origin would be advected east (across the Great South Channel) to GBK or north to GOM. Therefore, the most likely settlement area for CC-spawned larvae is within the SNE stratum, making this a major connectivity pathway. Significant CC-SNE time series correlations exist for both occurrence and abundance of settlement. However, it is important to note here that under the assumption that all CC settlement originates from the GOM, these correlations provide further evidence for GOM-SNE connectivity.

GBK/SNE (minor connectivity)

The seasonal profile of larval abundance in both GOM and GBK strata mirror their respective spawning seasons (lagged by ~+1 month), as would be expected for areas of self-recruitment that receive no external inputs (Fig. 3.11). In contrast, there are 2 distinct modes of larval abundance in SNE that occur both before and well after the local spawning season. The earlier mode coincides with winter spawning in the GOM and CC, while the later mode coincides with GBK spawning. The timing of these spawnings suggests that SNE receives larval inputs from multiple areas. The spatial distribution of larvae and juvenile settlement shows that GBK production does extend into the SNE stratum, which is consistent with the expected direction of the minority of larvae that are exported from GBK (Werner et al. 1996). A significant GBK-SNE time series correlation for settlement further corroborates this connectivity pathway. However, similar to the connectivity between GOM and SNE, we consider this a minor pathway, because: (1) SNE settlement also results from spawning in GOM, CC, and SNE itself; and (2) the majority of settlement resulting from GBK spawning likely occurs within the GBK stratum.

Discussion

Both the GOM and GBK strata appear to be areas of self-recruitment that receive few inputs from external sources, which supports maintaining a minimum of 2 stocks for managing Atlantic cod in US waters. However, there are several ways in which the current management/assessment paradigm is incongruent with the early-life connectivity between areas identified here (Fig. 3.15). Multiple lines of evidence suggest that juvenile cod found in the CC stratum most likely originate in the GOM, and seasonally include the offspring of both spring and winter spawners. It also appears likely that a portion of the juvenile settlement found in the SNE stratum originates from winter spawning in the GOM, in addition to CC, GBK, and SNE itself. Therefore, there are 2 connectivity pathways that cross the current management boundary: GOM-CC (major), and GOM-SNE (minor). While moving the CC stratum (statistical area 521) to the Gulf of Maine management unit would keep the major GOM-CC pathway intact, it would introduce a new issue by creating a boundary that intersects the major CC-SNE pathway. As such, it seems more biologically appropriate to combine the GOM, CC, and SNE strata into a single management unit that is distinct from a GBK-only stock (at least from an early life history perspective). This change would leave only a single minor connectivity pathway (GBK-SNE) to cross the management unit boundary.

In the context of observed settlement patterns, there were 9 time series correlations for juvenile occurrence that cross current management boundaries (7 for abundance). Moving only the CC stratum to the Gulf of Maine management unit would yield similar results (9 for occurrence; 8 for abundance). However, combining GOM, CC, and SNE would represent a significant improvement (2 for occurrence; 1 for abundance) by creating 2 management units with more internally homogenous settlement patterns.

Settlement Area

Spawning Group	GOM	CC	SNE	GBK
GOM Spring	C	C	x	x
GOM Winter	C	C	c	x
CC	x	x	C	x
SNE	x	x	C	x
GBK	x	x	c	C

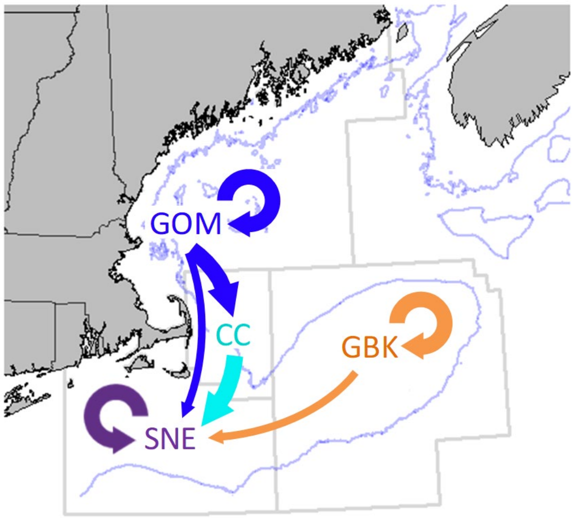


Figure 3.15. [left] Summary of the early life connectivity between spawning groups and settlement areas for Atlantic cod (*Gadus morhua*) in US waters. An uppercase "C" indicates major connectivity; a lowercase "c" indicates minor connectivity; an "X" indicates unlikely connectivity. The Gulf of Maine (GOM) stratum is defined by statistical areas 511-515, and includes 2 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.

The Transboundary Resource Assessment Committee (TRAC) is a separate process that governs the assessment and management of the eastern portion of the Georges Bank stratum that is shared between United States and Canada. This area includes the Northeast Peak of Georges Bank, which has been identified as a primary cod spawning location and is typically used as the release location for GBK-focused larval transport simulations. These simulation studies, as well as the empirical observations from ichthyoplankton surveys, suggest that the larvae produced by cod spawning at the Northeast Peak are broadly transported across Georges Bank, crossing the western stock boundary used for TRAC assessments. Spawning occurs on Georges Bank from January through April; a few settlement-capable juveniles from the early portion of this period are also captured broadly across the bank by the spring NEFSC bottom trawl survey. However, when the fall NEFSC bottom trawl survey covers this same area several months later, a much higher quantity of larger age-0 cod is found on the gravel-pebble habitat of the Northeast Peak (and none outside the TRAC management boundaries). This observation suggests that the eastern portion of Georges Bank used for the TRAC process is both a zone of self-recruitment and also exports some larvae to the western GBK and SNE strata. Modifying the management boundaries for US cod stocks as outlined above (i.e., 2 stocks: GOM-CC-SNE and GBK) would have the auxiliary benefit of improving consistency with the international process that manages the shared transboundary resource on eastern Georges Bank.

Even though this chapter has focused exclusively on the management domain of US cod stocks, it is important to consider the possibility for inputs of larvae from outside the system (i.e., adjacent Canadian waters). Cod spawn in February-March on Browns Bank, approximately 80 km to the northeast of Georges Bank (Campana et al. 1989; ICES 2005). The deep Northeast Channel that separates Browns Bank and Georges Bank is believed to be a barrier to larval transport

(Ruzzante et al. 1998), and the observed spatial distribution of cod eggs, larvae, and juveniles all show a clear discontinuity between the 2 banks (Figs. 3.7 and 3.8; Wigley and Serchuk 1992; Hanke 2000; Lough 2010). Although occasional "crossovers" of water masses from Browns Bank to Georges Bank do occur (Bisagni and Smith 1998; Lage et al. 2004), the products of cod spawning on Browns Bank are primarily advected northward along the southwestern coast of Nova Scotia or retained within a local gyre (Campana et al. 1989; Suthers and Frank 1989; ICES 2005).

A review of ichthyoplankton data collected by the Canadian government in the 1970s-1990s suggests that cod also spawn near the mouth of the Bay of Fundy, along the coast of Nova Scotia (Hanke 2000). Similar to the US side of the Gulf of Maine, there are 2 seasonal modes to the spawning activity of this group of cod: "spring" (February-March) and "fall" (October-November) (ICES 2005). The Canadian ichthyoplankton data suggest that most fall-spawned eggs and larvae remain in Canadian waters and are distinct from those that originate from within the US management domain (i.e., west of Grand Manan Island - Hanke et al. 2000). Recently settled juveniles are encountered on Browns Banks and along the southwest Nova Scotia in April, likely resulting from fall spawning along the Nova Scotia coast (Figs. 2.1, 3.8). In contrast, the distribution of spring-spawned cod eggs and larvae appears to extend from Browns Bank, along southwestern Nova Scotia, and across to eastern Maine (Figs. 2.1, 3.7; Berrien and Sibunka 1999; Morse 1994). Regardless, there is little evidence of juvenile settlement in Eastern Maine resulting from Nova Scotian spring-spawning cod (Fig. 3.8). Collectively, both US and Canadian ichthyoplankton data suggest that there is relatively little influx of cod larvae from the Scotian Shelf-Bay of Fundy region (Northwest Atlantic Fisheries Organization [NAFO] div. 4x) into the US management domain for Atlantic cod.

The spatial and seasonal patterns described in this chapter were stable over the decades examined: larval (1977-2017) and age-0 (1963-2017) cod were consistently found in the same areas at the same times of year. However, the relative abundance of different groups changed over time. For example, the mid-2000s appeared to be a good period for age-0 settlement originating from winter-spawning groups in the GOM-CC-SNE region, but not for GBK. The 1980s and 2000s were periods of higher age-0 settlement for GOM spring spawners. Unfortunately, there has been very little evidence of successful recruitment from GOM spring-spawners since 2010. Of all the cod spawning groups in US waters, the spring spawning cod of the GOM are perhaps the most vulnerable to climate change and warming ocean waters. Very little settlement has occurred where water temperature exceeds 16°C. In most years, much of SNE, GBK, and the southern portion of Cape Cod Bay (GOM) are all warmer than 16°C during the settlement period for spring-spawned cod (September - October). Therefore, suitable thermal habitat is far more constrained for this group than for others and will likely become further constrained in the future.

It is important to consider that the results and conclusions offered here only take into account regional patterns in early life history. Although the period of life between spawning and settlement is integral to population structure, much happens beyond the first year that is critically relevant to the definition of a stock. Our findings should be viewed in the context of the evidence presented in the remaining chapters in order to form a holistic perspective. Nonetheless, there are notable parallels between this early life history perspective on stock structure and previous genetic analyses: Kovach et al. (2010) found genetic similarities between winter spawning cod in the Gulf of Maine and cod west of the Great South Channel, and in southern New England. These results agree with the connectivity patterns described above. Similarly, Kovach et al. (2010) noted genetic differences between cod on eastern Georges Bank and those sampled in the Gulf of Maine, Cape Cod, or Southern New England. These findings largely support the early life history information, which suggests that eastern Georges Bank is a self-sustaining population. Lage et al. (2004) found genetic differences between cod on eastern Georges Bank and western Georges Bank, supporting the conclusion that connectivity from GBK to CC is unlikely. Further, Lage et al. (2004) also found evidence for reproductive connectivity between Cape Cod and southern New England, which agrees with the results of our analysis.

We are fortunate that there have been numerous studies focused on the transport of larval cod within the region, with each providing valuable insight on the possible structure of the population. However, there are notable transport pathways that have yet to be investigated. In particular, it is unclear which spawning area(s) are the fundamental drivers of the observed juvenile settlement south of Cape Cod (SNE stratum) in April/May. Studies focused on either GOM or GBK spawning grounds suggest that some larvae may be transported to SNE; however, the fate of larvae originating from CC or SNE spawning grounds remains largely unknown. In addition, it would be interesting to explore the Cape Cod Canal as a potential GOM/SNE transport pathway, given that cod larvae and juveniles are found in the area surrounding both ends of the canal in April/May.

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4. GENETIC MARKERS

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Abstract

Genetic markers are the gold standard for stock identification in fisheries science. Integrating data from neutral and adaptive genetic variation yields insight into gene flow and demographic connectivity, as well as into local adaptation and the influence of natural selection on traits with ecological relevance. Here, we reviewed 8 genetic studies from 1998 to 2019 that employed microsatellite DNA and genomewide single-nucleotide polymorphism (SNP) markers to assess population structure of Atlantic cod in US and adjacent Canadian waters. Across these studies, genetic data for major spawning populations in US waters were available consistently and with temporal replication. Our review revealed support for 5 biological populations: (1) spring spawning cod in the western Gulf of Maine (GOM); (2) winter-spawning cod in the western GOM winter plus Cape Cod, Nantucket Shoals, and Great South Channel; (3) cod spawning on western Georges Bank, east of the Great South Channel, and the Northeast Peak; (4) southern New England waters; (5) eastern GOM, although the data from spawning cod are lacking to resolve this population with confidence. Differences among cod populations are driven largely by adaptive genetic variation (i.e., regions of the genome under the influence of natural selection. Therefore, there are likely ecological, life history, behavioral, or physiological differences associated with the observed genetic variation. Populations were differentiated weakly by neutral genetic variation, a finding common for marine fish populations with large, historical, effective population sizes. Taken together, the genetic findings point toward biocomplexity in Atlantic cod populations that may be important for conferring resilience and ensuring adaptive capacity and evolutionary potential.

Introduction

Genetic markers are a powerful and widely used tool in fisheries stock identification (Cadrin 2005; Waples et al. 2008; Mariani and Bekkevold 2014). Data from genetic markers are useful for making inferences about stock structure because they provide information about genetic similarity among individuals within and among populations. When examined with a robust sampling design, genetic markers are temporally stable. Therefore, they are relevant for making inferences about reproductive cohesiveness or isolation, which are key metrics for drawing conclusions about population structure (Waples et al. 2008).

Neutral and Adaptive Genetic Variation

The majority of the variation that occurs in the genome is neutral genetic variation, which is not subject to the influence of natural selection because these genetic variants do not have a direct bearing on an organism's fitness (Kimura 1983). Variation at neutral genetic markers is influenced by the evolutionary and demographic processes of mutation, recombination, genetic drift, and dispersal/gene flow (Wright 1931). Of these processes, the latter 2 have the largest impact on populations over time scales relevant to fishery management. Genetic drift acts very slowly except in small populations, leaving gene flow as the primary parameter of inference from studies of neutral genetic variation.

Gene flow (the transfer of genetic material from one population to another) in marine systems results from the combined effects of successful adult or juvenile dispersal. Larval drift away from the natal spawning ground is largely a function of oceanographic currents. Given its influence by these processes, gene flow is used as a measure of demographic connectivity, such that groups that are connected by high levels of gene flow are considered a population unit. However, there is no clear criterion or threshold level of gene flow that confers reproductive isolation, and the levels of exchange needed to generate genetic or demographic independence may be very different. Indeed, a single individual disperser per generation can homogenize neutral genetic variation (one migrant per generation; Slatkin 1987), but populations can be demographically independent despite much higher levels of gene flow (Waples and Gaggiotti 2006; Waples et al. 2008). Further, marine fish populations are typically characterized by large population sizes and high dispersal ability, which both lead to high levels of gene flow and subtle patterns of population differentiation (Ward et al. 1994; DeWoody and Avise 2000).

While a large fraction of the genome is believed to be neutral to selective forces, other portions of the genome are influenced by natural selection. These genome regions house adaptive genetic variation associated with functional genes, which influence characteristics or traits that affect the fitness of the organism. Adaptive variation is often associated with environmental gradients (e.g., differences in temperature, salinity, or oxygen in marine environments), across which selection can act differentially on divergent phenotypes and their underlying genotypes. While fisheries management has long relied on defining management units in terms of demographic independence (i.e. using neutral genetic markers; Waples et al. 2008), considering data from adaptive genetic markers can reveal information about the ecological adaptation of populations to their local environments, which can further inform management unit designation (Schindler et al. 2010; Funk et al. 2012; Nielsen et al. 2012). Examining adaptive genetic variation therefore can aid in identifying populations with ecological distinctiveness, which is often a criterion for consideration in management contexts, including the US Endangered Species Act (Waples et al. 1991; Crandall et al. 2000).

Integrating data from both neutral and adaptive genetic markers provides a more complete picture of population structure than using either marker type alone, as this approach provides insight into the full suite of demographic and evolutionary processes at play. In this way, neutral and adaptive markers may group populations differently, according to the spatial patterns of drift, gene flow, and selection (Funk et al. 2012). For example, it is not uncommon, especially in marine systems, for populations to show local adaptation in the face of relatively high levels of gene flow (Conover et al. 2006; Barth et al. 2017). As a result, interpreting data from genetic markers requires acknowledging the complexity of inference caused by the different marker types and the evolutionary forces that shape them.

Types of Genetic Markers

Several classes of genetic markers have been used in studies of stock structure, with technological advancements over time. In this review, we will focus on 2 types of markers that have been used in studies of Atlantic cod (*Gadus morhua*) populations: microsatellite markers and single nucleotide polymorphisms (SNPs). Studies using these marker types will differ in the number of markers used and whether the markers target neutral or adaptive genetic variation.

Microsatellite markers are length polymorphisms composed of small repetitive sequences of 2-10 nucleotides per unit (Tautz 1989). For example, a dinucleotide repeat may contain the nucleotides GT repeated in tandem a variable number of times. Individual alleles vary in the number of repeats of a given unit. Microsatellites are typically thought to be neutral, but they may also be associated with genes through physical linkage within a chromosome; in this case, they serve as markers of adaptive genetic variation. Because of the cumbersome technology involved in microsatellite marker development and genotyping, studies typically are limited to the use of 8-20 microsatellite markers, although new approaches based on high-throughput sequencing recently have made it possible to efficiently genotype much larger microsatellite panels (e.g., Zhan et al. 2017; Lepais et al. 2019).

SNPs are single base differences at any position in the genome, occurring as the result of point mutations. Because they occur throughout the genome, SNPs may represent either adaptive or neutral variation (Kirk and Freeland 2011). Within any genome, there is a far greater (orders of magnitude) amount of neutral compared to adaptive SNPs. Typically, modern high-throughput sequencing technologies are used to generate data from SNP markers, enabling studies to use information from thousands to millions of loci, depending on the amount of the genome that is sequenced (Seeb et al. 2011). Reduced representation sequencing is focused on a small, random (unbiased) fraction of the genome and typically generates thousands to tens of thousands of SNPs. Whole-genome sequencing entails sequencing all of the nucleotides in an organism's genome and generates millions of SNPs (Davey et al. 2011). Restriction-site-associated DNA (RAD) sequencing is the most commonly used type of reduced representation sequencing to generate SNP markers for population genetic studies; it involves cutting the genome with one or more restriction enzymes and sequencing small portions of the resulting fragments (Davey et al. 2011). The large datasets generated for SNP markers require bioinformatics processing for analysis.

A third type of genetic polymorphism that occurs in some genomes is a chromosomal inversion. Here, a segment of the chromosome remains intact as a single linked block but is found in an inverted orientation in some individuals. In essence, the whole linked block is functioning as a single locus (marker) because it is inherited as a unit (by suppressed recombination during meiosis), even though it is composed of tens of thousands of SNPs.

Chromosomal inversions are known to play a role in cod population genetics, as there are 4 known large inversions on 4 different linkage groups (LGs; i.e. chromosomes) – LGs 1, 2, 7, and 12. These regions compose 7% of the entire cod genome and each one contains a large number of genes (Barth et al. 2017; Berg et al. 2016, 2017; Kirubakaran et al. 2016; Sodeland et al. 2016). Polymorphisms in these chromosomal inversions have been associated with differentiation of cod populations rangewide, in both the Northeast and Northwest Atlantic. Further, these inversions have been variously associated with resident/migratory and inshore/offshore ecotypes (Berg et al. 2016, 2017; Hemmer-Hansen et al. 2013; Kess et al. 2019; Kirubakaran et al. 2016; Sinclair-Waters et al. 2018; Therkildsen et al. 2013), thermal adaptation (Barney et al. 2017; Berg et al. 2017; Bradbury et al. 2010, 2013, 2014; Therkildsen et al. 2013), salinity (Barth et al. 2017; Berg et al. 2015), and oxygen concentrations (Berg et al. 2015).

Genetic Sampling Considerations and Caveats

A few sampling considerations are critical when using genetic data to make inference about stock structure for fisheries management. Firstly, for studies seeking to characterize the population genetic structure or to establish reference or baseline genotypes for future mixed stock analyses, the unit of sampling and analysis is the spawning population. Wherea fish spawns, not where it feeds or otherwise migrates to, determines reproductive and demographic isolation among groups. Accordingly, samples must be collected in a manner that is representative of the spawning population of a given location. To achieve this, fish should be sampled as either adults in known spawning condition or as recently spawned eggs or newly hatched larvae on an active spawning ground. In an ideal scenario, representative samples are collected in cooperation with experienced fishermen from active spawning aggregations along with metadata describing the exact sampling location and maturity status of each individual fish (e.g., Kovach et al. 2010; Kerr et al. 2018; Puncher et al. 2019). According to conventional maturity schedules used in fisheries science (Burnett et al. 1989; Morrison 1990), the maturity categories of ripe, ripe and running, or spawning are the most appropriate for this purpose, as they indicate active spawning. If actively spawning fish are not available, samples from spent (recently spawned) fish may be informative, with the caveat that it is possible that fish in spent condition have already left the spawning grounds. Fish categorized in other maturity stages (immature, developing, or resting) are not ideal for characterizing population genetic structure, given the extensive migratory movements of many marine fish during nonspawning seasons. For example, Wirgin et al. (2007) found greater genetic differences among samples of spawning cod than among opportunistic samples of cod at other life stages.

It is also important that samples are collected in a way that ensures observed genetic patterns reflect stable differences between locations. Sample collection should avoid overrepresentation of particular cohorts or related individuals and should control for fluctuations in environmental variables that may create interannual variation in the spatial distribution of ecotypes (e.g., variation in currents affecting settlement patterns). Within a single year, sampling should be more robust if conducted over multiple days or at least across multiple tows within a sampling location. The gold standard, however, is achieved by collecting samples in more than one year and demonstrating that the observed genetic structure is temporally stable (Waples et al. 2008; ICES 2009). In order to establish that a genetic structure is temporally stable, the samples must demonstrate that the allelic differences observed among locations in the same timeframe are meaningfully greater than those observed among years from the same location, and that the latter are not statistically significant (Waples 1998).

When spawning populations are sampled as above to characterize population genetic structure, the unit of analysis is the spawning aggregation, referenced by location and season of spawning. In some situations, there may be interest in sampling fish of unknown spawning origin as a mixed stock (i.e., a sample that may contain a mixed group of fish potentially from multiple spawning grounds outside of the spawning season). Analytically, such mixed collections of fish are treated differently than collections sampled from spawning aggregations. Individuals sampled in nonspawning condition or from a mixed stock can be assigned to their most likely spawning population of origin by using assignment tests (Hansen et al. 2001; Manel et al. 2005). Alternately, mixture analyses can be used to determine the proportional composition of groups to designated reference populations by using baseline genotypes (Pella and Milner 1987; Anderson et al. 2008). In the absence of these formal analyses, inference about genetic composition of mixed samples may also be made from spatial clustering analyses (e.g., Principal Component Analysis [PCA] or

Discriminant Analysis of Principal Components [DAPC]; Jombart et al. 2010) or Bayesian clustering methods (e.g., STRUCTURE; Pritchard et al. 2000).

Sample size considerations for genetic studies vary by marker type, number of markers used, and the extent of the genome covered by the markers. Population-level sampling of spawning aggregations generally target 50-100 individuals for microsatellite analyses of 8-20 markers (Ruzzante 1998), 20-30 individuals for RAD sequencing analyses of a few thousand markers, and potentially as few as 10-15 individuals for whole-genome sequencing studies that typically employ a few million SNPs. Fewer individuals are needed with larger marker panels because higher information content can be generated for each individual when more independent locations in the genome are analyzed. In other words, either adding more individuals or more markers will increase the statistical power to detect differentiation among groups. Indeed, studies and simulations have shown that sufficient power to detect population differences can be achieved with as few as 8-10 individuals for more than 1000 SNP markers (Willing et al. 2012; Nazareno et al. 2017). However, the number of markers and individuals per population needed for robust conclusions will be influenced by the genetic diversity of the system, and importantly, results from small sample sizes can be biased heavily by nonrandom sampling. For this reason, in most natural populations, robust sample sizes are required for population inference. Even larger sample sizes are needed for mixed stock analyses because this analysis uses genetic information from the whole sample and assigns it proportionally by reference population. Typically, a minimum of 100-200 individuals are required for robust mixed stock analyses. Power analyses should be conducted to demonstrate the statistical power of this approach for population assignments with the markers and genetic polymorphism of the particular study.

Review of Studies

In this section, we review the known studies of cod population genetic structure in US and adjacent Canadian waters, both chronologically and by genetic marker type. We begin our review with the earliest studies of population structure in this region, employing microsatellite markers. We do not discuss prior work focused on broadscale, rangewide genetic variation using mitochondrial DNA or allozymes, as these studies did not focus on the scale of biological populations that concerns us in this report. We summarize the key aspects of study design (including geographic focus, sample size, and other methodological caveats) and the key findings in relation to stock structure. Table 4.1 provides details of each study reviewed, including levels of genetic divergence, as measured by the fixation index (F_{ST}). Note that comparison of F_{ST} values across studies should be conducted with caution, given the different markers used and the variable influence of selection (Moen et al. 2008; Bradbury et al. 2013; Berg et al. 2016) and mutation (Hodgkinson and Eyre-Walker 2011) on different regions of the genome.

Table 4.1. Overview of key findings and genetic divergence, as measured by F_{ST}, for studies of Atlantic cod (*Gadus morhua*) population genetic structure in US/adjacent Canadian waters

Reference	Geographic scope	Sample sizes	Genetic markers	F_{ST} values[1]	Key findings[2]	Stock structure model supported[3]	Caveats and limitations
Ruzzante et al. 1998	Georges Bank, Browns Bank, Bay of Fundy	48 per location	5 microsatellite loci (including GMO 132*)	0.011 overall (across the 3 groups)	BSS	Georges Bank differentiated from Browns Bank	Relatively small sample size and not all fish in spawning condition
Lage et al. 2004	Nantucket Shoals (NS), Georges Bank (GB), Browns Bank (BB)	97 – 144 (NS and GB); 30 (BB)	5 microsatellite loci (including GMO 132) and Pan I**	0.0047 overall; 0.011 Browns Bank vs. Nantucket Shoals	BSS, NV	Nantucket Shoals differentiated from Georges Bank; connectivity between Georges and Browns Banks	Only 30 fish from Browns Bank; limited geographic scope and few markers.
Weiss et al. 2005	West and east sides of Great South Channel	78 (east), 168 (west)	5 microsatellite loci	0.011	BSS	Great South Channel separates Georges Bank from spawning in Cape Cod area	Limited geographic scope; few markers unique to this study, unknown if adaptive or neutral
Wirgin et al. 2007	western Gulf of Maine (wGOM. spring and winter), Cape Cod, Georges Bank, and non-spawning New York Bight	855 mixed samples; 343 spawning adults (27-100 per location)	6 microsatellite loci (including GMO 132, Pan I, and 2 Single Nucleotide Polymorphism markers (SNPs)	0.007 overall; 0.0095 -0.013 wGOM spring vs. winter; 0.022 wGOM spring vs. Cape Cod; 0.012 Cape Cod vs. Georges Bank	BSS, FSS	>1 stock within wGOM; differentiation of Cape Cod and Georges Bank	Few markers, some sample sizes small; not all US spawning groups sampled
Kovach et al. 2010	12 spawning aggregates in wGOM, Southern New England and northeastern Georges Bank	1581 samples (n = 31-158, with temporal replication); most in spawning condition	10 microsatellite loci (including Gmo 132); Pan I, 5 SNPs	0.0085 spring vs. winter wGOM; 0.0044 overall; 0.0011 neutral only	BSS, FSS, NV, AV	3 spawning complexes: (1) northern spring-spawning coastal complex; (2) southern complex (winter and fall spawning in wGOM, Cape Cod and	No samples from western Georges Bank, Great South Channel area, eastern GOM, or adjacent Canadian waters

						southern New England); (3) Georges Bank	
Barney et al. 2017	Spring and winter wGOM; northeastern Georges Bank	10-11 individuals from each of 3 groups	54,030 exonic SNPs and focus on chromosomal inversions on LG 2, 7 ,12	0.09 – 0.17 for pairwise comparisons by LG 2, 7, 12; 0.0001 genomewide exonic SNPs	BSS, FSS, AV, CG	Three spawning complexes are genetically distinct, with adaptive differences driven by LG 2, 7, 12	Small sample sizes without metadata; exonic SNPs may be conserved (non-neutral); potential error with finding that winter-spawning wGOM are most differentiated (inconsistent with all other studies)
Clucas et al. 2019a	Spring and winter wGOM; northeastern Georges Bank, eastern GOM (eGOM) mixed fishery	15-24 per each of 3 groups in spawning condition and nonspawning from eGOM	3128 SNPs	0.0073 – 0.02 pairwise all loci; 0.0047 – 00.12 pairwise neutral loci only (across the 3 spawning groups)	BSS, FSS, NV, AV	Three spawning complexes are genetically distinct; eGOM may be comprised of a mixed stock or a group of fish from nearby Canadian waters	Scope limited to the 3 spawning complexes; source of eGOM could not be resolved.
Clucas et al. 2019b	15 spawning aggregates in US waters, 2 in Canadian waters (NAFO regions 4VsW – eastern Scotian Shelf, 3Ps – St. Pierre bank), and 3 nonspawning areas in eGOM	306 samples; 11-25 (typically 15) from each of 20 spawning aggregates/locations	Nearly 11 million SNPs	0.011 – 0.05 pairwise all loci; 0.0054 – 0.0017 pairwise across groups neutral loci only	BSS, FSS, NV, AV, CG	Five genetically distinct groups: (1) spring-spawning wGOM; (2) fall and winter spawning wGOM + Cape Cod; (3) Georges Bank; (4) southern New England; (5) putatively eGOM	Analyzed samples from wGOM, but not in multiple years, raises uncertainty about temporal stability; origins of eastern GOM could not be resolved.

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[1] F_{ST}s are not directly comparable across studies that use different markers (e.g., SNP-based estimates tend to be higher than estimates derived from microsatellites and estimates that include adaptive loci are higher than those that include

exclusively neutral loci). Even within a particular marker type, the number and genomic region of the markers will influence the F_{ST} estimate.

[2] Key findings reveal one or more of the following aspects of genetic structure: Broad-scale structure (BSS), Fine-scale structure (FSS), Neutral Variation (NV; as evidenced by statistically significant divergence at neutral F_{ST}), Adaptive Variation (AV; as revealed by statistically significantly elevated divergence at adaptive genetic markers), Candidate genes underlying population differences (CG).

[3] All studies focused in US waters revealed inconsistencies with the current 2-stock model; the key nature of these inconsistencies are given here, as well as the genetically distinct groupings revealed by the study.

*Gmo 132 is a microsatellite marker known to be nonneutral (i.e., linked to a genome region under selection).

*Pan I is a single nucleotide polymorphism (SNP) that codes for an integral membrane protein, pantophysin, found in cytoplasmic transport vesicles and is known to be under the influence of natural selection.

Studies of Population Structure with Microsatellite Markers and Pan I

The first studies of cod population genetic structure in US waters used <20 genetic markers, including microsatellites and a few targeted SNPs (Lage et al. 2004; Weiss et al. 2005; Wirgin et al. 2007; Kovach et al. 2010). One SNP, at the Pan I locus, was particularly informative for differentiating populations. It codes for an integral membrane protein, pantophysin, found in cytoplasmic transport vesicles and is known to be under the influence of natural selection and associated with behavioral, life history, and environmental variation (Jónsdóttir et al. 2008; Arnason et al. 2009). These studies primarily focused on a few sampling areas within the western Gulf of Maine, the waters around Cape Cod, and the northeastern peak of Georges Bank; therefore, with one exception (Lage et al. 2004), these early studies were not able to address connections with adjacent Canadian waters. Below, we consider each study individually.

Wirgin et al. (2007) sampled 855 individuals from mixed collections of larval, juvenile, and adult samples from the western Gulf of Maine (GOM), Georges Bank, and the Great South Channel. Analyses with 7 microsatellite markers identified genetic heterogeneity within the western GOM samples, caused by divergence of a mixed collection of juveniles from Massachusetts Bay. In a second phase of the study, the authors used 6 microsatellite loci, Pan I, and 2 additional SNPs to analyze 343 spawning adults (n = 27 - 100 per location) sampled from spring and winter-spawning populations in Ipswich Bay and winter-spawning cod in Stellwagen Bank, Cape Cod (the waters offshore of Chatham, MA), and the northeastern peak of Georges Bank, as well as a nonspawning collection of cod in the New York Bight. The spring-spawning collection from Ipswich Bay was differentiated from all other spawning aggregations and the New York Bight nonspawning collection. Georges Bank was also differentiated from western GOM and Cape Cod waters, whereas there was connectivity among winter-spawners in the western GOM, Cape Cod, and the nonspawners in New York Bight. These findings were inconsistent with the 2-stock model of cod structure based on 3 lines of evidence: (1) genetic heterogeneity within the Gulf of Maine, (2) connectivity between western GOM and southern New England, and (3) differentiation between Georges Bank and Cape Cod.

The latter finding of heterogeneity within what is considered the Georges Bank stock (Georges Bank and waters to the south, including Cape Cod, Nantucket Shoals, and southern New England) was consistent with a prior study by Lage et al. (2004). Using 5 microsatellite markers and Pan I, these authors found differentiation between cod spawning on Nantucket Shoals (n = 97) and the northeastern peak of Georges Bank (n = 144). Further support for the differentiation of Georges Bank and the Nantucket Shoals/ Cape Cod waters is provided by Weiss et al. (2005), using a different suite of 5 microsatellite markers than any of the aforementioned studies. This study found spawning adults sampled west of the Great South Channel (n = 168) to be genetically distinct from those sampled east of the Great South Channel on Georges Bank (n = 78). Larvae (n = 46) sampled west of the Great South Channel were assigned to the western spawning sampling area, while assignment of juveniles (n = 343) was not conclusive, likely because of the mixed sample, low resolution of markers, and the small genetic differences between spawning populations.

Lage et al. (2004) also found connectivity between a spawning cod from the northeastern peak of Georges Bank (n = 144 across 2 years) and 30 individuals (from 1 year) from a spawning ground on nearby Browns Bank in Canadian waters. As part of a much larger study across Canadian waters, Ruzzante et al. (1998) found the opposite result, using a similar suite of 5 microsatellite markers and sample sizes of 48 individuals. Differences in the results of these 2 studies may stem from relatively small sample sizes and differences in spawning condition of sampled fish (only 60% of Browns Bank cod were in spawning condition in the study of Ruzzante et al. [1998]). Two other key findings from this study may have some bearing on our interest in US waters: (1) cod south of the Laurentian Channel (Bay of Fundy, Georges Bank, and Scotian Shelf) were strongly differentiated from populations to the north of it; (2) within the southern banks, 3 areas emerged as genetically distinct: Georges Bank, western Scotian Shelf (Browns Bank and Bay of Fundy), and eastern Scotian Shelf (Banquereau Bank and Western Bank).

Kovach et al. (2010) expanded the work of Wirgin et al. (2007) with a comprehensive study of 1581 individuals in spawning condition (primarily ripe/ripe and running, with a few developing and spent fish in some collections) from 12 spawning aggregations in US waters and 2 collections of nonspawning cod from Platts Bank (spent and resting) and New York Bight (resting). Analyses with 10 microsatellite markers, Pan I, and 5 additional SNPs identified genetic structure largely consistent with 3 broad spawning complexes: the northern spring spawning complex, the southern complex, and Georges Bank. The northern spring spawning complex feature cod that spawn in the inshore waters of western GOM in the spring time (May/June) in Massachusetts Bay, Ipswich Bay, and Bigelow Bight.The southern complex include cod that spawn primarily in the winter, variably from November to April, in inshore western GOM in Ipswich Bay, Massachusetts Bay, the nearshore banks of Jeffreys Ledge and Stellwagen, in Cape Cod waters of Nantucket Shoals, and in southern New England on Cox Ledge. The Georges Bank complex contains cod that spawn on the northeastern peak of Georges Bank (Fig. 1). Nonspawning adults from Platts Bank were similar to the northern spring complex, and those from New York Bight were similar to the southern complex. This genetic structure was shown to be stable over a 5-year period, based on replicated samplings across 2006-2008 and on comparison with the samples collected in 2003 and analyzed in Wirgin et al (2007). Further, age-0 juveniles collected in Massachusetts Bay and Cape Cod Bay in the spring and fall could be assigned back to their spawning complex of origin. Lastly, weak differentiation of cod in Nantucket Shoals and Cox Ledge suggested the possibility for finer scale population structure beyond the 3 primary complexes.

The markers used in the study of Kovach et al. (2010) included 2 outlier loci known to be under the influence of natural selection. Polymorphisms at these loci have been associated with variation in temperature, depth, salinity and inshore-offshore migration patterns (Pampoulie et al. 2006). The genetic structure identified with the full suite of these markers, including the outliers, could not be recovered with the neutral markers alone because of very small levels of neutral genetic differentiation (F_{ST} values close to zero), suggesting either recent or currently ongoing gene flow in the face of adaptive genetic differentiation. The major genetic discontinuities, however, were supported by a subset of the neutral loci.

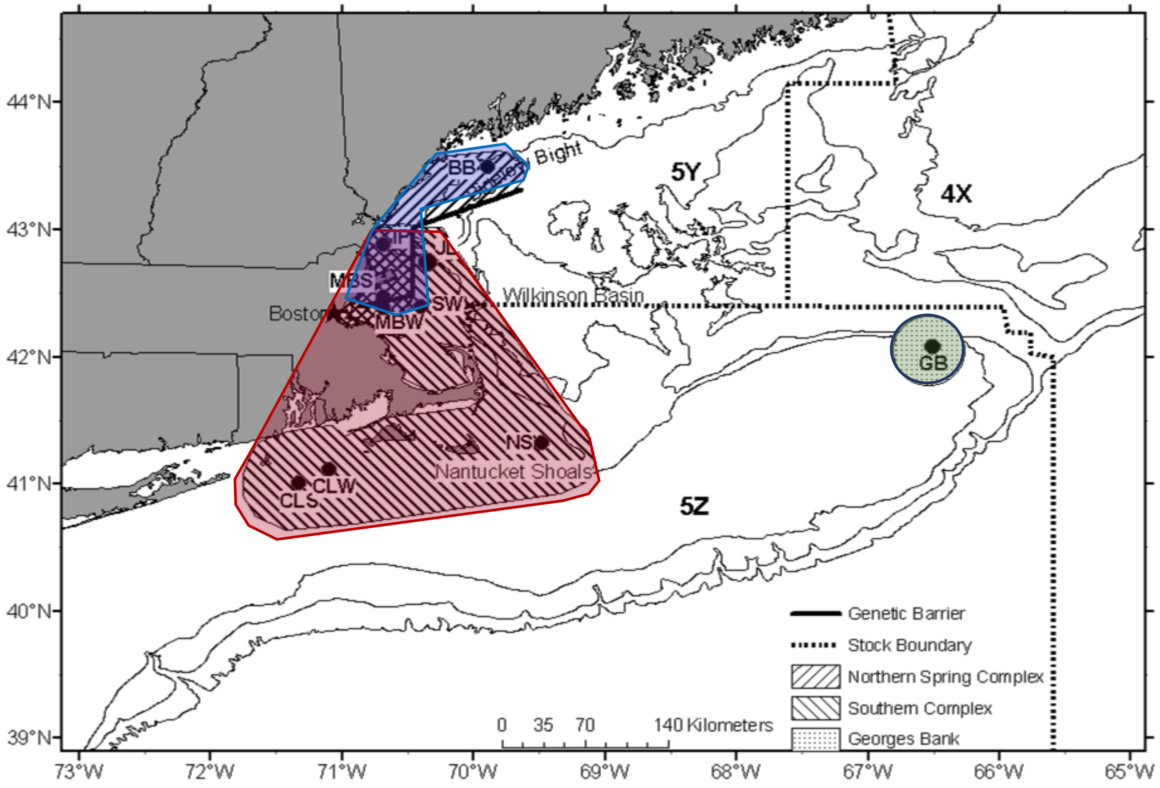

Figure 4.1. Three genetically distinct spawning complexes of Atlantic cod (*Gadus morhua*) identified in US waters by the study of Kovach et al. (2010) by using microsatellite markers and Pan I. The northern spring complex (blue shaded hatching) comprises spawning aggregates in Massachusetts Bay (MB), Ipswich Bay (IP), and Bigelow Bight (BB) in May and June. The southern complex (red shaded hatching) is composed of fall and winter spawning aggregates in Massachusetts Bay (MB), Ipswich Bay (IP), Jeffreys Ledge (JL), Stellwagen Bank (SW), Nantucket Shoals (NS), and Cox Ledge (CLW) in December/January and Cox Ledge Spring (CLS) in March/April. The Georges Bank complex was only sampled from the northeastern peak of Georges Bank. Figure modified with permission from Kovach et al. (2010).

The findings from these first studies, above, collectively provide evidence that:

- the Gulf of Maine stock is composed of at least 2 discrete populations that spawn, sometimes in the same inshore locations in the wGOM, in different seasons (winter and spring)
- there is some degree of connectivity between cod in the western Gulf of Maine and cod that spawn offshore of Cape Cod and in southern New England
- the cod that spawn in Georges Bank are distinct from the remainder of the cod considered in that stock (those that spawn in the waters of the Cape Cod area and southern New England)
- finer scale differences may also occur among geographically separate populations, (e.g., southern New England vs. Gulf of Maine);

- nonneutral markers drive the patterns of genetic differentiation, a finding which suggests the population structure reflects differential adaptation of populations to local environmental conditions.

The collective evidence from genetic studies, summarized above, largely influenced a model of cod structure put forth in Zemeckis et al. (2014; reproduced in Fig. 4.2 below), which showed inconsistencies with the currently accepted 2-stock management model. Nonetheless, some knowledge and sampling gaps remained at this time. In particular, (1) none of these early microsatellite studies included samples collected from the eastern GOM; (2) only one, very limited study of Weiss et al. (2005), included samples from the Great South Channel and western Georges Bank area; and, (3) with the exception of the conflicting findings of Lage et al. (2004) and Ruzzante et al. (1998), these earlier studies did not incorporate samples from adjacent Canadian waters.

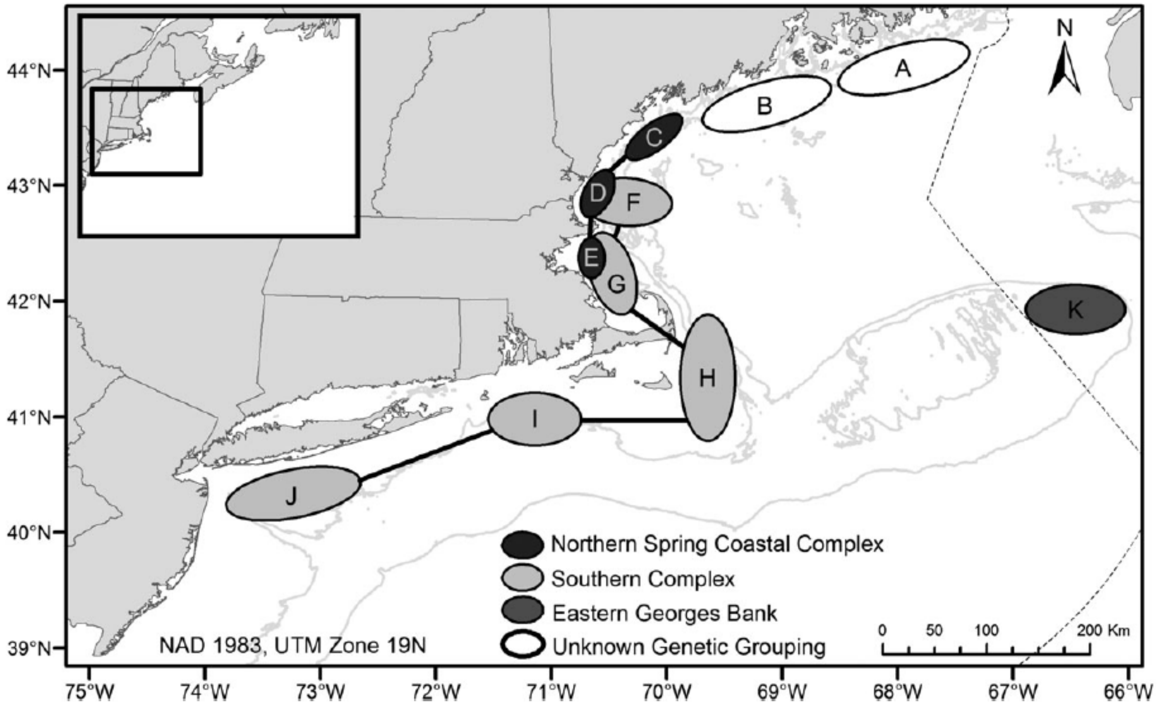

Figure 4.2. Model of Atlantic cod (*Gadus morhua*) stock structure proposed by Zemeckis et al. (2014), largely based on evidence from genetic studies using microsatellite markers and Pan I. Three metapopulation complexes are depicted, largely following the findings of Kovach et al. (2010). The northern spring coastal complex includes cod spawning in waters of coastal southern Maine, Ipswich Bay, and Massachusetts Bay in the spring time. The southern complex includes cod spawning inshore and nearshore Ipswich Bay and Massachusetts Bay, off of Cape Cod, Nantucket Shoals, and southern New England waters, and with extrapolation to the New York Bight based on prior tagging studies and genetic samples of non-spawning cod. Eastern Georges Bank complex comprises cod spawning on the Northeast Peak of Georges Bank. In the eastern Gulf of Maine the is a fourth group with unknown genetic make up because of the lack of data from this depleted area. Figure adapted with permission from Zemeckis et al. (2014).

Studies of Population Structure with Genomewide SNPs

A series of recent studies using more powerful panels of SNPs leveraged from high resolution genomic methods has largely confirmed the patterns identified in the above-described microsatellite and Pan I studies and provides additional insights into the complexity of cod population structure. In the first of these studies, Barney et al. (2017) focused primarily on the regions of the genome found in the known chromosomal inversions on LG 2, 7, and 12, which had been previously shown to differentiate cod populations broadly within the Northeast and Northwest Atlantic (Bradbury et al. 2014). Barney et al. (2017) were the first to show these inversions to be polymorphic within the GOM and Georges Bank area. The authors used whole-genome sequencing and extracted 54,030 exonic SNPs (found in the coding regions of the genome, termed exons) for their population analyses. Of those SNPs, 33,915 were found in LGs 2, 7, and 12, both within and outside of the linkage blocks containing the chromosomal inversions, and 20,115 were found elsewhere in the genome. These SNPs were used to evaluate 10-11 individuals sampled from each of the 3 spawning groups identified in Kovach et al. (2010) – winter and spring spawners in western GOM and cod spawning on Georges Bank. The authors found that adaptive variation played a key role in differentiating the winter and spring spawning populations in the western GOM and those on Georges Bank. They found candidate genes linked to temperature associated physiological differences and a large number of such genes on LG 2 that differentiated the winter and spring spawning populations.

While the overall finding of adaptive genetic differentiation among the 3 spawning groups corroborated other studies, one inconsistency in the findings of Barney et al. (2017) was that of greater genetic differentiation of the winter spawning population from the other 2. All other studies of these populations (Wirgin et al. [2007]; Kovach et al. [2010]; Clucas et al. [2019a, 2019b]) have found the spring spawning population to be the most genetically differentiated spawning group within these waters. This inconsistency in the study of Barney et al. (2017) may be a result of small sample sizes (n = 10-11), which may have led to imprecise estimates of allele frequencies. Additionally, metadata describing the reproductive maturity of the sampled fish were unavailable. Barney et al. (2017) also found no evidence for neutral differentiation among these 3 populations, with very small F_{ST} values, suggesting complete panmixia. The study's use of exonic SNPs for estimating neutral divergence makes it difficult to compare with neutral estimates of other studies that include SNPs from noncoding portions of the genome. Exons are conserved regions of the genome subject to purifying selection, which reduces genetic variation. Therefore, exonic SNPs are less likely to show patterns of population differentiation unless they are under strong divergent selection because of selective constraints.

Using RAD sequencing, Clucas et al. (2019a) identified a panel of 3,128 SNPs randomly distributed across the cod genome, which they used to analyze genetic variation across winter and spring spawning populations in Ipswich Bay and Massachusetts Bay, cod spawning on the northeastern peak of Georges Bank, and a nonspawning population of cod sampled from the Maine Center for Coastal Fisheries' Sentinel Survey in the eastern GOM (Henry 2013; Rodrigue 2017). The latter provided the first genetic evaluation of cod in this depleted region of the eastern GOM, where aggregations of spawning cod have not been observed since the 1990s. Analyses of 15-24 cod per population showed clear support for divergence between the winter and spring spawning populations in the western GOM, as well as fine-scale differences between cod spawning in the 2 bays within the same season. Cod spawning on the northeastern peak of Georges Bank were differentiated from both spawning populations in the western GOM, and the spring spawning wGOM population was the most divergent of all spawning populations. The cod sampled from the

Sentinel Survey in the eastern GOM could not be decisively linked to either of the 3 spawning groups, suggesting a few possible hypotheses: that this sample may represent a genetically distinct population, a mixed sample, or cod that migrated to the eastern GOM from Canadian waters. The nonspawning condition of these fish preclude firm conclusions about the population genetic structure of the eastern GOM.

As was true of the earlier microsatellite studies described above, most of the genetic differentiation revealed by the 3,128 SNPs in Clucas et al. (2019a) was driven by nonneutral loci. When 47 outlier loci (SNPs with statistically significantly elevated levels of divergence as measured by F_{ST}) and another 106 SNPs located in the chromosomal inversions on LG 2, 7, and 12 were removed, the genetic differences (magnitude of F_{ST}; see Table 1) were much smaller and the patterns of structure weaker. However, the differences among the 3 primary groups (winter GOM, spring GOM and Georges Bank) were recovered by discriminant analysis of principal components (DAPC). The 3 LGs factored strongly in shaping the genetic patterns in this study, primarily in differentiating spring-spawning western GOM from both winter-spawning western GOM and Georges Bank. Identification of 47 additional outlier loci suggested that other portions of the genome may also be important in differentiating these populations.

In the largest scale genomic study of cod population structure to date, Clucas et al. (2019b) used nearly 11 million SNPs recovered from low-coverage whole-genome sequencing of 306 individuals from 20 sampling locations, including all known spawning aggregations in US waters and 2 locations in nearby (but not adjacent) Canadian waters. All samples were collected from actively spawning (or recently spawned) fish, except those in the eastern GOM. US spawning samples included 8 spawning aggregations in the western GOM (4 spawning in winter and 4 in spring); 3 areas in the waters offshore of Cape Cod, on the Nantucket Shoals, and the Great South Channel; 2 in southern New England on Cox Ledge; 1 on the western most edge of Georges Bank just east of the Great South Channel; and 1 on the northeastern peak of Georges Bank. Samples collected from nonspawning cod were also analyzed from 3 areas in the eastern GOM: midcoast in the Penobscot Bay area, inshore in the eastern most portion of the GOM, and offshore in the eastern GOM. Canadian spawning aggregations were sampled on either side of the Laurentian Channel (on the eastern Scotian Shelf and on St. Pierre Bank) offshore of Newfoundland.

The findings of Clucas et al. (2019b) revealed complex patterns of population structure driven largely by regions of the genome likely to be under natural selection. The allele frequencies from all polymorphisms across the whole genome in a principal component analysis (PCA), revealed a clustering of populations. Within US waters, the spring spawning populations in the western GOM clustered distinctly from the winter spawning populations, and winter and spring spawners from the same bays (Ipswich Bay and Massachusetts Bay) clustered more clearly by their spawning season rather than geographic location. Cod sampled from the Cape Cod/Nantucket Shoals/Great South Channel area clustered with the winter spawners in the western GOM, but cod in southern New England clustered separately and were positioned at the far end of the first principal component axis. Cod sampled from eastern and western Georges Bank were positioned proximate to one another in the PCA and intermediate to the winter and spring spawners in the western GOM, albeit nearer to the winter spawners. Nonspawning cod collected in the eastern GOM showed some variability, they but clustered largely with winter spawners in the western GOM and in the Cape Cod region. Cod sampled in Canadian waters were the most divergent from all populations in US waters and from each other.

The observed genetic structure was driven largely by the 4 chromosomal inversions (LGs 1, 2, 7, and 12), as a PCA generated solely from haplotype frequencies of these 4 inversions appeared very similar to the whole genome PCA. However, when examined separately, these 4 LGs did not group the populations in exactly the same way. In particular, LG1 largely differentiated the 2 Canadian populations from all populations in US waters, while at LG 2, 7, and 12 the spring-spawning western GOM group showed more similarity to the Canadian samples than the other US samples did. There were also subtle differences in the grouping of Georges Bank and southern New England across these 3 LGs that pointed to some finer-scale structuring in these regions.

Elevated genetic divergence was also found in several other regions of the genome outside of the chromosomal inversions. The polymorphisms within these differentiated regions of the genome were associated with several candidate genes with known functions that may play a role in adaptive differences of these population groups. In particular, 2 hormone receptor genes, a follicle stimulating hormone receptor (FSHR) and an estrogen receptor-beta (ESR2), were found to be highly differentiated between the spring-spawners in the western GOM and all other populations, except the Canadian samples from St. Pierre Bank, which also spawn in the spring time. Clucas et al. (2019b) suggested that this genetic difference may underlie a mechanism for the difference in spawning time of these populations. Another potentially relevant polymorphism occurred in a region that contained 2 heat shock protein genes, known to play a role in thermal tolerance. This region differentiated the southern New England samples from other cod populations in a clinal fashion, suggesting differentiation in local adaptation of cod in thermal tolerance along a latitudinal temperature gradient. In summary, the whole genome analysis of Clucas et al. (2019b) highlighted the role of adaptive genetic variation in driving population differentiation and showed that different parts of the genome distinguished populations differently, suggesting that complex patterns of adaptive diversity contribute to biocomplexity of cod population structure.

Clucas et al. (2019b) concluded that there are 4 or 5 genetically distinct groupings of cod in US waters: (1) spring-spawning cod western GOM; (2) winter-spawning cod in western GOM and fall and winter-spawning cod in the Cape Cod and Nantucket Shoals area, including the western part of the Great South Channel (statistical area 521); (3) cod spawning on western and eastern Georges Bank; (4) cod spawning in southern New England waters (coastal areas south of the Cape Cod/Great South Channel area); and (5) potentially cod spawning in the eastern GOM, with the caveat that conclusions could not be reached in the absence of data from spawning cod in this area (Fig. 4.3). When the adaptive loci (polymorphisms in the chromosomal inversion regions and the additional outlier regions of the genome) were removed from the dataset, the remaining neutral datasets showed very little differentiation among populations; however, differences among these major groupings were upheld. Neutral loci also indicated some gene flow between Georges Bank and the Cape Cod/Nantucket Shoals/Great South Channel area, which was not apparent with the adaptive loci. While this study is the most robust to date in terms of sampling effort (extensive sampling of cod in spawning condition from the major known spawning aggregations) and a comprehensive genome-wide set of markers was used, a few limitations remained. First, the 15 individuals sampled from the western Georges Bank were from a single year, and therefore the study was unable to demonstrate temporal stability. In contrast, other regions in this study had been sampled in multiple years in prior work, and those prior analyses demonstrated temporal stability. In addition, the genetic composition of the eastern GOM remains unresolved until data from spawning or larval cod are available from this region.

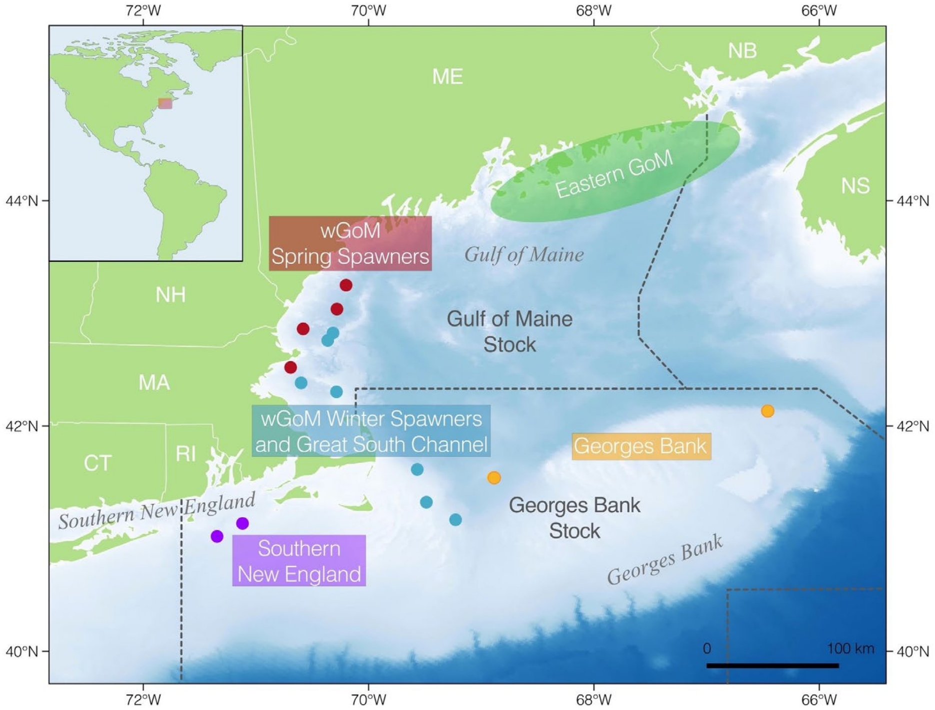

Figure 4.3. Model of Atlantic cod (*Gadus morhua*) population structure put forth in Clucas et al. (2019b). Four genetically differentiated spawning groups are indicated with color coding as follows: (1) western Gulf of Maine (GOM) spring – Massachusetts Bay, Ipswich Bay, and Bigelow Bight (red); (2) western GOM winter plus Cape Cod – Massachusetts Bay, Ipswich Bay, Jeffreys Ledge, Stellwagen Bank, Cape Cod, Nantucket Shoals, and Great South Channel (blue); (3) Georges Bank – western Georges Bank, east of the Great South Channel, and Northeast Peak (orange); (4) southern New England – Cox Ledge (purple). The circled area comprising eastern GOM is a fifth potentially distinct population, although the data from spawning cod are lacking to resolve this. Dotted lines depict current US management unit boundaries. Figure reproduced from Clucas et al. (2019b) under a Creative Commons License.

Recent findings from another study using >5000 SNPs with Restriction-site Associated DNA (RAD sequencing) provides evidence of transboundary gene flow across the US and Canadian border (Puncher et al. 2021). That study also revealed an eastern corridor of connectivity linking the Bay of Fundy with Browns Bank and eastern Georges Bank. This latitudinal path of gene flow is similar to the corridor of movement identified in the west that links the winter spawning cod of the wGOM with Cape Cod and the Nantucket Shoals. Another preliminary finding from that study is the clustering of samples from the western Georges Bank (near 68ºW) near samples from the Great South Channel. Given the contrast with the results of Clucas et al. (2019b), these findings suggest that western Georges Bank may be a mixing area, and different collections of samples may represent genetically different groups of fish. Alternatively, it is important to note, that even including these 2 studies, sampling of the western Georges Bank has been sparse and temporally unreplicated.

In summary, the findings of studies from genomewide SNPs largely build upon the earlier microsatellite studies summarized above. They provide higher resolution and reveal additional details about the complexity of population structure, with the following key points:

- There is a greater complexity of population structure than recognized by the US 2-stock model, with at least 4 genetically distinct spawning aggregations in US waters.
- Spring-spawning cod in the western GOM are the most genetically distinct from all other cod spawning in US waters, including winter-spawning aggregations in the same inshore bays. They share some similarities with more northern Canadian populations, particularly those that also spawn in the spring.
- Genetic differentiation is driven primarily by regions of the genome under the influence of natural selection. Some of these genome regions hold genes with ecological or physiological functions (reproduction, thermal tolerance) that differ among populations. Different parts of the genome group spawning populations differently, so these complex patterns of adaptive differentiation across the genome suggest multifaceted selection pressures and local adaptation among spawning populations.
- When the adaptive portions of the genome are excluded, neutral loci alone reveal a much lower amount of divergence, but they still support differentiation among the main population groupings.

Mixed Stock Analyses

Relatively little attention has been given to the assignment of mixed stock fisheries to spawning population of origin in US waters, compared to the above described work on population structure. One study focused on assigning fish from a modern GOM commercial fishery to either winter or spring-spawning western GOM populations (Kerr et al. 2018). First, temporal stability was demonstrated by comparing a sample of 160 spawning cod sampled on the spawning grounds in 2014-2015 (samples distributed across Ipswich Bay and Massachusetts Bay in the winter and spring) with 274 archived samples from Kovach et al. (2010), collected in 2006-2008 from the same 2 bays and spawning seasons. Datasets generated from 12 microsatellite markers were compared across the 2 time periods. Significant genetic differentiation, as measured by pairwise F_{ST} and Analysis of Molecular Variance, was found for all comparisons of winter and spring spawning groups, while no significant genetic variation was attributed to sampling the same bays and spawning seasons across years. This consistency provides strong evidence for temporal stability, especially when combined with prior evidence for stability of these populations across the 5 years between sample collections for the studies of Wirgin et al. (2007) and Kovach et al. (2010), together providing compelling evidence for long-term stability (2003 - 2015) in the winter and spring spawning populations.

Given this demonstrated temporal stability, the study described in Kerr et al. (2018) combined the genotypes for the 2006-2008 and 2014-2015 samples to generate a full microsatellite dataset of 434 individuals. This dataset served as a reference for a mixed stock analysis of the fishery. The dataset had reasonably high resolution for discriminating among populations, with an F_{ST} of 0.0135 for winter and spring spawners overall. Assignment scores from Discriminant Analysis of Principal Components (DAPC) were 78% and 74% for individual fish to the winter and spring populations, respectively. Power analyses of the mixed stock assignments (which estimated the overall proportion of fish from different spawning groups in a mixed sample) indicated considerably higher correct assignment rates but depended on the proportional composition of the mixed groups.

For the modern commercial fishery, mixed stock samples were available from 131 individuals sampled during 9 separate collections, from western GOM statistical areas 513 and 514 in 6 different months (March, May, June, July, December, and January). These mixed stock samples were collected as representative of the modern fishery in the wGOM region. These samples were assigned to 1 of the 2 reporting groups (winter and spring) by using a conditional likelihood approach. The full collection (all 131 samples) was slightly biased toward the winter spawners (60:40; Fig. 4.4). When analyzed by season, the winter mixture (December, January) consisted of 77% winter spawners and the summer mixture (June, July) consisted of 80% spring spawners, while the spring mixture (March, May) comprised a more even mix of both winter (61%) and spring (39%) spawners (Fig. 4.4). This finding makes sense if spring and winter spawning populations have only temporary residence in the western GOM and subsequently undertake migrations either up and down the coast or offshore (Chapter 7). It also highlights that the period between March and May is when the fishery is the most mixed between these 2 seasonal spawning components.

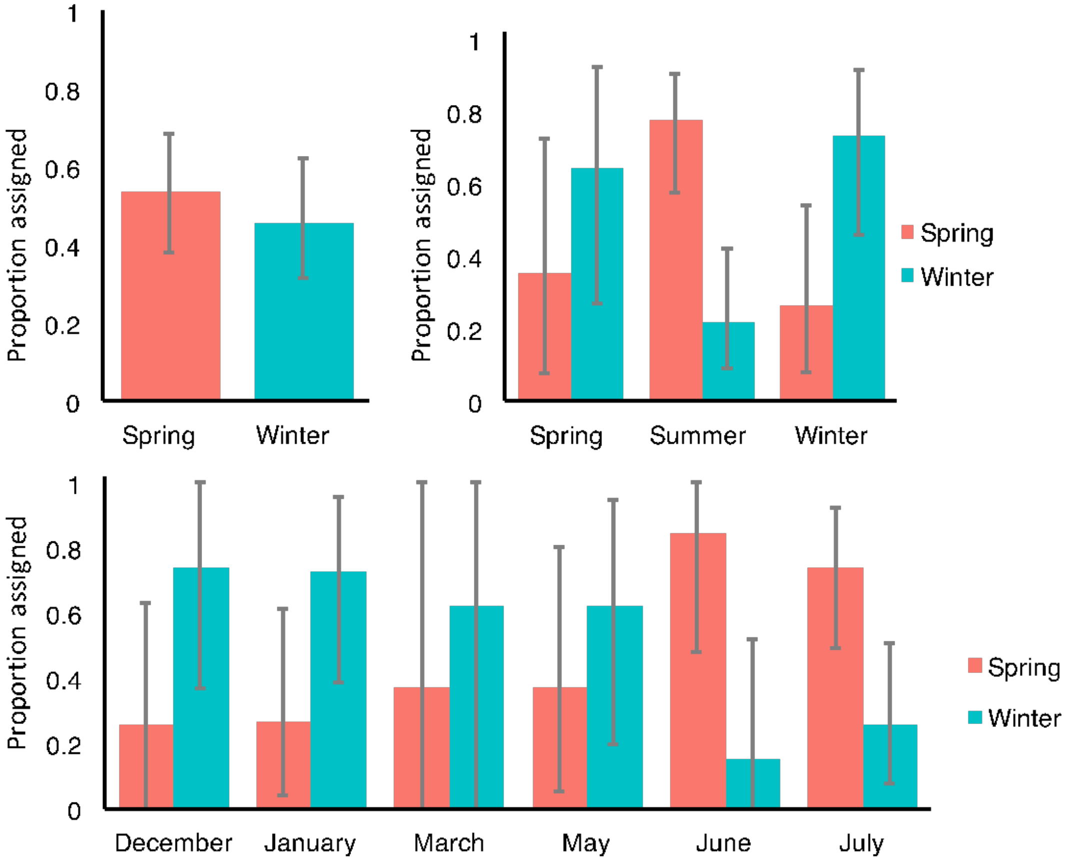

Figure 4.4. Proportional assignments to spring (red bars) and winter (blue bars) spawning populations of Atlantic cod (*Gadus morhua*) from mixed stock analyses of commercial fishery catches. Top left: across all samples collected, assignments are relatively evenly split toward spring and winter populations. Top right: by season, a greater proportion of assignments are to the winter population (about 70% on average) in the spring and winter months, while a greater proportion are assigned to the spring population in the summer months. Bottom panel: by month, assignments are stronger (60-77%) to the winter population in December, January, March, and May) and stronger (70-85%) to the spring population in June and July. Samples were collected, as representative of the modern western Gulf of Maine (GOM) fishery, by a fisherman conducting simulated fishing trips in statistical areas 513 (southern portion) and 514 of the western GOM.

These mixed stock analyses demonstrate the utility of genetic markers for differentiating individuals of an unknown mixed grouping and provide insight into the seasonal differences in the western GOM fishery. The work to date is limited in its spatial scope and exclusive focus on the western inshore GOM, as well as by the use of only 2 reporting groups – winter and spring spawning western GOM spawners. These limitations stem from the limits of the resolution of the microsatellite data. Future work with mixed stocks fishery assignments should leverage the recent genomic studies and seek to use high resolution SNPs in an effort to assign fish of unknown origin to the 5 groupings identified in the work described above. The much greater degree of differentiation among groups within SNP outlier regions along with preliminary work with a subset of SNPs from Clucas et al. (2019a) suggest that finer discriminatory power is possible to the population or bay level (Kerr et al. 2018). To achieve these goals, development of a high-resolution SNP panel array would be useful and, with the appropriate logistical and financial support, could potentially lead to relatively efficient identification of fish to population origin, in a similar manner as is used to manage the Pacific salmon (*Salmonidae*) fishery.

Temporal Comparisons

DNA analysis of historical samples can yield insight about population structure in the past and help compare it to that of contemporary times. In fisheries research, these samples can come from archived otoliths or scales collected in systematic assessment surveys or from the commercial fishery (Nielsen and Hansen 2008). This type of historical DNA analysis can allow for reconstructing past population structure and identifying potential changes in genetic diversity or variation over time. This approach holds promise in US waters for (1) filling in gaps in our knowledge of the eastern GOM that exist because of the collapse of this fishery, and (2) testing hypotheses about prior population diversity (e.g., Ames 2004). If population components have been lost over time, this information should be uncovered in genotypes obtained from historical analyses.

One study builds on the mixed stock analysis study reported above and addresses the question of changes in population structure in US waters over time Kerr et al. (2018). Archived otoliths were obtained from the commercial fishery collection curated by NOAA Fisheries' Northeast Fisheries Science Center (NOAA NEFSC). The spawning condition of these samples was unknown. Microsatellite genotypes were generated from 232 individuals in 2 time periods, (1979-1982 and 1989-1992) from statistical areas 513, 514 (in both time periods), and 515 (in the latter time period) in the western GOM, for a total of 5 spatiotemporal groupings. These samples were compared with both the modern commercial fishery of 2014-2015 and the winter and spring spawning reference populations. All 5 groups of otolith samples were found to be genetically distinct from the 4 modern spawning populations, with F_{ST} values ranging 0.018 - 0.045 which are substantially larger than the genetic distances among the modern cod populations. While differentiated from both modern spawning groups, the historical samples were more divergent from the winter spawners than from the spring spawners and also strongly divergent from most of the modern fishery sample collections, with the exception of the June and July collections. Mixed stock analysis of the historical fishery samples indicated strong majority assignments to the spring spawning population (75-95% for all statistical areas and time periods; Fig. 4.5). However, an important limitation of this analysis is that it can only assign individuals to 1 of the 2 reporting groups and cannot account for unsampled populations. Therefore, the best interpretation of these findings is that the historical samples were more similar to today's spring spawning population than to today's winter spawning populations, and the historical fishery had a different composition than that of the modern fishery (which is more heavily dominated by the winter-spawning population). While the F_{ST} results suggest that the historical fishery was composed of populations with a different genetic signature from the modern winter and spring spawning populations in Ipswich Bay and Massachusetts Bay, the historical mixed stock analysis study was not designed to directly test this hypothesis.

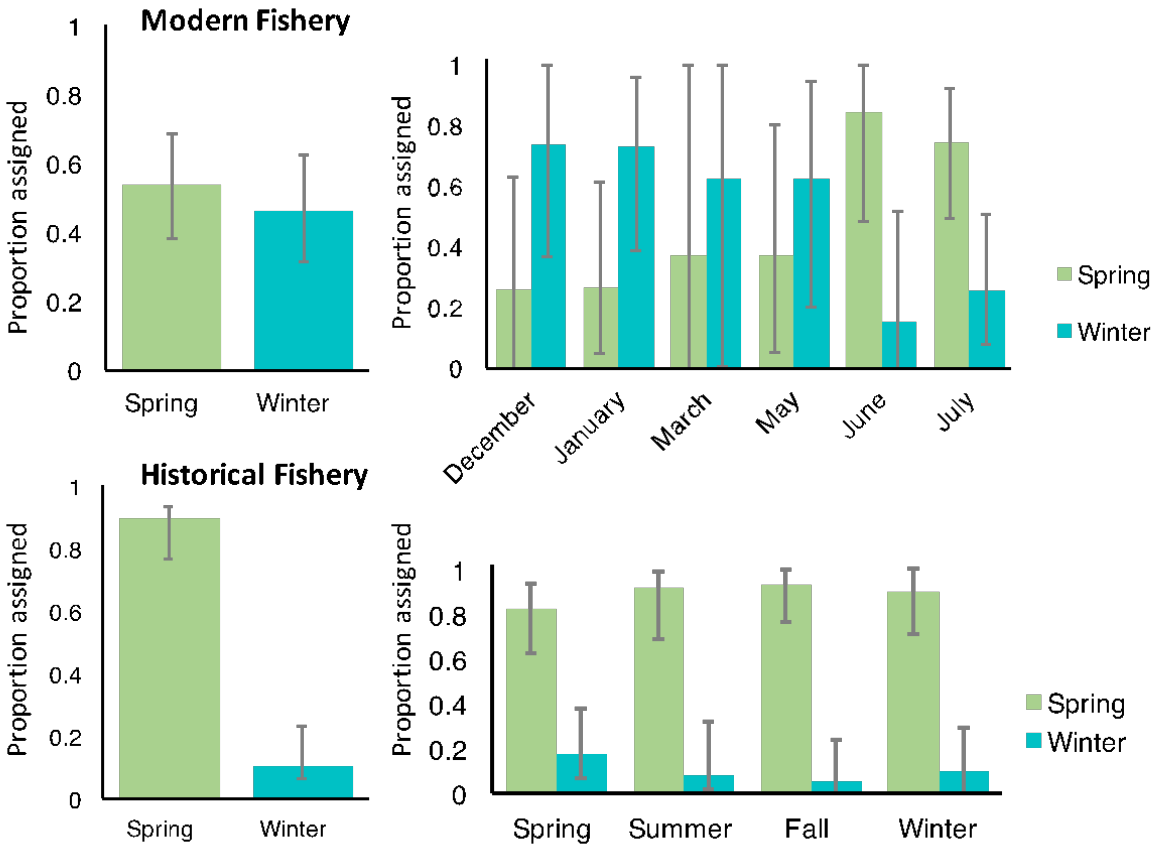

Figure 4.5. Comparison of proportional assignments to winter (blue bars) and spring (green bars) spawning groups of Atlantic cod (*Gadus morhua*) from mixed stock analyses of the modern commercial fishery (top panel) and the historical fishery (bottom panel). Overall (left 2 panels), the modern fishery is more evenly composed of spring and winter spawners (about 60:40), with a prevalence of spring spawners in June and July and winter spawners in December, January, March, and May (right panels). In comparison, the historical fishery consisted almost exclusively of spring spawners overall and in each season. This difference suggests a shift in the composition of the fishery from historical to modern times.

In further work reported in Kerr et al. (2018), genetic diversity, as measured by allelic richness (sample-size corrected number of microsatellite alleles per population), was found not to differ between historical and modern samples, with the exception of a slight reduction in the diversity of the modern spring-spawning population. This finding points toward change in allele frequencies, rather than to a decrease in genetic diversity, driving the genetic differences observed between historical and modern samples. Specifically, a shift in allelic composition away from spring-spawning genotypes and toward the winter-spawning genotypes is indicated by comparison of the historical and modern fishery.

Further work with higher resolution markers and finer scale sampling of fish in known spawning condition is needed to more clearly evaluate the structure of cod populations in the past and to determine whether genetically distinct population components have been lost. One shortcoming of the analysis of historical fishery samples is that reproductive status of these fish is unknown. This information gap can be resolved by using samples from the NOAA NEFSC bottom trawl survey archive. At the time of writing, an ongoing study out of Cornell University and the University of New Hampshire (N. Lou, N. Therkildsen, G. Clucas, A. Kovach) is focused on whole genome sequencing analysis of historical otolith samples collected in spawning condition with specific location data (statistical area). This study will compare the historical genomic signatures with those of modern populations.

Synthesis

In this concluding section, we synthesize findings reviewed in this chapter into a consensus view of population genetic structure for cod in US and adjacent Canadian waters, describe the interpretations from neutral and adaptive genetic markers and the implications of the genetic structure for management, and outline the remaining knowledge gaps and priority areas for future research.

Consensus Model of Population Genetic Structure

Cod spawning in US and adjacent Canadian waters have a population genetic structure that is more complex than recognized by the current US 2-stock model or the 3-stock model for the international region (Gulf of Maine, Georges Bank, western Scotian Shelf/Bay of Fundy), with heterogeneity within and connectivity between the currently defined stocks.

Two genetically distinct groups (spring and winter spawning populations) show temporal stability in their genetic structure from 2003-2015 in the western Gulf of Maine (wGOM). Spring spawners in the wGOM are genetically distinct from all other spawning populations in US and adjacent Canadian waters; in some genomic regions, wGOM spring spawners are more similar to Canadian populations of Northwest Atlantic Fisheries Organization (NAFO) management areas 4VsW (eastern Scotian Shelf) and 3Ps (St. Pierre Bank) than to US populations.

Cod spawning in the Cape Cod, Nantucket Shoals, and Great South Channel area are more genetically similar to winter spawning cod in the wGOM than they are to Georges Bank cod. Cod spawning in southern New England show genetic differentiation from Georges Bank, Cape Cod, and Gulf of Maine cod. Cod spawning on Georges Bank from east of the Great South Channel (western Georges Bank) to the Northeast Peak are genetically differentiated from cod spawning west of the Great South Channel in the Cape Cod area, southern New England, and the GOM. There is some variability among studies on the genetic group membership of cod spawning on western Georges Bank, and therefore the precise geographic location of the split between the Cape Cod /western GOM and Georges Bank is not yet resolved.

The fit of eastern GOM (statistical areas 511 and 512) into the population structure model is not yet well resolved because of the lack of spawning fish in this area. Analyses of nonspawning cod suggest there may currently be connectivity with western GOM and/or Georges Bank and that there may be inshore/offshore differences or differences between Penobscot Bay and area 512. There may be a mixture of fish using this area during the nonspawning season.

Cod spawning on Browns Bank share genetic similarities with those on eastern Georges Bank, suggesting exchange across the Northeast Channel.

Cod populations in US and adjacent Canadian waters are differentiated from the Canadian populations found farther north on the eastern Scotian Shelf (4VsW) and St. Pierre Bank (3Ps).

Synthesis of genetic data suggests the following groups, depicted in Fig. 4.6:

1. western GOM spring-spawning
2. western GOM winter-spawning and Cape Cod area
3. Georges Bank
4. southern New England
5. eastern Gulf of Maine
6. Browns Bank, western Scotian Shelf, and Bay of Fundy

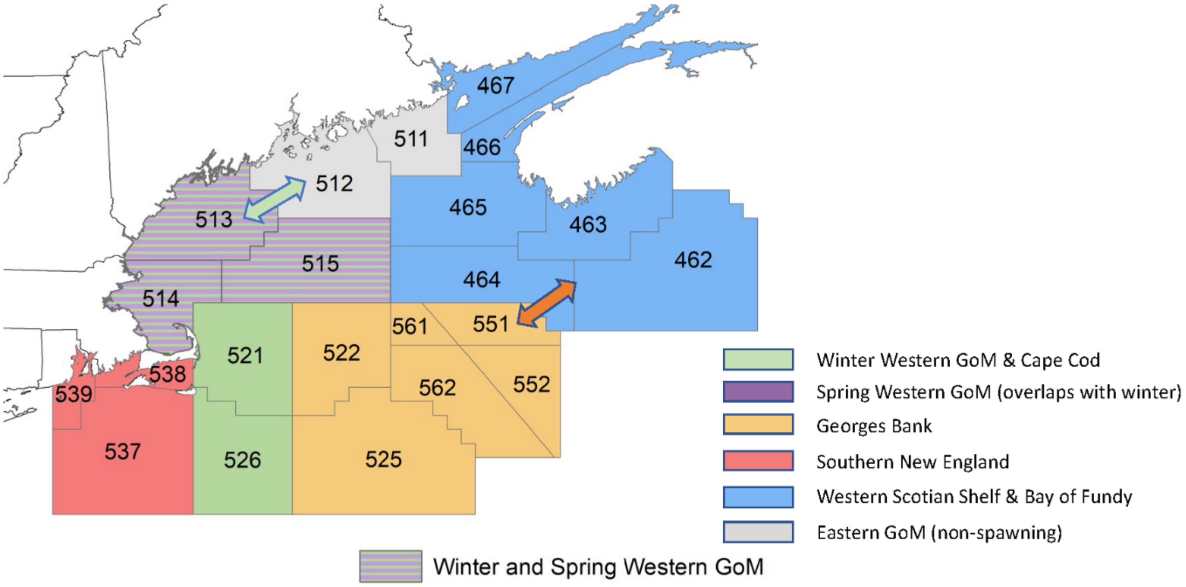

Figure 4.6. Model of Atlantic cod (*Gadus morhua*) population genetic structure in US and adjacent Canadian waters. Six genetically differentiated spawning groups are denoted by statistical area, based on known spawning locations as follows: (1) spring-spawning cod in the western Gulf of Maine (GOM; purple); (2) winter-spawning cod in the western GOM winter plus Cape Cod, Nantucket Shoals, and Great South Channel; (3) cod spawning on western Georges Bank, east of the Great South Channel, and the Northeast Peak; (4) southern New England waters; (5) eastern GOM, which may be a distinct population, although the data from spawning cod are lacking to resolve this; (6) western Scotian Shelf and Bay of Fundy. The purple/green hatched area comprising areas 513, 514, and 515 denotes the same spatial areas used separately by genetically distinct winter and spring spawning populations. Data from nonspawning cod in area 512 suggest connectivity with the western GOM winter spawning population (indicated by the green arrow). In addition, some level of connectivity exists between the western Scotian Shelf and Georges Bank via Browns Bank(areas 462 and464), as indicated by orange arrow).

Inference from Neutral and Adaptive Variation and Chromosomal Inversions

Differences among cod populations are driven largely by regions of the genome under the influence of natural selection (i.e., adaptive genetic variation). This distinction means that there are likely functional (ecological, life history, behavioral, or physiological) differences associated with the observed genetic variation.

The majority of the observed genetic differences occur within 4 chromosomal inversions, which also have been associated with population structure in other parts of the cod range, including Canadian, Icelandic, and Norwegian waters. Across broad spatial scales these chromosomal inversion regions have been associated with environmental variation in water temperature, salinity, depth, and oxygen, as well as with stationary/migratory ecotypes. Numerous genes associated with temperature-driven physiological processes have been identified in portions of these inversions. Although the exact functional role that these inversions play in differentiating among US cod populations is not yet understood, the highly elevated levels of differentiation in these regions suggest ecologically relevant differences in adaptations of cod to these environmental drivers.

- The inverted genomic regions differentiate US populations from more northern Canadian populations on the eastern Scotian Shelf (4VsW) and St. Pierre Bank (3Ps), although the western GOM spring spawners have genotypes intermediate to those of the Canadian populations and the rest of US samples.
- Similar linkage group genotypes between these northern Canadian cod and spring-spawning wGOM cod are also found in the Bay of Fundy and Browns Bank, suggesting cod in these areas may share similar adaptations to shared environmental or other drivers.

In addition to the 4 chromosomal inversion regions, other portions of the genome exhibit differences among these populations. These "outlier" regions contain genes that function in reproduction (female hormone receptors) and thermal tolerance (heat shock proteins). These genes may be targets of natural selection that underlie adaptive differences among these populations.

Neutral variation among populations is minimal. This finding suggests there may be some ongoing gene flow among populations or that the populations have not been differentiated long enough for neutral divergence to accumulate. Even very low levels of gene flow could eliminate neutral differentiation between populations while divergent selection can maintain large allele frequency differences even when levels of connectivity are relatively high. Adaptive differentiation in the face of gene flow is a phenomenon observed in other cod populations elsewhere in the range. Further, in marine fish populations with large effective population sizes, such as Atlantic cod, it takes a great deal of time for neutral genetic differences to occur among populations and much ecologically relevant population structure is undetectable by genetic markers. Given this insight, the observed differences among US and Canadian populations described in this chapter have likely been in place for centuries or more.

Implications of Cod Population Genetic Structure for Management

While the interpretation of the extensive, genomewide data summarized in this chapter is undoubtedly complex in the context of management, a few key take home messages readily emerge. First, while the genetic variation observed among populations in the GOM and surrounding waters is quite small as measured by the F_{ST} statistic, the observed structure is consistently detected across multiple, independent studies and marker types and is temporally stable, suggesting there are meaningful implications for population structure. Small but significant levels of genetic differentiation are common in marine fishes as a result of their high dispersal potential and large effective population sizes (Hauser and Carvalho 2008). Careful sampling design with temporal and spatial replicates, as across the many studies described in this chapter, therefore, confirm that the weak genetic structure is biologically meaningful. There is now a great deal of evidence that even very small F_{ST} values among marine fish populations can coincide with migration rates that are sufficiently low to suggest demographic independence (Waples et al. 2008).

The observed genetic variation provides strong evidence for a greater complexity of population structure than currently recognized by the 2-stock model. The 5 population genetic groupings put forth in the synthesis model are consistent with aspects of prior hypothesized stock structures (e.g., Wise 1963) and with data from other disciplines, including tagging, natural markers, early life history stages, and oceanographic currents.

It is not uncommon, especially in marine systems, for populations that are only weakly differentiated at neutral markers to exhibit differentiation at adaptive loci as a result of divergent selection pressures. This adaptive divergence underlies differential ecological adaptation and suggests there may be unique ecological and functional diversity among populations (Crandall et al. 2000; Funk et al. 2012). Adaptive genetic variation is a component of biocomplexity, which – along with morphological, behavioral, physiological, and life history variation – may be highly relevant to fishery management (Hilborn et al. 2003; Ruzzante et al. 2006; Therkildsen et al. 2013). Maintaining adaptive variation, along with other forms of biocomplexity, could be key to ensuring adaptive capacity or evolutionary potential (Nicotra et al. 2015; Mable 2019). Biocomplexity may also confer resilience, and loss of intraspecific genetic diversity has been linked to reduced population stability and reduced resilience to exploitation and changing environmental conditions (Hilborn et al. 2003; Schindler et al. 2010; Kerr et al. 2010a, 2010b). The latter may be particularly relevant to the Gulf of Maine, in light of its rapidly changing water temperatures and the finding of genetic polymorphisms that are linked to putative thermal tolerance and other temperature associated gene functions.

Remaining Knowledge Gaps and Future Research Needs

A vast amount of new high-resolution genomic data has recently come to bear on the topic of cod population structure, confirming results of earlier genetic studies and providing new insights about the complexity of biological population structure. While these efforts reveal a clear consensus view, a few knowledge gaps remain. Firstly, the level of connectivity between western Georges Bank (i.e., the area east of the Great South Channel) and the Cape Cod area is yet not fully resolved. Further, the precise geographic location of the boundary between the Cape Cod/western GOM and Georges Bank populations is unclear (in the 68°W or 69°W area), because of small sample sizes on the east side of the Great South Channel in the studies to date. Resolving these uncertainties requires further research from samples of spawning cod in this region, obtained from multiple tows in additional years (i.e., beyond the ones reviewed in this chapter), with analyses to evaluate temporal variation. Additionally, knowledge gaps remain for the eastern GOM, from which modern spawning cod samples are unavailable to provide a picture of current genetic structure. Given the lack of spawning cod in this region today, results of an ongoing historical analysis using archived otoliths from cod sampled in spawning condition by the NOAA NEFSC trawling survey in the 1980s and 1990s will be informative for reconstructing the genetic composition of this region in the past. To more clearly identify the origin of cod that occur in this region during the nonspawning season today, further studies using mixed stock analyses with large sample sizes of both juveniles and adults collected from the Sentinel Survey and the NOAA NEFSC trawling survey are warranted.

The amount of mixing among the Bay of Fundy, Browns Bank, and northeastern Georges Bank requires additional study as well, as the measures of genetic similarity among these locations appears to vary from 1 year to the next (Puncher et al. 2021). This research should be combined with hydrodynamic data in order to elucidate the influence of annually changing water currents. Connectivity of these regions with the eastern GOM also warrants future study. Mixed stock analysis using juvenile samples collected in more locations in both US and adjacent Canadian waters would enhance our understanding of the connectivity among the stocks.

Lastly, it may become necessary to develop tools to aid assessment of sympatric winter and spring spawning western GOM cod and possibly other populations that may occur in mixed stocks. To this end, it would be beneficial to use highly informative SNP markers (both adaptive and neutral) to develop a robust genetic screening assay.

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5. LIFE HISTORY

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Abstract

Life history traits often define stock structure because of their relevance to population productivity. Such phenotypic traits helped establish the 2 Atlantic cod (*Gadus morhua*) management units during the 1970s. Here, we accessed a bottom trawl time series, 1970-2017, to examine these life history traits: abundance and distribution, size at age 2, and age and length at maturity. During this 48-year period, cod abundance declined, and its distribution contracted within each management unit. Cod size and maturity differed between the 2 management units with 4 notable deviations: (1) size difference between units eroded over time as Gulf of Maine fish have become larger and Georges Bank fish smaller; (2) both length and age at maturity declined early in the 48-year period, but coherent spatial clusters were identifiable throughout the time series; (3) both growth and maturity rates indicated mixing of fish between the southern part of the Gulf of Maine management unit and the Great South Channel portion of the Georges Bank management unit; and (4) there were persistent differences in growth and maturity between western and eastern portions of the Georges Bank unit. At a broad-scale, these life history traits support at least 2 management units, but the variation of traits within units and apparent mixing of traits between units raise questions about stock numbers and boundaries. Continued monitoring is warranted to determine if these traits remain dynamic over time and space.

Introduction

Many marine species have multiple, fine-scale subpopulations, each with varying levels of productivity and exploitation rates, requiring management measures that address this biocomplexity (Altukhov 1981; Ricker 1981; Cadrin et al. 2014). Atlantic cod (*Gadus morhua*) in US waters has been described as a metapopulation consisting of multiple subpopulations and many finer-scale spawning components (Smedbol and Stephenson 2001; Zemeckis et al. 2014). Scientific uncertainty related to cod stock structure has been identified as a key factor contributing to difficulties in managing the rebuilding of cod populations in US waters (Annala 2012; NEFSC 2017).

Life history traits, such as distribution, growth, and maturation, provide direct insights into the productivity and resilience of fish stocks. Because collecting life history information is already a part of fishery monitoring programs, these data are typically available to inform an interdisciplinary review of a species' stock structure (McBride 2014a). The current 2-unit management model for cod in US waters was based, at least in part, on standardized trawl survey results that depicted distribution, abundance, growth, and maturity within the Northwest Atlantic Fisheries Organization's [NAFO] Divisions 4, 5, and 6 (i.e., Gulf of Maine, NAFO 5Y; Georges Bank, 5Z; New York Bight, 6A; Canadian waters of the Gulf of Maine, 4X) (see Chapter 2 this volume, for description of areas). For example, in terms of distribution, Serchuk and Wood (1979) concluded from the near absence of juvenile cod in survey tows from Block Island, RI, to Cape Hatteras, NC, that the cod from that area were not self-sustaining and likely part of the Georges Bank management unit (e.g., a migratory component). In terms of growth, Penttila and Gifford (1976) reported a significant difference in the mean lengths-at-age for young cod collected in 3 areas: the Gulf of Maine, Georges Bank, and off Cape Cod/southern New England. In terms of maturity, Livingston and Dery (1976) reported differences in age at maturity between Gulf of Maine, Georges Bank, and Browns Bank (NAFO unit 4X). Together with other information about traditional fishing areas, tagging studies, parasite infestation, and differences in spawning times, it was concluded that minimal exchange of cod occurred between the Gulf of Maine and Georges Bank, but extensive mixing occurred between Georges Bank and in the southern New England/Mid-Atlantic region (Serchuk and Wood 1979; Serchuk and Wigley 1992; Zemeckis et al. 2014).

Subsequently, changes in Atlantic cod life history traits have been noted. The spatial distribution of cod offshore from the US Mid-Atlantic seaboard north through the Gulf of Maine and Canadian waters has contracted since the 1960s (Begg et al. 1999; Zemeckis et al. 2014; NEFSC 2017). In the Gulf of Maine, the distribution of cod has become concentrated in its southwestern portions for several decades now (Ames 2004; NEFSC 2017), while on Georges Bank, an apparent gap in distribution has emerged between the eastern and western portions of the Georges Bank management unit (Begg et al. 1999; Zemeckis et al. 2014).

Although spawning and genetic stock structure will be addressed in separate chapters (Chapters 3 and 4, both this volume), these aspects help explain the spatial and temporal metapopulation structure of cod (Zemeckis et al. 2014). Historically, cod spawned along coastal Maine, but many of these spawning components were extirpated by the 1940s leaving very low cod abundance in its wake (Ames 2004; NEFSC 2017). The western Gulf of Maine consists of genetically distinct winter and spring-spawning subpopulations (Kovach et al. 2010) with peak spawning occurring in November-December and May-June, respectively (Berrien and Sibunka 1999). Both subpopulations spawn near the 50 m isobath primarily in Massachusetts Bay and Ipswich Bay (Siceloff and Howell 2013; Dean et al. 2014; Zemeckis et al. 2019). The northeast peak of Georges Bank is considered the most productive and consistent offshore cod spawning site, where spawning occurs at 20-90 m depth and peaks seasonally during January-April (Colton and Temple 1961; DeCelles et al. 2017). Spawning also occurs in the western portion of the Georges Bank management unit in the areas around the Great South Channel, Cape Cod, and Nantucket Shoals at 20-55 m depth and peaks seasonally during November-December (Berrien and Sibunka 1999; DeCelles et al. 2017). Cod spawning also occurs in southern New England around Coxes Ledge with a peak in spawning from December to February (Berrien and Sibunka 1999).

Investigations of growth have been examined by using otolith-derived ages and from tag-recapture data. Begg et al. (1999) found a persistent pattern of slow growth for cod from Gulf of Maine, faster growth on western Georges Bank, and fastest growth on eastern Georges Bank by examining otolith-derived ages from1970 to 1997. Tallack (2009, 2011) used the tag recapture method and reported similar results: tagged cod recaptured from 2003 to 2008 had faster growth rates but smaller asymptotic size on Georges Bank and slower growth but largest size in the Gulf of Maine. Tallack (2009) also reported evidence that fish tagged near Cape Cod were smaller and younger and appear to disperse with age into the eastern portion of Georges Bank and the Gulf of Maine.

Investigations of maturity have also continued to show spatial structure, as well as temporal variability. For example, Begg et al. (1999) reported that cod from the Georges Bank management unit matured at younger ages and greater lengths than Gulf of Maine cod, and O'Brien (1999) reported that the age at maturity declined for both stocks from 1970 to 1998 (see also Hunt 1996; Barot et al. 2004; Miller et al. 2018). Investigations into maturity have left finer-scale variability relatively unexplored.

As we approached this reevaluation of Atlantic cod stock structure, we noted 3 issues to address. First, Annala (2012) identified a need to update the available data, which we do here, up to 2017. Second, comparisons of model-based growth coefficients by Begg et al. (1999) and Tallack (2009, 2011) may be correlated with different maximum length estimates for different areas (i.e., the Brody growth coefficient [k] versus an asymptotic length [L_∞]) and are simply difficult to fit based on small samples of large fish (L_∞). Third, a few studies report finer-scale analyses, such as comparing cod life history traits between eastern and western Georges Bank (Penttila and Gifford 1976; Begg et al. 1999; Tallack 2009), whereas others compare only between current management units without scrutiny of finer-scale geographic variation. Although these situations may arise from data limitations beyond the control of the investigators, we attempt to mitigate them in our reevaluation of stock structure as outlined below.

This study draws on the NOAA Northeast Fisheries Science Center bottom trawl survey as a single, updated source of data to evaluate cod distribution, abundance, growth, and maturity across a latitudinal range from 35°N to 45°N between 1970 and 2017. Although other long-term surveys exist, (e.g., US state waters, Fisheries and Oceans Canada [DFO] federal waters), coverage varied both spatially and temporally, which precludes any straightforward pooling of these data sources. In analysis, we avoided model-based estimates of growth and instead used direct measures of size at age 2, as originally used by Penttila and Gifford (1976). To examine fine-scale structure, we post-stratified growth and maturity data into statistical areas arranged hierarchically within the Georges Bank and Gulf of Maine management units. These findings update aspects of cod life history for comparison and integration with the findings from other stock identification tools used in this Technical Memorandum (e.g., tagging, genetics, natural markers), working towards an interdisciplinary review of cod stock structure in US waters.

Methods and Materials

Life History Sampling

Several surveys were considered for evaluation of Atlantic cod life history, as discussed in the section on "Overview of the approach" below. However, pooling of multiple surveys presented complications that we choose to avoid in this initial review. Here, cod were collected from a single fishery-independent bottom trawl survey for groundfish operated by NOAA's Northeast Fisheries Science Center (hereafter referred to as "the NOAA bottom trawl survey"). This survey operated across the geographic range of interest for defining cod stock boundaries: throughout Northwest Atlantic Fisheries Organization areas 5Z (southern New England and Georges Bank) and 5Y (Gulf of Maine), in parts of 4X (Bay of Fundy, Scotian Shelf), as well as further south (6A-C; Block Island Sound to Cape Hatteras), as described in Chapter 2 (this volume). Tows were assigned with a stratified, random sampling design within inshore and offshore waters (Politis et al. 2014), and latitude and longitude positions reported here are from the beginning of the trawl tow.

Although this survey began in the 1960s (Reid et al. 1999), sampling for age and maturity began in 1970 (Penttila and Gifford 1976). Sampling stopped in 2 Canadian areas during this period: parts of the Scotian Shelf in 1979 and Browns Bank after 1987. As a result, while data from these specific statistical areas of Canada are included in initial geographic plots, they are not included in subsequent cluster analysis because comparisons across the entire period are not possible. We end sampling in all other areas with 2017, resulting in a 48-year time series. Sampling occurred twice each year: spring (approximately March-May) and fall (September-November). Specific dates and number of tows vary by season and year (Table 5.1).

Catch data (number per tow and kg per tow) of cod were recorded for each tow. Individual fish lengths (fork length; 1 cm) were measured for at least a subsample from large tows (Reid et al. 1999). Age of individual cod, in years, was determined by using otoliths to assign an age based on the number of complete annuli and the edge type (Penttila and Dery 1988). Sex and maturity of individual cod were assigned by visually inspecting the dissected gonad following Burnett et al. (1989).

Table 5.1. Specific dates and number of tows per season (spring, fall) and year (1970-2017) by the Northeast Fisheries Science Center's bottom trawl survey.

Year	Spring surveys					Fall surveys			
	Start date	End date	Tows[1]	Tows[2]		Start date	End date	Tows[1]	Tows[2]
1970	3/12	4/29	342	288		9/5	11/20	312	301
1971	3/9	5/5	419	311		9/29	11/19	334	310
1972	3/8	4/27	366	306		9/28	12/5	646	646
1973	3/16	6/4	495	495		9/26	11/19	451	451
1974	3/13	5/4	416	416		9/23	11/10	379	379
1975	3/4	5/11	305	270		10/7	11/18	406	406
1976	3/4	5/7	384	384		9/28	11/22	340	340
1977	3/19	5/19	355	355		9/26	12/15	419	419
1978	3/21	5/24	397	397		9/7	11/21	556	556
1979	3/22	5/11	477	477		9/13	11/18	600	588
1980	3/18	5/7	468	468		9/18	11/15	420	420
1981	3/19	5/24	395	395		9/16	11/7	421	416
1982	3/11	5/8	443	420		9/14	11/11	449	411
1983	3/7	4/30	428	401		9/13	11/9	476	407
1984	3/2	4/24	407	391		9/11	11/6	433	337

Tows[1]: the total number of tows completed

Tows[2]: the final number of tows used for plotting abundance after quality control

Table 5.1, continued. Specific dates and number of tows per season (spring, fall) and year (1970-2017) by the Northeast Fisheries Science Center's bottom trawl survey.

1985		2/26	4/12	391	371		9/10	11/15	368	339
1986		3/4	4/27	368	361		9/14	11/5	364	352
1987		3/24	4/28	349	334		9/11	11/5	335	316
1988		3/5	4/20	321	314		9/13	10/27	326	307
1989		2/28	4/13	299	291		9/11	11/9	342	321
1990		3/6	4/17	322	311		9/12	10/24	345	332
1991		3/6	4/16	333	324		9/10	10/24	354	328
1992		3/3	4/16	326	307		9/9	10/27	353	324
1993		3/9	4/29	329	319		9/8	10/26	339	325
1994		3/1	4/27	345	326		9/7	10/27	341	331
1995		3/7	4/27	335	325		9/6	10/26	360	326
1996		3/6	4/29	350	335		9/10	10/31	365	320
1997		3/4	4/23	345	327		9/4	10/30	369	327
1998		3/3	4/20	374	360		9/22	11/9	374	332
1999		3/2	4/22	329	322		9/21	11/10	346	339
2000		3/16	5/3	333	324		9/6	10/20	337	329
2001		2/28	4/30	325	317		9/5	10/22	339	330
2002		3/6	4/25	331	317		9/4	10/25	342	321
2003		3/6	4/27	332	321		9/7	10/31	336	322
2004		3/3	4/21	332	326		9/10	10/27	319	311
2005		3/4	4/21	334	329		9/7	11/4	332	322
2006		3/8	4/19	344	339		9/6	10/25	367	357
2007		3/8	4/27	363	355		9/5	10/31	349	342
2008		3/7	5/3	344	335		9/3	11/13	441	341
2009		2/27	5/9	436	369		9/13	11/18	381	328
2010		2/28	5/2	403	372		9/9	12/3	374	334
2011		3/3	5/10	382	340		9/6	11/14	374	326
2012		2/29	5/3	396	350		9/7	11/10	396	363
2013		3/5	5/8	407	377		9/6	11/19	392	365
2014		3/31	5/31	314	286		9/10	11/12	441	359
2015		3/14	5/6	401	372		9/2	11/5	408	370
2016		4/8	6/6	375	351		9/9	11/9	396	378
2017		3/7	5/12	385	353		10/20	11/18	143	130

Data Processing

Although changes (both vessel and gear related; e.g., Azarovitz 1981) to the survey have taken place, no conversion calculations were performed on the raw data. In terms of the decommissioning of the NOAA Ship Albatross IV in 2008 and transfer of operations to the NOAA Ship Henry Bigelow, calibration tows between these vessels demonstrate that the latter catches more fish that are smaller and younger fish than the former (Brooks et al. 2010). Tows were not used if they failed quality control metrics (i.e., Station-Haul-Gear criteria > 136 or Type-Operational-Gear-Acquisition criteria > 132; Politis et al. 2014).

Data for the 48-year period were pooled into eight 6-year periods (i.e., 1970-1975, etc.) to balance sample size with temporal discreteness. This convention of the same 6-year periods was followed for abundance, growth, and reproductive analyses.

Size at age 2 was used as a proxy for growth during the immature or early mature phase. A total of 14,042 age-2 cod were caught north of 35°N, with at least 3,200 individuals of either sex in each season, and only 80 without sex determined (Table 5.2). Median adjusted size at age 2 was about 8 cm larger in the fall than spring, so seasons were always kept separate.

Table 5.2. Adjusted spring and fall fork length (cm) quintile boundaries for age-2 Atlantic cod (*Gadus morhua*) males and females collected by the NOAA bottom trawl surveys, 1970-2017. Number of individuals = n.

Season	Sex	0%	20%	40%	60%	80%	100%	n
Spring	Male	16.5	31.5	36.5	40.3	44.4	64.0	3701
Spring	Female	13.8	30.8	35.4	39.8	44.6	59.7	3260
Fall	Male	22.7	38.3	43.2	47.4	52.4	69.2	3605
Fall	Female	23.7	38.8	43.2	47.6	52.7	72.0	3396

Differences in survey timing could introduce bias in determining size at age 2, because such difference could vary by weeks within a season and between regions and years. To adjust for this, the fish age was increased above 2.0 by the day of the year, and the resulting quotient of size and fractional age was multiplied by 2.25 for fish collected in spring and 2.75 for fish collected in fall. This adjustment created an index of size at age 2 for April 1 and October 1, respectively. Additional bias in age resulting from different spawning seasons – spring versus fall (Chapter 3, this volume) – and its effect on size at age could not be accounted for with the methods used here.

Hunt (1996) reported sexual dimorphism in Atlantic cod, but females did not become consistently larger than males until after age 3. Here, the mean difference in adjusted size at age 2 between sexes was small, ~0.5 cm in both seasons, but statistically significant ($P_{spring} = 0.02$ vs. $P_{fall} = 0.03$; 2-sample Student's t-test with the Welch approximation for heteroscedasticity of variance as indicated by Levene's test for spring). However, the direction of this difference was not consistent, as the spring mean of females was smaller than males (37.6 vs. 38.1 cm), but the fall mean of females was larger than males (45.6 vs. 45.2 cm). In terms of transparency, sexes were kept separate for initial spatial analysis (i.e., descriptive maps), but all 14,042 age-2 fish were pooled later to achieve adequate sample sizes for season-specific summary statistics and corresponding cluster analysis of size at age 2.

Finally, individual age-2 fish were assigned to growth quintiles (smallest to largest sizes at age 2) using all years of data, 1970-2017, but partitioned by sampling season and sex (Table 5.2). Quintiles were assigned color-based growth rates, from purple being the smallest or slowest growing quintile to red being the largest or fastest-growing quintile (Fig. 5.2), to be used later for spatial analysis.

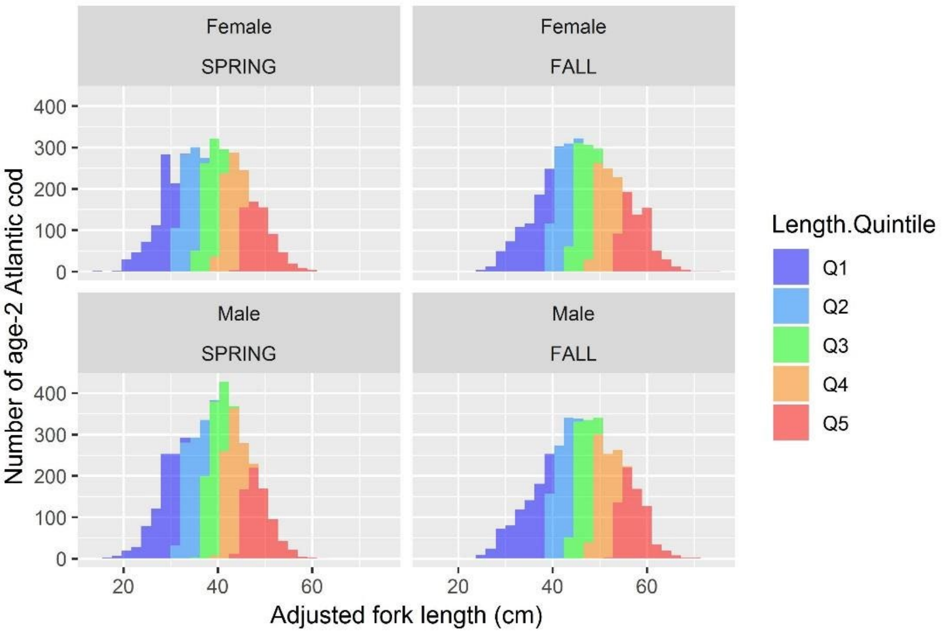


Figure 5.1. Partitioning of size along a quintile gradient: slowest (purple [or dark blue]) to fastest (red) growing age-2 Atlantic cod (*Gadus morhua*) collected by the NOAA bottom trawl survey, 1970-2017. Fork length was adjusted for date of capture, as described in the text. See Table 5.2 for specific boundary values for each quintile.

We examined female cod collected by the spring NOAA bottom trawl survey for maturity data. These totaled 14,710 individuals ranging from 5 to 150 cm fork length and from 0 to 17 years old (Table 5.3). Fish were assigned a maturity class by visually inspecting the gonads at sea (Table 5.3), but for these analyses, the data were collapsed into 2 classes (i.e., a binary response: either immature [1 immature class] or mature [the remaining classes]).

No spatial segregation of immature or mature females in either season was identified. Therefore, these data were fitted to a generalized linear model by using a logit link function, and the resulting coefficients were used to calculate the median length at maturity (L_{50}) and age at maturity (A_{50}) as well as the associated standard errors, by using dose.p from R's MASS package (R Development Core Team 2014). All other data wrangling and statistical analyses were computed with R software, as well.

Spatial Analysis

Abundance, growth, and maturity were first plotted in a descriptive manner and mapped without consideration of past or current stock boundaries (Fig. 5.2). Abundance data were plotted without regard to sex for both biomass per tow in each season (Figs. 5.3A, B) as well as number per tow (Figs. 5.3C, D). Initially, adjusted size-at-age-2 data were plotted at the individual fish level separately by seasons and sexes, and maturity parameters were estimated for females in spring aggregated at 1° × 1° latitude-longitude resolution.

For cluster analysis, data were aggregated by statistical areas, which are used for reporting fish landings (Halliday and Pinhorn 1990; Chapter 2, this volume). These were assigned an "Area_stock," label, a combination of the numerical statistical area used for reporting landings and an abbreviated geographic description of this area and how it fits into the current management units for cod. For example, primary Canadian statistical reporting areas are in the 400s, US areas included in the current stock assessment areas are 500s and 600s. The descriptive abbreviations identify the Scotian Shelf (SS), Bay of Fundy (BF), Gulf of Maine (GOM), Georges Bank (GB), southern New England (SNE), and the New York Bight (NYB), with some areas subdivided as north (No.), south (So.), central (Ce.), west (W), and east (E). Some adjacent statistical areas were combined because of low sample sizes. A map of these statistical areas is depicted in Fig. 5.2 (see also Chapter 2, this volume).

Table 5.3. Number of female Atlantic cod (*Gadus morhua*) collected in spring NOAA bottom trawl surveys, 1970-2017. Data are organized by fork length bins (left, 0 = 0-9 mm), or whole age (right, years), and maturity class (Immature [I], Developing [D], Ripe [R], Ripe and running [U], Spent [S], and Resting [T]).

Length (10 cm)	Maturity Class					
	I	D	R	U	S	T
0	2	0	0	0	0	0
1	409	2	0	0	0	3
2	1175	17	0	0	0	56
3	1282	53	7	1	6	438
4	1069	211	27	1	48	1360
5	429	259	58	3	180	1954
6	145	237	67	4	260	1638
7	20	185	70	4	222	1015
8	3	183	41	14	196	509
9	0	107	30	10	91	232
10	0	42	18	2	52	105
11	0	28	10	2	24	44
12	0	8	2	0	10	16
13	0	3	1	0	3	6
14	0	0	0	0	1	0

Age (yr)	Maturity Class					
	I	D	R	U	S	T
0	2	0	0	0	0	0
1	1290	9	0	0	0	27
2	2006	161	13	0	34	1020
3	840	237	56	5	241	2403
4	287	305	92	7	269	1995
5	55	276	57	6	230	1020
6	14	137	48	7	129	466
7	5	87	33	4	76	208
8	1	40	10	7	49	88
9	1	33	8	1	29	35
10	0	11	7	3	13	28
11	0	14	3	1	7	9
12	0	6	1	0	6	6
13	0	1	0	0	2	3
14	0	3	2	0	3	3
15	0	1	0	0	0	4
16	0	1	0	0	2	0
17	0	0	0	0	0	1

These statistical areas form the basis of cod stock assessments because they represent the fundamental unit for which much of the fisheries data are collected. Presently, cod are assessed and managed domestically as 2 stocks in the United States in the following statistical areas: the Gulf of Maine (areas 511-515) and Georges Bank (areas 537-539, 521, 522, 525, 526, 551, 522, 561, 562). These 2 sets of the "500" statistical areas are referred to later in the text as "management units," to reflect that they are the current, status quo depictions of stock structure in the United States. In addition to these geographic units used in the United States, US and Canadian fisheries agencies annually complete a separate, bilateral assessment of eastern Georges Bank only (areas

551-2, 561-2) through the Transboundary Resource Assessment Committee (TRAC). The outcomes of this assessment are considered in the domestic management process of the full Georges Bank unit. In addition, catches of cod from NAFO area 6 (statistical areas in the 600s) are included in the assessment of the full Georges Bank management unit described above (e.g., NEFSC 2012).

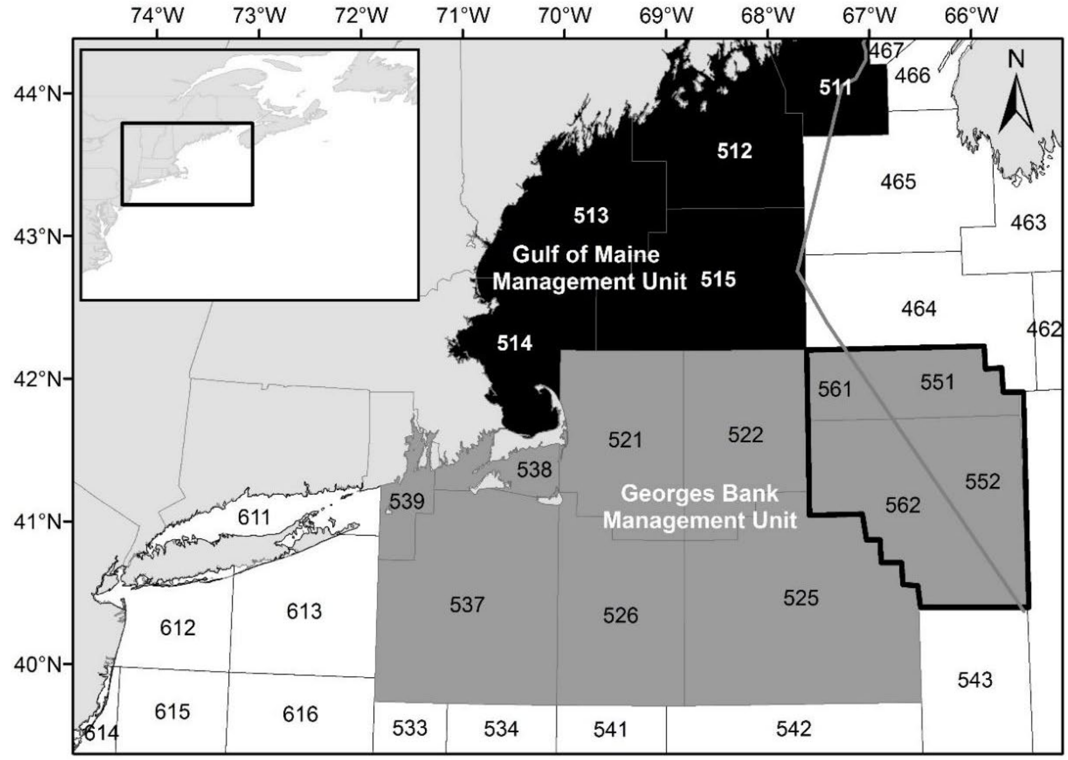


Figure 5.2. Current management units applied to Atlantic cod (*Gadus morhua*) in US waters and the enumerated statistical areas. The eastern portion of Georges Bank (outlined in bold) is managed jointly between the United States and Canada as a transboundary resource, and the Hague Line, delineating US from Canadian marine territory, is indicated as a gray chevron.

Divisive cluster analysis (DIANA), using the "cluster" and "dendextend" packages in R, tested how well the growth and maturity data conform to the cod stock boundaries used in the US stock assessment and management process (e.g., Cope and Punt 2009). "Growth" phenotypes, by statistical area and season, were clustered by using the mean and standard deviation of the adjusted size at age 2. "Maturation" phenotypes, by statistical area and considering both length and age at maturity, were clustered using the median and standard error of the estimate. Clusters were performed for 2 periods: (1970-1975 and 2012-2017) to determine the stability of this phenotypic stock structure at the initial and most recent periods of the NOAA bottom trawl survey time series.

Sample size was also considered here but as a selection criterion and not as a cluster variable because small sample sizes could lead to an inaccurate or imprecise estimate. For growth clustering, only statistical areas with 5 or more fish were used. For maturation clustering, only areas with a sample size > 30 were used.

Results

Distribution and Abundance

Spring distribution of cod ranged broadly offshore of the Delmarva peninsula and northward to Cape Cod, across Georges Bank, and well into the Gulf of Maine, including in Canadian waters (Fig. 5.3A). In fall, cod were rarely distributed west of 72°W or south of 40°N, and they were uncommon even on the southern flank of Georges Bank (Fig. 5.3B). Over time, the southern part of the spring distribution has contracted, with few cod observed south or west of Block Island Sound (approximately 41.3°N, 71.7°W) since the 1990s. Although biomass is presented in the text, there were no qualitative differences in patterns based on numbers of cod per tow (Figs. 5.3 C, D).

On Georges Bank, the distribution of cod has contracted over the period 1970-2017 and is now concentrated on the northeast peak. West of Georges Bank, from Cape Cod and into the Great South Channel area, there is a concentration of cod that is more contiguous with the southern Gulf of Maine than with Georges Bank. Both concentrations appear to have existed since the 1970s but are more obvious now that cod are less dense across the entire region in recent decades (Figs. 5.3-5.4).

On the US side of the Gulf of Maine, abundance has consistently been highest in the southwest part and lower in the northern part, particularly offshore of downeast Maine, and the open, central part of the Gulf of Maine. In Canadian waters, cod have been consistently present on the Scotian Shelf and in the Bay of Fundy; however, the disappearance of fish on Browns Bank, evident in the last 5 panels, 1988-2017, is an artifact created when sampling was stopped there in the 1980s.

In summary, during the last 5 decades, 1970-2017, the cod population distribution has become more aggregated, and is now primarily concentrated into 2 areas: (1) the southwest part of the Gulf of Maine, extending into the Great South Channel, and (2) on the northeast peak of Georges Bank.

Size at Age 2 – Descriptive

At a broad-scale, age-2 cod were distributed widely throughout the Gulf of Maine as well as across Georges Bank (Figs. 5.4-5.6). They occurred less frequently offshore of southern New England and further west (> 72°W) and south (< 40°N): mostly in spring, less so in fall; mostly in the first 6-year period, 1970-1975, and less so in later periods.

Age-2 cod were segregated by size along a general latitudinal gradient in the first 3 decades, approximately 1970-2000, but these spatial differences have diminished in recent years (Fig. 5.5 [spring data], Fig. 5.6 [fall data]). Early in the time series, the above average sizes of cod (orange-red) were mostly on Georges Bank and distributed along the Mid-Atlantic seaboard from Cape Cod to Cape Hatteras. The below average sizes of cod (purple-blue) were mostly distributed in the Gulf of Maine and on the Scotian Shelf and Browns Bank. Spatial size-segregation of age-2 fish between these 2 regions broke down sometime after 2000-2005, particularly stemming from the near absence of larger fish (red quintile) in any area. These patterns were evident for both males and females, plotted separately in Figures 5.5, 5.6.

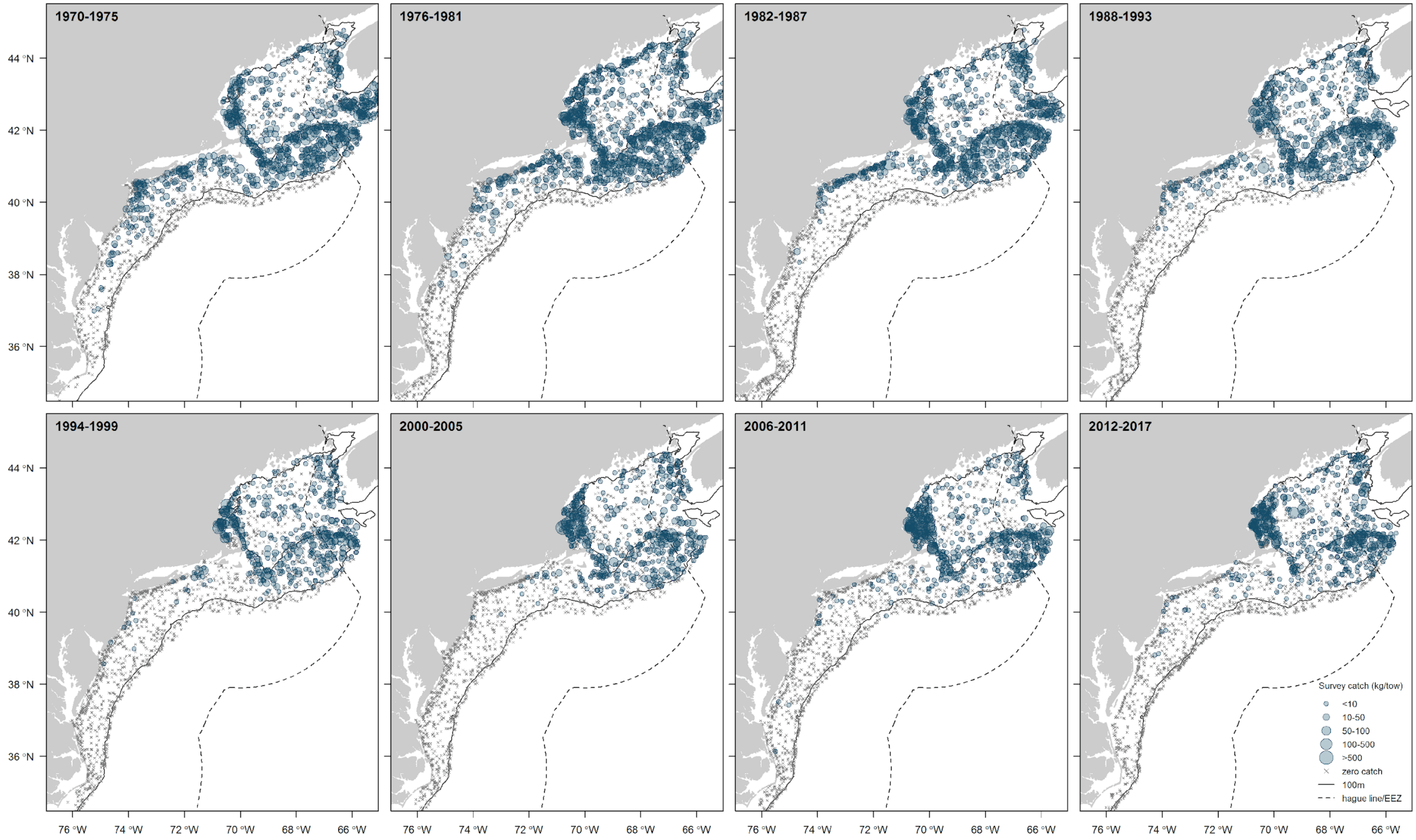


Figure 5.3A. Spring distribution and biomass (aggregate weight per tow) of Atlantic cod (*Gadus morhua*) during eight 6-year periods, 1970-2017, of the NOAA bottom trawl survey. See next page for fall data. The solid isobath = 100 m, and the dashed line delineates the 200 mile exclusive economic zone. Data for numbers per tow in spring are depicted in Fig. 5.3C.

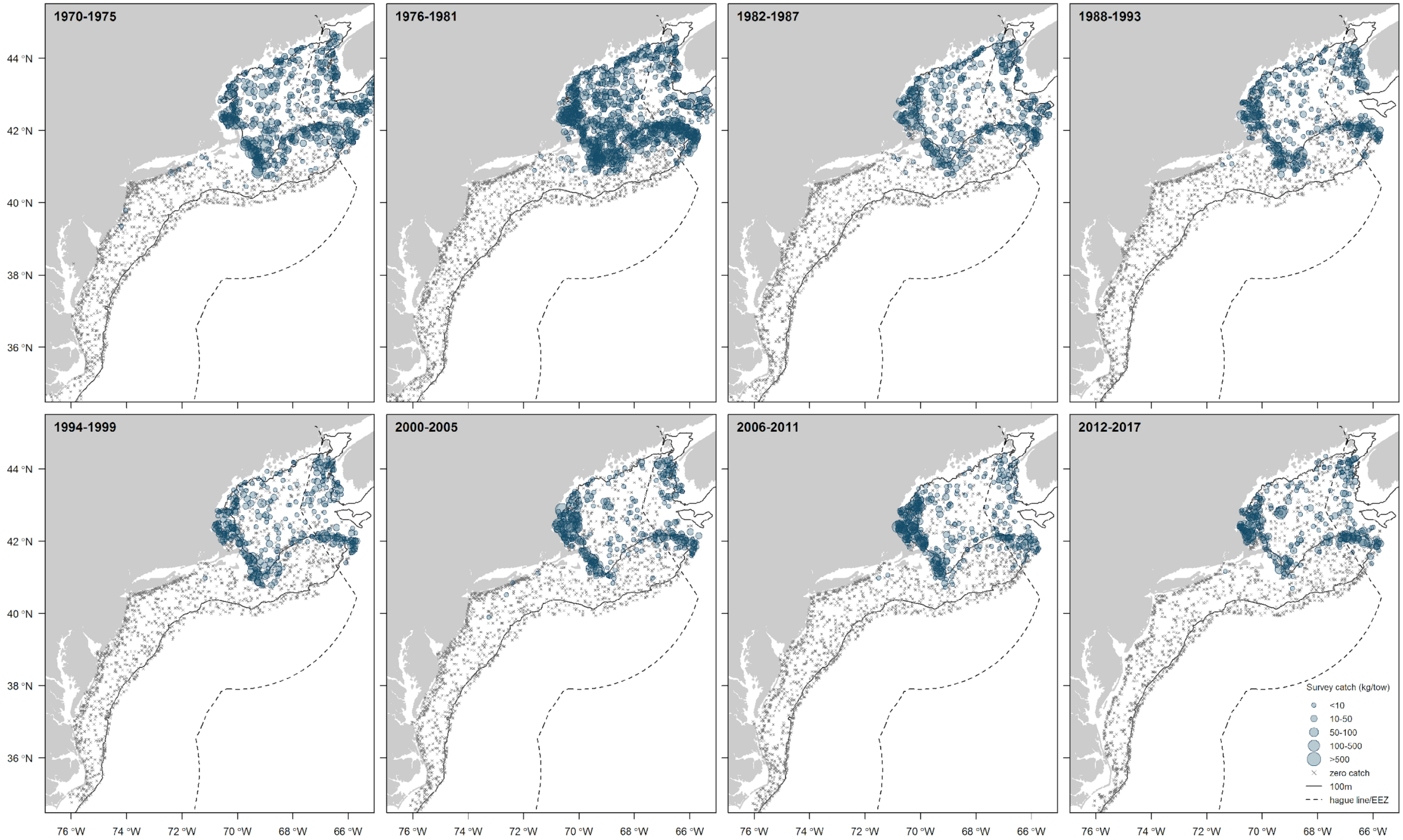


Figure 5.3B. Fall distribution and biomass (aggregate weight per tow) of Atlantic cod, (*Gadus morhua*) during eight 6-year periods, 1970-2017, of the NOAA bottom trawl survey. Data for numbers per tow in fall are depicted in Fig. 5.3D.

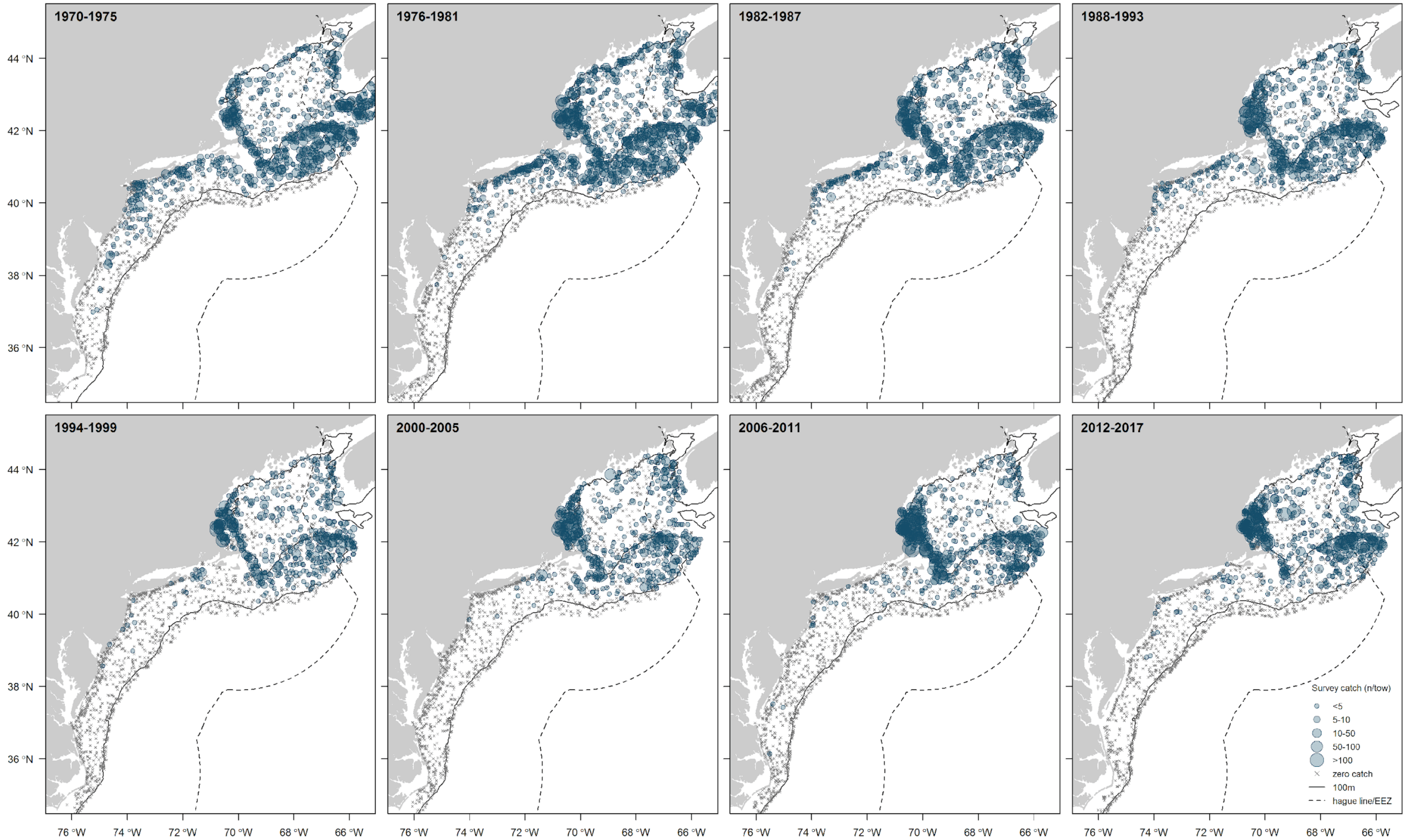


Figure 5.3C. Spring distribution and abundance (number per tow) of Atlantic cod (*Gadus morhua*) in eight 6-year periods, 1970-2017, of the NOAA bottom trawl survey. The solid isobath = 100 m, and the dashed line delineates the 200 mile exclusive economic zone. Spring biomass values are presented in Fig. 5.3A.

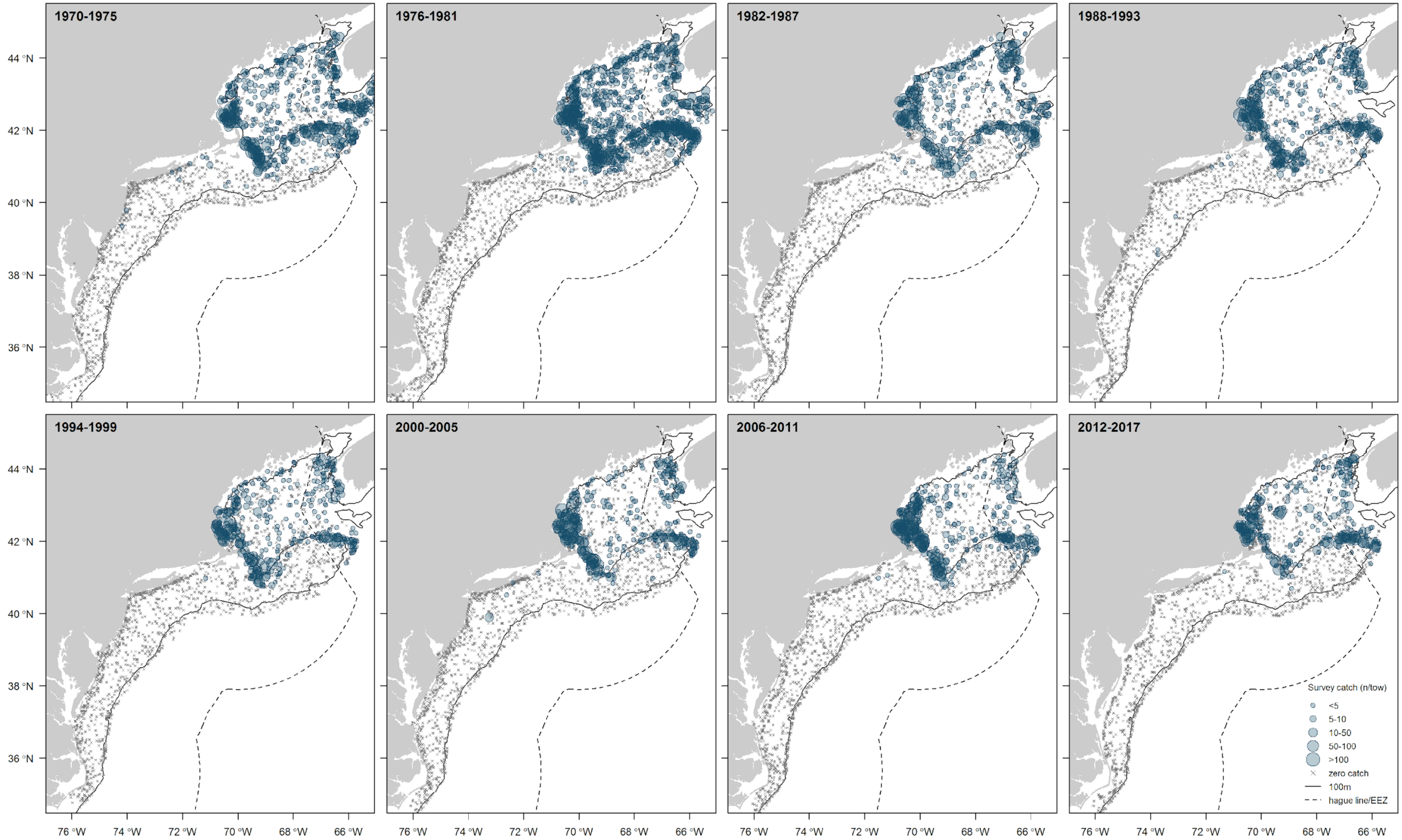


Figure 5.3D. Fall distribution and abundance (number per tow) of Atlantic cod (*Gadus morhua*) in eight 6-year periods, 1970-2017, of the NOAA bottom trawl survey. The solid isobath = 100 m, and the dashed line delineates the 200 mile exclusive economic zone. Fall biomass values are presented in Fig. 5.3B.

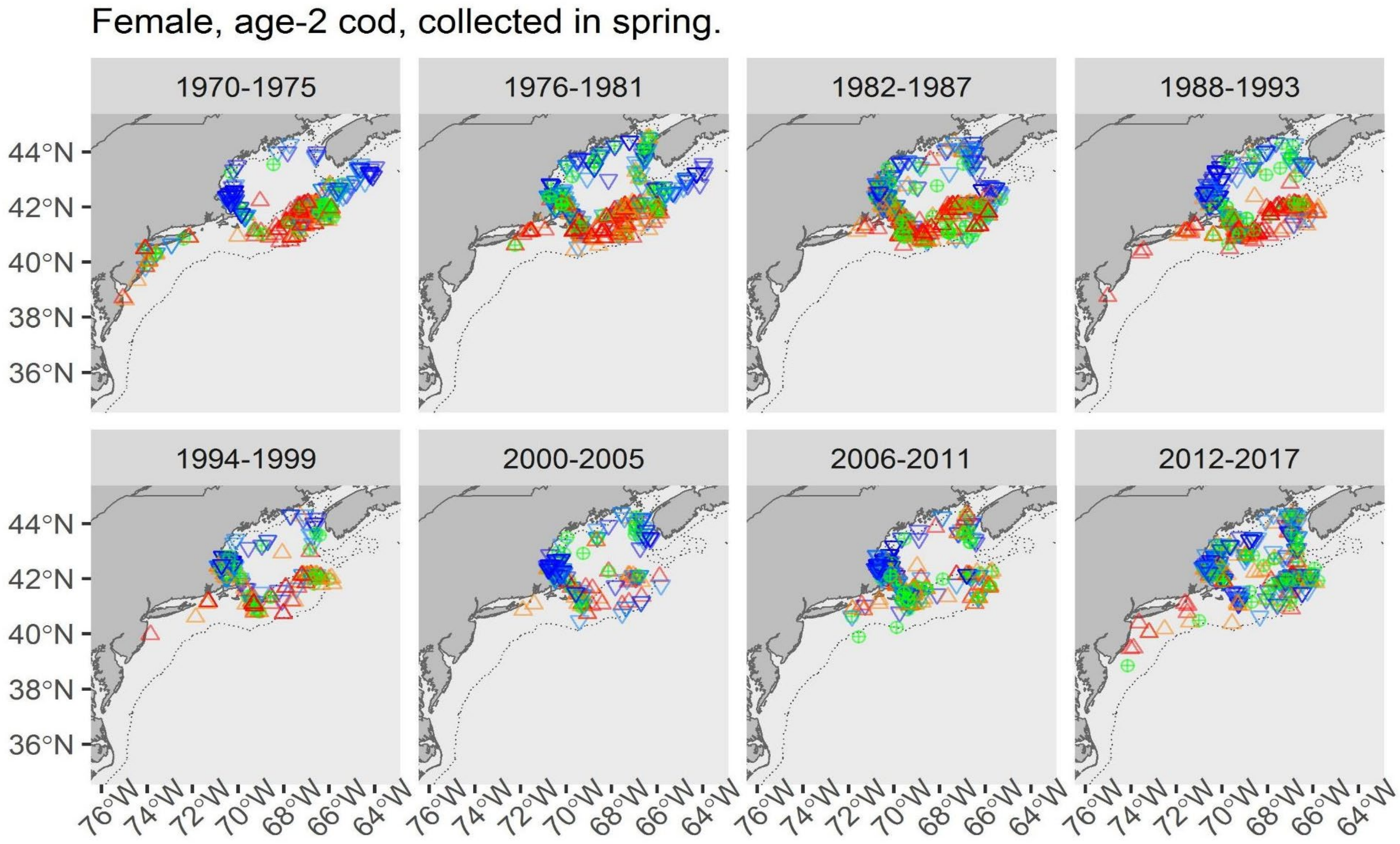


Figure 5.4A. Spring distribution of female age-2 Atlantic cod (*Gadus morhua*) grouped in eight 6-year periods, 1970-2017. Color coding is translucent to reveal overlay of points, using a color spectrum from Fig. 5.1 to indicate a size-at-age gradient. Smaller (purple-blue; quintiles 1-2) fish are also marked with upside-down triangles, medium (green; quintile 3) fish with a crossed-circle, and larger (orange-red; quintiles 4-5) fish with right side-up triangles. The dotted isobath = 100 m.

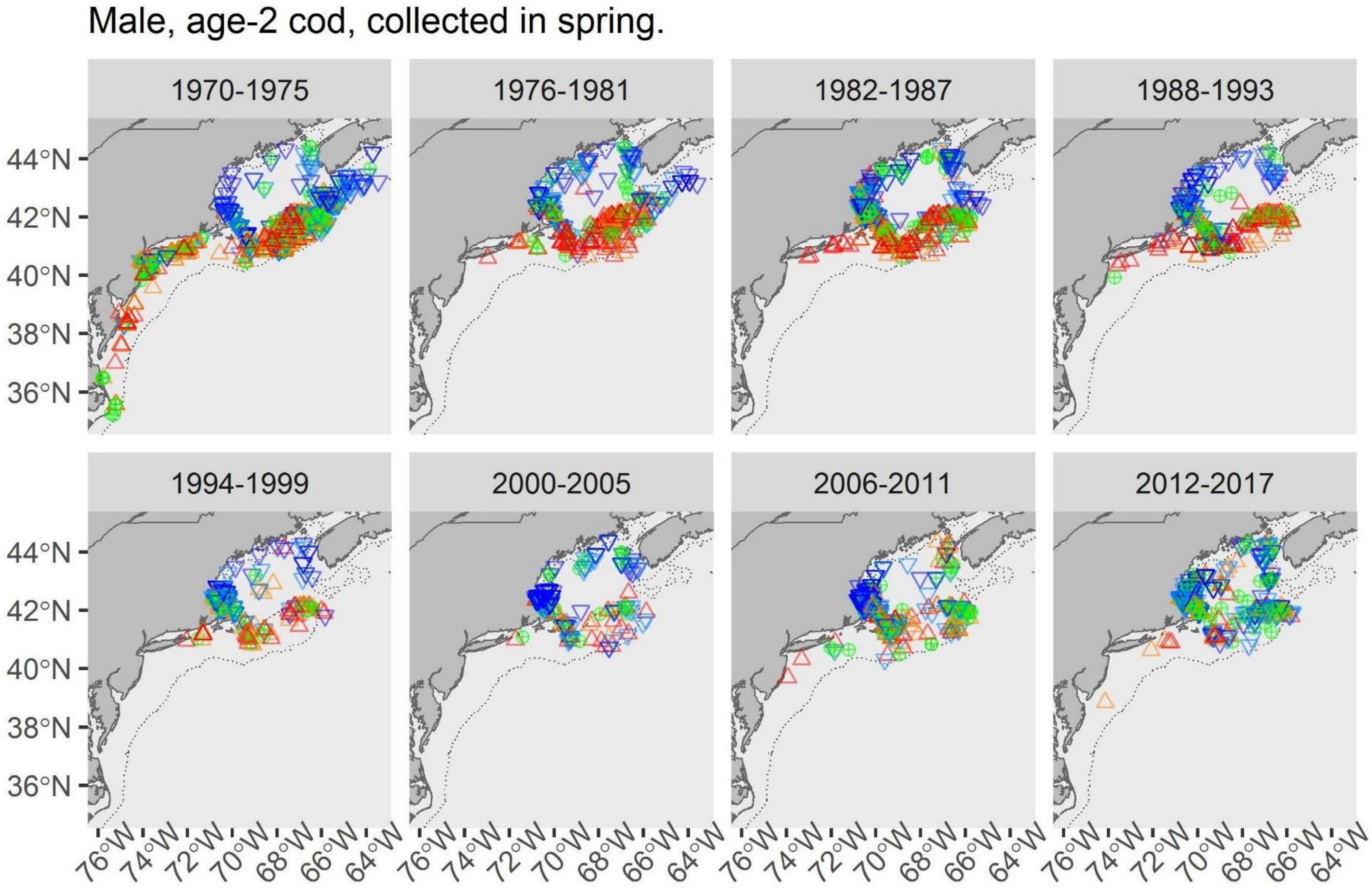


Figure 5.4B. Spring distribution of male age-2 Atlantic cod (*Gadus morhua*) grouped in eight 6-year periods, 1970-2017. Color coding is translucent to reveal overlay of points, using a color spectrum from Fig. 5.1 to indicate a size-at-age gradient. Smaller (purple-blue; quintiles 1-2) fish are also marked with upside-down triangles, medium (green; quintile 3) fish with a crossed-circle, and larger (orange-red; quintiles 4-5) fish with right side-up triangles. The dotted isobath = 100 m.

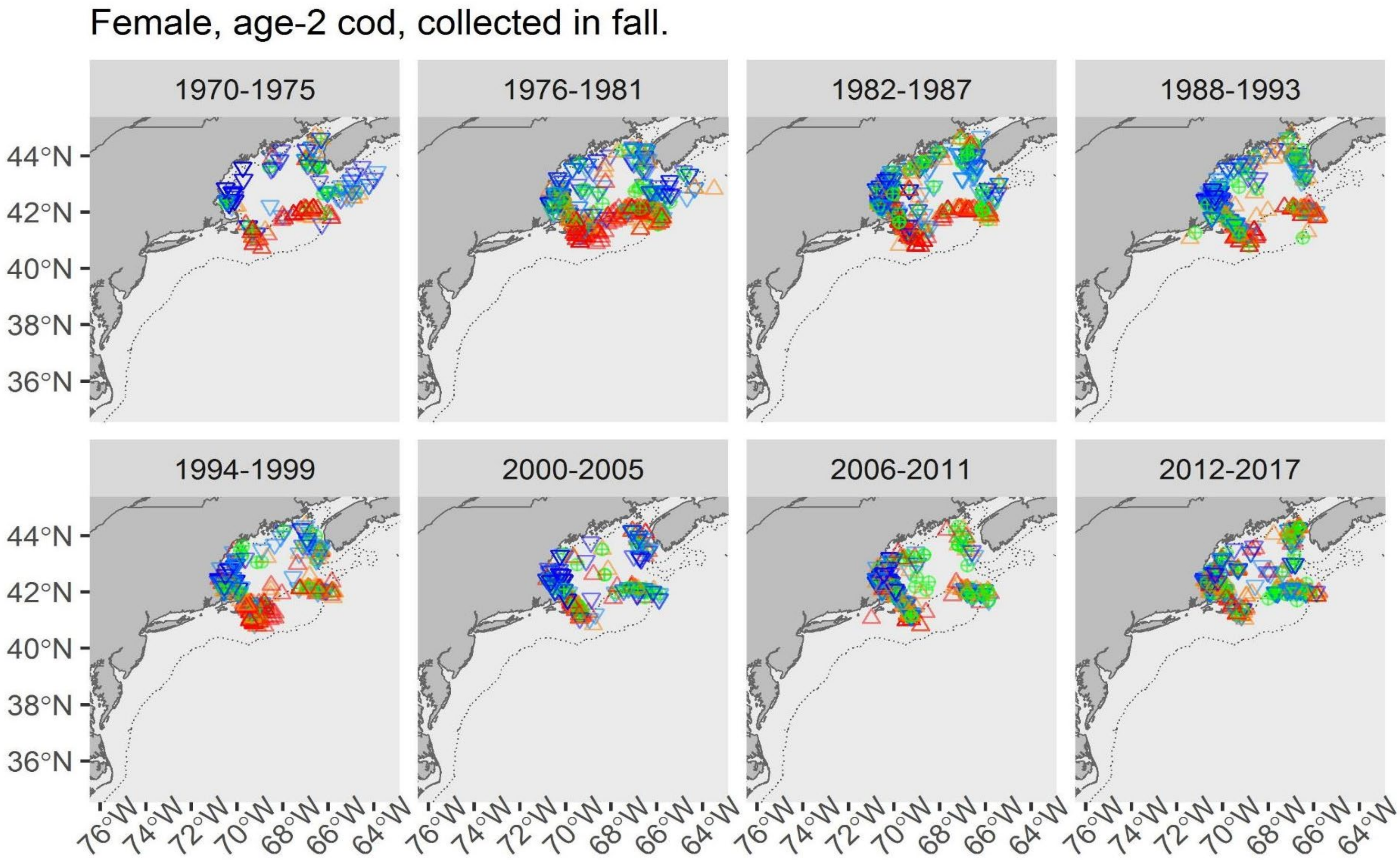


Figure 5.4C. Fall distribution of female age-2 Atlantic cod, (*Gadus morhua*) grouped in eight 6-year periods, 1970-2017. Color coding is translucent to reveal overlay of points, using a color spectrum from Fig. 5.1 to indicate a size-at-age gradient. Smaller (purple-blue; quintiles 1-2) fish are also marked with upside-down triangles, medium (green; quintile 3) fish with a crossed-circle, and larger (orange-red; quintiles 4-5) fish with right side-up triangles. The dotted isobath = 100 m.

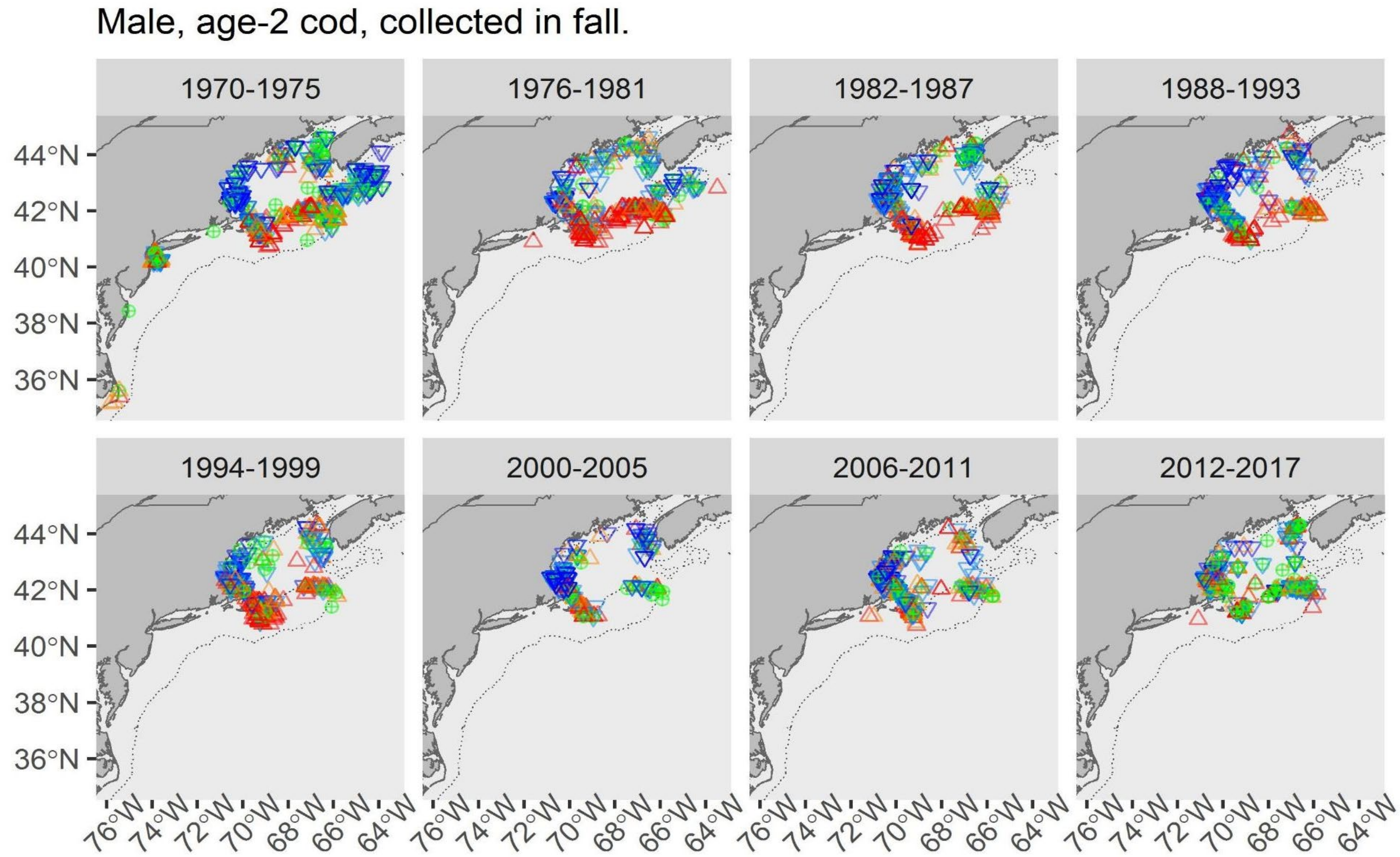
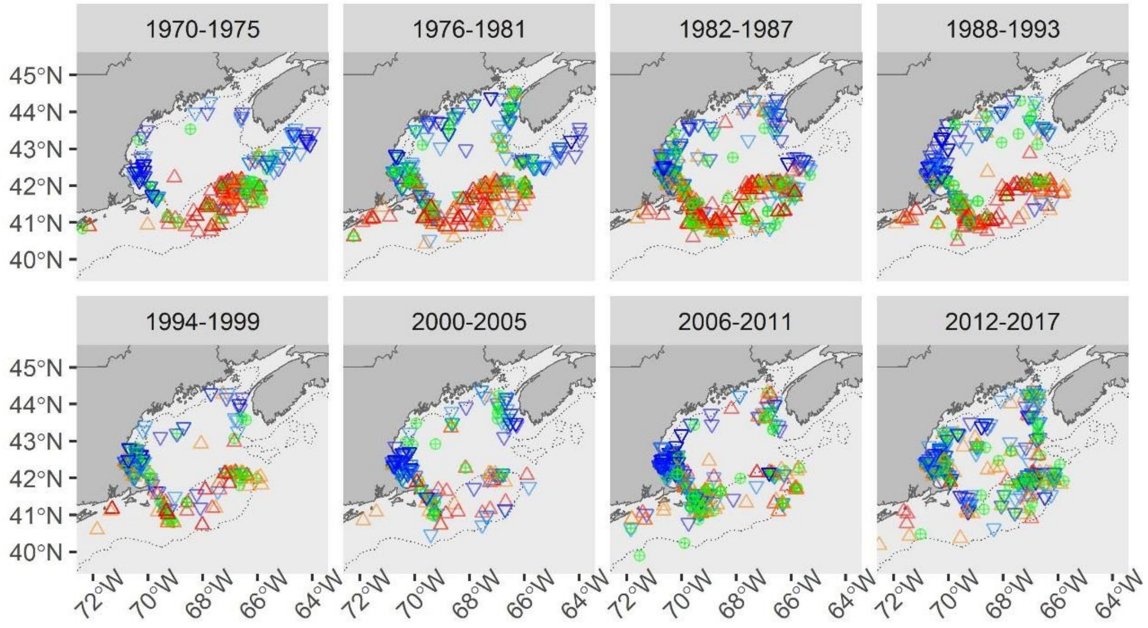
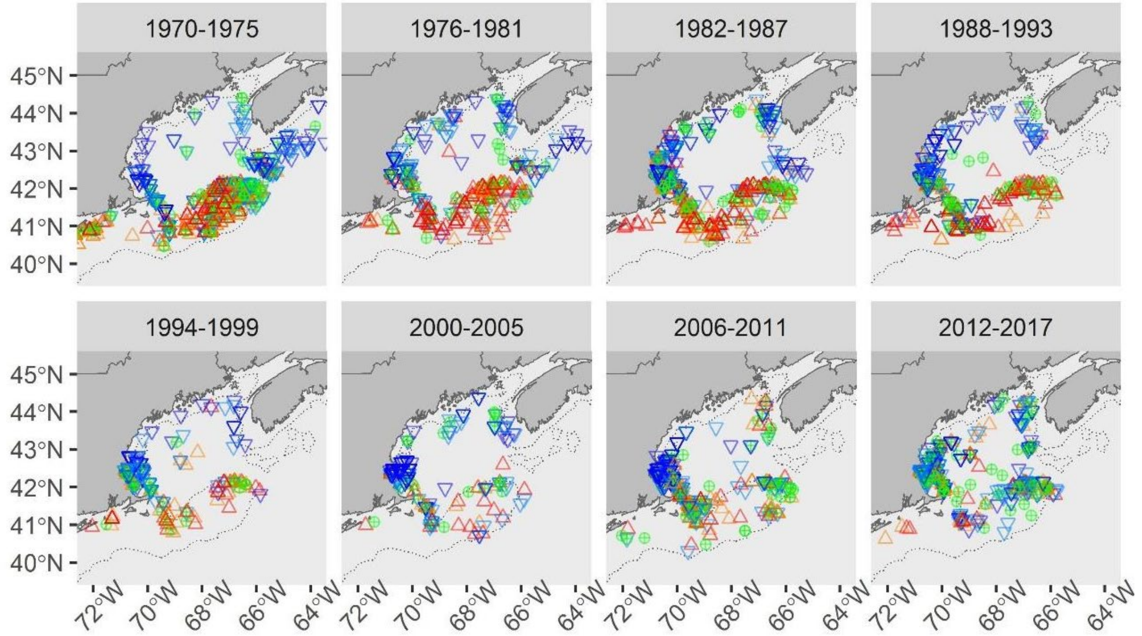


Figure 5.4D. Fall distribution of male age-2 Atlantic cod (*Gadus morhua*) grouped in eight 6-year periods, 1970-2017. Color coding is translucent to reveal overlay of points, using a color spectrum from Fig. 5.1 to indicate a size-at-age gradient. Smaller (purple-blue; quintiles 1-2) fish are also marked with upside-down triangles, medium (green; quintile 3) fish with a crossed-circle, and larger (orange-red; quintiles 4-5) fish with right side-up triangles. The dotted isobath = 100 m.



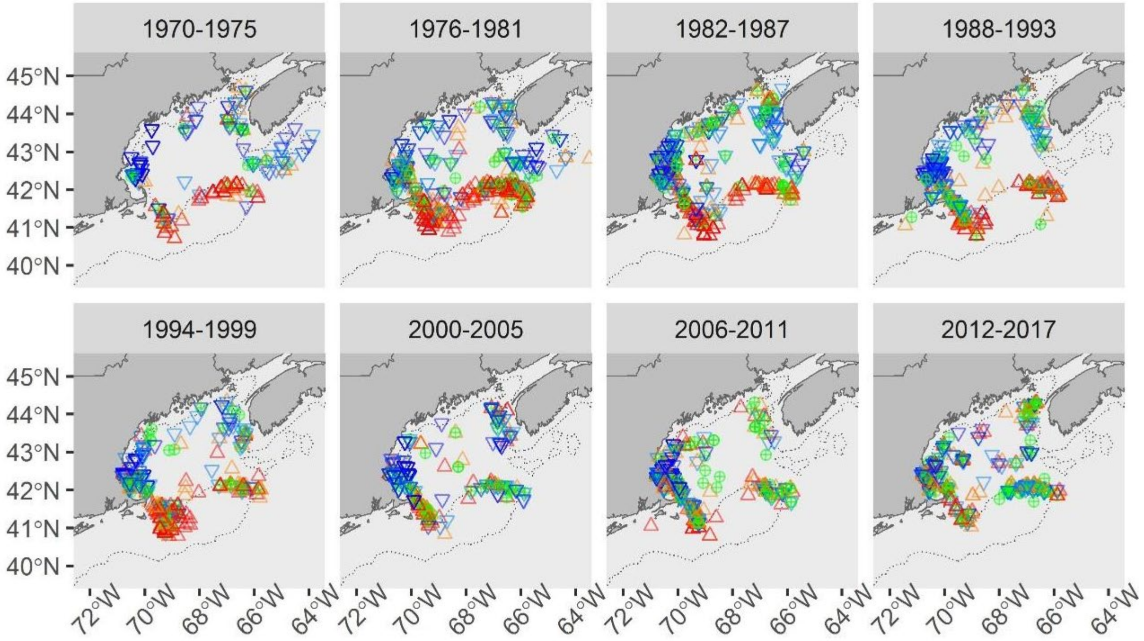
Female, age-2 cod, collected in spring.



Male, age-2 cod, collected in spring.

Figure 5.5. A closer look at the spring geographic distribution of female (top) and male (bottom) age-2 Atlantic cod (*Gadus morhua*) 1970-2017.

Female, age-2 cod, collected in fall.



Male, age-2 cod, collected in fall.

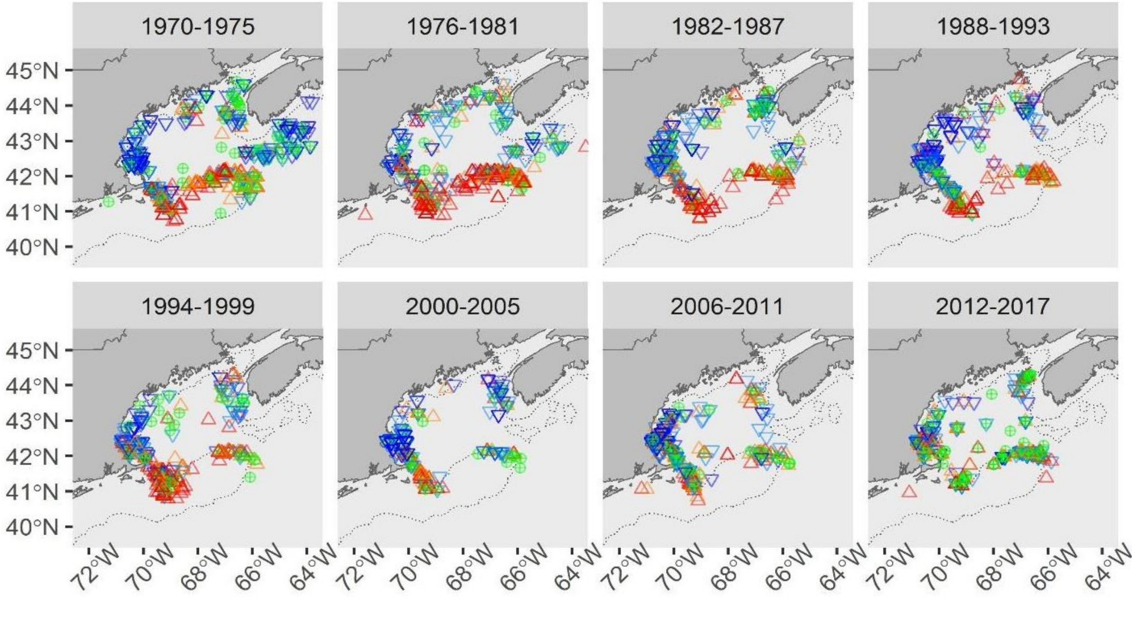


Figure 5.6. A closer look at the fall geographic distribution of female (top) and male (bottom) age-2 Atlantic cod (*Gadus morhua*) 1970-2017.

Sample sizes vary from period to period, reaching lowest values during 1994-2005, but > 200 fish were available to plot per sex, season, and period (Table 5.4).

Table 5.4. Number of age-2 Atlantic cod (*Gadus morhua*) by sex and 6-year seasonal periods, for all tows > 35°N, and the reduced number of fish from examining only the "close-up" spatial scale (< 72°W and > 40°N, in parentheses).

Period	Spring		Fall	
	Female	Male	Female	Male
1970-1975	322 (285)	1060 (822)	242 (240)	792 (688)
1976-1981	487 (481)	396 (390)	576 (575)	479 (478)
1982-1987	648 (648)	533 (531)	536 (536)	460 (460)
1988-1993	384 (381)	392 (388)	430 (430)	380 (380)
1994-1999	232 (231)	217 (216)	403 (403)	378 (378)
2000-2005	250 (250)	227 (227)	282 (282)	217 (217)
2006-2011	496 (495)	422 (419)	455 (455)	459 (459)
2012-2017	441 (434)	454 (452)	472 (472)	440 (440)

Size at Age 2 – Cluster Analysis

In spring, mean size of age-2 cod was lower in the Gulf of Maine management unit ($\text{range}_{1970\text{-}1975}$: 28.1-36.5 cm; $\text{range}_{2012\text{-}2017}$: 32.1-40.2 cm), than in the Georges Bank management unit ($\text{range}_{1970\text{-}1975}$: 35.4-45.6 cm; $\text{range}_{2012\text{-}2017}$: 35.4-45.1 cm) (Table 5.5). Fish from Gulf of Maine statistical areas 513 and 514 ranked among the smallest 3 means in both the first and last periods, but size at age 2 increased by 14-21% in both statistical areas between the first and last periods (1970-1975 and 2012-2017). Modest increases in mean size at age 2 were also noted for cod in statistical areas 521, 537-539, and 612-614. In contrast, fish from Georges Bank areas 522, 525, 561, 562 were largest during 1970-1975, but size at age 2 decreased 13-19% in these 4 areas by 2012-2017. All this change suggested spatial restructuring of the growth phenotypes between the beginning and end of the time series and resulted in a narrowing of the differences in size at age 2 between the 2 management units.

Table 5.5. Spring adjusted sizes at age 2, for Atlantic cod (*Gadus morhua*) aggregated by statistical areas and by the first period, 1970-1975, and the most recent period, 2012-2017, of the NOAA bottom trawl survey. The Area_stock label denotes the statistic area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Size is reported as the mean (mean), standard deviation (sd), number of fish (n), and percent difference in mean values between the 2 periods (% diff.). Percent differences are not calculated for areas with < 5 fish per area-period, and these values will not be included in subsequent cluster analysis (Fig. 5.7).

Area_stock	1970-1975			2012-2017			% diff.
	mean	sd	n	mean	sd	n	
463-5 GOM-SS	32.9	4.72	126	35.1	4.88	62	6.7
466-7 GOM-BF	36.5	3.72	5	35.0	4.51	18	-4.1
511 GOM-No.	32.8	1.91	2	36.5	5.71	30	
512 GOM-No.	33.8	4.21	5	32.1	4.77	18	-5.0
513 GOM-So.	29.4	4.62	8	33.6	6.65	47	14.3
514 GOM-So.	28.1	4.38	92	34.1	5.08	266	21.4
515 GOM-Ce.	35.7	3.36	2	40.2	4.58	81	
521 GB-W	35.4	6.03	114	37.1	6.16	119	4.8
522 GB-W	45.6	4.68	64	37.0	5.06	25	-18.9
525 GB-W	42.8	4.67	105	35.4	4.12	10	-17.3
537-9 GB-SNE	41.3	3.88	9	44.5	2.99	8	7.7
551 GB-E	41.8	4.59	185	37.3	5.08	121	-10.8
552 GB-E	39.6	3.86	103	37.3	5.57	13	-5.8
561 GB-E	43.4	5.59	92	37.6	5.06	47	-13.4
562 GB-E	44.1	4.41	127	37.7	4.66	20	-14.5
612-4 NYB	39.7	5.04	228	45.1	3.37	6	13.6

The results of the cluster analysis suggested that the spring adjusted sizes of age-2 cod during 1970-1975 were more spatially segregated between Georges Bank and the Gulf of Maine compared to those in 2012-2017 (Fig. 5.7). In the first period, 1970-75, the growth patterns of all statistical areas on Georges Bank, except 521, were clustered separately from areas within the Gulf of Maine, but together with fish from southern New England and the New York Bight. Statistical area 521, which has been historically assigned as part of the Georges Bank management unit, is geographically in proximity to Cape Cod and the western part of the Great South Channel. In the most recent period, 2012-2017, spatial segregation of growth by statistical areas became less coherent. For example, while growth patterns in Gulf of Maine areas 512-515 clustered together, as did the southern New England and the New York Bight, the remaining Georges Bank and Gulf of Maine areas were mixed together in 1 large cluster.

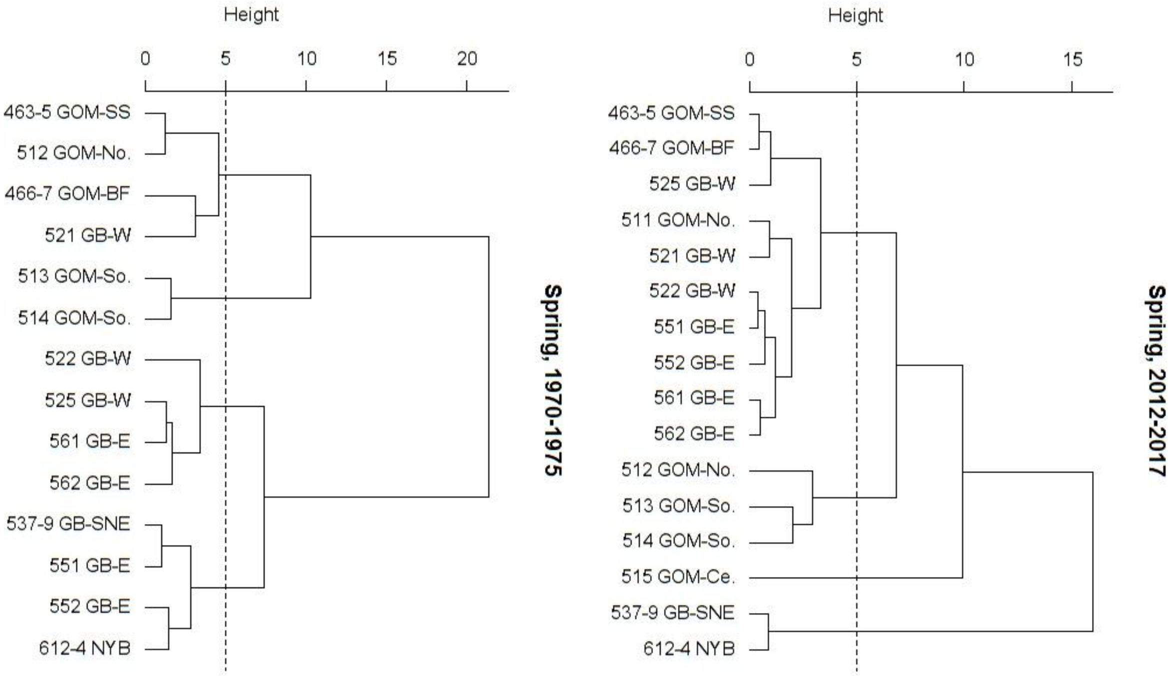


Figure 5.7. Divisive clusters of adjusted spring size at age 2 for Atlantic cod (*Gadus morhua*) aggregated by statistical catch areas (mean, sd; see Table 5.5). The Area_stock label denotes the statistic area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Two periods are selected among the range of years: an early period (left) versus the most recent period (right). Statistical areas with low sample sizes (i.e., < 5 individuals/period; Table 5.5) were not included in the cluster analysis. An arbitrary height value of 5 is marked with a dashed line to aid in comparing between seasons and periods, and to demark an initial number of clusters.

In fall, mean size of age-2 cod was also lower in the Gulf of Maine management unit (range$_{1970\text{-}1975}$: 34.8-43.8 cm; range$_{2012\text{-}2017}$: 43.0-47.6 cm) than in the Georges Bank management unit (range$_{1970\text{-}1975}$: 45.9-53.2 cm; range$_{2012\text{-}2017}$: 43.7-50.6 cm) (Table 5.6). As observed in spring catches, fish from statistical areas 513 and 514 ranked among the smallest 3 means in both the first and last periods, and size at age 2 increased in these 2 areas by 24-25% between the first and last periods (1970-1975 and 2012-2017). Mean size at age 2 also increased in statistical area 521, but to a lesser extent. In contrast, fish from Georges Bank areas 522, 551, 561 were very large during 1970-1975, but size at age 2 dropped 9-17% in these statistical areas by 2012-2017. Again, this difference suggested spatial restructuring of the growth phenotypes, specifically a narrowing of the range in sizes at age 2, between fish in the Gulf of Maine and Georges Bank management units from the beginning to the end of the time series.

Cluster analysis confirmed that fall adjusted size distributions of age-2 cod from 1970 to 1975 were more spatially segregated between Georges Bank and the Gulf of Maine management units compared to 2012-2017 (Fig. 5.8). Again, fish from statistical area 521 stood out as not being classified with the Georges Bank management unit from 1970 to 1975, whereas fish from all the Georges Bank and Gulf of Maine statistical areas were jumbled together in a spatially incoherent manner during 2012-2017.

Table 5.6. Fall adjusted sizes at age 2, for Atlantic cod (*Gadus morhua*) aggregated by statistical areas and by the first period (1970-1975) and the most recent period (2012-2017) of the NOAA bottom trawl survey. The Area_stock label denotes the statistic area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Size is reported as the mean (mean), standard deviation (sd), number of fish (n), and percent difference in mean values between the 2 periods (% diff.).

Area_stock	1970-1975			2012-2017			% diff.
	mean	Sd	n	mean	sd	n	
463-5 GOM-SS	41.3	5.66	104	43.9	6.02	44	6.3
466-7 GOM-BF	43.8	4.46	29	47.6	5.62	26	8.7
511 GOM-No.	43.1	6.11	29	45.8	4.53	38	6.3
512 GOM-No.	43.6	8.37	24	43.3	8.39	8	-0.7
513 GOM-So.	34.8	5.65	34	43.0	4.71	51	23.6
514 GOM-So.	34.8	5.81	219	43.6	5.70	208	25.3
515 GOM-Ce.			0	46.4	6.50	33	
521 GB-W	45.9	6.98	205	49.0	5.85	129	6.8
522 GB-W	52.4	5.03	33	43.7	4.50	40	-16.6
525 GB-W	53.2	8.24	3			0	
537-9 GB-SNE	46.5		1	56.3		1	
551 GB-E	50.9	5.14	86	46.1	4.24	270	-9.4
552 GB-E	47.2	4.57	37	50.6	8.41	2	
561 GB-E	53.1	3.76	51	44.2	3.61	64	-16.8
562 GB-E	50.3	2.98	11			0	
612-4 NYB	47.6	4.00	90			0	

In summary, Atlantic cod size at age 2 increased substantially in several statistical areas of the Gulf of Maine management unit but decreased substantially in several statistical areas on Georges Bank management unit from 1970-1975 to 2012-2017, a change which has weakened the growth signal that readily distinguished these 2 management units. Statistical area 521, assigned in US stock assessments to Georges Bank, was clustered repeatedly with the Gulf of Maine assessment unit. Some fish from southern New England (537-539), which were assigned as part of the Georges Bank management unit, were clustered with either fish from Georges Bank (551, 552) or the New York Bight (612-614), both contiguous areas to southern New England. However, any inferences regarding the structure of cod in southern New England need to be treated with caution, given the paucity of samples in statistical areas 537-539.

Plotting individual cod size at age 2 depicted fluctuations around a relatively stable value in the Gulf of Maine, including the Scotian Shelf, but the length of age-2 cod declined on both western and eastern Georges Bank, particularly evident in the spring (Fig. 5.9). As a result, at a broad-scale, size segregation at age 2 initially existed between cod within the Gulf of Maine and Georges Bank assessment boundaries, but this devolved after approximately 2 decades and is no longer evident 50 years later.

Female Maturity – Descriptive

Without consideration of a spatial structure of cod maturity, a declining trend in female size at maturity was evident over the time series. The base model with only length as a predictor of maturity (Akaike information criterion [AIC] = 9932) was markedly improved by adding 6-year periods to the model (AIC = 9230). The best performing model was the full model of fish length, time period, and their interaction (AIC = 9125).

The median size at maturity, L_{50}, initially at about 50 cm fork length, declined rapidly in the first few periods before appearing to stabilize at a lower value, around 40 cm (Table 5.7).

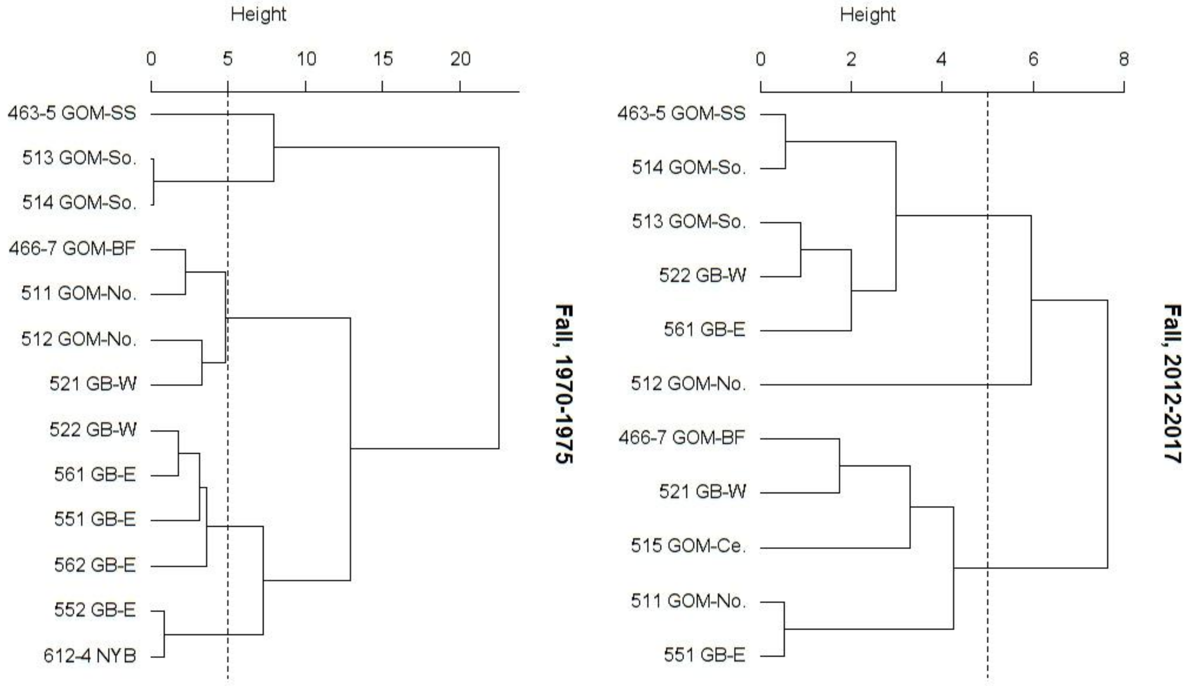


Figure 5.8. Divisive clusters of adjusted fall size at age-2 Atlantic cod (*Gadus morhua*) aggregated by statistical areas (mean, sd; see Table 5.6). The Area_stock label denotes the statistic area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Two periods are selected among the range of years: an early period (left) versus the most recent period (right). Statistical areas with low sample sizes (i.e., < 5 individuals/period; Table 5.6) were not included in the cluster analysis. An arbitrary height value of 5 is marked with a dashed line to aid in comparing between seasons and periods, and to demark an initial number of clusters.

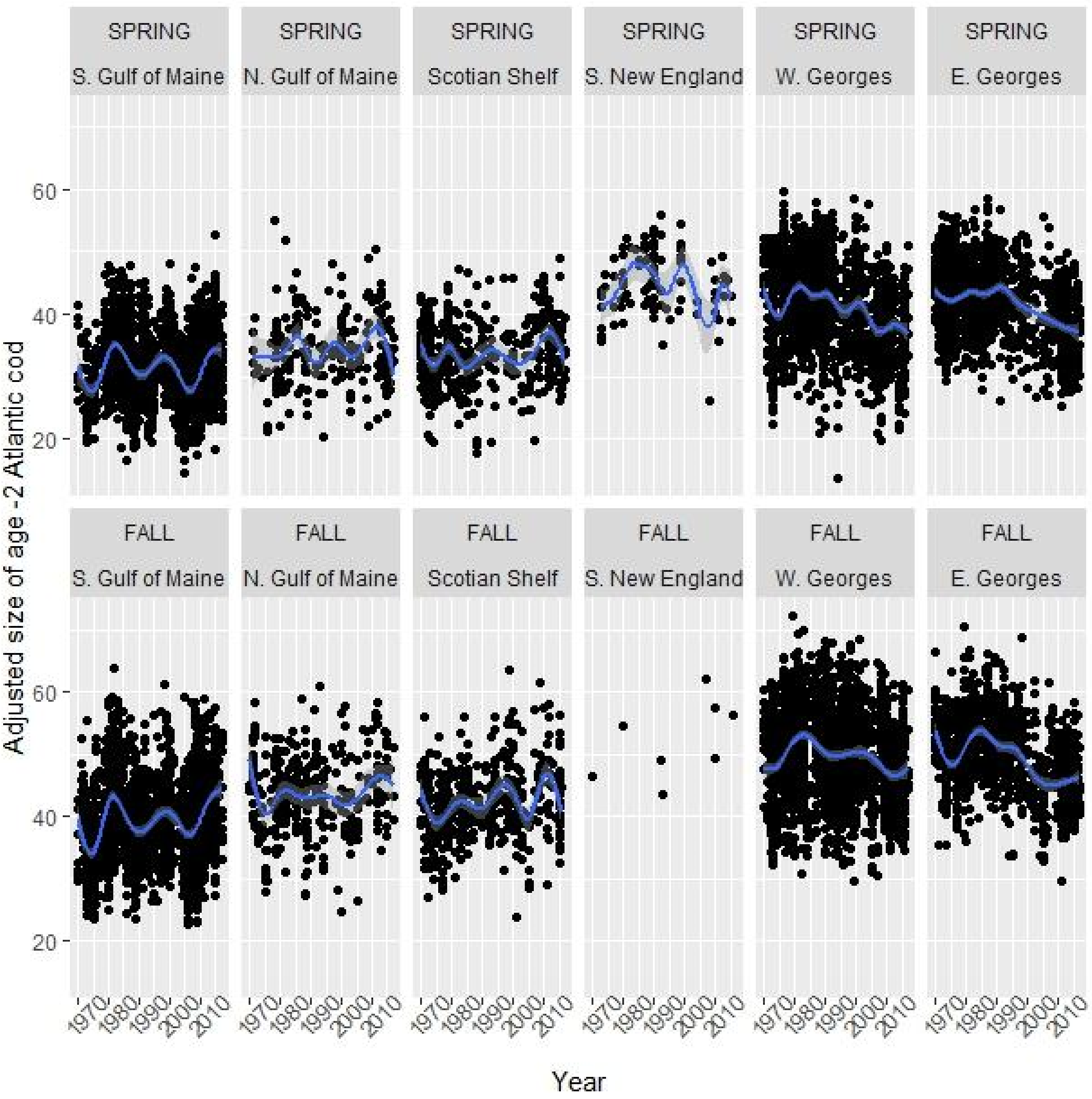


Figure 5.9. Annual trends in adjusted size (length, cm) of individual age-2 Atlantic cod (*Gadus morhua)* by region and season during the period 1970-2017. Data are aggregated by statistical areas into the following regions: Northern Gulf of Maine (511-512), Southern Gulf of Maine (513-514), Scotian Shelf (463-465), southern New England (537-539), Western Georges Bank (521-522 and 525-526), and Eastern Georges Bank (551-552 and 561-562). The blue trend line is a Generalized Additive Model fit ('y ~ s(x, bs = "cs")') as part of the ggplot2 package in R (R Development Core Team 2014).

Table 5.7. Period-specific median size (cm) and age (years) at maturity (L_{50}, A_{50}), standard errors (SEs), and number of females (n) used for fitting the logit model. Data are for female Atlantic cod (*Gadus morhua*) from the spring NOAA bottom trawl survey.

Period	L_{50}	SE(L_{50})	A_{50}	SE(A_{50})	n
1970-1975	52.4	0.487	2.92	0.0501	1781
1976-1981	46.9	0.467	2.58	0.0407	2211
1982-1987	38.2	0.589	1.89	0.0452	2152
1988-1993	40.2	0.581	2.20	0.0440	1779
1994-1999	38.0	0.560	2.16	0.0480	1081
2000-2005	42.4	0.621	2.50	0.0535	1356
2006-2011	41.2	0.386	2.57	0.0368	2080
2012-2017	39.7	0.362	2.23	0.0375	2270

Age at maturity was also best explained when incorporating a time element. The base model with only age as a predictor of maturity (AIC = 11495) was markedly improved by adding 6-year periods to the model (AIC = 11046). The best performing model was the full model of fish age, time period, and their interaction (AIC = 11007).

The median age at maturity, A_{50}, initially at almost 3 years of age, declined a full year in the first 3 periods, 1970-1987, before appearing to stabilize at a lower value, around 2.2-2.5 years (Table 5.7).

In addition to this declining trend in length and age at maturity over time, the L_{50} and A_{50} values also varied spatially (Fig. 5.10). Estimates were restricted to 1°×1° cells with >30 individual females, and several cells with insufficient sample sizes to estimate maturation make it difficult to see a pattern within each period; however, in the following section, a spatial pattern is evident from cluster analysis based on statistical areas.

Female Maturity – Cluster Analysis

Length at maturity was larger in the Gulf of Maine management unit than for fish in the Georges Bank management unit but only during 1970-1975 ($\text{range}_{\text{GOM}}$: 54.3-57.6 cm; range_{GB}: 44.5-55.7 cm) (Table 5.8). The L_{50} estimates were smaller and overlapped more between the areas during 2012-2017 ($\text{range}_{\text{GOM}}$: 37.8-50.5 cm; range_{GB}: 35.8-47.4 cm). The L_{50} estimate declined between these 2 periods in 9 out of 10 statistical areas, averaging -23% across all 10 statistical areas with sufficient data (n > 30) to estimate parameters.

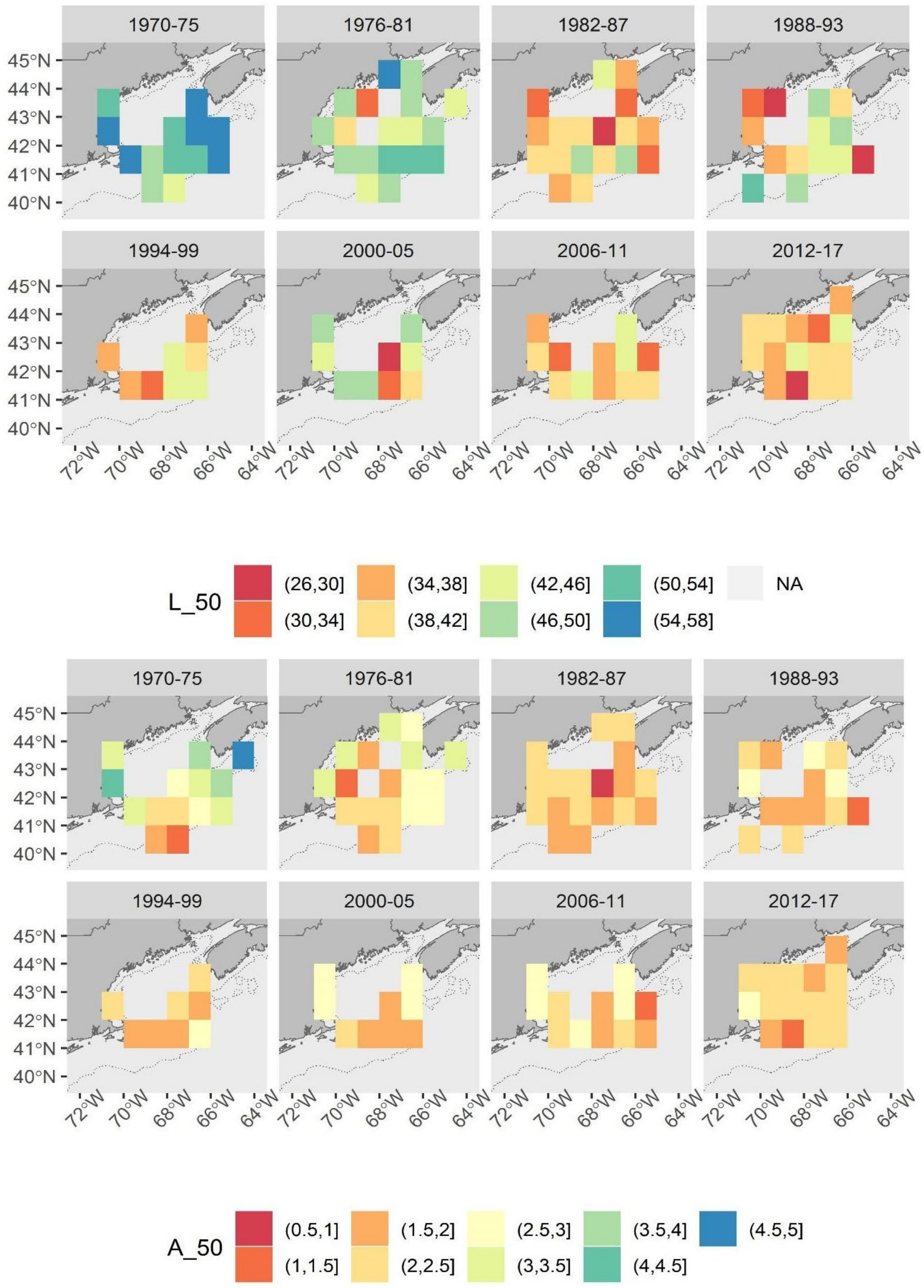


Figure 5.10. Modeled values of length (L_50, cm; top) or age (A_50, years; bottom) at maturity of female Atlantic cod (*Gadus morhua*) based on spring observations from the NOAA bottom trawl survey. Data were aggregated spatially in 1° (latitude and longitude) units north of 40°N and east of 72°W, as well as temporally in eight 6-year periods, 1970-2017.

Table 5.8. Estimates of size at maturity for female Atlantic cod (*Gadus morhua*) by statistical areas for 1970-1975 and 2012-2017 of the NOAA bottom trawl survey time series. See methods and Fig. 5.2 for description on the Area_stock label. Size is reported as the median length at maturity (L_{50}), standard error (SE), number of fish (n), and percent difference in mean values between the 2 periods (% diff.). Values were not estimated if the number of fish was ≤ 30.

Area_stock	1970-1975			2012-2017			% diff.
	L_{50}	SE	n	L_{50}	SE	n	
463-5 GOM-SS	56.0	1.26	305	39.2	1.79	168	-30.0
466-7 GOM-BF			19			30	
511 GOM-No.			15	37.8	2.25	33	
512 GOM-No.			16	50.5	9.27	35	
513 GOM-So.	57.6	2.47	75	42.3	1.23	197	-26.6
514 GOM-So.	54.3	2.54	144	40.1	0.55	687	-26.2
515 GOM-Ce.			12	40.2	1.41	150	
521 GB-W	51.7	1.69	123	37.3	1.08	175	-27.9
522 GB-W	51.0	2.93	130	36.5	2.85	70	-28.4
525 GB-W	47.3	3.81	106	35.8	2.84	31	-24.3
537-9 GB-SNE			18			16	
551 GB-E	55.7	0.98	226	39.2	0.93	318	-29.6
552 GB-E	44.5	0.91	74	47.4	2.02	119	6.5
561 GB-E	53.1	2.40	48	41.0	1.84	151	-22.8
562 GB-E	48.7	1.19	128	39.4	1.63	70	-19.1
612-4 NYB	47.6	1.23	181			7	

Cluster analysis demonstrated that the length at maturity distributions were well segregated between the Gulf of Maine and Georges Bank in both periods (Fig. 5.11). However, there was evidence of variation within the Georges Bank management unit because statistical areas 521-22 (western Georges Bank) clustered more closely with the Gulf of Maine statistical areas than with the eastern Georges Bank statistical areas. Females from area 512 in 2012-2017 had a particularly high L_{50} and large standard error, resulting in an independently assigned cluster for this area in the Gulf of Maine.

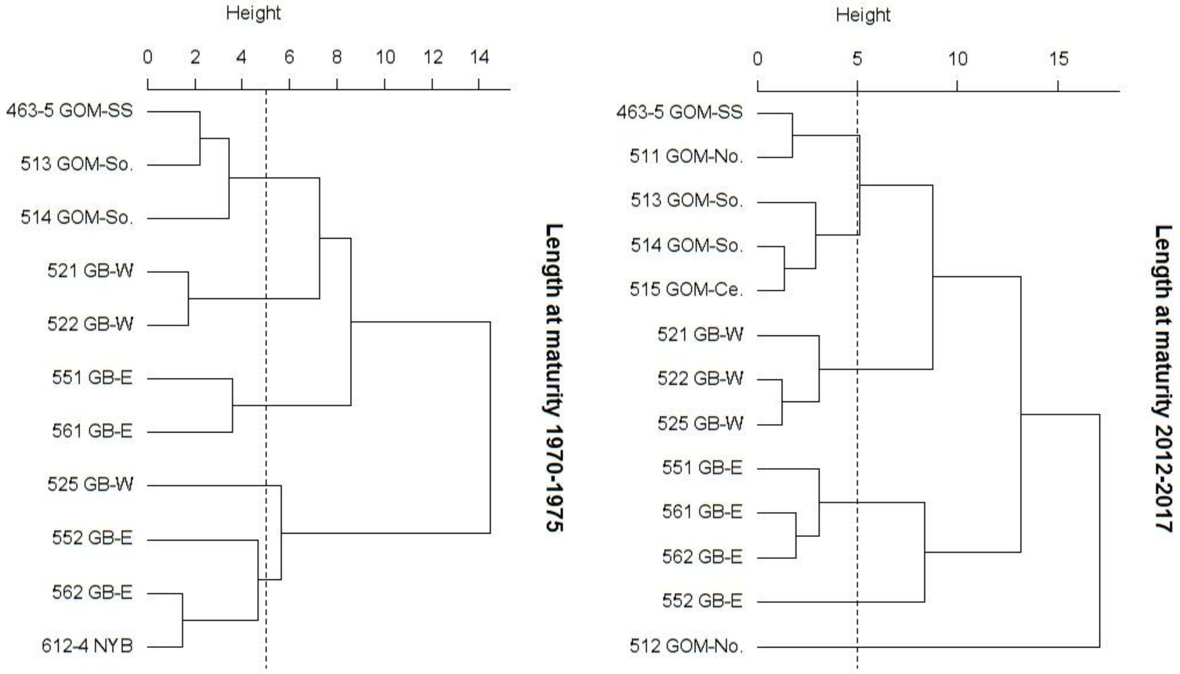


Figure 5.11. Divisive clusters of length at maturity (median, standard error) for female Atlantic cod (*Gadus morhua*) collected in spring and aggregated by statistical areas. The Area_stock label denotes the statistical area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Two periods are selected among the range of years: an early period (left) versus the most recent period (right). Statistical areas with low sample sizes (i.e., $\leq$ 30 females/period; Table 5.8) were not included in the cluster analysis. An arbitrary height value of 5 is marked with a dashed line to aid in comparing between seasons and periods and to demark an initial number of clusters.

Age at maturity was older in the Gulf of Maine management areas than in the Georges Bank management areas but only during 1970-1975 (range$_{GOM}$: 3.7-4.4 yr; range$_{GB}$: 1.9-2.9 cm) (Table 5.9). The A_{50} estimates were younger and overlapping between the areas during 2012-2017 (range$_{GOM}$: 1.9-2.9 cm; range$_{GB}$: 1.7-2.8 cm). The A_{50} estimate declined between these 2 periods in 8 out of 10 statistical areas, averaging -23% across all 10 statistical areas.

Table 5.9. Estimates of age at maturity for female Atlantic cod (*Gadus morhua*) by statistical areas and by an early period, 1970-1975, and the most recent period, 2012-2017, of the NOAA bottom trawl survey. Age is reported as the median age at maturity (A_{50}), standard error (SE), number of fish (n), and percent difference in mean values between the 2 periods (% diff.). Values were not estimated if the number of fish was $\leq$ 30.

Area_stock	1970-1975			2012-2017			% diff.
	A_{50}	SE	n	A_{50}	SE	n	
463-5 GOM-SS	3.74	0.128	305	2.16	0.150	168	-42.2
466-7 GOM-BF			19			30	
511 GOM-No.			15	1.94	0.178	33	
512 GOM-No.			16	2.86	0.374	35	
513 GOM-So.	3.88	0.332	75	2.45	0.114	197	-36.9
514 GOM-So.	4.41	0.277	144	2.54	0.062	687	-42.4
515 GOM-Ce.			12	2.13	0.105	150	
521 GB-W	2.91	0.109	123	1.87	0.107	175	-35.7
522 GB-W	2.49	0.197	130	1.71	0.388	70	-31.3
525 GB-W	1.89	0.446	106	1.77	0.504	31	-6.3
537-9 GB-SNE			18			16	
551 GB-E	2.88	0.092	226	2.06	0.120	318	-28.5
552 GB-E	2.48	0.132	74	2.85	0.203	119	14.9
561 GB-E	2.57	0.237	48	2.06	0.265	151	-19.8
562 GB-E	2.30	0.105	128	2.35	0.163	70	2.2
612-4 NYB	2.47	0.892	181			7	

Cluster analysis demonstrated that the age at maturity distributions were well segregated between the Gulf of Maine and Georges Bank in both periods (Fig. 5.12). Again, in the early period (1970-1975) statistical areas 521-522 clustered more closely with the Gulf of Maine management unit. However, in the most recent period (2012-2017), the 4 major clusters were almost perfectly ordered: (1) northern Gulf of Maine, (2) southern/central Gulf of Maine, (3) western Georges Bank (with 551 from eastern Georges), and (4) eastern Georges Bank.

In summary, despite spatially broad, double-digit percentage declines in both L_{50} and A_{50} from 1970-1975 to 2012-2017, the spatial segregation of both length and age at maturity clustered into either the Gulf of Maine and Georges Bank assessment units. An exception is that in 3 of the 4 comparisons, parts of the western Georges Bank (particularly areas 521 and 522) clustered more closely with Gulf of Maine areas. Assignment of southern New England areas (537-539) was not possible in either period because of low sample size, but the adjoining New York Bight area (612-614) did align with Georges Bank during 1970-1975.

Discussion

This study examined a single source of sampling over a broad scale of space and time – from Cape Hatteras, NC, United States, to Cape Sable Island, NS, Canada, over a 48-year period – demonstrating spatial and temporal dynamics in multiple life history traits of Atlantic cod: distribution and abundance, size at age 2, and size and age at maturity. Because measures of abundance and vital rates are inputs to regional cod stock assessments, they have been monitored regularly for decades and they were considered in early efforts to delineate cod stocks. Our historical review confirms that all the life history traits examined here have changed since the 1970s, which emphasizes the need for this reevaluation and for continued monitoring in the future.

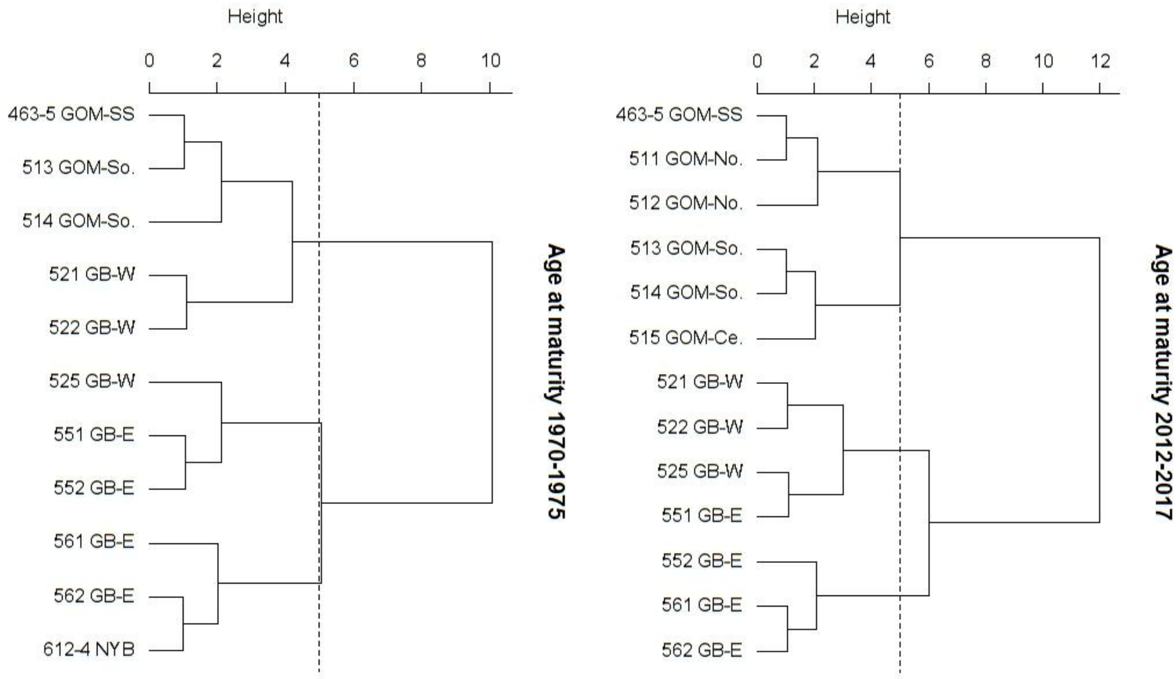


Figure 5.12. Divisive clusters of age at maturity (median, standard error) for female Atlantic cod (*Gadus morhua*) collected in spring and aggregated by statistical areas. The Area_stock label denotes the statistical area number and an abbreviated description of the area; see methods and Fig. 5.2 for further details. Two periods are selected among the range of years: an early period (left) versus the most recent period (right). Statistical areas with low sample sizes (i.e., ≤ 30 females/period; Table 5.8) were not included in the cluster analysis. An arbitrary height value of 5 is marked with a dashed line to aid in comparing between seasons and periods and to demark an initial number of clusters.

Distribution and Abundance

Most reports reiterate Earll's (1880) southern distributional limit as Cape Hatteras (35°N). In this analysis, we uncovered unpublished records from a single cruise in November-December 1972 that recorded cod south of Cape Hatteras, as far south as northern Florida (30°N). This event is unusual and appears to be the result of a strong year class in the early 1970s (Serchuk and Wood 1979) as well as an unusual sampling cruise track, both in southern range of stations and late into winter conditions. In most years the southern distributional record was well north of 35°N. The overall pattern of decreasing abundance with decreasing latitude south of 40°N is most likely associated with the temperature tolerance of Atlantic cod (Fig. 5.13). Cod's total thermal niche, -1.5 to 19°C (Righton et al. 2010; Zemeckis et al. 2017), is not broad enough to occupy temperatures along the Mid-Atlantic seaboard year round, which seasonally gets warmer than 20°C (Friedland and Hare 2007; McBride 2014b). Moreover, cod has a narrower niche (1-8°C) during the spawning season and an optimal growth range of 8-10°C (Righton et al. 2010).

Seasonal migrations identified in our survey area have long been noted by others (e.g., Grosslein 1973). Temperature shifts from spring to fall (Fig. 5.13) are likely the driver of strong seasonal shifts in distribution and abundance (e.g., cod move off the southern flank of Georges Bank in fall). Temperatures associated with capture of age-2 cod are higher in fall than in spring (< 15 versus < 10°C; Fig. 5.14). One segment of the cod population that has suffered, in particular, is what Wise (1963) regarded "the New Jersey coastal cod," a distinct group that migrated to southern New England during the warmer months; this group is greatly reduced in abundance based on distributional maps.

The southern distributional limit of cod moved northward from 1970 to about 2000, and since the 1990s, very few cod were observed south or west of Block Island Sound (approximately 41.3°N, 71.7°W). This shift may be due to interactions between a warming trend along the US east coast (Friedland and Hare 2007; Pershing et al. 2015; Miller et al. 2018) and the declining abundance of cod. In the case of the Georges Bank cod management unit, spawning stock biomass declined from 60,000-90,000 metric tons (mt) during 1970-1990 to < 30,000 mt during 2000-2010 (NEFSC 2012). Synoptic analysis of both climate effects and fishing pressure have shown both drivers affecting the distribution of regional fish stocks (Adams et al. 2018a).

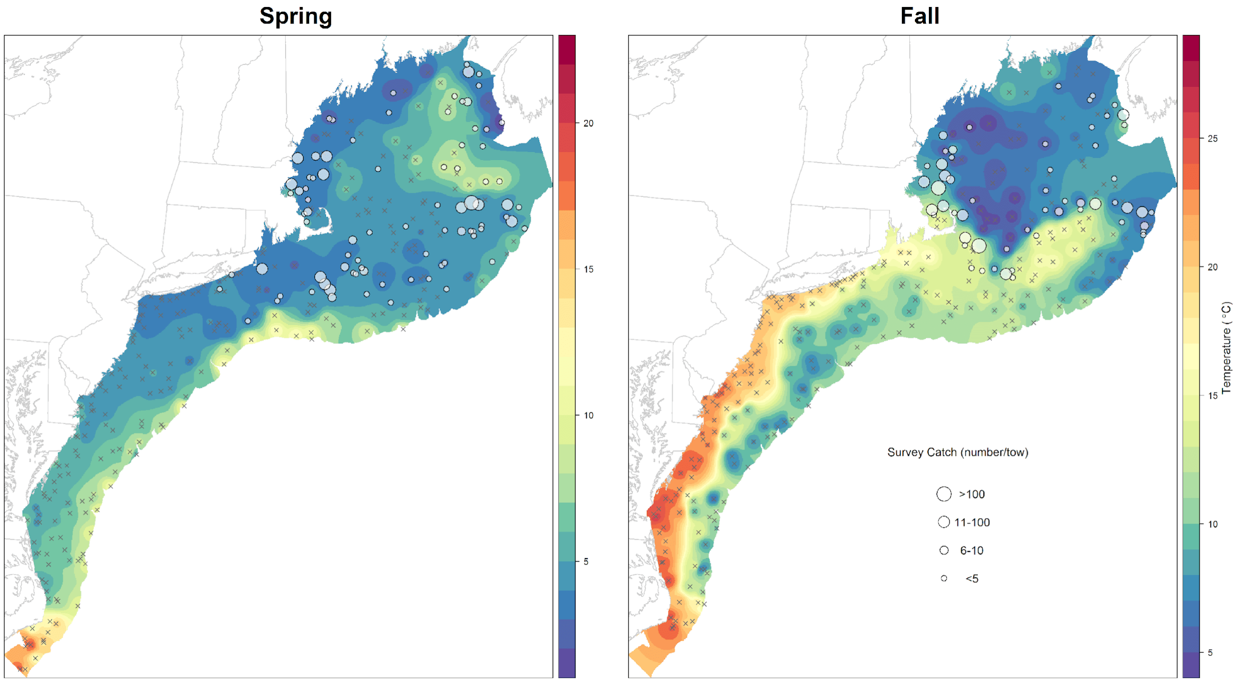


Figure 5.13. Seasonal distribution of Atlantic cod (*Gadus morhua*) in relation to modeled bottom temperature in 2004.

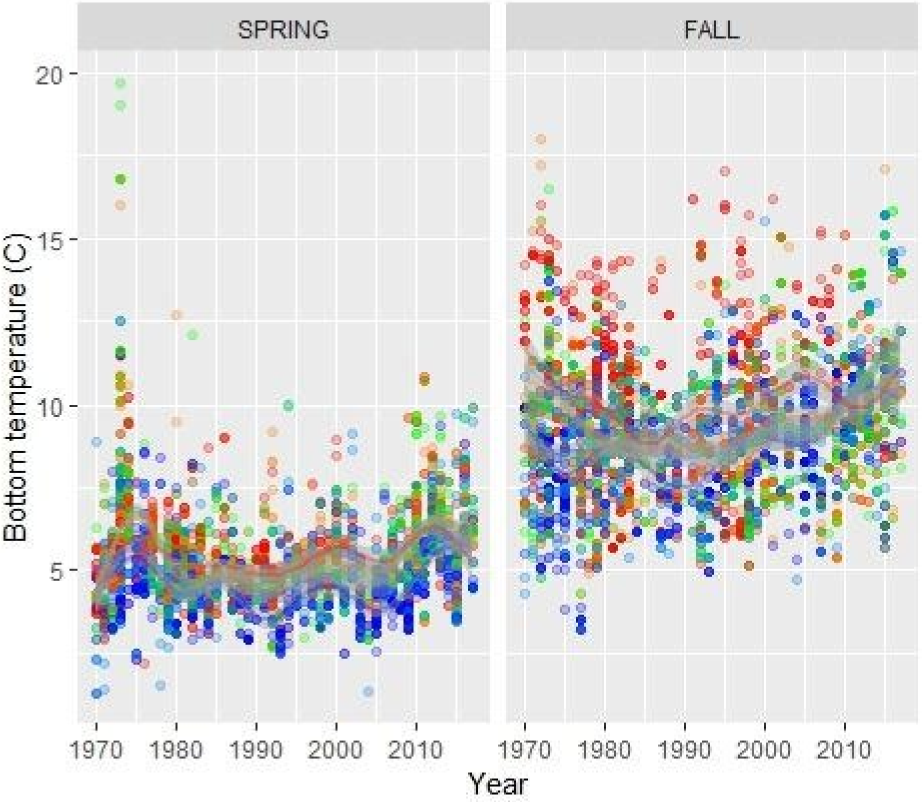


Figure 5.14. Age-2 Atlantic cod were associated with different bottom temperature at capture during spring (right) and fall (left) seasons. No annual trend was evident from 1970 to 2017, but larger fish were found in warmer temperatures. The individual points are color coded by quintiles of size at age 2, as in Fig. 5.1. The predictive, solid lines (with shaded 95% confidence intervals) for each quintile are fit to the data by general additive modeling in R.

Also evident in 1970-2017, the cod population has aggregated into 2 areas: (1) the southwest part of the Gulf of Maine and extending into the Great South Channel and (2) on the northeast peak of Georges Bank. Ames (2004) and Alexander et al. (2009) documented entire spawning groups delepeted along the Maine coast, and abundance in this region has fluctuated at very low levels since the 1970s. Concentration of cod on Georges Bank appears to be more recent, as witnessed during the 1970-2017 period. These patterns of aggregation were also noted by Begg et al. (1999), examining data from 1967 to 1997, who attributed this trend to declining population size. Notable among the plots of geographic distribution is the continuous aggregation of cod from the southern Gulf of Maine, around eastern Cape Cod, and into the Great South Channel because this aggregation spans statistical areas 514 and 521, which are assigned to the Gulf of Maine and Georges Bank management units, respectively (Fig. 5.15). The continuous distribution of cod from the southern Gulf of Maine, to the east of Cape Cod, and into the Great South Channel was also identified by several fishermen (Chapter 8, this volume).

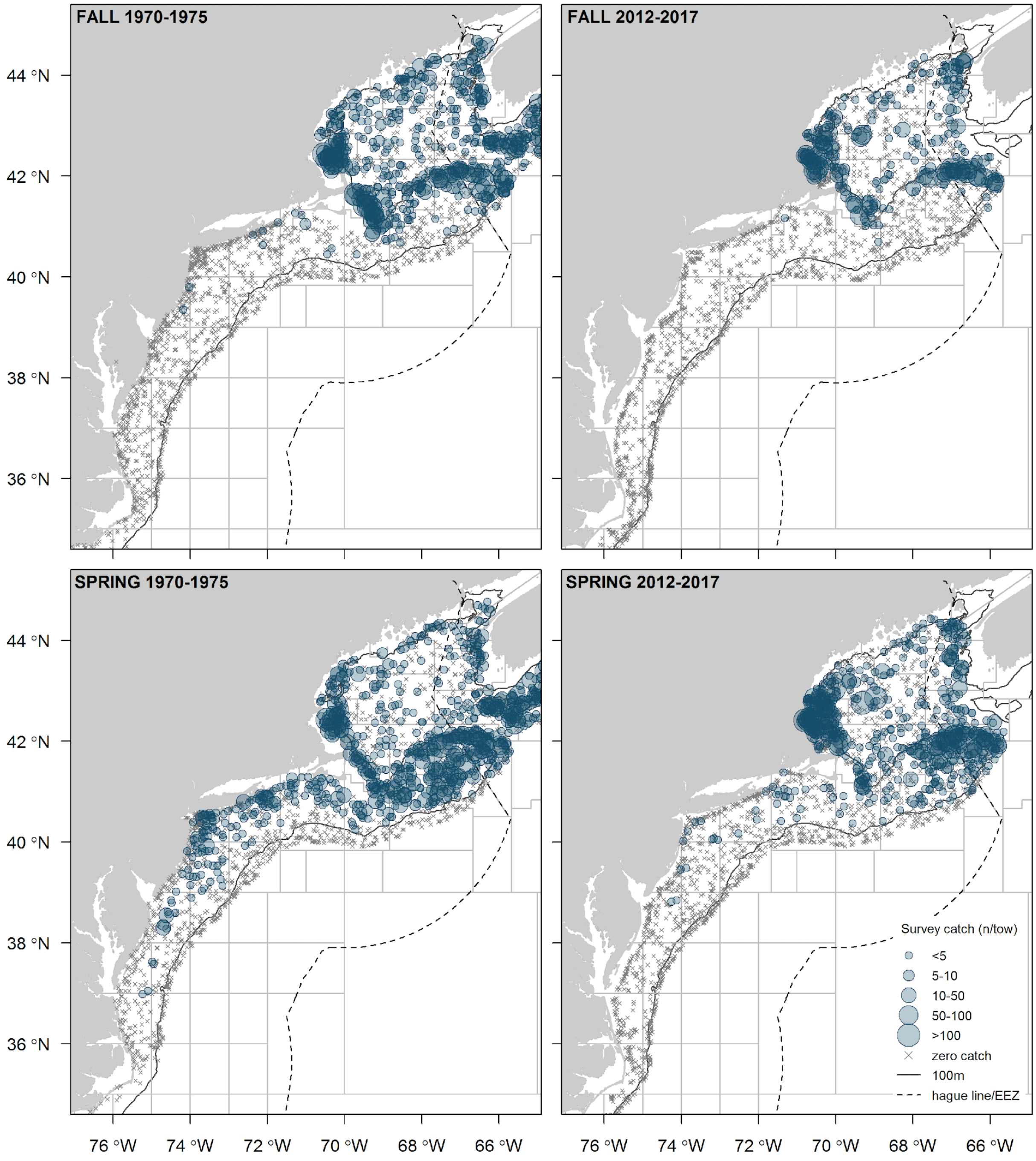


Figure 5.15. Distribution and abundances (number of fish per tow) of Atlantic cod (*Gadus morhua*) during the first period (1970-1975) and the most recent period (2012-2017) of the NOAA bottom trawl survey during fall (top) and spring (bottom). Overlayed are the statistical area boundaries. See Chapter 2 (this volume) for more details on areas.

Size at Age 2

Size at age 2 varied widely among cod, from 14 to 72 cm, and was related to both sampling location and period. Cod from the Gulf of Maine management unit were consistently smaller than those from the Georges Bank unit, but the degree of difference changed during the time series. Size at age differences were first noted for young cod by Penttila and Gifford (1976), who reported that cod collected during 1970-1974 from eastern Georges Bank were significantly larger than cod from western Georges Bank cod (southern New England, including the Great South Channel), which were larger than cod from the Gulf of Maine management unit. These differences were consistent (both seasons) for age-1 and age-2 cod, less so for age-3 and older fish. Begg et al. (1999) also reported that growth rates were highest for eastern Georges Bank, typically greater than western Georges Bank, and lowest for Gulf of Maine, based on interpreting the Brody growth coefficient from the von Bertalanffy model. Finally, Tallack (2009) reported strong differences in growth among the Gulf of Maine, Georges Bank, and Bay of Fundy management units, as well as within unit variation between western and eastern George Bank, based on tag recaptures from 2003 to 2008.

In reference to the current 2 management units used domestically in the United States, our reexamination of 1970-1975 data found size at age 2 in statistical area 521 misaligned with the areas within the Georges Bank management unit; instead it clustered with Gulf of Maine areas. This misalignment suggests that the differences between western and eastern Georges Bank is driven largely by a misalignment of a single statistical area to the western Georges Bank, which is potentially influenced by connectivity with the southern Gulf of Maine.

Chapter 3 (this volume) also concluded that there is connectivity of cod early life stages between the Gulf of Maine and statistical area 521, based on their examination of the spatial and temporal distribution of cod larvae, a review of larval transport studies, and correlation analyses. They conclude that the majority of observed settlement in statistical area 521 originates from spawning events in the Gulf of Maine. Chapter 7 (this volume) also notes that adults tagged in statistical area 521 move in all directions, including between the 2 management units. The high degree of cod larvae dispersal and adult movements around Cape Cod provide a mechanistic explanation for why cod life history in this statistical area is often clustered with the Gulf of Maine management unit, instead of the Georges Bank unit to which this statistical area is assigned.

Up to about 2010, a size at age signal existed between 3 areas: Gulf of Maine, western Georges Bank, and eastern Georges Bank. However, this historic area-specific growth signal since has broken down, to the point that strong differences between these 3 areas have diminished and that size at age 2 is relatively homogeneous between US statistical areas in the last decade or so. Three process hypotheses may explain this change: (1) warming in this region has become physiologically stressful, more so on Georges Bank than in the Gulf of Maine; (2) the composition of spring versus winter-spawners has changed over time, favoring the latter which are larger at the first few age classes and more common in the Gulf of Maine management unit; or (3) prolonged and intense fishing has removed faster growing fishing genotypes, resulting in fishing-induced evolution, which is most evident for the Georges Bank cod stock. There is also a measurement error hypothesis that the switch from the NOAA Ship Albatross IV to the NOAA Ship Henry Bigelow had led to reduced differences between regions. We explore each of these hypotheses in detail below.

Warming in this region has been recognized repeatedly in both the Gulf of Maine and Georges Bank management units with potential effects on Atlantic cod (Pershing et al. 2015; Miller et al. 2018; Sguotti et al. 2019). Nonetheless, Miller et al. (2018) modeled growth of

Georges Bank cod during spring 1970-2014 and showed that bottom temperature positively affected size at age during the first year of life, which does not suggest that temperatures on Georges Bank have reached some threshold that would reduce cod growth in this management unit. We reject hypothesis 1 as a causative factor slowing growth of Georges Bank cod.

Shifts in size at age 2 may be a result of changes in cohort structure, such as an area that was dominated historically by spring-spawning cod are dominated now by winter-spawned cod. This change may occur where spawning occurs in both the spring and winter, specifically in the southwest Gulf of Maine, where cod are aggregated. Because the winter-spawned cod experience nearly a full year of growth before the first annulus is marked on their otolith, whereas the spring-spawned cod experience only a partial year, winter-spawned cod are larger at a common age in the first few years, when age is assigned by examining otoliths. Dean et al. (2019) developed an otolith-based method to discriminate between these spawning cohorts in the Gulf of Maine and found that spring-spawned cod were the dominant cohort during the 1980s and through the mid-1990s, after which the winter-spawned cohort became dominant to today. Lefebvre et al. (2021) also report changes in proportions of winter and spring-spawned cod between decades. While these findings reveal a mechanism for why size at age may have increased in at least certain statistical areas of the Gulf of Maine during this time period, it does not explain why size at age 2 decreased on Georges Bank.

Cod in both management units have experienced high mortality over time, which has led to lower spawning stock biomass and numbers overall. Reduced density may promote faster growth if resources become more available, either relatively or absolutely. However, faster growth was only suggested in the Gulf of Maine, and it may be conflated with spawning origin if an increase of size at age 2 is the result in shifting composition of spring versus winter-spawned cohorts, as specified in the previous paragraph. More concerning is that high fishing mortality has removed fast-growing genotypes out of the population. This possibility has been reported for many marine fish populations, including US stocks of cod (i.e., fishing-induced evolution; Barot et al 2004). Presumably, fast growing genotypes of cod are being removed in both management units, and if so, historically reduced size at age 2 will likely persist for decades, even after lowering fishing mortality, confounding the historical growth signal of cod stock structure as well as reducing fisheries yield for each stock (Law 2000; Conover et al. 2009).

Finally, measurement error is a concern because of the various changes that occur during the 48-year time series. We focus here on the switch between NOAA Ship Albatross IV in 2008 and transfer of operations to the NOAA Ship Henry Bigelow. The latter catches more cod, and these are smaller and younger than catches by the former (Brooks et al. 2010), which could result in a bias of slower growing cod being caught. Qualitatively, this does not appear to be the case. First, the shift to slower growing fish on Georges Bank is evident in the period 2000-2005 (Figs. 5, 6), before the switch in vessels. Second, it is not clear why this calibration issue would lead to larger fish in the Gulf of Maine but smaller fish in the Georges Bank management unit. Third, the cod that are aged are sampled in a stratified-random manner with respect to length bins, which would down-weight the influence of Bigelow sampling more cod that are smaller and younger. A more qualitative analysis would require reconstructing the original, pre-stratified samples and simulating the size at age of subsampled cod, which is beyond the scope of this study, and will not necessarily lead to a different conclusion, but we discuss it here to be complete.

Female Maturity

Historical estimates of age at female maturity showed that Gulf of Maine cod had the oldest age at maturity: 4 years, Gulf of Maine (Cape Ann, MA); 3.5, Browns Bank; 2.9, Georges Bank (Earll 1880; Livingston and Dery 1976). Over time, median length and age at maturity declined dramatically based on the analyses here and those published elsewhere (Hunt 1996; Begg et al. 1999; O'Brien 1999; Barot et al. 2004; Miller et al. 2018).

Although such temporal trends have been associated with increasing water temperatures for some marine species (Shapiro Goldberg et al. 2019), bottom temperature did not improve modeling of maturity parameters for Georges Bank cod (Miller et al. 2018). As pointed out for size at age 2, it is more likely that this decrease in both L_{50} and A_{50} is a response to overfishing of these populations, which has been seen in many heavily exploited fishes (Trippel 1995; Laugen et al. 2014). Although age at maturity in the most recent period (2012-2017) was highly structured into 4 largely geographically coherent clusters, the spatial tendency is for L_{50} (both periods) and A_{50} (1970-1975) from western Georges Bank statistical areas to cluster with Gulf of Maine areas. This finding supports a misalignment of select western areas, particularly statistical areas 521-522, within the Georges Bank management unit.

Overview of the Approach

A strength of these analyses is the use of a single time series across nearly 5 decades and over a relevant spatial scale, using standard methods to examine abundance, size at age 2, and maturity schedules. A mixed set of data sources could have been used if statistical sampling designs were appropriately matched or adjusted throughout the time series and corresponding quality checks occurred for sample processing between laboratories. For example, Du Pontavice et al. (2018) integrated fishery-independent (survey beam trawl) and fishery-dependent (commercial landings) sources and calibrated the results during a short period of sampling (2010-2015). We considered including other bottom trawl monitoring datasets, but each choice presented complications we have avoided here. For example, Canada DFO has a trawl survey across a partially overlapping area but at a different time of year (Andrushchenko et al. 2018). There are inshore surveys in the Gulf of Maine and around Cape Cod but these started later, each in different decades (i.e., trawl surveys operated by Maine-New Hamphire[1] and Massachusetts[2], respectively). The Connecticut Department of Energy and Environmental Protection has a spring and fall trawl survey of Long Island Sound, a large estuarine system not sampled by the NOAA bottom trawl survey, but the median number of cod collected has been zero (1984-2019; range 0-109. However, nearly all the cod collected in this survey have been collected since 2003 suggesting a trend over time (CT-DEEP[3], Annual Reports). The Northeast Area Monitoring and Assessment Program samples inshore areas from Cape Cod to the Chesapeake Bight in both spring and fall since 2008, but it collects very few cod (0-15 individuals per year; NEAMAP[4], Annual Reports). In addition, quality assurance would be necessary to compare ages and maturity classifications among these

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[1] [MEDMR] Maine Department of Marine Resources, [NHFGD] New Hampshire Fish and Game Department. Maine – New Hampshire inshore trawl survey annual reports. https://www.maine.gov/dmr/science-research/projects/trawlsurvey/index.html

[2] [MADMF] Massachusetts Division of Marine Fisheries. Trawl survey annual reports. https://www.mass.gov/service-details/review-trawl-survey-updates

[3] [CT-DEEP] Connecticut Department of Energy and Environmental Protection. Annual Reports. https://portal.ct.gov/DEEP/Fishing/Fisheries-Management/Long-Island-Sound-Trawl-Survey

[4] [NEAMAP] Northeast Area Monitoring and Assessment Program. Atlantic cod summary data. http://fluke.vims.edu/mrg/neamap_abundance/AtlanticCod.htm

programs. That is not to dissuade further efforts to combine datasets to address specific questions, but here, it was not a simple matter of pooling all these data, as such differences would require extensive explanation for evaluation and interpretation.

Another strength is to aggregate the data in a hierarchical manner to test for coherence between fine-scale statistical areas and large-scale management units. Specifically, we employed cluster analysis to look for coherence between the data assigned to nested spatial units, as outlined by Cope and Punt (2009) for common fishery data. A corollary to using finer-scale measurements is that we avoided model-based estimates of growth. For example, a seminal, model-based approach by Begg et al. (1999) noted unrealistic estimates of von Bertalanffy growth parameters when samples sizes were low in the 1990s, even when the data were pooled by only the 2 management units. Bayesian methods may assist in fitting realistic parameters to such data-limited situations, but the application of this approach by Adams et al. (2018b) still reported the greatest uncertainty for sampling units that had the smallest sample sizes, which constrains the inference possible for testing alternative stock structure hypotheses.

There are some weaknesses of this analysis, including limited sample sizes in some statistical areas, particularly but not limited to the New York Bight, southern New England, Browns Bank, and the central Gulf of Maine. Still, the clustering approach followed guidelines proposed by Cope and Punt (2009) to use multiple years of data per period and samples with low coefficients of variation. Also, the origin of season spawning (spring versus winter) is not directly known in our samples, but as discussed, this may explain the temporal instability of the size at age results. Finally, in concordance with temperatures rising, the forage for cod may be shifting, as documented for larval cod by Friedland et al. (2013), but the effects of these ecosystem shifts on cod life history traits and stock structure cannot be explored by our approach.

These temporal dynamics in Atlantic cod life history are highly relevant for assessment and management because they affect yield. At a very broad-scale, there is a spatial pattern in these life history traits that supports at least 2 management units. However, the temporal instability of growth and maturation rates raise additional questions. Growth and maturation rates arise from both environmental and genetic components that may be difficult to tease apart (Swain and Foote 1999; Begg 2005). Life history parameters may change over ecological time scales because of environmental influences (e.g., temperature) or population dynamics (e.g., density-dependence) (McBride 2014a), and they can be subject to fisheries-induced evolution (Kuparinen and Merilä 2007; Enberg et al. 2009) or phenotypic plasticity (e.g., Grabowski et al. 2009). Continued sampling is warranted to determine if these changes arise from environmental plasticity, which may rebound quickly if conditions revert to original settings, or from fishing-induced evolution, which may only reverse in response to reduced fishing pressure over several generations of cod.

Conclusions

The value of life history traits as inputs to stock assessment has resulted in decades of monitoring data across relevant spatial scales and revealed spatial and temporal dynamics of abundance and distribution, size at age 2, and size and age at maturity. This reevaluation of these specific life history traits supports earlier divisions of Atlantic cod into at least 2 management units, but also suggests that select areas of western Georges Bank are not only different than eastern Georges Bank, they are more aligned with the Gulf of Maine. The loss of the size-at-age “stock structure signal” over time is confounding, and brings up the question of whether this change arises from environmental plasticity, which may rebound quickly if conditions revert to original settings, or from fishing-induced evolution, which may only reverse in response to reduced fishing pressure over several generations of cod.

Life history patterns contribute to our interdisciplinary review of cod stock structure but do not appear to be leading indicators identifying stock structure of cod (Chapter 9, this volume). In particular, the significant temporal and spatial dynamics in these life history traits, coupled with low sample sizes in specific period-area combinations, make them more of a complementary approach to consider among the other disciplines explored in this volume.

Regardless, the dynamic nature of the specific life history traits analyzed here suggest they could continue to change in the future, and thereby continue to inform stock structure, stock assessment, and fishery management. It appears that current allocations of sampling in recent years have achieved well-balanced sample sizes across areas, which should be maintained. Alignment of future life history trait analysis within an interdisciplinary context is recommended as a recurring process-oriented approach to investigate stock structure and dynamics of Atlantic cod.

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6. NATURAL MARKERS

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Abstract

Natural markers are naturally induced characteristics that can be used to identify members of a population, stock, or finer-scale grouping of organisms (e.g., contingent). Elemental and isotopic fingerprints, genetic markers, growth patterns and shape recorded in otoliths, and parasites are all examples of natural markers with demonstrated success in identifying and tracking populations. The natural markers applied to Atlantic cod (*Gadus morhua*) to date include otolith characteristics (chemistry, shape, and structure), tissue characteristics (stable isotopes concentrations and fatty acid profiles), body characteristics (color type, morphometrics, and meristics), and other features, such as parasites and genetics, the latter of which is reviewed separately in this Technical Memorandum. Natural markers (otolith chemistry, structure, and morphometrics) support winter and spring spawners as unique groups in the Gulf of Maine. This finding is also supported by genetic evidence. Morphometric results also suggest that there may be 2 unique groups of cod on eastern and western Georges Bank. These results are in broad agreement with genetic analyses, tagging studies, and fishermen's ecological knowledge of Atlantic cod. Parasite infestation rates suggest separation between the northern Gulf of Maine, central Gulf of Maine, Georges Bank, and southern New England cod. Natural markers are a valuable tool, not only to identify cod stocks or separate stock components in mixed catches, but also to lend inference about natural history of populations, (e.g., meristics often follow a latitudinal cline or morphometrics suggest whether groups of fish are migratory or resident).

Introduction

Natural markers are naturally occurring traits that can be used to identify members of a population, stock, or more discrete grouping of fish. Some of these traits may be readily recorded without special equipment, such as measuring fish body shape or counting parasites types or numbers. Other natural markers can require additional, sometimes specialized laboratory analyses, such as measuring the chemical composition of otoliths or genome sequencing. The ease of measuring some natural markers often allows more than one natural marker to be recorded in a single study. The challenge is identifying a marker, or group of markers, that is sufficiently distinct to identify the population, stock, or group of interest. Among fishes, there are many natural markers that have demonstrated success in identifying or tracking populations or finer-scale groups; these include: elemental and isotopic fingerprints, genetic markers, growth patterns and shape recorded in otoliths, and parasites (Cadrin et al. 2014). Some multidisciplinary investigations of population structure have found natural markers to be the most informative basis for stock identification (e.g., horse mackerel [Trachurus trachurus] Abaunza et al. 2008). Once the utility of a natural marker is established, it can be applied in stock discrimination, where the origins of mixed-stock samples are apportioned to multiple stocks (Waldman et al. 1988).

Natural markers may be representative of fish genotype, phenotype, or both. The use of genetic markers to characterize fish genotype is addressed in Chapter 4. Here, we describe natural markers that are observable as phenotypes. Phenotypic differences between groups in natural markers may reflect genetic differences, environmental differences, or some combination of both (Swain et al. 2005; Heino 2014). In general, even genetically similar fish that reside in different environments are expected to exhibit physical dissimilarities because of the influence of the unique conditions to which they are exposed (Swain et al. 2005). In some instances, natural markers can reveal subtle population structure or life-cycle patterns that may not be detected by genetic applications alone, such as contingent structure, which is not necessarily genetically inherited but explained by phenotypic plasticity and social behavior (Kerr et al. 2010; McBride 2014). A key advantage of phenotypic characteristics is that they reflect both the influence of natural selection and the environment. Nevertheless, in many instances it can be challenging to distinguish between differences that have a genetic basis and those that have been environmentally induced (Swain et al. 2005). Information gathered from phenotypic markers are often combined with genetic data and movement information for more robust inference regarding stock structure.

In this chapter, we review the best available science on the application of natural markers to the study of Atlantic cod (*Gadus morhua*) stock structure in the northwest Atlantic (NAFO Divisions 5 and 6 and interactions with 4X; Fig. 1.1). The natural markers applied to cod include otolith characteristics (chemistry, shape, and structure), tissue characteristics (stable isotopes concentrations and fatty acid profiles), body characteristics (color type, morphometrics, and meristics), and other features, such as parasites.

Review of Natural Markers Applied to Atlantic Cod

Otolith Characteristics: Chemistry, Shape, and Structure

Otoliths are calcified structures within the inner ear of fish which grow throughout a lifetime by accumulating calcium carbonate, preserving a detailed record of the chemistry of the environment experienced by an individual fish and its growth history over time (Campana et al. 1999; Kerr and Campana 2014). Otolith characteristics, including chemical composition, shape, and macro- and microstructure, have been identified as informative natural markers relevant to understanding population structure and the natal origin of fish.

Otolith chemistry

There is a considerable body of work that has established the utility of otolith chemistry as a useful natural marker of fish stock structure and tracer of fine-scale habitat use of fish indicative of alternative life history types (Campana 2005; Elsdon et al. 2008; Kerr and Campana 2014). This technique depends on geographic variation in water chemistry (e.g., coastal vs. offshore gradients) or other factors (e.g., temperature, salinity) that influence the chemistry of otoliths such that fish that inhabit different environments exhibit differences in their otolith chemical composition (Kerr and Campana 2014). In addition to environmental differences, the chemical composition of fish otoliths can also be influenced by fish physiology (Sturrock et al. 2015) and genetics (Clarke et al. 2011). Applications of this approach often focus on analysis of otolith cores composed of the first few months up to a year of otolith growth, which provide insight on natal origin of fish. However, whole otolith analysis is used as well to demonstrate lifetime differences in habitat use. Of the 3 pairs of fish otoliths, the sagitta, lapillus, asteriscus, the sagitta is most frequently used because of its size, with limited examples of applications to the lapillus and asteriscus.

There are several examples of past applications of otolith chemistry to cod in US and Canadian waters, as well as ongoing work that is relevant to understanding population structure of cod in US waters. Early on, Campana et al. (1994) used otolith chemistry to characterize cod collected at 5 spawning grounds in the northwest Atlantic (Chéticamp [Cape Breton, Canada], the riptide in the Bay of Fundy [Canada], Georges Bank, Newfoundland, and Iceland). The study found significant differences among concentrations of 14 isotopes across spawning sites. However, differences between sites were small resulting in low classification accuracy between spawning sites based on discriminant analysis (30% jackknife accuracy). Campana and Gagne (1995) expanded on this approach, evaluating cod otoliths from 7 spawning grounds (the 5 previously mentioned and the Gulf of St. Lawrence and Eastern Scotian Shelf) for 34 isotopes to test for differences in chemical composition. The highest level of discrimination was based on sagittal otoliths between Scotian Shelf and Gulf of St. Lawrence fish (i.e., 90 - 98% accuracy). In addition, discriminant analysis based on a subset of isotopes analyzed in lapillar otoliths also revealed relatively high classification success (average 83% accuracy) with the highest error rate associated with the discrimination of Georges Bank and adjacent Bay of Fundy riptide samples, which may suggest connectivity between these areas or reflect similar chemical signatures across adjacent areas. These early applications of otolith chemistry to cod in the northwest Atlantic demonstrate that this technique has the capacity for accurate discrimination of cod spawning populations over a large geographical range.

Additional studies by Campana and others in Canadian waters demonstrated the utility of otolith microchemistry for mixed stock assignments with high classification accuracy. Campana et al. (1999) used otolith elemental chemistry to conduct a mixed stock analysis on cod overwintering in the Gulf of St. Lawrence. Four populations were identified within this region, including: (1) northern Gulf of St. Lawrence, (2) southern Gulf of St. Lawrence, (3) southern Newfoundland, and (4) eastern Scotian Shelf. The authors used the stock composition analysis of the individual trawl samples to develop maps of population specific abundance and distribution during winter. Campana et al. (2000) also demonstrated the utility of whole otolith elemental analysis of Atlantic cod for stock identification within the Gulf of St. Lawrence. Where aggregations of mixed stocks occurred on both feeding (summer) and overwintering grounds, the elemental fingerprints of the source spawning aggregations were different enough that mixed stock analysis could identify cod stock composition.

Recent work by Kerr et al. (2018) applied otolith microchemistry to discriminate between winter and spring spawning cod in the Gulf of Maine (collections in Massachusetts Bay and Ipswich Bay; sampling years 2012-2016; n = 252). Significant differences in the elemental fingerprint of cod otoliths (age one and whole otolith) were evident between the 2 spawning groups (Figure 6.1), supporting a previous genetic study that identified the 2 groups as temporally distinct spawning populations (Kovach et al. 2010). Stepwise discriminant function analysis with jackknife prediction was used to classify Atlantic cod based on age one otolith chemistry to spawning time (winter and spring), and classification success was relatively high at 74%. There were also significant differences, albeit smaller in magnitude, in otolith chemistry based on capture location.

However, these differences did not support accurate classification of fish to location of capture. This study illustrates the utility of otolith chemistry for discrimination of winter and spring spawners in the inshore Gulf of Maine. Application of this technique to samples representative of the fishery (collected 2015-2016) revealed the composition of fish was dominated by winter spawners (ranging from 55 to 65% across years; Figure 6.2).

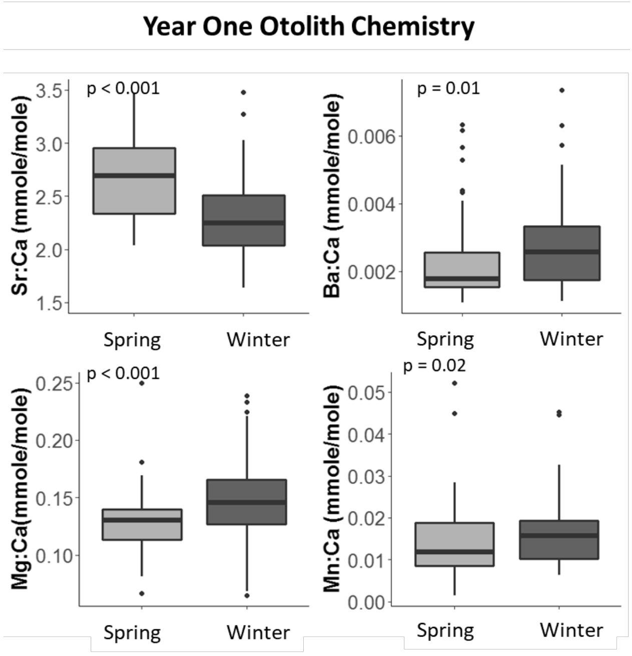

Figure 6.1. Elemental ratios from the first year of life (age-0 region of otoliths) of Atlantic cod (*Gadus morhua*) sampled from winter and spring spawning populations in the Gulf of Maine. Figure modified with permission from Kerr et al. (2018).

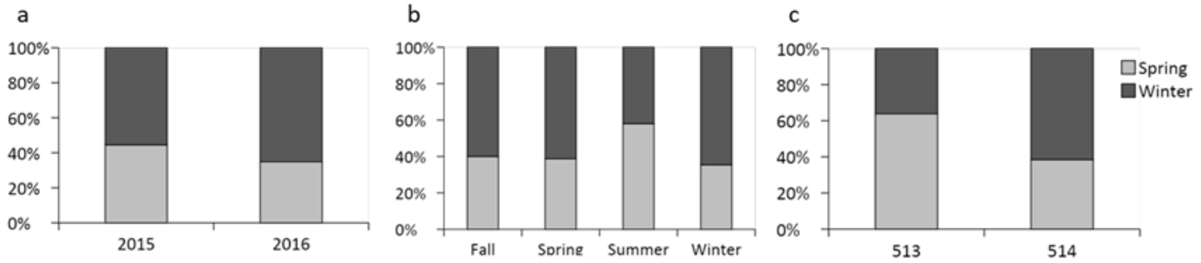

Figure 6.2. Mixed stock composition of fishery collected Atlantic cod (*Gadus morhua*) (a) over time (2015-2016), (b) across statistical areas (513 and 514), (c) and by season. Data are presented by using random forest classification approach. Figure modified with permission from Kerr et al. (2018).

Otolith shape

Otolith shape has been shown to have great utility in stock discrimination and has been applied to other cod stocks, informing separation of eastern and western Baltic cod (Hüssey et al. 2016) and Norwegian coastal cod and Northeast Arctic cod (Stransky et al. 2008). Otolith shape is known to be influenced by a combination of genetic and environmental factors with fish of different origin and life histories exhibiting shape variation that can be used to discriminate between stocks (Vignon and Morat 2010).

Campana and Casselman (1993) applied otolith shape analysis to classify cod populations in the northwest Atlantic. They applied the technique to otoliths from fish in spawning condition collected at 19 sites in US (Gulf of Maine and Georges Bank) and Canadian waters, as well as Iceland. They found that classification accuracy was wide ranging. In general, samples from the Gulf of Maine region were accurately classified to region (61-80% correct classification), but there was poor classification success for other regions: (1) Eastern Scotian Shelf, (2) St. Lawrence, (3) Newfoundland, and (4) Iceland. It is important to note that this was an early application of this approach and technical developments have occurred since this implementation (Stransky 2014). Thus, although there are few current applications to cod in the northwest Atlantic, this technique has a strong potential for utility in cod stock discrimination based on successful application in other regions.

Otolith structure

Otolith "growth signatures" have been established as a powerful tool for stock identification (Brophy 2014). The relative growth of otolith annuli is known to be related to growth of the fish, and changes in fish and otolith growth are expected to occur ontogenetically, but otolith growth will also vary spatially and temporally in response to different oceanic conditions, as well as from genetic differences that may influence metabolism (Brophy 2014). Annual, seasonal, and daily growth patterns have been used to distinguish groups of fish with different growth histories (Brophy 2014). Otolith structure, specifically the size of year one otolith growth, has been successfully applied to discriminate cod stocks off the coast of Norway (Norwegian coastal cod from Northeast Arctic cod; Berg et al. 2005) and, more recently, in the Gulf of Maine (winter and spring spawners; Dean et al 2019; Lefebvre et al. 2021).

An analysis of otoliths from spring and winter spawning cod in the Gulf of Maine revealed distinct early growth patterns between the 2 spawning populations (Dean et al. 2019; Figure 6.3). Although the diameter of the first annulus was the primary discriminating feature, the age of fish upon capture was also important, suggesting a difference in mortality rates between groups. By using a logistic regression model fit to training data (n = 577) and evaluating the model through cross-validation, individuals were correctly classified with 81% accuracy, and the overall subpopulation mixture was predicted within 1%. Applying the model to a broader population dataset (n = 1642) revealed that spring-spawned cod are more prevalent within closed fishing areas and therefore experience a lower mortality rate. However, despite dominating older age classes and comprising a relatively large fraction of the spawning stock, these spring cod currently contribute little to annual recruitment. Significant differences in growth and mortality were found between the 2 groups, where winter spawners grow and mature at a faster rate, but spring spawners reach a larger maximum size. These apparent differences in vital population rates (i.e., mortality, productivity, growth, maturity) have important consequences for assessment models and management measures that assume homogeneity across the stock.

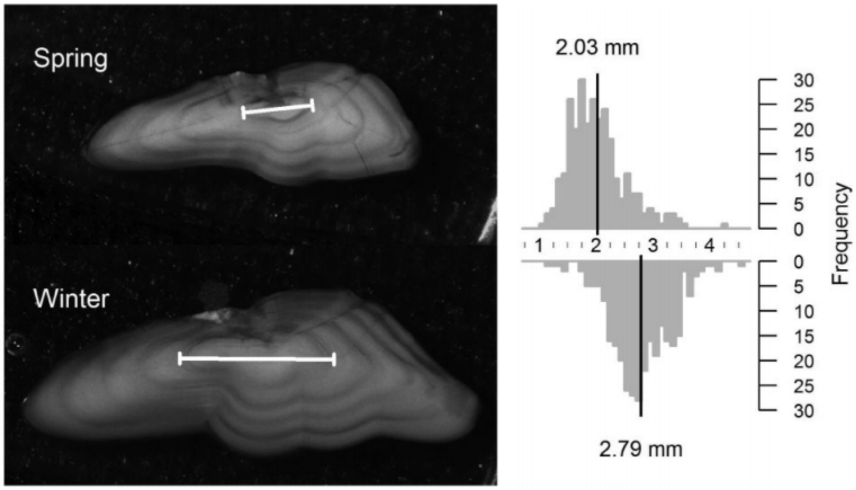

Figure 6.3. The diameters of the first annulus differed between spring and winter spawning Atlantic cod (*Gadus morhua*). [Left] Otolith cross-sections from 2 age 4 cod, both captured in spawning condition. The one at top was captured in May, while the one at bottom was captured in December. The diameter of the first annulus (A1) 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. Figure modified with permission from Dean et al. (2019).

In addition, ongoing work by Kerr et al. (2018) identified significant differences in otolith growth of winter and spring spawning cod from the Gulf of Maine beyond age 1 (i.e., ages 1-2 and 4-5). The largest differences in otolith growth were evident in the width of the age 1 annulus between winter and spring spawning cod. Persistent growth differences later in life align with Dean et al. 2019 observations of differences in vital rates between winter and spring spawners.

Body Characteristics: Meristics, Morphometrics, and Color Morphs

Color morph

Variation in the color of Atlantic cod has long been recognized and has been explored as a stock identification technique. Gosse and Wroblewski (2004) noted that color morphs of cod are common in the waters of Labrador and Newfoundland and that cod in Gilbert Bay, Labrador, which feed primarily on invertebrates commonly exhibit a golden-brown color and are colloquially known as “the golden cod of Labrador.” These golden-brown cod were held in a net pen for 3 months and fed a fish based diet. The color of the cod changed over the holding period, as the experimental fish lost much of their golden-brown pigmentation, and the ventral surface became lighter, as the fish adopted a more “typical” countershading pattern (Figure 6.4A). Similarly, a local morph of “red cod” were also held for 3 months and fed a fish based diet. Over time, the red pigment on the cod gradually transitioned to a brownish color, and the ventral surface of the cod became lighter (Figure 6.4B). Taken together, these findings suggest that coloration in cod is strongly influenced by diet and is not a stable marker. Nevertheless, Wroblewski et al. (2005) suggested that color can be used as part of interdisciplinary stock composition analysis to aid in distinguishing resident and migratory cod groups in mixed fishery catches.

Sherwood and Grabowski (2010) reported that “red cod” are commonly observed near Cashes Ledge (Ammen Rock) in the Gulf of Maine, and the presence of red cod in the Gulf of Maine was also noted by Bigelow and Schroeder (1953) and confirmed by Conroy (2016).

Sherwood and Grabowski (2010) sampled cod from Cashes Ledge over a 3 year period (2007-2009) and investigated the growth, diet, morphometrics, and isotope signatures of these fish. The authors noted an abrupt cutoff in the color (red to green ratio; RGR) of cod caught around Cashes Ledge, with higher red to green ratios for cod captured in shallow waters near Ammen Rock. Red cod grew slower and reached smaller asymptotic sizes than olive cod, based on von Bertalanffy growth curves. The 2 color morphs selected different prey, which was reflected in their $\delta^{13}C$ and $\delta^{15}N$ ratios. Red cod primarily fed on lobsters, crabs, and benthic fish, while the olive cod primarily consumed pelagic shrimp. The body shape of red and olive cod also differed, with red cod exhibiting shorter snouts, deeper bodies, and more slender tails. Using body shape, cod could be classified back to their color type with 84% accuracy. Based on the observed differences in growth, morphometry, habitat, and diet, red cod may exhibit a unique life history strategy in the Gulf of Maine (i.e., more sedentary and shallow-living). Indeed, follow up work (Conroy et al. 2017) showed that red cod at Cashes Ledge inhabit shallower depths and exhibit more sedentary behavior, as indicated by acoustic telemetry. In this example, 2 color morphs were consistent with other evidence of ecological specialization, whether from other natural markers or applied markers (i.e., tags). However, further work is needed to determine whether these red cod represent a genetic ecotype that is distinct from olive cod, or if it is a conditional life history strategy (i.e., contingents). A common garden experiment would help to elucidate this problem.

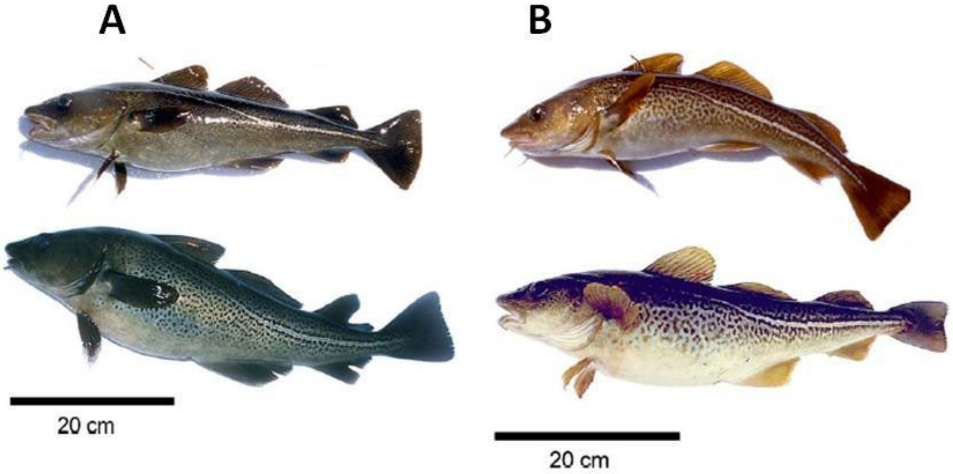

Figure 6.4. Color changes observed in Atlantic cod (*Gadus morhua*) from Gilbert Bay, Labrador, observed over a 12 week holding period. (A) the original coloration of the cod at the start of the holding period. These cod are colloquially referred to as "brown cod," as indicated by the brownish pigment on the fins and ventral side of the fish. By the end of the holding period, the brown coloration had largely disappeared from the cod, and the ventral surface had lightened (bottom picture). (B) the original (top) and final (bottom) coloration of the "red cod" over the 12 week holding period. Note the loss of the red pigment, and the lightening of the ventral surface that occurred during the experiment. Figure modified with permission from Gosse and Wroblewski (2004).

Meristics

Meristic characters are features of fish that can be counted. External body features such as fin rays, gill rakers, and scales, and internal features such as vertebrae, pterygiophores, and branchiostegal rays can be used in meristic analyses (Waldman 2005). The formation of meristic characters is influenced by environmental factors, such as temperature, pH, salinity, oxygen levels, food availability, and the growth of an individual (Barlow 1961), as well as genetics. Meristic values for a body feature are usually determined during early life history and can be useful for stock identification because they indicate that early development occurred under different conditions or in separate areas (Chase 2014). There is generally an inverse relationship between water temperature and the counts of meristic features, known as Jordan's rule (Chase 2014). Meristic characters are inexpensive to obtain and relatively easy to analyze, and as a result, they have been used in stock identification research for over a century. Waldman (2005) and Chase (2014) provide an excellent overview of case studies where meristic characters have been used to investigate stock structure.

Meristic characters, especially vertebrae and fin ray counts, have been applied extensively to investigate Atlantic cod stocks in Canadian and European waters. In a multidisciplinary study, Martin (1953) employed a combination of meristics, tagging, life history data, and parasites to examine the stock structure of cod off Nova Scotia and the Gulf of St. Lawrence. Mackenzie and Smith (1955) also used vertebral counts to examine the stock structure of cod in Canadian waters and documented at least 4 populations in the Gulf of St. Lawrence and 7 populations on the Scotian Shelf. They also used vertebral counts to study the seasonal migrations of cod on the Scotian Shelf. Over 3 decades, Templeman (1981) analyzed the vertebral counts of nearly 45,000 cod ranging from the Scotian Shelf to western Greenland and found geographic variation related to temperature and latitude, with higher vertebral counts associated with more northern samples. Pepin and Carr (1993) used a combination of meristics, morphometrics, and genetics to investigate the stock identity of cod on the Grand Banks and found low reclassification rates (<50%), suggesting a single cod stock inhabited the study area. Swain et al. (2001) used vertebral counts to examine the stock composition of cod harvested in the Laurentian Channel winter fishery. In a common garden experiment, Loken and Pedersen (1996) demonstrated that vertebral number in Norwegian cod is determined both by genetics and temperature.

Despite the utility of meristic characters for investigating the stock identity of Atlantic cod, this technique has not been routinely applied in US waters or the Bay of Fundy. In an early study, Schmidt (1930) investigated vertebral counts of cod taken from Nantucket Shoals (mean = 51.9) and Mt. Desert Island (mean = 53.0). Later, Templeman (1962) reported similarities in vertebral counts between cod taken from the Northeast Peak of Georges Bank (mean = 52.7) and Browns Bank (means ranged from 52.5 to 53.0), although the sample sizes were not reported. Given the utility and cost effectiveness of this approach, meristic characters may be informative for future multidisciplinary stock identification studies in the region.

Morphometrics

General morphometry (i.e., body shape analysis) has long been used to aid in identification of stock structure in fish (Meng and Stocker 1984; Haddon and Willis 1995; Begg and Waldman 1999; Cadrin and Silva 2005). Morphometrics are known to be influenced by both genetics and the environment, which can lead to subtle differences in body shape among populations (Swain et al. 2005). For example, some populations may exhibit more migratory behavior, whereas others may be more sedentary, and these behavior adaptations may lead to differences in body shape (e.g., migrants should be more streamlined than residents, Morinville and Rasmussen 2008). Differences in diet among regions may also drive differences in body shape.

Sherwood and Grabowski (2010) identified body shape differences in cod in the central Gulf of Maine (Cashes Ledge) with red cod having deeper bodies, shorter snouts, and more slender tails than normal (olive) cod which is likely a result of their sedentary behavior, but could also be related to a more crustacean dominated diet (i.e., large crabs and lobsters).

Sherwood and Grabowski (2012) sampled 370 cod in the Gulf of Maine and on Georges Bank between from 2007-2009 using hook and line (Figure 6.5). Morphological characters were measured with a box truss network, and step-wise discriminant function analysis was used to classify samples to their original spatial grouping. Samples from Georges Bank and the Gulf of Maine could be classified to their original groups with an accuracy of 70%. However, classification accuracy was higher for samples taken from eastern and western Georges Bank (77%), and the authors concluded that "there is some important structure on Georges Bank that is not captured by the current stock definitions." The morphometric results suggested that cod on eastern Georges Bank were more streamlined that western Georges Bank cod, which may be reflective of differences in their migratory behaviors.

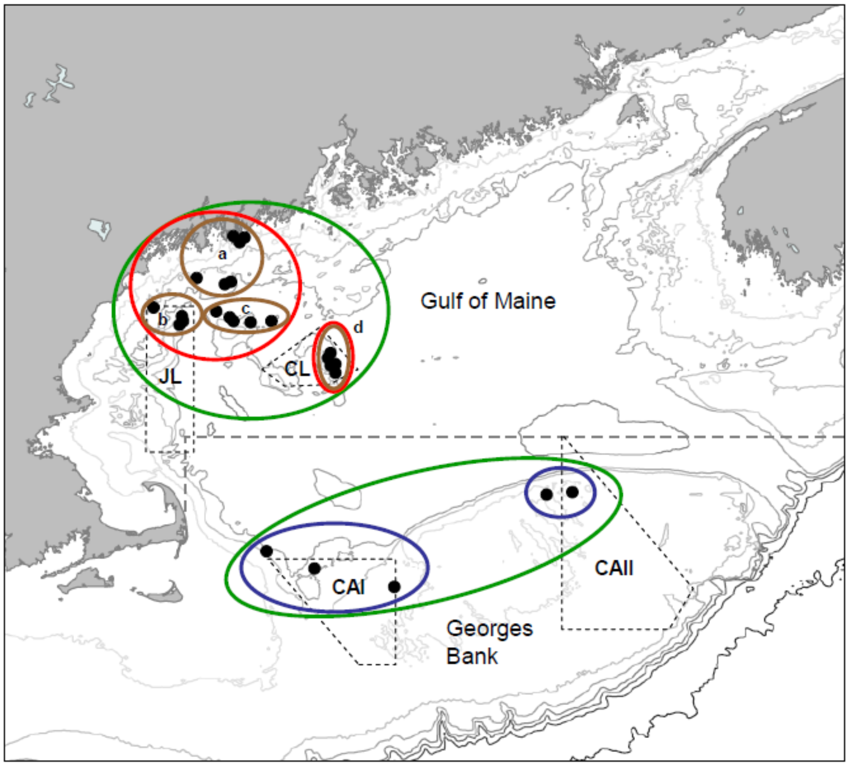

Figure 6.5. Map of Gulf of Maine (GOM) and Georges Bank (GB) showing location of sampling sites (black dots) for Atlantic cod (*Gadus morhua*) morphometric analysis (Sherwood and Grabowski 2012). Green ellipses indicate groupings for comparison 1 (Gulf of Maine vs. Georges Bank), blue ellipses are groupings for comparison 2 (eastern vs. western GB), red ellipses are groupings for comparison 3 (eastern vs. western GOM), and brown ellipses are groupings for comparison 4: (a) Bigelow Bight and Sheepscot Bay; (b) Jeffreys Ledge (JL); (c) Platts Bank; (d) Cashes Ledge (CL). Dashed polygons show 4 year-round closed areas: closed area I (CAI); closed area II (CAII); Cashes Ledge closured area (CL); Jeffreys Ledge (JL) or western Gulf of Maine closure area. Dashed line shows division between GOM and GB stocks. Figure contributed by G. Sherwood.

The results of Sherwood and Grabowski (2012) also pointed to fine-scale structure within the Gulf of Maine, where samples from the eastern (Cashes Ledge) and western (Bigelow Bight, Platts Bank, and Sheepscot Bay) Gulf of Maine could be assigned to their group of origin with 91% classification accuracy. The authors concluded that there may be population structuring within the Gulf of Maine that is not accounted for in management but noted that little corroborating information from other disciplines (e.g., tagging and genetics) was available to support this conclusion. Interestingly, cod on Platts Bank, which is an intermediate distance offshore between the eastern (Cashes Ledge) and western (Bigelow Bight and Sheepscot Bay) sample locations, grouped with samples from both the eastern and western areas, suggesting this area may serve as a boundary between populations (Figure 6.5). This boundary also agreed well with Ames' (2004) substock delineations (i.e., western and midcoast subpopulations).

Kerr et al. (2018) included morphometric methods among a suite of others for investigating the differences between spring and winter spawning cod in both Massachusetts Bay and Ipswich Bay. A box-truss network was created with 12 homologous landmarks, and 22 linear measurements and discriminant function (DF) analysis were performed, based on 260 near spawning condition fish from the 4 spawning groups. The largest discrimination was between Massachusetts Bay and Ipswich Bay fish along the first discriminating axis (DF1), rather than between spring and winter spawning cod. Discrimination of spring and winter spawning cod in both bays were distinguishable along DF2. Overall, 82% of cod were correctly reclassified back to their original groupings suggesting that body shape alone is a good means of discriminating between spawning groups. Massachusetts Bay, in particular, had very high reclassification rates (90%). Overall reclassification rates were slightly higher (84%) when color (red-green ratio) was added as a discriminating variable. These reconstructions consistently show that spring spawning cod are more streamlined regardless of location, and therefore probably more migratory than winter spawning cod.

Tissue Characteristics: Stable Isotope Concentrations and Fatty Acid Profiles

Fatty acid profiles have been used as natural marks for stock identification for several marine species, including cod (Grahl-Nielsen 2005, 2014). The fatty acid composition in the tissues of a fish is influenced by several factors including their genotype diet, and environmental conditions (Kirsch et al. 1998; Grahl-Nielsen 2005, 2014). Over 20 fatty acids have been used as stock identification markers, and principal component analysis is typically used to quantify differences amongst groups (Grahl-Nielsen 2005).

Fatty acids have been used to differentiate cod stocks on the Faroe Plateau and the Faroe Bank (Joensen et al. 2000). Furthermore, fatty acid profiles of cod muscle and heart tissue from Northeast Atlantic stocks (Faroe Bank, Faroe Plateau, Northwest Iceland, Norway-Barents Sea, and Denmark-Skagerrak) have demonstrated high classification accuracy for stock identification (89%; Joensen et al. 2014). Fatty acid profiles have not been applied for the purpose of stock identification of Atlantic cod in US waters to date.

Tissue stable isotope concentrations have not been routinely applied to investigate cod stock structure in US waters. Sherwood and Grabowski (2016) investigated the tissue stable isotope signatures of cod inside and outside of the groundfish closed areas (Closed Areas I and II, Cashes Ledge, and Jeffreys Ledge) in US waters. Although this study was not specifically designed to investigate stock structure, they did find differences in the $\delta^{13}C$ and $\delta^{15}N$ ratios of cod inside and outside of the closed areas, suggesting that cod within closed areas consumed a wider range of prey items.

Parasites

The utility of parasites as a natural marker to identify connectivity and stock structure has been identified in many species, in many oceans, and in several reviews (e.g., MacKenzie 1987; Timi 2007; Catalano et al. 2014). Cod have an abundance of parasites across their range: a single study identified 57 different parasites in eastern Atlantic cod (Perdiguero-Alonso et al. 2008), and a review of the literature identified 107 proto-/metazoan parasites of cod (Hemminson and MacKenzie 2001).

In the northwest Atlantic, Sherman and Wise (1961) studied infestation rates of the parasitic copepod, Lernaeocera branchialis, across New England's waters. These rates, which declined with latitude, were interpreted to represent 4 stocks of cod: (1) a heavily infested group in the northern Gulf of Maine, (2) a moderately infested group of central and southern Gulf of Maine cod, (3) a lightly infested group on Georges Bank, and (4) a group free of infestation in the southern New England region. These rates supported previous unpublished tag return data (Wise 1963) and indicated the usefulness of Lernaeocera for distinguishing groups of cod across broad areas. In Canadian waters, use of parasites in defining stock structure was reported by Martin (1953; unspecific as to taxa or methods used), as well as in research reported for the Gulf of St. Lawrence (McClelland and Marcogliese 1994 [nematodes]; McClelland and Melendy 2011 [multiple parasites]), and Newfoundland (Khan and Tuck 1995 [multiple parasites]).

The potential utility of parasites for analysis of cod stock structure has been realized in the past but has been largely unexplored in recent years. Analysis of parasites remains relevant because fish can be readily screened for parasites from fishery-dependent or fishery-independent collections and because there is an historical benchmark for comparison. Nonetheless, several challenges remain: (1) sampling at an appropriate scale and with a framework to infer population-level processes, (2) partnering with appropriate taxonomic expertise for parasites, (3) and selecting parasites with appropriate life histories to address the questions of stock connectivity or separation. Furthermore, there is the issue of assuming that the dynamics of the parasite population is stationary in time and space. For example, an increase in infection rates in a region could be interpreted as an increase/immigration of a particular group of cod, when in reality it may be caused by the spread of the parasite. Recent ecological knowledge suggests that parasite loads in southern New England, such as offshore of Rhode Island, may no longer be zero, in contrast to historical reports by Sherman and Wise (1961), warranting consideration of the biology of both the host and the parasite.

Multiple Natural Markers

Genetic and genomic methods are oftentimes applied in combination with other natural markers and can serve as effective and complementary tools to other techniques, such as otolith chemistry or body morphometrics, in the identification of stock structure (Campana 2005; Sturrock et al. 2012; Cadrin et al. 2014). Genetics can provide insight about spawning group origins, whereas other techniques, like otolith chemistry and body morphometrics, can provide insight on the spatial behavior and life history type (resident vs. migratory) of cod (Secor et al. 2001; Morinville and Rasmussen 2008; Sherwood and Grabowski 2010). Applying modern, genomic tools can further characterize ecological diversity by identifying adaptive variation among populations.

The number of natural markers necessitates a strategic approach to match them–with each other or with other stock identification methods–so as to investigate cod biology and ecology in an integrated manner. In ongoing work by Kerr et al. (2018), a combination of genetics, genomics, otolith chemistry, otolith structure, morphometric, and color analysis was applied to winter and spring spawning fish from the 2 main spawning locations in the Gulf of Maine (Ipswich Bay and Massachusetts Bay) to characterize their genetic, spatial, and life history diversity. Genetic analysis indicated significant neutral and adaptive genetic differentiation between winter and spring spawners sampled over multiple years and suggested limited connectivity as well as ecological differentiation in these 2 spawning populations. Otolith chemistry analysis indicated significant differences in elemental ratios of winter and spring spawners that suggested differences in environmental conditions experienced early in life and potentially in the habitat used by these groups over their lifetime. Morphometric analysis indicated that winter and spring spawning cod exhibit significant differences in body shape, with winter spawners having features often associated with a more resident life history (deeper bodied and shorter head) than spring spawners. These 3 methods provided largely congruent results; taken together, these point toward biocomplexity of Atlantic cod on a fine scale, consistent with local adaptation and ecological divergence.

Using mixed stock analysis, Kerr et al. (2018) also compared the relative contribution of these 2 spawning complexes in commercial catches from 3 periods: (1979-1982, 1989-1992, and 2012-2016). Genetic and otolith analyses indicated that the composition of the fishery has changed over time: a greater proportion of winter spawners populate the fishery today compared with the past. Furthermore, the genetic data suggest that the historical fishery may have been characterized by a greater diversity than it is today.

Synthesis of Findings to Date

- The natural markers applied to Atlantic cod in US waters for stock identification include otolith characteristics (chemistry, shape, and structure), body characteristics (color type, morphometrics, and meristics), and other features, such as parasites.
- The morphometric results of Sherwood and Grabowski (2012) suggest that cod on eastern and western Georges Bank may compose unique groups, although the boundary between these groups could not be identified. These results are in broad agreement with genetic analyses (e.g., Kovach et al. 2010; Chapter 4), tagging studies (Wise 1963; Hunt et al. 1999; Tallack 2009; Chapter 7), and fishermen's ecological knowledge (Chapter 8).
- Natural markers (otolith chemistry, structure, and morphometrics) support winter and spring spawners as unique groups. This finding is in agreement with genetic analyses (Kovach et al. 2010).
    - Otolith chemistry analysis indicated significant differences in elemental ratios of winter and spring spawners, both early in life and across their lifetime, reflecting differences in environmental conditions experienced early in life and potential differences in habitat use by these groups over their lifetime.
    - Morphometric analysis indicated that winter and spring spawning cod in the western Gulf of Maine exhibit significant differences in body shape with winter spawners having features often associated with a more resident life history (deeper bodied and shorter head) than spring spawners.
    - Otolith structure analysis identified significant differences in year-one growth between the winter and spring spawning cod. Associated analysis revealed differences in growth and mortality between the winter and spring spawning cod in the western Gulf of Maine, where winter spawners grow and mature at a faster rate, but spring spawners reach a larger maximum size.

    - Otolith chemistry, body morphometrics, and otolith structure provided largely congruent results, and taken together, the results point toward biocomplexity of Atlantic cod on a fine scale, consistent with local adaptation and ecological divergence.
- Parasite infestation rate suggests separation between the northern Gulf of Maine, central Gulf of Maine, Georges Bank, and southern New England cod.

Further Research Needs and Priorities

- Natural markers have been more widely applied for cod in the Gulf of Maine and on Georges Bank but have not been routinely used for cod in southern New England, Nantucket Shoals, or the Great South Channel. Applying natural markers to samples collected in these regions would provide complementary information to results collected through other disciplines, like genetics and tagging.
- Meristic characters have proven useful for stock identification of Atlantic cod but have not been routinely applied in US waters. Given their low cost, utility, and ease of collection, future multidisciplinary stock identification studies should consider investigating meristic characters.
- Examining otolith shape has great potential but has not been applied extensively to cod in US waters.
- Based on historical studies and information from fishermen, parasitological investigation in the Gulf of Maine region may be a cost-effective approach to stock identification.
- Examining color morphs for cod may have utility for stock composition analysis. However, color morphs are often defined by using colloquial names or qualitative criteria, and coloration is rarely quantified, which can make interpretation and comparisons difficult. Therefore, we recommend that quantitative metrics of color, such as those employed by Sherwood and Grabowski (2010), be used whenever possible to aid in the interpretation of results.

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7. APPLIED MARKERS

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Abstract

A comprehensive review of conventional and electronic tagging of Atlantic cod (Gadus morhua) in the Gulf of Maine region and adjacent areas (NAFO divisions 4X, 5, 6) and analysis of available conventional and archival tag data show persistent patterns of movement and residence. Published tagging studies and updated analyses of available tagging data, including nearly 200,000 tag releases and nearly 12,000 recaptures as well as information from acoustic and archival tags, were used to identify major patterns of residence and movement among regions and fishing grounds. Tagging data since the 1990s indicates little movement of cod between the eastern and western Scotian Shelf; cod groups within the Bay of Fundy, the western Gulf of Maine, southern New England, and the Mid-Atlantic Bight are relatively sedentary. Conversely, there is substantial movement from Browns Bank to the Bay of Fundy and the western Scotian Shelf, from the Great South Channel to the western Gulf of Maine, and from eastern Georges Bank to Browns Bank. Analysis of residence and dispersal of distinct spawning groups among fishing grounds suggests high residence and fidelity to spawning areas in the western Gulf of Maine and the Bay of Fundy, moderate spawning site fidelity on eastern Georges Bank with some post-spawning dispersal, and greater dispersal from the "Cape Cod" spawning grounds. Major movement patterns are consistent among studies and across recent decades of tagging studies, but the frequency of residence and movement vary.

Introduction

Tagging studies can inform inferences of the degree of connectivity among distinct population components. Conventional tags document movements from release to recapture location (Hall 2014), and electronic tags provide information on movement trajectories, habitat utilization, behavior, and spawning dynamics (DeCelles and Zemeckis 2014). Fishery recaptures of conventional tags are influenced by spatiotemporal patterns in fishing effort, but information from electronic tags is largely fishery-independent.

The objective of this chapter is to contribute to an interdisciplinary evaluation of Atlantic cod (Gadus morhua) stock identity by (1) reviewing all published information on cod tagging in the Gulf of Maine and adjacent areas (NAFO divisions 4X, 5, 6) from conventional and electronic tagging and (2) analyzing movement patterns among fishing grounds with the available conventional and archival tag data in the context of putative spawning groups, as identified from early life history and genetic information (Chapters 3 and 4, this volume). This summary extends and synthesizes previous reviews (Schroeder 1930; McKenzie 1956; Wise and Jensen 1960; Templeman 1962; Loehrke and Cadrin 2007; Wang et al. 2009; Clark and Emberley 2010; Zemeckis et al. 2014b) drawing on source material and conclusions from previous reviews.

Review of Conventional Tagging Studies

The earliest tagging studies of New England cod were in association with hatchery experiments (Tarr 1884). Smith (1902) tagged and released 4,000 cod from Woods Hole, MA, and reported recaptures on Nantucket Shoals and in the Mid-Atlantic Bight. Rich (1925) tagged on Nantucket Shoals, and tagging continued annually until 1932, primarily on Nantucket Shoals but also in other areas (Higgins 1934). Schroeder (1930) reviewed data from tagging on Nantucket Shoals and concluded that the group of cod on Nantucket Shoals is mostly distinct from those to the north and east, but cod from Nantucket Shoals move off Rhode Island and to the Mid-Atlantic Bight in fall. Wise (1958) tagged cod off New Jersey in winter and confirmed the seasonal pattern described by Schroeder (1930).

Higgins (1929) reviewed tagging data throughout the Gulf of Maine region and concluded that cod from northern Massachusetts Bay to eastern Maine and the offshore Gulf of Maine banks were relatively sedentary, but cod from Massachusetts Bay tended to migrate to the south. Tagging off the coast of Maine had mostly local recaptures, and some moved east (Higgins 1933), but the cod off the Maine coast were not considered to be connected to those on the Georges Bank and Browns Bank (Higgins 1934). Wise and Jensen (1960) reviewed this historical tagging information and concluded that cod in the Gulf of Maine are relatively sedentary. Higgins (1931) described tagging on Browns Bank and concluded that most movement was north and northeast with a little to the south and west. Tagging on Georges Bank suggested that most fish stayed in the region with some movement to Browns Bank and less to Nantucket Shoals and southward (Higgins 1931).

McKenzie (1956) reviewed recapture patterns of cod tagged in the Bay of Fundy, the Scotian Shelf, and the Gulf of St. Lawrence. Only a few cod were tagged in the Bay of Fundy in 1938 and 1939, and all were recaptured in the Bay of Fundy, except 1 cod tagged off St. Andrews that was recaptured on Georges Bank. McKenzie (1956) concluded that cod tagged in summer inshore from the Bay of Fundy and other inshore locations on the Scotian Shelf are mostly stationary, with little offshore mixing. Recaptures of cod tagged off Machias Seal Island (western Scotian Shelf, area 465, Figure 1.1) were generally eastward in summer and westward and deeper in winter. By contrast, all recaptures of cod tagged off Shelburne (southeast Nova Scotia, area 463) were to the north, suggesting little movement to the western Scotian Shelf, Gulf of Maine, Browns Bank, or Georges Bank from the eastern Scotian Shelf. Templeman (1962) reviewed the tagging information reported by McKenzie (1956) and noted that only 11 of 2,200 recoveries from cod tagged off the eastern Scotian Shelf (Fundian Channel to the Laurentian Channel) were recaptured on New England fishing grounds. In an interdisciplinary evaluation of stock identity of cod in the Bay of Fundy, Hunt and Neilson (1993) analyzed these tagging data by adjusting for patterns in fishing effort, and they found extensive movement between the eastern and western Bay of Fundy.

Wise (1963) completed a regional, 4-year tagging investigation to study New England cod stock structure. Most cod tagged on the northeast peak of Georges Bank during the spawning season (March-April 1957) were recaptured on eastern Georges Bank (64%), and some moved to Browns Bank and the western Scotian Shelf (36%). Most cod tagged on Browns Bank during the spawning season (February-March 1957) were recaptured on Browns Bank (86%), with some movement of cod to eastern Georges Bank (14%). Most cod tagged off Chatham (Cape Cod, MA) in February-March 1957 were recaptured in the Great South Channel (74%), and some moved to the Gulf of Maine (15%), southern New England/Mid-Atlantic Bight (6%), Georges Bank (3%), and the Scotian Shelf (1%). Recaptures of cod tagged on Georges Bank and Browns Bank were distributed almost entirely on offshore banks and the western Scotian Shelf, but recaptures of cod tagged off Chatham were distributed throughout the region (from the Mid-Atlantic Bight to the Scotian Shelf). Wise and Jensen (1960) and Wise (1963) concluded that cod on eastern Georges Bank have limited mixing west of 68°W, but some older fish move to southwestern Nova Scotia.

Perkins et al. (1997) tagged 4,191 cod in Sheepscot Bay (southern Maine) during March-July, 1978-1983. Almost all of the 255 reported recaptures with known locations (97%) were in the western Gulf of Maine, but 4 (2%) were recaptured in Canadian waters, and 3 (1%) were recaptured on Georges Bank. A large portion were recaptured near the tagging location during subsequent spawning seasons and recaptures were reported near the spawning site up to 6 years later. The pattern of tag recaptures suggests spawning site fidelity (Zemeckis et al. 2014a) and demonstrates that cod form aggregations offshore of the spawning site before and after spawning in spring.

Hunt et al. (1999) tagged more than 22,000 cod in the region from 1984 to 1997, primarily on Georges Bank and Browns Bank and adjusted 2,400 tag recoveries for fishing patterns and reporting rates. They also summarized tagging on the eastern Scotian Shelf from 1978 to 1981 and concluded that there is little exchange between the eastern Scotian Shelf and the Gulf of Maine region. Most cod tagged on eastern Georges Bank were recaptured on eastern Georges Bank (54%), some moved to the Browns Bank and the western Scotian Shelf (34%), western Georges Bank (10%), the Great South Channel (1%), and the Gulf of Maine (1%), and no recaptures were reported on Nantucket Shoals or southern New England/Mid-Atlantic Bight. Most cod tagged on Browns Bank were recaptured on Browns Bank, the western Scotian Shelf, and the Bay of Fundy (62%), some moved to Georges Bank (12%), the Gulf of Maine (6%), the Great South Channel (1%), and Nantucket Shoals (1%), and no recaptures were reported in southern New England/Mid-Atlantic Bight. Clark and Emberley (2010) reanalyzed these data and showed that most movements from Browns Bank to Georges Bank were from releases on western Browns Bank.

Howell et al. (2008) tagged 27,772 cod in the western Gulf of Maine and reported 1,334 recaptures, adjusted by the relative number of recaptures in each area as a proxy for fishing effort. They reported concentrations in Ipswich Bay and Massachusetts Bay in winter and spring associated with spawning, dispersal throughout the western Gulf of Maine after spawning, and spawning site fidelity (i.e., multiyear recoveries on the spawning grounds) while remaining resident to the area and sedentary (mean rate of travel <0.2 km/day).

Clark and Emberley (2010) summarized results from tagging approximately 14,000 cod in the Bay of Fundy in 2001-2002 and approximately 6,000 cod off southwest Nova Scotia in 2003-2004. Cod tagged in the Bay of Fundy were mostly recaptured on the western Scotian Shelf and Bay of Fundy, with relatively few returns on Georges Bank and in the western Gulf of Maine. They compared this recovery pattern with cod tagged east of Browns Bank, which were mostly recaptured on the Scotian Shelf with few recaptured west of Browns Bank.

Tallack (2009, 2011) summarized movement information from the Northeast Regional Cod Tagging Program, which tagged 114,467 cod from the Bay of Fundy to southern New England and reported 6,540 recaptures. Movement analyses accounted for tag loss and tagging-induced mortality and weighted releases and recaptures for resource, fishing, and reporting patterns. There was some residence within management units (e.g., Gulf of Maine, Georges Bank), but also considerable movement among areas, including extensive movement between the Great South Channel and western Gulf of Maine, and the Great South Channel and western Georges Bank, some mixing between the Bay of Fundy and offshore banks, movement between Georges Bank and the Scotian Shelf, but little movement from Georges Bank to inshore New England.

Loehrke (2014) analyzed recaptures of 2,572 cod tagged on spawning grounds during spawning seasons from the Northeast Regional Cod Tagging Program and the Massachusetts Marine Fisheries Institute. He analyzed both unweighted data and recaptures weighted by approximations of local exploitation rates. Movement patterns varied among spawning groups, from sedentary (southern New England) to dispersive (eastern Georges Bank).

In addition to acoustic and archival tagging (described below), Zemeckis et al. (2017) tagged 2,368 spring-spawning cod in Massachusetts Bay with conventional tags and reported recaptures of 223 cod (196 with location). Most recaptures were in the western Gulf of Maine, except for 12 (6%) that moved to the Great South Channel (521) and 1 (1%) that moved to coastal Maine (512). Almost half of the recaptures were during a subsequent spring-spawning season, and 10 (5%) were within 6 km from the release position, indicating spawning site fidelity. Some were also recaptured at other spawning locations in Ipswich Bay and Massachusetts Bay during the spawning season, suggesting some mixing among spring-spawning groups within the western Gulf of Maine.

In summary of published conventional tagging studies in the region:

There is little movement of cod between the eastern Scotian Shelf and the Gulf of Maine regions (including Browns Bank, the Bay of Fundy, Georges Bank, and more southern waters), and there appears to be a distinct and persistent boundary off southeast Nova Scotia, with negligible movement to or from the eastern Scotian Shelf (4W) and little overlap between southeastern Scotian Shelf (463) and the western Scotian Shelf (464-465; McKenzie 1956; Hunt et al. 1999; Clark and Emberley 2010).

There is little dispersal of cod from the Bay of Fundy (Halliday 1971; McKenzie 1956; Hunt and Neilson 1993; O’Brien and Worcester 2009; Tallack 2009, 2011), but recent tagging suggests some movement to the western Gulf of Maine, western Scotian Shelf, and Georges Bank (Clark and Emberley 2010).

Cod in the Gulf of Maine, including coastal Maine (Higgins 1933, 1934; Perkins et al. 1997) and the western Gulf of Maine (Higgins 1929; Wise and Jensen 1960; Howell et al. 2008; Liu 2019; Zemeckis et al. 2017), are relatively sedentary with some movement to the south (Tallack 2009, 2011; Loehrke 2014).

There is extensive movement from the Great South Channel to the western Gulf of Maine, with some movement to southern New England, Georges Bank, and the western Scotian Shelf (Wise 1963; O’Brien and Worcester 2009; Tallack 2009, 2011; Loehrke 2014).

There is extensive movement between eastern Georges Bank and the western Scotian Shelf, but little movement across 68oW, between eastern Georges Bank and western Georges Bank (Higgins 1931; Templeman 1962; Wise and Jensen 1960; Wise 1963; Hunt et al. 1999; O’Brien and Worcester 2009; Tallack 2009, 2011; Loehrke 2014).

There is extensive movement between Nantucket Shoals and the Mid-Atlantic Bight (Smith 1902; Schroeder 1930; Wise 1958; Wise and Jensen 1960; Wise 1963; Loehrke 2014).

Review of Spawning Dynamics from Acoustic Tagging Studies

Studying the spawning dynamics of Atlantic cod, including their behavior and spatial ecology, provides valuable information for investigating stock structure. For example, information about spawning site fidelity, residency on spawning sites, and connectivity among spawning sites provides insights into the mixing among spawning components and subpopulations. These findings are valuable when included with conventional tagging data and other stock identification techniques as a part of an interdisciplinary approach to investigating stock structure. Acoustic telemetry is an excellent tool for studying cod spawning dynamics because they track the movements of individual fish over multiple spatial and temporal scales without the reliance on recaptures and associated uncertainties (e.g., heterogeneous fishing patterns and reporting rates; tag shedding).

Several studies have applied acoustic telemetry to study cod spawning dynamics in the Gulf of Maine. For example, Siceloff and Howell (2013) investigated the spawning dynamics of spring-spawning cod (n = 26) in Ipswich Bay in 2006 by using a combination of moored acoustic telemetry receivers and active tracking with a boat-mounted directional receiver. Individual cod utilized home ranges ≤ 60 km2 (mean = 41 km2) with a high degree of spatial and temporal overlap in the detection of multiple fish. Spawning activity was associated with specific humps and ridges, and the mean residence time of individual fish on the spawning grounds was 30 days (range = 8-53 days), primarily during May and June. The authors concluded that cod in the western Gulf of Maine aggregate around fine-scale bathymetric features, utilize relatively small areas during spawning, are highly mobile within these areas, and tend to move as a group.

Elsewhere in the Gulf of Maine, other studies examined cod spawning dynamics in Massachusetts Bay, including both spring-spawning and winter-spawning cod. Dean et al. (2014) tagged spring-spawning cod (n = 70) with acoustic transmitters within the Spring Cod Conservation Zone (SCCZ) in 2010 and 2011. Cod movements were tracked with a VEMCO Positioning System that provided fine-scale (e.g., <10m) position estimates of tagged cod while they aggregated to spawn and identified sex-based and diel patterns in space use and aggregation behavior. Females remained aggregated in one small location during daytime with little variability within and between years. During daytime, males formed separate but adjacent aggregations over a larger area. At night, males sought out individual territories, and females made periodic excursions to the male territories with spawning events appearing to occur at night. The mean residence time of cod on the spawning ground was 38 days with cod primarily resident from May through July. Cod exhibited multiyear spawning site fidelity (up to 4 consecutive years) with respect to this spawning site in the SCCZ, with 47 (95%) tagged individuals exhibiting spawning site fidelity after adjusting for fishing mortality, natural mortality, and skipped spawning (Zemeckis et al. 2014a). Spawning site fidelity serves as one of multiple mechanisms contributing to the formation and maintenance of the observed metapopulation structure of cod in US waters by limiting the connectivity among subpopulations. However, acoustic telemetry detections and conventional tag recaptures also documented connectivity among spawning sites in Massachusetts Bay and Ipswich Bay, where some tagged fish were detected or recaptured at multiple spawning sites within the same spawning season (Zemeckis et al. 2017). Although there is a high rate of spawning site fidelity, there is also connectivity among inshore spawning sites via adult movements, which contributes to gene flow among spring-spawning cod in the Gulf of Maine and is consistent with results from genetics studies (e.g., Kovach et al. 2010).

Zemeckis et al. (2019) described the spatial and temporal distribution of cod spawning during the winter in Massachusetts Bay by using acoustic telemetry receivers deployed either at fixed locations or on mobile autonomous gliders. Tagged cod exhibited spawning site fidelity and spawning primarily occurred from early November through January. The spatial distribution of spawning was largely consistent during 3 years of monitoring and was concentrated in multiple hotspots in Massachusetts Bay and near the northwest corner of Stellwagen Bank in depths greater than 50 m. Results from this study demonstrate that there are multiple focal points of spawning during the winter in Massachusetts Bay and that there is some connectivity among these locations with fish tagged throughout the study site aggregating in multiple locations. Furthermore, results from this study confirmed findings from previous studies, where despite a disparity in spawning season between spring-spawning and winter-spawning cod in Massachusetts Bay, they utilize similar areas during their respective seasons.

Methods and Materials

Residence and Movement Patterns from Conventional Tags

Available data were analyzed to tabulate residence and movement among areas and regions to standardize information across tagging studies at a common spatial scale (statistical area) that is pertinent to management and assessment boundaries (Table 7.1). Data were available from logs keypunched from Schroeder (1930), 2 tagging studies by Fisheries and Oceans Canada (DFO; Hunt et al. 1999; Clark and Emberley 2010), the Northeast Regional Cod Tagging Program (NERCTP; Tallack 2009, 2011), the Massachusetts Marine Fisheries Institute (MA MFI; Loehrke 2014), and the Massachusetts Spring Cod Conservation Zone (MA SCCZ; Zemeckis et al. 2017).

Schroeder's logs include tag releases by the US Bureau of Fisheries in the 1920s. Cod were caught with hook gear in less than 50 fathoms, and those in good condition were tagged on the caudal fin with uniquely numbered metal crimps (Schroeder 1930). Many of the records in Schroeder's logs were keypunched by NOAA Fisheries' Northeast Fisheries Science Center (NEFSC), but logbook 3 is missing, and logbooks 11-12 have not been keypunched (Michael Palmer, personal communication). Schroeder (1930) summarizes results for 24,739 cod tagged from the Great South Channel to New Jersey 1923-1929, but the keypunched logs include 30,149 releases from the Gulf of Maine to southern New England, 1923-1927.

Canada DFO provided 2 cod tagging datasets for releases on Georges Bank in 1994-1996 (Hunt et al. 1999) and for cod tag releases on the Scotian Shelf 2001-2004 (Clark and Emberley 2010). Cod were captured with short trawl tows, and viable cod were tagged with T-bar tags at the base of the first dorsal fin (Hunt et al. 1999).

As reported in detail by Tallack (2009, 2011), the NERCTP tagged cod (T-bar tags at the base of the dorsal fin) throughout New England and the Bay of Fundy. Each tagging organization targeted fishing grounds which have been traditionally considered key spawning or feeding grounds or were considered important for studying movement of Atlantic cod. Cod tagging trips took place year-round from March 2003 through July 2005, with peak tagging seasons in spring and autumn of each year. Outreach for reporting tag recoveries included shirts, hats, lottery reward, and high reward tags.

The Massachusetts Marine Fisheries Institute (MFI) targeted spawning groups and adopted the same tagging protocol as the NERCTP (Loehrke 2014). Spawning cod were tagged with T-bar tags from the western Gulf of Maine, the Great South Channel and Nantucket Shoals, Georges Bank, and southern New England. Zemeckis et al. (2017) tagged spawning cod in spring in Massachusetts Bay with T-bar tags.

Table 7.1. Tagging data available for analysis of residence and dispersal patterns of Atlantic cod (*Gadus morhua*) (including Supplemental Materials (SM) letter for results).

Study	Reference	Release Area(s)	Years	Months	Releases	Recaptures	SM
Schroeder logs	Schroeder 1930	all US areas	1923-1927	Jan-Oct	30,149	2,150	A
Fisheries and Oceans Canada (DFO) 1994	Hunt et al. 1999	Georges Bank and Gulf of Maine	1994-1996	Mar-Dec	5,067	262	B
Northeast Regional Cod Tagging Program (NERCTP)	Tallack 2011	all areas	2002-2003	Jan-Dec	114,473	6,784	C
Massachusetts Marine Fisheries Institute (MFI)	Loehrke 2014	all US areas	2000-2014	Jan-Dec	37,460	1,900	D
DFO 2001-2004	Clark and Emberley 2010	Scotian Shelf	2001-2004	Jan-Dec	10,000	472	E
Massachusetts Spring Cod Conservation Zone (MA SCCZ)	Zemeckis et al. 2017	Massachusetts Bay	2010-2013	Apr-Jul	2,368	223	F
				Totals	199,517	11,791	G

We standardized the spatial analyses by adopting the spatial stratification based on statistical areas for reporting fishing effort and catch (Figure 7.1) previously defined by Hunt et al. (1999) and Zemeckis et al. (2017). Reporting conventions and reporting area boundaries were consolidated and standardized to reflect major fishing grounds (Rounsefell 1948; Halliday and Pinhorn 1990). Statistical areas were also grouped into regions that reflect putative spawning groups, as identified in Cournane et al. (Chapters 2 and 3, this volume).

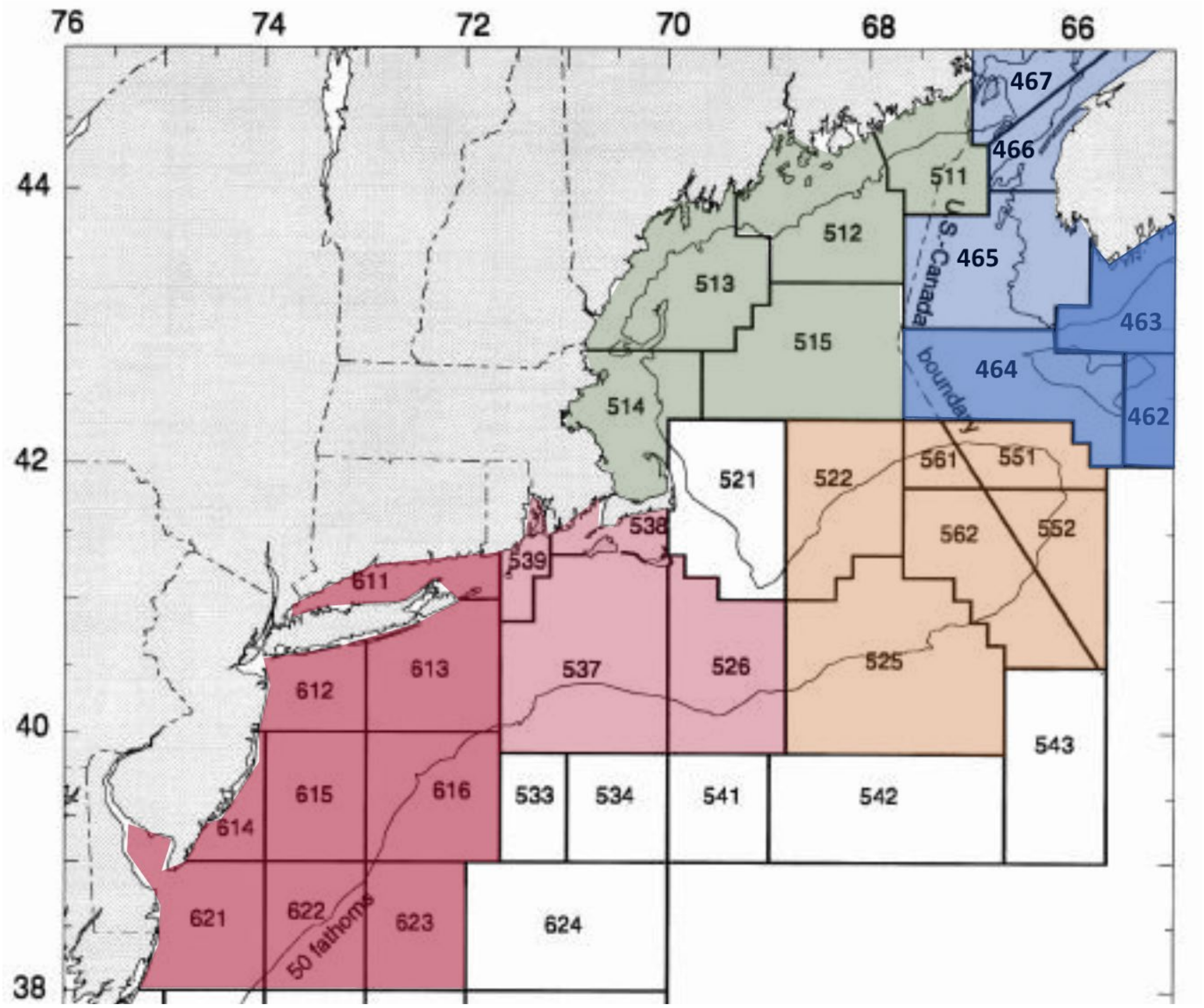

Figure 7.1. Spatial stratification based on statistical areas for reporting fishing effort and catch of Atlantic cod (Gadus morhua) (dark blue: eastern Scotian Shelf; medium blue: Browns Bank; light blue: Bay of Fundy; green: Gulf of Maine; white: Great South Channel; orange: Georges Bank; light red: southern New England; dark red: Mid-Atlantic Bight).

Matrices of residence and movement were compiled from release and recapture records that included tag release date and location, fish size at release, and recapture date and location. Matrices were derived separately in 2 ways: (1) for all recaptures (with known location) and (2) for recaptures of fish tagged during the spawning season, on the spawning grounds. Spawning seasons and areas were revised from those defined by Loehrke (2014), as identified in Chapters 3, 4, and 8 (genetics, early life history, and fishermen's ecological knowledge), recognizing that some of these areas have multiple persistent spawning locations:

Western Gulf of Maine Winter Spawners (513-514, Oct-Jan)
Western Gulf of Maine Spring Spawners (513-514, Apr-Jul)
Cape Cod (521, 526; Oct-Jan)
Eastern Georges Bank (522, 551, 552, 561, 562; Dec-May)
Western Scotian Shelf/Bay of Fundy (466-467, Jan-May)
Southern New England (537, 539; Nov-Mar)

Recaptures of each spawning group were compiled by seasonal period to indicate spawning site fidelity and post-spawning dispersal: (1) spawning season of release, (2) post-spawning seasons (i.e., recaptures during months when spawning does not occur for each group), and (3) subsequent spawning seasons (e.g., recaptures during spawning months and after at least one post-spawning season). Recapture patterns were depicted with bag plots (Rousseeuw et al. 1999), which are bivariate extensions of box plots, including a polygon that encompasses 50% of the data, an outer "fence" which approximates a 95% confidence region, and statistical outliers, as applied to cod tagging data by Loehrke (2014). Bag plots were presented by season for spawning groups with >50 recaptures per season.

Residence and dispersal matrices were derived for each study and for all studies combined, except for the Schroeder logs from the early 1900s, which indicated some differences in cod distribution, fishing effort and movement patterns.

Recapture data were not adjusted for patterns of local fishing effort, because estimates of catch and effort by statistical area are uncertain, some estimates of fishing mortality may be unreliable (e.g., Georges Bank; NEFSC 2017), and previous efforts to adjust tagging data have produced similar results as unweighted data (Tallack 2009, 2011; Loehrke 2014). Therefore, attempts to adjust tagging data for fishing patterns may introduce more uncertainty (Loehrke 2014).

Habitat Occupancy and Movements from Archival Tagging

Archival data storage tags (DSTs) record data on the environmental conditions experienced by tagged animals, including variables such as depth, temperature, and salinity. DSTs can be externally attached or surgically implanted, and they need to be physically recovered to download the environmental data archived on the tags. Geolocation involves the estimation of daily positions via a likelihood model that compares the environmental data recorded by the tags with oceanographic model predictions and inclusion of an animal movement model. Therefore, DSTs provide semi-fishery-independent data on animal movements because they need to be physically recovered (i.e., typically by fishermen), but geolocation yields movement data from the entire period before an animal is caught, or "at liberty" (in comparison to conventional tagging where only release and recapture locations are known). Combining estimated daily positions into the most probable track for cod at liberty permits investigation of migration patterns and space use, which are valuable for examining stock structure and mixing among subpopulations.

Spring-spawning cod in Ipswich Bay were tagged with DSTs in 2006 (n = 200) (Siceloff 2009; Siceloff and Howell 2013). Data from DSTs recovered as a part of this study were used to investigate cod habitat occupancy and off-bottom movements, as well as to infer movements based on comparisons with environmental and bathymetry data in the region. However, recovered DSTs from this study were not included in geolocation analyses.

Spring-spawning cod were also tagged with DSTs (n = 266) in the Spring Cod Conservation Zone (SCCZ) in Massachusetts Bay from 2010-2014 (Zemeckis 2016; Zemeckis et al. 2017). The depth and temperature data from the DSTs were used to investigate seasonal habitat occupancy. Recovered DST data were also used in geolocation analyses that assigned daily position estimates to statistical areas. This geolocation method relied on depth and temperature data from the DSTs with tidal-based exclusion and an observational likelihood model with movement constraints and activity level classifications (Zemeckis 2016; Zemeckis et al. 2017). The observational model compared the depth, bottom water temperature, and tidal information from the DSTs with estimates from the Northeast Coastal Ocean Forecasting System (NECOFS

2013), which is based on the Finite-Volume Community Ocean Model (FVCOM: Chen et al. 2006). The statistical area with the greatest score of likelihood was chosen as the most likely daily position for a given fish with the consideration of movement constraints based on cod behavior, physiology (i.e., swimming capabilities), and geolocation limitations. To investigate movement patterns, assignments to statistical areas were grouped among all individuals and summarized by seasonal period.

Additional DST tagging was conducted throughout US waters from December-April 2001-2011 by the Massachusetts Marine Fisheries Institute (MFI; Liu 2019). DSTs were released in the Gulf of Maine, Great South Channel, and Nantucket Shoals, and Southern New England. Depth and temperature data recorded by the DSTs were used to describe the seasonal habitat occupancy of cod tagged in each region. A subset of the DST data recovered as a part of this long-term effort to understand cod movement patterns and stock structure were analyzed by Gröger et al. (2007) who employed a tidal-based algorithmic geolocation method to estimate daily positions by using a direct comparison of environmental data from the DSTs with oceanographic model predictions. Data from recovered DSTs and analyzed by Gröger et al. (2007) were combined with that from the larger dataset of DSTs recovered as a part of the MFI tagging efforts and geolocated with a hidden Markov model (HMM) developed by Liu et al. (2017). The HMM framework from Liu et al. (2017) contains a likelihood model that compares tag-recorded environmental data (depth, temperature, tidal characteristics) with those derived from an oceanographic model and a behavior model that constrains the horizontal movement of the fish in order to estimate the most likely daily location. The most probable track was then selected as that which maximizes the overall probability score of the whole sequence of daily locations while the fish was at liberty. For each of the 3 tagging regions, the most probable track for each fish was plotted, and the probability distributions from all fish were pooled as an estimate of the utilization distribution (based on the methods of Galuardi and Lutcavage 2012) for each group to estimate core use areas (Liu 2019).

Results

Residence and Movement Patterns from Conventional Tags

Frequencies of residence and movement among the broad areas in Figure 7.1 are reported for all recaptures with known location and for seasonal recaptures of fish tagged during the spawning season on spawning grounds. Results are combined from multiple tagging studies since the 1990s. Residence and movement for each study in Table 7.1 among each statistical area in Figure 7.1 are reported in Supplemental Materials A-G. Nearly all cod released with conventional tags in each study were larger than the size at maturity (Figure 7.2).

The summary of all recaptures by statistical area indicates both high residence as well as substantial movements, depending on the region (Table 7.2; Figure 7.3; Supplemental Materials G), similar to those reported by Tallack (2009, 2011). There were 8,351 reported recaptures with a reliable recapture position. There was 93% residence in the Bay of Fundy/western Scotian Shelf (462, 463, 464, 465, 466, 467), 92% residence in the Gulf of Maine (511, 512, 513, 514, 515), 69% residence in the Great South Channel (521, with substantial movement to the Gulf of Maine), 76% residence on Georges Bank (522, 525, 551, 552, 561, 562, with substantial movement to Browns Bank), 88% residence in southern New England (526, 537, 539), and 100% residence in the Mid-Atlantic Bight (621, 625, 626).

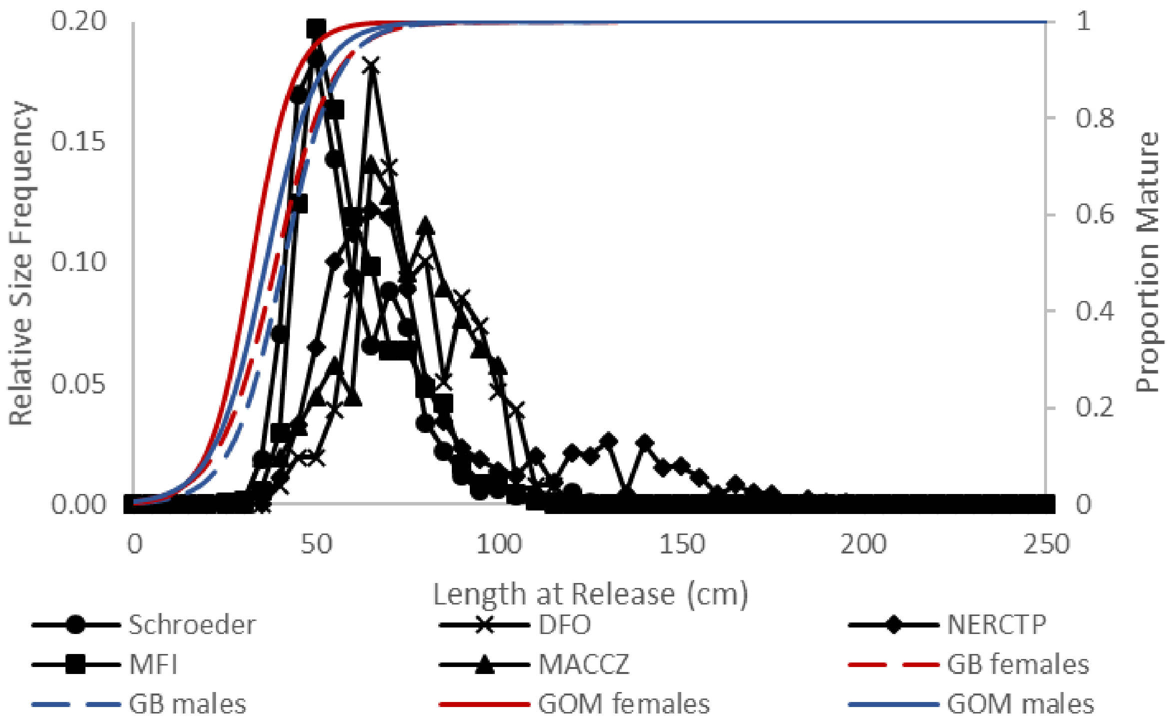

Figure 7.2. Size frequency of Atlantic cod (*Gadus morhua*) tagged and recaptured in the Northeast Regional Cod Tagging Program (NERCTP) (release size, black line) and estimates of maturity at size (colored lines) from O'Brien et al. (1993). Fisheries and Oceans Canada (DFO), the Massachusetts Marine Fisheries Institute (MFI), and the Massachusetts Spring Cod Conservation Zone (MACCZ). Georges Bank = GB and Gulf of Maine = GOM.

Table 7.2. Proportion of tag recaptures of Atlantic cod (*Gadus morhua*) from multiple tagging studies (Table 1; Hunt et al. 1999; Tallack 2011; Loehrke 2014; Clark and Emberley 2010; Zemeckis et al. 2017) by region of release and recapture (colors indicate relative proportion). Regions include Bay of Fundy-western Scotian Shelf (BOF), Gulf of Maine (GOM), Great South Channel (GSC), Eastern Georges Bank (EGB), and Southern New England/Mid-Atlantic Bight (SNEMA).

	Recapture Area				
Release Area	Bay of Fundy	Gulf of Maine	Great South Channel	Eastern Georges Bank	Southern New England/ Mid-Atlantic Bight
Bay of Fundy/W Scotian Shelf	0.93	0.03	0.00	0.04	0.00
Gulf of Maine	0.02	0.92	0.03	0.02	0.01
Great South Channel	0.00	0.17	0.69	0.08	0.04
Eastern Georges Bank	0.19	0.02	0.03	0.76	0.00
S. New England/Mid Atlantic Bight	0.00	0.01	0.08	0.01	0.92

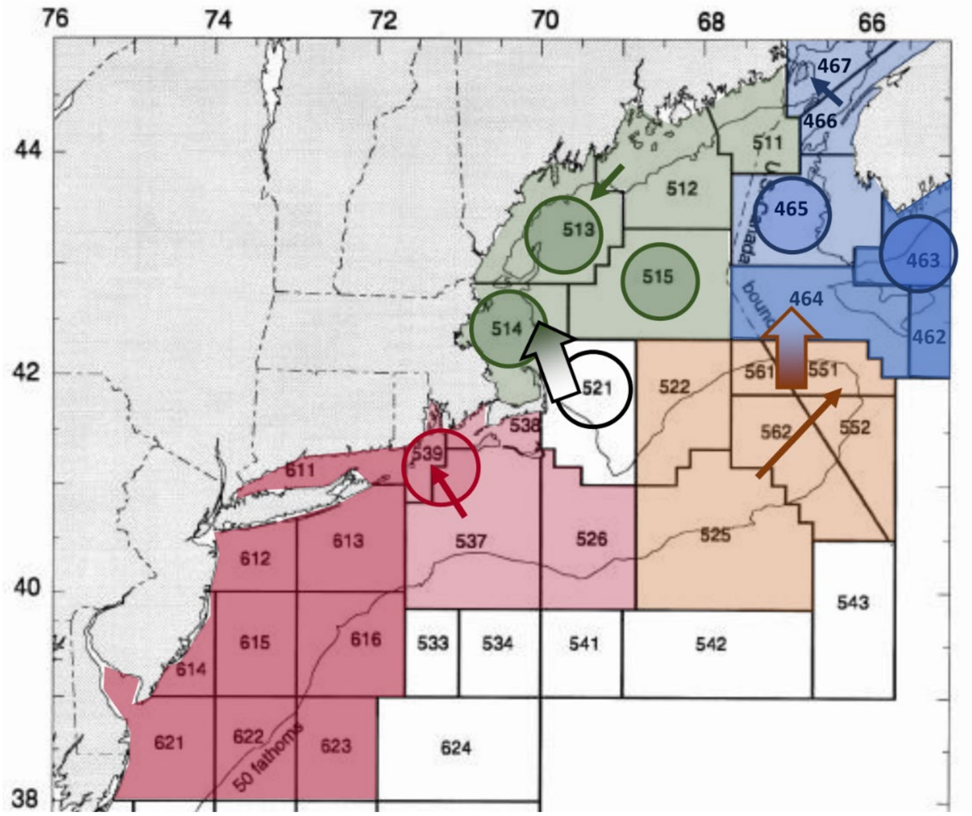

Figure 7.3. Major patterns of Atlantic cod (*Gadus morhua*) movement among regions (multicolor arrows: >10% movement), movement within regions (solid colored arrows: >50% movement from statistical area), and residence within statistical areas (circles: >50% residence in statistical area) from combined tagging studies.

Residence within and movement between individual statistical areas (Supplemental Materials Table G1) were similar to those generalized by Tallack (2011). Residence and movement from statistical areas indicates >50% residence on the western Scotian Shelf (463), the southern Bay of Fundy (465), southern ME-NH (513), southwest Gulf of Maine (514), central Gulf of Maine (515), Great South Channel (521), RI Sound (539) and off Delaware (621). Substantial movement (>50%) was from the northeast Bay of Fundy (466) to the northwest Bay of Fundy (467), from midcoast ME (512) to southern ME-NH (513), from southwest Georges Bank (525) to northeast Georges Bank (551), from offshore southern New England (537) to RI Sound (539), and from off MD (625, 626) to off DE (621). Although the number of tag releases from eastern ME were limited, more were recaptured in the Bay of Fundy than in other areas of the Gulf of Maine (Supplemental Materials Table G1).

Western Gulf of Maine winter spawners demonstrated strong spawning site fidelity (Table 7.3). Nearly all (99%) of recaptures during the same release season (95 with reported recapture location) were recaptured in the spawning area (513-514, western Gulf of Maine). Of the 290 recaptures with known recapture position in the post-spawning period, 93% were in the spawning area, and 6% moved to the Great South Channel (521), Georges Bank (522, 562), and southern New England (537, 538). In subsequent spawning seasons there was 93% residence in the Gulf of

Maine, 92% residence in the spawning area, 2% movement to the central Gulf of Maine (515), and 6% movement to the Great South Channel and southern New England. Distribution of winter-spawning cod was concentrated in the western Gulf of Maine during the spawning season (Figure 7.4) and distributed more broadly during the post-spawning season (Figure 7.5).

Table 7.3. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Tallack 2011; Loehrke 2014) of cod tagged during the winter-spawning season (October-January) in the western Gulf of Maine (513-514) and recaptured during the same spawning season of release, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions.

Season of Recapture	Browns Bank	western Gulf of Maine	central Gulf of Maine	Great South Channel	eastern Georges Bank	southern New England
Release	0.00	0.99	0.01	0.00	0.00	0.00
Post-spawning	0.00	0.93	0.01	0.02	0.02	0.02
Subsequent Spawning	0.00	0.92	0.02	0.03	0.00	0.03

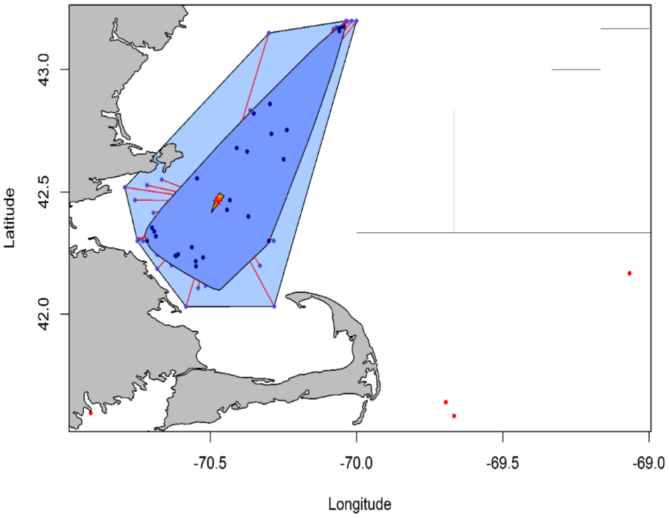

Figure 7.4. Recaptures of western Gulf of Maine winter spawning of Atlantic cod (*Gadus morhua*) during the spawning season (October-January), with median recapture position (red asterisk), area with 25% of recaptures (yellow), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

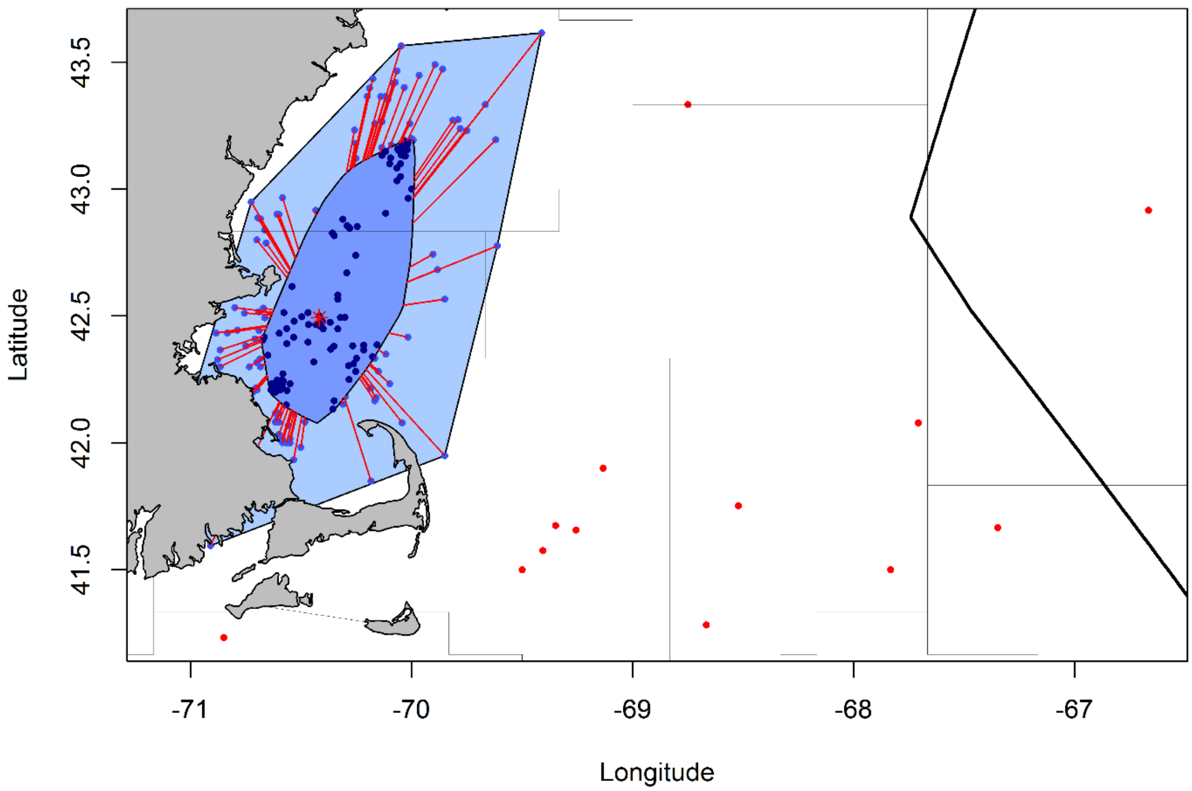

Figure 7.5. Recaptures of western Gulf of Maine winter spawning of Atlantic cod (*Gadus morhua*) during the post-spawning season (February-September), with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

Western Gulf of Maine spring spawners also demonstrated high spawning site fidelity (Table 7.4). Of the 1036 recaptures during the same release season with known recapture location, there was 97% residence in spawning area (513-514, western Gulf of Maine) and 2% movement to Great South Channel (521). There were 1138 recaptures with reported recapture location during the post-spawning season, with 91% residence in spawning area, 5% movement to the Great South Channel (521), 1% to central Gulf of Maine (515), 1% to Georges Bank (522, 525, 551, 561), and 2% to southern New England (526, 538). Similar to the results reported by Loehrke (2014) and Zemeckis et al. (2017), the 501 cod recaptured in subsequent spawning seasons with location information had 95% residence in the spawning area, 1% movement central Gulf of Maine (515; 96% residence in the Gulf of Maine), 2% to Great South Channel (521), and 2% to Georges Bank (522, 525, 551, 561). Most recaptures of spring-spawning cod from the western Gulf of Maine were recaptured in the western Gulf of Maine, with some overlap with the Great South Channel during both the spawning and post-spawning seasons (Figures 7.6-7.7).

Table 7.4. Recaptures from combined studies (Tallack 2011; Loehrke 2014; Zemeckis et al. 2017) of Atlantic cod (*Gadus morhua*) tagged during the spring-spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions.

Season of Recapture	Browns Bank	western Gulf of Maine	central Gulf of Maine	Great South Channel	eastern Georges Bank	southern New England
Release	0.00	0.97	0.00	0.02	0.00	0.00
Post-spawning	0.00	0.91	0.01	0.05	0.01	0.02
Subsequent Spawning	0.00	0.95	0.01	0.02	0.02	0.00

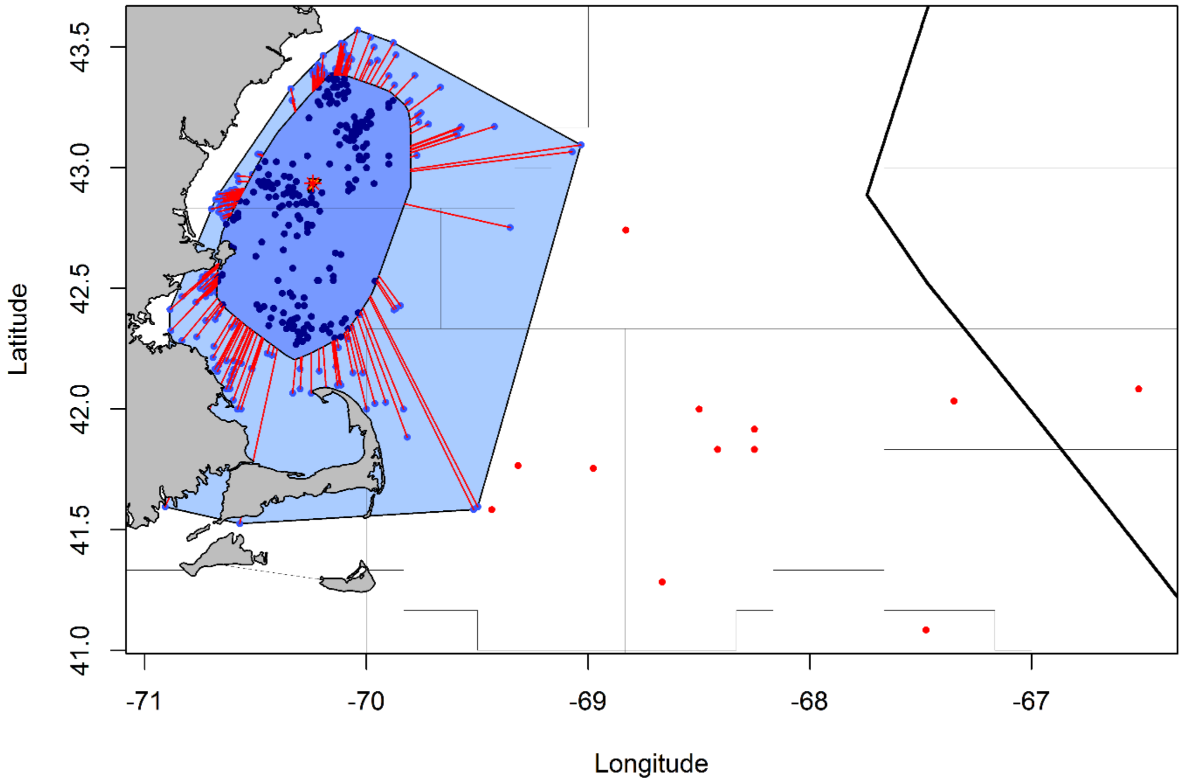

Figure 7.6. Recaptures of western Gulf of Maine spring-spawning Atlantic cod (*Gadus morhua*) during the spawning season, with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

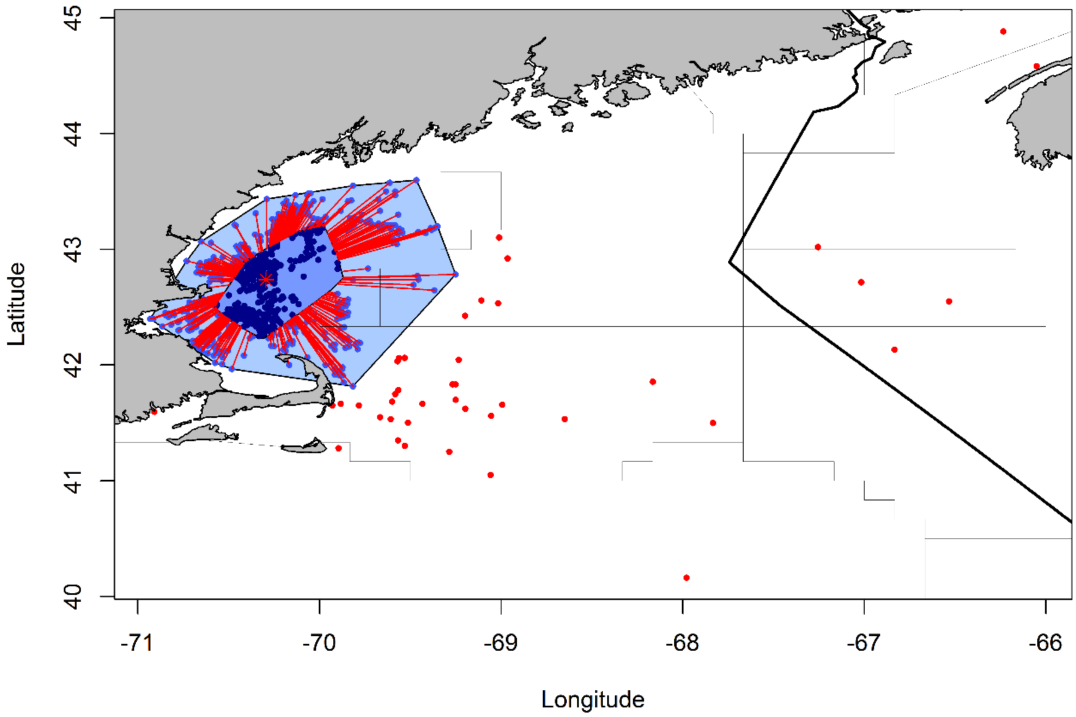

Figure 7.7. Recaptures of western Gulf of Maine spring-spawning Atlantic cod (*Gadus morhua*) during the post-spawning season, with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue) and outliers (red dots).

Eastern Georges Bank spawners demonstrated high spawning site fidelity and dispersal in the post-spawning season (Table 7.5). During the release season (183 recaptures with locations) there was 96% residence on eastern Georges Bank (522, 525, 551, 552, 561, 562), 2% movement to the western Scotian Shelf and Bay of Fundy (464, 465), 1% movement to the western Gulf of Maine (513, 514), and 1% to the Great South Channel (521). During the post-spawning season (746 recaptures with locations), there was 70% residence on eastern Georges Bank (522, 525, 551, 552, 561, 562), 26% movement to the Scotian Shelf-Bay of Fundy (461, 462, 463, 464, 465, 466, 467), 3% movement to the Great South Channel (521), and 2% movement to the Gulf of Maine (511, 512, 513, 514, 515). During subsequent spawning seasons (274 recaptures with locations), there was 72% residence on eastern Georges Bank, 22% movement to the Scotian Shelf/Bay of Fundy (461, 462, 463, 464, 465, 466), 3% movement to the Great South Channel (521), 2% movement to the Gulf of Maine (511, 514), and 2% movement to Nantucket Shoals (526). The majority of recaptures of eastern Georges Bank spawners were on eastern Georges Bank, Browns Bank, and the western Scotian Shelf during the spawning season (Figure 7.8) and mostly in Canadian waters during the post-spawning season (Figure 7.9).

Table 7.5. Recaptures from combined tagging studies (Hunt et al. 1999; Tallack 2011) of Atlantic cod (*Gadus morhua*) tagged during the spawning season (December-May) on eastern Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November) and subsequent spawning seasons. Colors indicate relative proportions.

Season of Recapture	W. Scotian Shelf-Bay of Fundy	Gulf of Maine	Great South Channel	eastern Georges Bank	southern New England
Release	0.02	0.01	0.01	0.96	0.00
Post-spawning	0.26	0.02	0.03	0.70	0.00
Subsequent Spawning	0.22	0.02	0.03	0.72	0.01

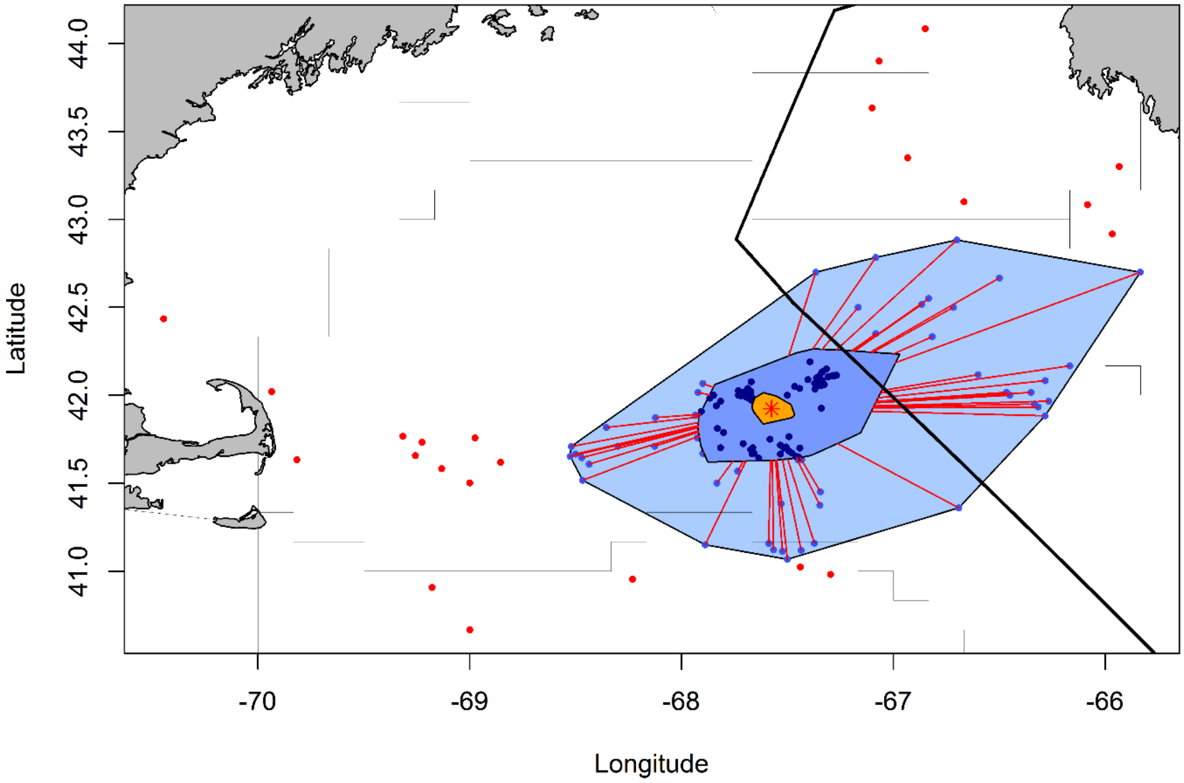

Figure 7.8. Recaptures of eastern Georges Bank spawning Atlantic cod (*Gadus morhua*) during the spawning season, with median recapture position (red asterisk), area with 25% of recaptures (yellow), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

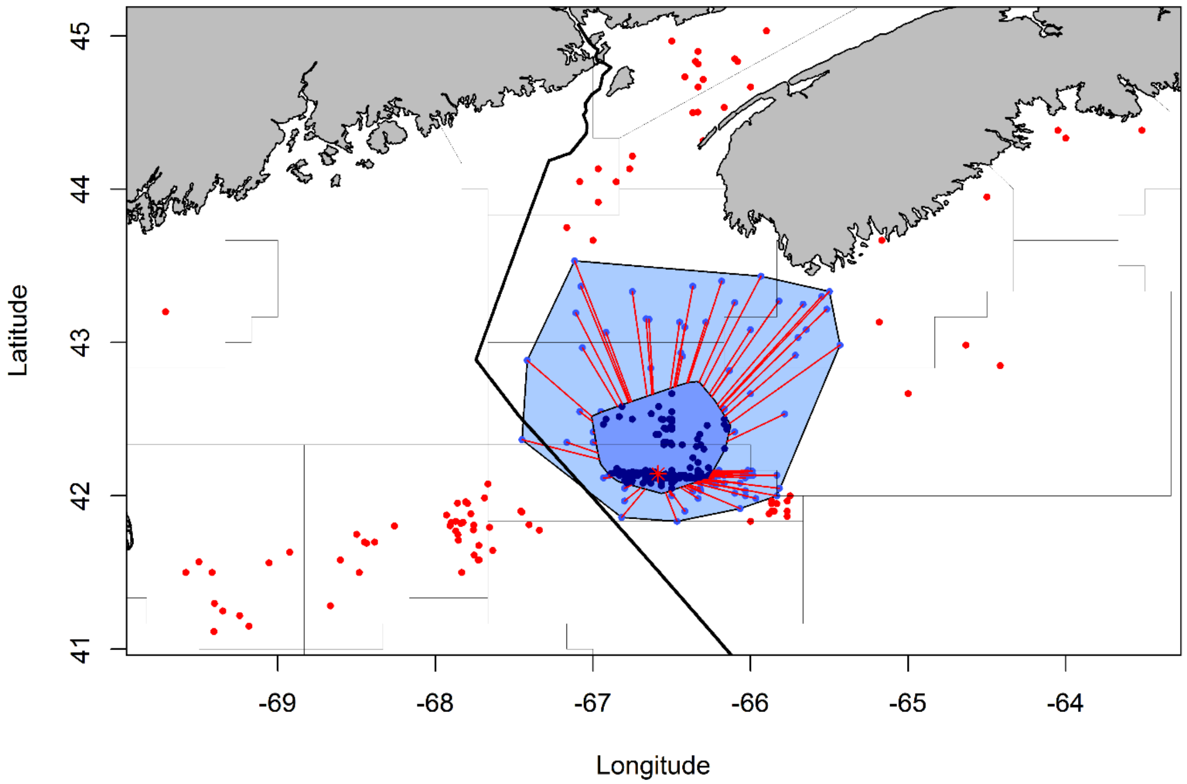

Figure 7.9. Recaptures of eastern Georges Bank spawning Atlantic cod (*Gadus morhua*) during the post-spawning season, with median recapture position (red asterisk, inside inner blue envelop), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

Western Scotian Shelf/Bay of Fundy spawners demonstrated high spawning site fidelity (Table 7.6). There was 100% residence in the spawning area (463, 464, 465, 466, 467) during the release season (146 recaptures with locations) as well as 100% residence in the Bay of Fundy (466, 467). During the post-spawning season (503 recaptures with locations), there was 94% residence in the spawning area, 4% movement to Georges Bank (522, 551), and 2% movement to the Gulf of Maine (511, 513). During subsequent spawning seasons (168 recaptures with locations), there was 92% residence in the spawning area, 5% to Georges Bank (522, 551, 561), 3% movement to the Gulf of Maine (511, 513), and 1% to Mid-Atlantic Bight (621, off DE-MD). Much of the 2000-2002 tagging (Clark and Emberley 2010) was in area 465 (southwest Scotian Shelf, between Browns Bank and German Bank), in a fishery near at the boundary of the Bay of Fundy, Browns Bank, and the Scotian Shelf. Most of the recaptures of spawning cod tagged in the western Scotian Shelf-Bay of Fundy stayed in the spawning area during the spawning season (Figure 7.10) and mostly in the Bay of Fundy during the post-spawning season (Figure 7.11).

Table 7.6. Recaptures from combined tagging studies (Clark and Emberley 2010; Tallack 2011) of Atlantic cod (*Gadus morhua*) tagged during the spawning season (January-May) in the Bay of Fundy (466-467) and recaptured during the same spawning season, the post-spawning season (June-December), and subsequent spawning seasons. Colors indicate relative proportions.

Season of Recapture	W. Scotian Shelf/Bay of Fundy	Gulf of Maine	eastern Georges Bank	Mid-Atlantic Bight
Release	1.00	0.00	0.00	0.00
Post-spawning	0.94	0.02	0.04	0.00
Subsequent Spawning	0.92	0.03	0.05	0.01

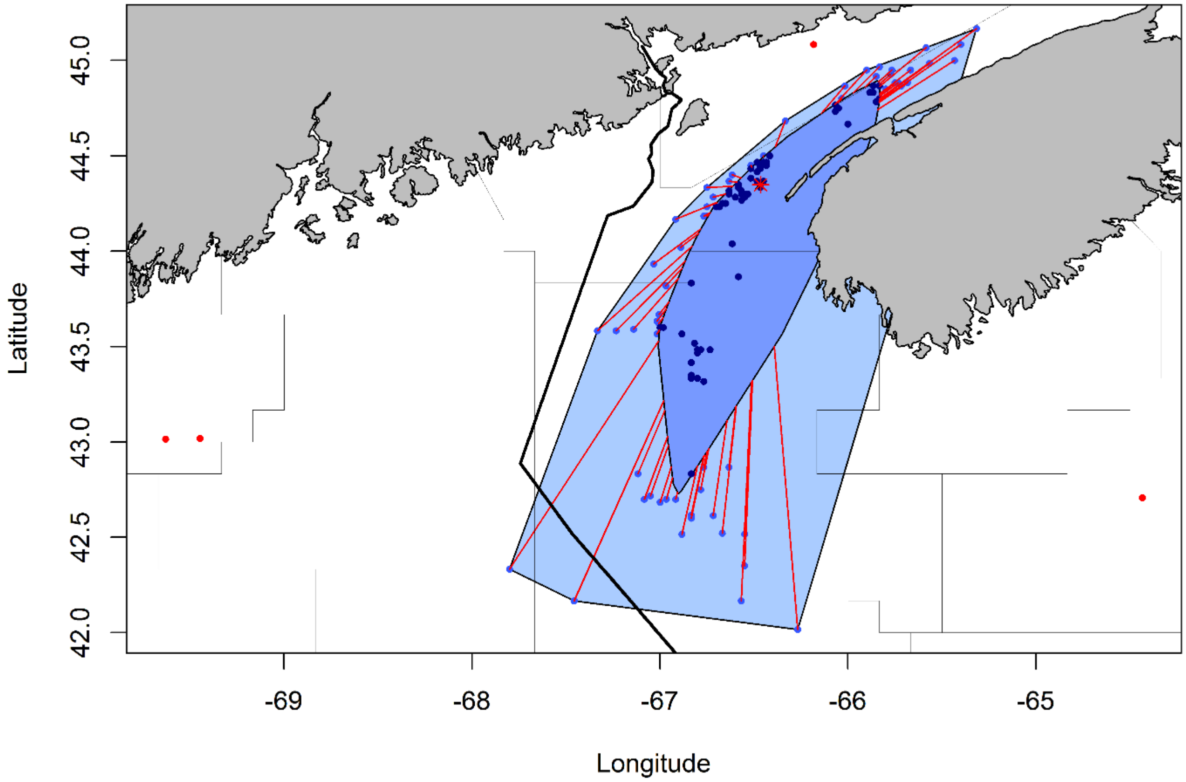

Figure 7.10. Recaptures of western Scotian Shelf and Bay of Fundy spawning Atlantic cod (*Gadus morhua*) during the spawning season, with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

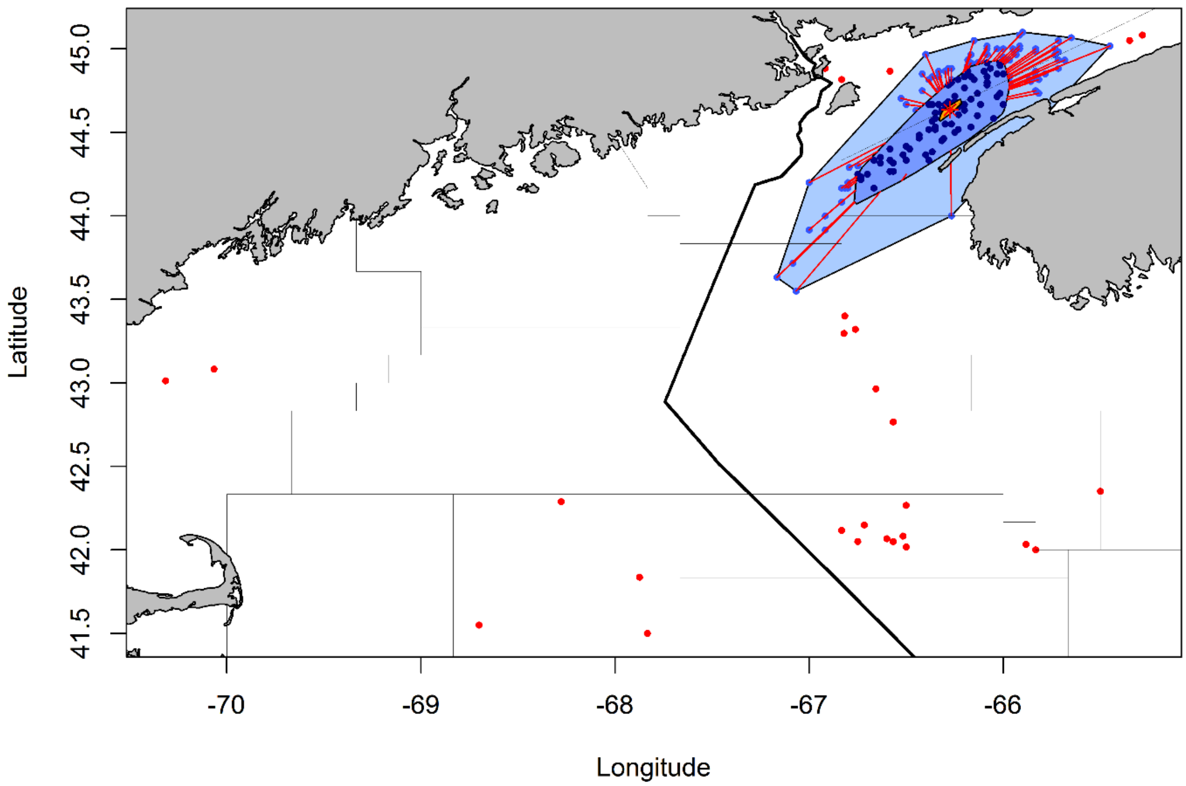

Figure 7.11. Recaptures of western Scotian Shelf and Bay of Fundy spawning Atlantic cod (*Gadus morhua*) during the post-spawning season, with median recapture position (red asterisk), area with 25% of recaptures (yellow), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

Cape Cod spawners demonstrated less residence and greater dispersal (Table 7.7), and these results are similar to those reported by Wise (1963), Tallack (2009, 2011), and Loehrke (2014). During the release season (57 recaptures with locations), there was 84% residence in the spawning area (521-526, Great South Channel-Nantucket Shoals), 7% movement to southwestern Gulf of Maine (514), 7% to eastern Georges Bank (522, 551, 561), and 2% movement to the Mid-Atlantic Bight (616, Hudson Canyon). During the post-spawning season (348 recaptures with locations), there was 65% residence in spawning area, 21% movement to the Gulf of Maine (513, 514, 515), 11% to eastern Georges Bank (522, 525, 551, 561), 3% to southern New England (537, 538, 539), and 1% to the Mid-Atlantic Bight (612, 613, off Long Island). During subsequent spawning seasons (68 recaptures with locations), there was 59% residence in the spawning area, 28% movement to the western Gulf of Maine (513, 514), 6% to Georges Bank (522, 525, 551), 4% to southern New England (537, 538, 539), 1% to the Mid-Atlantic Bight (612 off Long Island), and 1% to Browns Bank (464). Most Cape Cod spawners were recaptured in the Great South Channel and western Gulf of Maine during both the spawning and post-spawning seasons (Figures 7.12 and 7.13), with some movement to Georges Bank during the post-spawning seasons.

Table 7.7. Recaptures from the Northeast Regional Cod Tagging Program of Atlantic cod (*Gadus morhua*) tagged during the spawning season (October-January) in the Cape Cod area (521) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions.

Season of Recapture	Browns Bank	Gulf of Maine	Nantucket Shoals/Great South Channel	Georges Bank	Southern New England	Mid Atlantic Bight
Release	0.00	0.07	0.84	0.07	0.00	0.02
Post-spawning	0.00	0.21	0.65	0.11	0.03	0.01
Subsequent Spawning	0.01	0.28	0.59	0.06	0.04	0.01

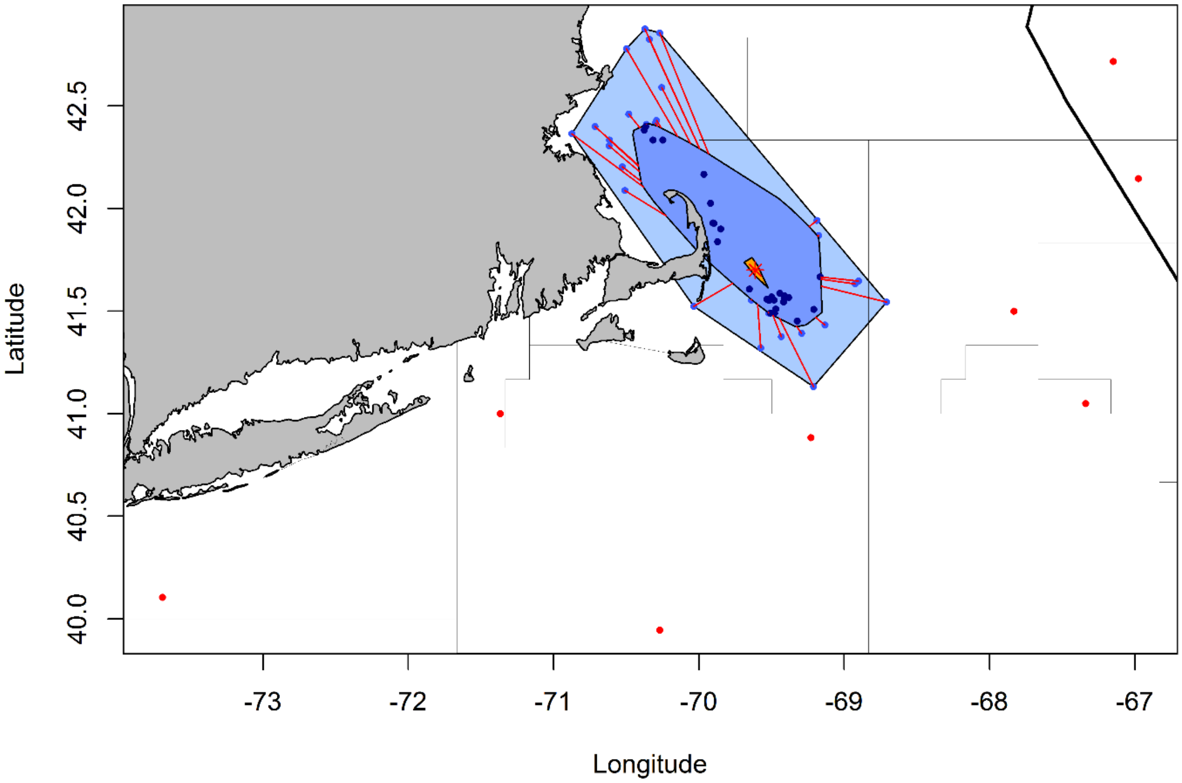

Figure 7.12. Recaptures of spawning Atlantic cod (*Gadus morhua*) tagged in the Cape Cod area during the spawning season, with median recapture position (red asterisk), area with 25% of recaptures (yellow), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

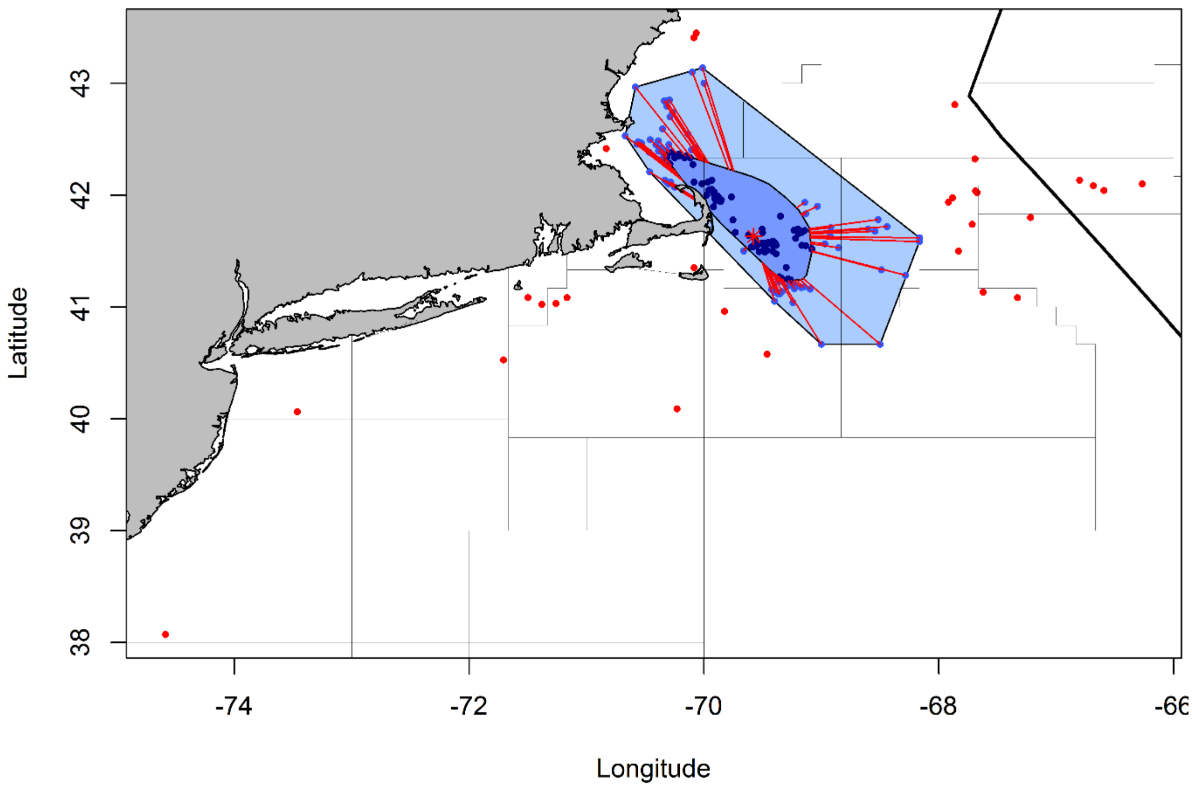

Figure 7.13. Recaptures of spawning Atlantic cod (*Gadus morhua*) tagged in the Cape Cod area during the post-spawning season, with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue), and outliers (red dots).

Southern New England spawners demonstrated high spawning site fidelity (Table 7.8). During the release season (139 recaptures), there was 99% residence in the spawning area (537, 538, 539), with some movement to the Mid-Atlantic Bight (611, 613). During the post-spawning season (42 recaptures), there was 74% residence in southern New England, 19% movement to the Great South Channel (521), and 5% movement to the Mid-Atlantic Bight (612, 613). During subsequent spawning seasons (19 recaptures), there was 95% residence in southern New England and 5% movement to the Great South Channel (521). There were no recaptures of southern New England spawners on eastern Georges Bank. Most spawning cod tagged in southern New England were recaptured in the area (Figure 7.14).

Table 7.8. Recaptures from the Massachusetts Marine Fisheries Institute of Atlantic cod (*Gadus morhua*) tagged during the spawning season (December-May) off southern New England (537, 539) and recaptured during the same spawning season, the post-spawning season (November-March), and subsequent spawning seasons. Colors indicate relative proportions and outlines indicate residence in area of release.

Season of Recapture	Gulf of Maine	Great South Channel	Southern New England	Mid-Atlantic Bight
Release	0.00	0.00	0.99	0.01
Post-spawning	0.02	0.19	0.74	0.05
Subsequent Spawning	0.00	0.05	0.95	0.00

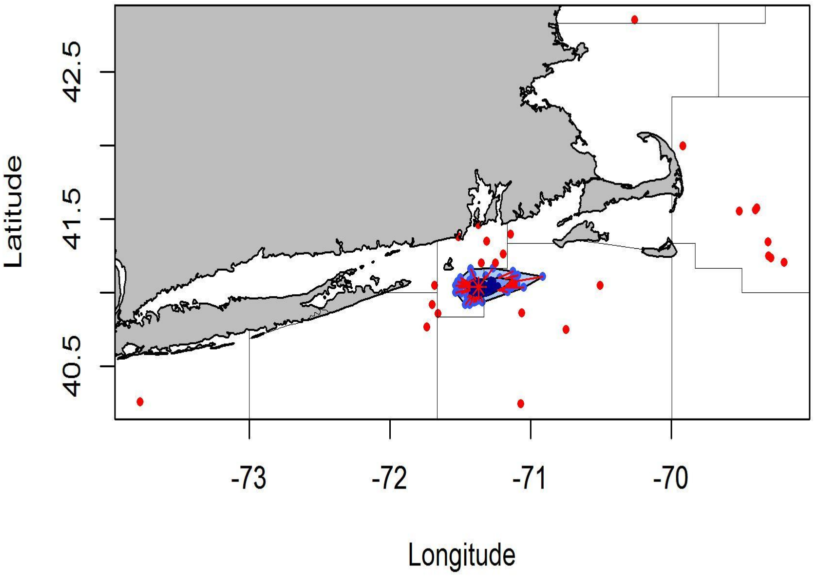

Figure 7.14. Recaptures of spawning Atlantic cod (*Gadus morhua*) tagged in southern New England, with median recapture position (red asterisk), area with 50% of recaptures (dark blue), approximately 95% of recaptures (light blue) and outliers (red dots).

Habitat Occupancy and Movements from Archival Tagging

Archival tags were deployed on fewer cod than were tagged with conventional tags, but geolocation provides information on movement throughout the deployment. The sampling design of archival tagging was to tag spawning cod to evaluate residence on spawning grounds and dispersal after spawning. Deployments with data suitable for geolocation (e.g., time at liberty, tag settings, data quality) were selected for geolocation.

DSTs recovered from spring-spawning cod in Ipswich Bay (n = 25) by Siceloff and Howell (2013) showed that most cod left the Ipswich Bay spawning ground during May and June and dispersed throughout the Gulf of Maine. Cod demonstrated little off-bottom movement while on the spawning ground, but most adopted various location-specific off-bottom movement behaviors after leaving the inshore spawning ground and moving to deeper waters post-spawning. A total of 49 DSTs was recovered from tagging in the SCCZ in Massachusetts Bay with the mean of 115 days at liberty (range = 9-635 days) (Zemeckis 2016; Zemeckis et al. 2017). The coldest temperatures were experienced from March through July, which roughly overlaps with the spring-spawning season, with an increase over the summer and fall to the warmest months from September through January. Cod typically inhabited waters from 45-175 m depth (mean = 93 m, range = 3-268 m). The deepest waters were generally occupied in February and March, and the shallowest when likely present on the inshore spawning grounds in May and June.

The geolocation results for cod tagged in the SCCZ in Massachusetts Bay indicated that cod were primarily residential within the Gulf of Maine. There were 751 positions estimated for 36 fish during the spring-spawning season (16 April–15 July). Cod were mainly located in statistical areas 514 (92%) and 513 (6%) during this period. Cod also demonstrated a high degree of residency in the Gulf of Maine after the spawning season, but a greater proportion of positions came from other statistical areas. For example, from 16 July – 15 October (365 positions, 18 fish), 62% of positions were in 514, 17% in 513, 9% in 512, and 3% in 465. One fish was estimated to occupy occupied statistical area 521 for 35 days during this time period, which represents ~10% of days during this period and movement into the Georges Bank management unit. However, little movement south of Cape Cod or to Georges Bank was estimated for other individuals. During the 16 October–15 January period (70 positions, 4 fish), most positions were assigned to statistical areas 514 (17%), 512 (64%), and 465 (11%). Most positions during the 16 January–15 April period (24 positions, 4 fish) were assigned to statistical area 514 (46%) or 512 (42%).

Most probable tracks from 88 DST deployments on Atlantic cod from the MFI tagging studies show dispersal patterns similar to those from conventional tags. There were 19 DSTs recovered from cod tagged in the western Gulf of Maine on Stellwagen Bank or in Massachusetts Bay (mean days at liberty = 67 days, range = 21-105 days), most of which were tagged in March or April 2001 (n = 10) and were included in Gröger et al. (2007) or they were released during March 2007 (n = 7). These fish occupied the shallowest depths from April through June, which could be indicative of feeding on Stellwagen Bank. In contrast, deeper depths were occupied from December through February, which may indicate inshore spawning during the winter in Massachusetts Bay, but sample sizes are low for these months. The coldest water temperatures were occupied from February through March, while the warmest water temperatures were occupied from December and January. Geolocation results for these fish demonstrate that cod in this region are likely to be primarily residential in the western Gulf of Maine (Figure 7.15). Results from the HMM geolocation model suggested some movement from the western Gulf of Maine to the Great South Channel, but these movements were less frequent than estimated for a subset of these fish by Gröger et al. (2007). Therefore, geolocation results are sensitive to the chosen geolocation method, but the more statistically robust and rigorously validated HMM method is expected to produce more accurate results.

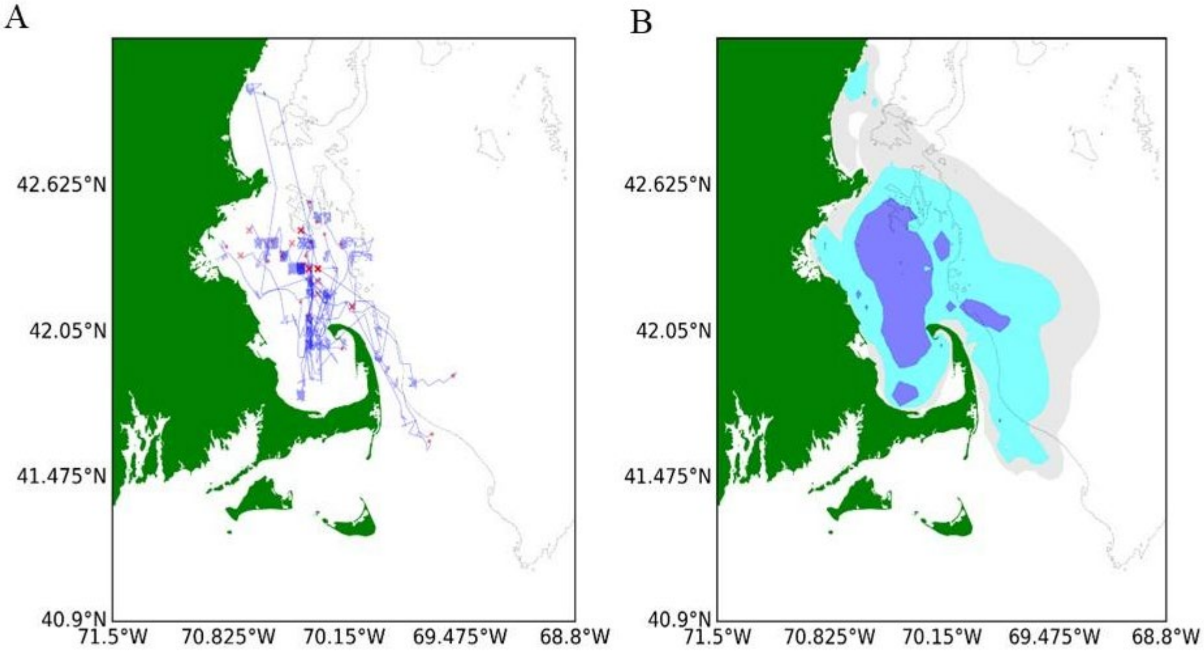

Figure 7.15. Geolocation results for recovered data storage tags (n = 19) from Atlantic cod (*Gadus morhua*) that were tagged in the western Gulf of Maine as a part of long-term tagging studies by the Massachusetts Marine Fisheries Institute (MFI), including (A) the most probable track for each individual (red X = tagging locations, red dots = reported recovery locations) and (B) a plot of the utilization distribution (blue = 68%, teal = 95%, gray = 99%) to estimate the space use of this group of fish, from Liu (2019).

The 5 cod tagged with DSTs in the Great South Channel and Nantucket Shoals were recovered that had data suitable for analysis ranged 15-124 days at liberty. Three of these fish were tagged in deep water (175 m) in the Great South Channel during March 2008, while the remaining fish were tagged in shallower waters (40 – 50 m) southeast of Chatham, MA, in November 2006 and December 2009. The low sample size of recaptures from this region provides limited data to investigate the habitat occupancy of cod tagged in these regions. All 5 of these fish tagged in the Great South Channel were recaptured in the Gulf of Maine, and both the most probable tracks and utilization distribution results provided additional evidence of connectivity among the Great South Channel and the Gulf of Maine (Figure 7.16).

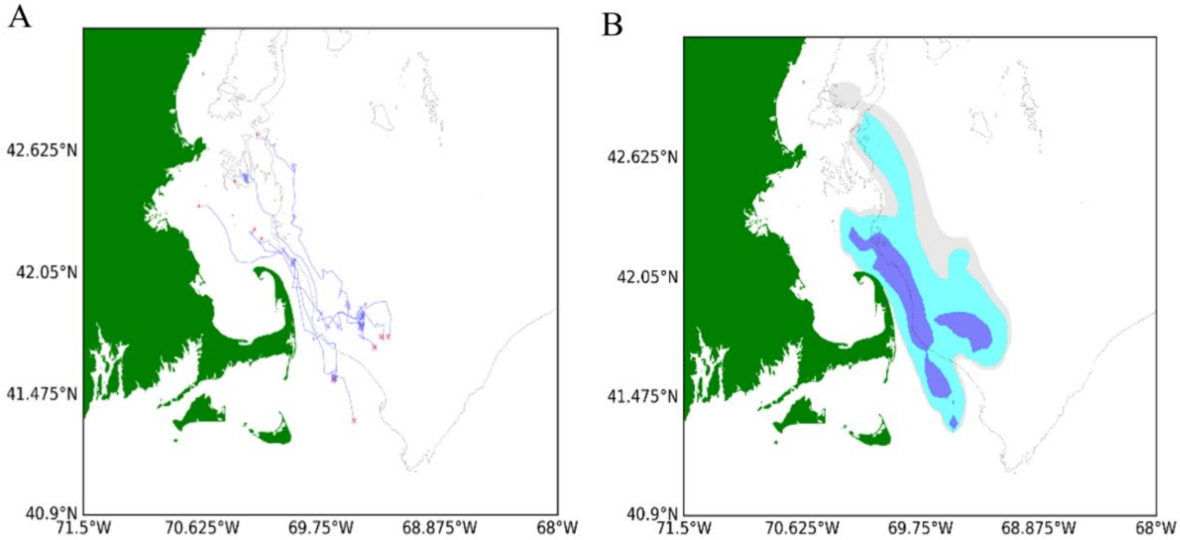

Figure 7.16. Geolocation results for recovered data storage tags (n = 5) from Atlantic cod (*Gadus morhua*) that were tagged in the Great South Channel and Nantucket Shoals as a part of long-term tagging studies by the Massachusetts Marine Fisheries Institute (MFI), including (A) the most probable track for each individual (red X = tagging locations, red dots = reported recovery locations) and (B) a plot of the utilization distribution (blue = 68%, teal = 95%, gray = 99%) to estimate the space use of this group of fish, from Liu (2019).

The 64 DSTs recovered from cod tagged with DSTs in southern New England waters ranged 4-429 days at liberty. The seasonal habitat occupancy data demonstrate that cod tagged in southern New England typically utilize a relatively narrow depth range of approximately 40-90 m, which is shallower than most of the fish tagged in other regions. The coldest water temperatures occupied by cod in southern New England occurred from February through May. The warmest water temperatures occupied by cod occurred from September through November, and these temperatures are generally warmer than the warmest temperatures experienced by cod tagged in other regions. Geolocation results suggest that cod tagged in southern New England were primarily residential in this area with some movement to the south towards the offshore canyons along the continental edge and southwest into the Mid-Atlantic Bight (Figure 7.17). Two fish were estimated to have moved to the Great South Channel, 1 of which was estimated to have also moved into the Gulf of Maine.

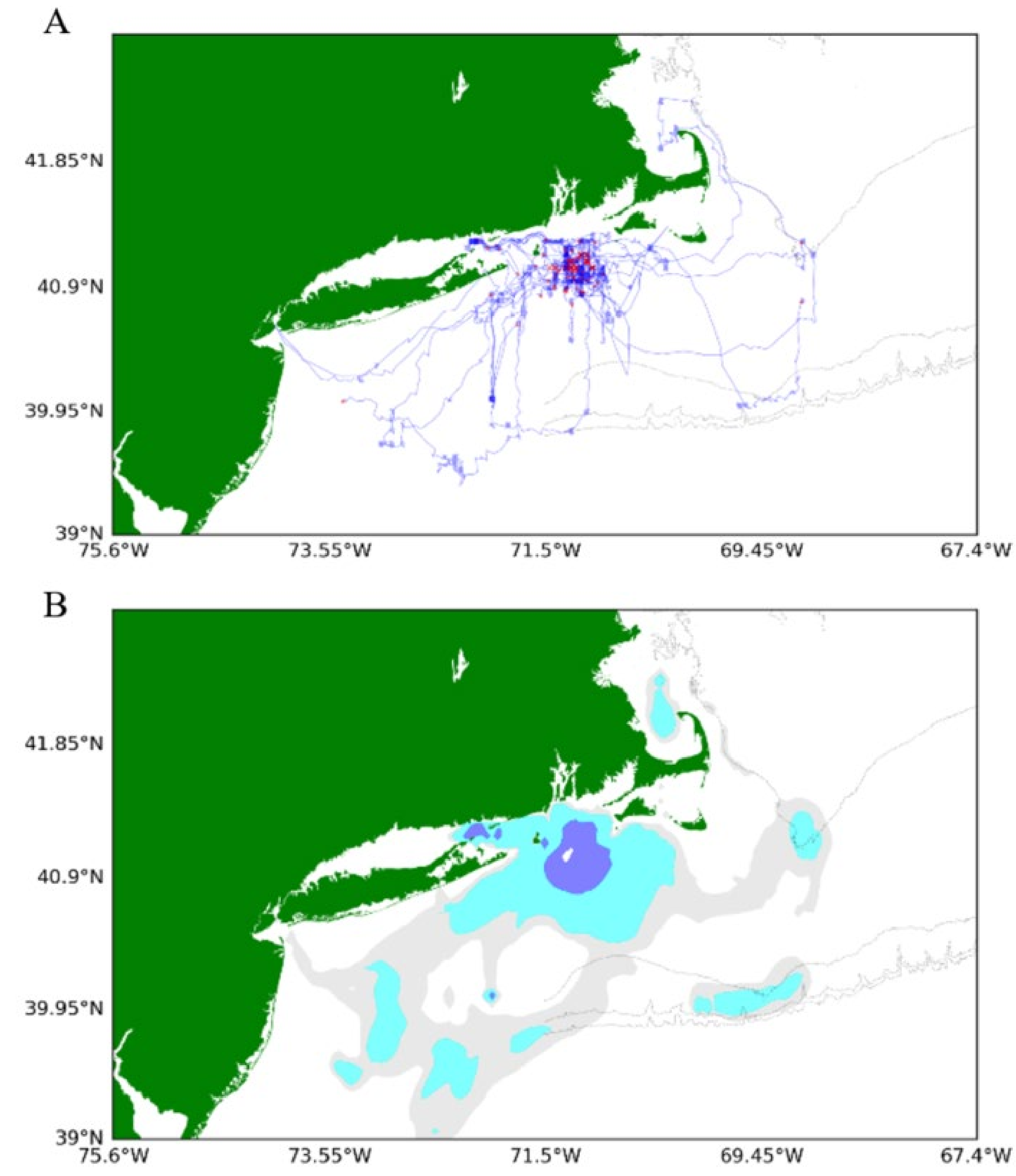

Figure 7.17. Geolocation results for recovered data storage tags (n = 64) from Atlantic cod (*Gadus morhua*) that were tagged in southern New England as a part of long-term tagging studies by the Massachusetts Marine Fisheries Institute (MFI), including (A) the most probable track for each individual (red X = tagging locations, red dots = reported recovery locations) and (B) a plot of the utilization distribution (blue = 68%, teal = 95%, gray = 99%) to estimate the space use of this group of fish.

Discussion

Some of the major patterns of residence, spawning site fidelity, and movement from tagging data appear to be persistent over decades. For example, the Northeast Regional Cod Tagging Program data (2002-2003 releases) show that cod in the Gulf of Maine are relatively sedentary with limited movement from the western Gulf of Maine to the Great South Channel (2%; Table 7.2) and western Georges Bank (2%, 522, 525), similar to the historical tagging (Higgins 1929, 1933, 1934; Perkins et al. 1997). Recent tagging data also confirm that there is extensive movement from the Great South Channel to the western Gulf of Maine (e.g., 17% movement from 521 to 514, Table 7.2), similar to the results reported by Wise (1963). Recent data also show greater movement from eastern Georges Bank to the Bay of Fundy and western Scotian Shelf (19%, Table 7.2) than to the Great South Channel (3%) similar to historical (Higgins 1931; Wise 1963) and contemporary (Hunt et al. 1999) tagging studies. The apparent boundary on western Georges Bank (approximately 68°W) identified by Wise (1963) is supported by recent tagging data because there was 6% movement from the Great South Channel (521) to western Georges Bank (522, 525), but only 2% movement to eastern Georges Bank (551, 552, 561, 562). Although the Northeast Regional Cod Tagging Program did not have releases on the western Scotian Shelf (462, 463, 464, 465), the apparent boundary between the western Scotian Shelf and the eastern Scotian Shelf off southeast Nova Scotia persisted over several decadal tagging studies (McKenzie 1956; Hunt et al. 1999; Clark and Emberley 2010).

Other patterns of residence and dispersal have changed since the early 1900s. Some regional movement patterns indicated from analysis of the Schroeder tagging logs (Schroeder 1930) were considerably different than those observed in tagging programs since the 1990s. The number of releases and recaptures off coastal Maine (512) also suggest much greater distribution of cod and fishing effort in that area in the early 1900s relative to recent decades. As described by Clark and Emberley (2010), dispersal from the Bay of Fundy appears to have increased. Historical tagging suggested more residence in the Bay of Fundy (Halliday 1971; McKenzie 1956; Hunt and Neilson 1993), than did the Northeast Regional Cod Tagging Program data. Similar to the 2001-2002 tagging reported by Clark and Emberley (2010), the Northeast Regional Cod Tagging Program data suggested 17% dispersal of cod from the Bay of Fundy, including to the western Scotian Shelf (9%), Gulf of Maine (5%), and Georges Bank (3%).

The major patterns of residence and movement are consistent with information on stock identity from other disciplines. The apparent boundaries off southeast Nova Scotia (McKenzie 1956; Hunt et al. 1999; Clark and Emberley 2010) and on western Georges Bank (Wise and Jensen 1960; Wise 1963) are consistent with geographic variation in genetics between the eastern Scotian Shelf, eastern Georges Bank, and the Great South Channel (Chapter 4, this volume). The apparent spawning site fidelity of western Gulf of Maine winter spawners (Table 7.2), western Gulf of Maine spring spawners (Table 7.3), and spawners on eastern Georges Bank (Table 7.5) may maintain the genetic differences among those groups (Chapter 4). Conversely, the lower residence and greater dispersal of spawning cod from the Cape Cod grounds (e.g., 28% of cod tagged during the spawning season on Nantucket Shoals and in the Great South Channel were recaptured in the western Gulf of Maine in subsequent spawning seasons; Table 7.7) suggest greater reproductive connectivity with other groups and may explain their genetic similarity with the western Gulf of Maine and possibly southern New England (Chapter 4). The greater movement from the Great South Channel to the western Gulf of Maine (16%, Table 7.2) is also consistent with geographic variation in size at age, in which cod from the Great South Channel are more similar to those in the Gulf of Maine than those on Georges Bank (Chapter 5, this volume).

Inferences of residence and movement from conventional tags are constrained by spatiotemporal patterns in fishing effort and reporting rates. However, conclusions about broad-scale residence and movement appear to be robust to these effects because results are similar to those from archival tags, which are much less constrained by fishery variables. In addition, the stability in tagging results over decades with different fishing patterns and fishery regulations, and the similarity of results from previous studies that attempted to account for fishing patterns (Hunt et al. 1999; Howell et al. 2008; Loehrke 2014) further corroborate the general patterns described here.

The tagging data available for exploring movement patterns of cod in the Gulf of Maine and adjacent areas (NAFO divisions 4X, 5, 6) are superlative, but some information gaps remain. The low abundance of cod in the eastern Gulf of Maine continues to be a challenge for tagging, and more tag releases would be valuable, particularly of spawning cod from that area. Small pop-up satellite tags may help to obtain data in the region despite low fishing effort. The recent studies of spawning dynamics for spring spawners in Ipswich Bay (Siceloff and Howell 2013), spring spawners in Massachusetts Bay (Dean et al. 2014; Zemeckis et al. 2014a; Zemeckis et al. 2017), and winter spawners in Massachusetts Bay (Zemeckis et al. 2019) show that advanced technologies can improve our understanding of spawning site fidelity and dispersal of other spawning groups that are currently active. For example, acoustic tagging of spawning cod on Cox Ledge would improve our understanding of their spawning dynamics. The recent delineation of spawning grounds on Georges Bank from Fishermen's Ecological Knowledge (Chapter 8, this volume) can be used to design conventional and electronic tagging studies to quantify movement patterns of those spawning groups.

Conclusion

There is a wealth of mark-recapture observations focused on regional stocks of Atlantic cod that spans more than 100 years and includes more than 200,000 tag releases and 10,000 recaptures. Major patterns of regional residence and movement have been similar among tagging studies since the early 1900s. There is little movement of cod between the Gulf of Maine region and the eastern Scotian Shelf. Cod in the western Gulf of Maine and the Bay of Fundy are relatively sedentary, but there is some movement between the western Gulf of Maine and the Great South Channel. There is extensive movement between eastern Georges Bank and the western Scotian Shelf and historically between Nantucket Shoals and the Mid-Atlantic Bight. 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, high spawning site fidelity on eastern Georges Bank with some post-spawning dispersal, and greater dispersal from the Cape Cod spawning grounds. Major movement patterns are consistent among studies, but the frequency of residence and movement vary among studies.

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Supplemental Materials A. Schroeder Logs

There were 2,097 reported recaptures from the keypunched Schroeder logs with recapture positions. Cod were tagged from eastern Gulf of Maine to the Mid-Atlantic Bight from 1923- 1927, with some reported recaptures up to 6 years at liberty. There was high regional residence as well as some substantial regional movements (Table A1a). Regional residence was 97% in the Gulf of Maine, 36% in the Great South Channel, and 28% in southern New England. Substantial regional movements (>10%) were from the Great South Channel to the Gulf of Maine (20%); from Georges Bank to the Gulf of Maine (20%) and to the Mid Atlantic Bight (20%); and from southern New England to the Mid-Atlantic Bight (40%), to the Gulf of Maine (17%), and to the Great South Channel (13%). There was >50% residence in statistical areas (Table A1b) off eastern ME (511), midcoast ME (512), southern ME-NH (513), and southwest Gulf of Maine (514), but not in the Great South Channel (521).

There were many more releases and recaptures from midcoast ME (512) than reported in more recent tagging studies, indicating much more fishing in that area in the early 1900s. Some regional movement patterns were considerably different than those observed in more recent tagging programs (e.g., less movement from Georges Bank to the western Scotian Shelf, more movement from Georges Bank to the Gulf of Maine and to the Mid-Atlantic Bight, and more movement from the Great South Channel and southern New England to the Mid-Atlantic Bight). The number of releases and recaptures off coastal Maine (512) also suggests much greater distribution of cod and fishing effort in that area than in recent decades. Therefore, these results were not pooled with those from more recent tagging. With the possible exception of the Cape Cod spawning group (640 recaptures from releases in area 521), there was an insufficient number of recaptures from currently active spawning groups to support a seasonal breakdown of recaptures.

Table A1a. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Schroeder logs by statistical area of release (Rel.) and recapture. Colors indicate geographic regions (green: Gulf of Maine; dark green: western Gulf of Maine; white: Great South Channel; orange: Georges Bank; red: southern New England/Mid-Atlantic Bight); and outlines indicate regional residence.

	Recapture Area																										
Rel.	461	463	465	466	467	511	512	513	514	515	521	522	525	551	552	562	526	537	538	539	611	612	613	614	615	621	?	Sum
511						26	22																				2	50
512	4	3	4	5	3	29	1104	6	12		1					1											4	1176
513	1						4	141	1	3	6	4					1		1								1	163
514				1			2		4												1	1		1				10
521	1				1	1	85	7	34		225		1			5	48	8	5	24	18	83	17	37	4	16	20	640
551									1					1	1						1							4
561															1													1
526	1						6				4											1		1				13
537								2			1							2		1								6
538											1						1	1		8	4	5	8				6	34
Sum	7	3	4	6	4	56	1223	156	52	3	238	4	1	1	2	6	50	11	6	33	24	90	25	39	4	16	33	2097

Table A1b. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Schroeder logs by statistical area of release (Rel.) and recapture, expressed as the proportion of known-area recaptures from each release area. Outlines indicate residence in each area.

	Recapture Area																									
Rel.	461	463	465	466	467	511	512	513	514	515	521	522	525	551	552	562	526	537	538	539	611	612	613	614	615	621
511	0	0	0	0	0	0.54	0.46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
512	0.00	0.00	0.00	0.00	0.00	0.02	0.94	0.01	0.01	0	0.00	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0
513	0.01	0	0	0	0	0	0.02	0.87	0.01	0.02	0.04	0.02	0	0	0	0	0.01	0	0.01	0	0	0	0	0	0	0
514	0	0	0	0.10	0	0	0.20	0	0.40	0	0	0	0	0	0	0	0	0	0	0	0.10	0.10	0	0.10	0	0
521	0.00	0	0	0	0.00	0.00	0.14	0.01	0.05	0	0.36	0	0.00	0	0	0.01	0.08	0.01	0.01	0.04	0.03	0.13	0.03	0.06	0.01	0.03
551	0	0	0	0	0	0	0.00	0	0.25	0	0	0	0	0.25	0.25	0	0	0	0	0	0.25	0	0	0	0	0
561	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	1.00	0	0	0	0	0	0	0	0	0	0	0
526	0.08	0	0	0	0	0	0.46	0	0	0	0.31	0	0	0	0	0	0	0	0	0	0	0.08	0	0.08	0	0
537	0	0	0	0	0	0	0.00	0.33	0	0	0.17	0	0	0	0	0	0	0.33	0	0.17	0	0	0	0	0	0
538	0	0	0	0	0	0	0.00	0	0	0	0.04	0	0	0	0	0	0.04	0.04	0	0.29	0.14	0.18	0.29	0	0	0

There are too few recoveries from the western Gulf of Maine releases (n = 173), Georges Bank releases (n = 5), and southern New England releases (n = 53) from the Schroeder logs to support seasonal recovery matrices.

The Schroeder logs include many tag releases from midcoast Maine (512) and many recaptures from those releases. Bigelow and Schroeder (1953) report that

> off the western coast of Maine, according to Capt. E. E. Hahn, former superintendent of the Boothbay Harbor hatchery, cod spawn from late February or early March until the last of May, with the production of eggs at its peak in March; they spawn from March through May off the eastern Maine coast, and cod eggs (and hence spawning cod) have been recorded in spring in the Bay of Fundy.

There were no releases from 512 in February or March, but recaptures from releases in April-May (Table A2) suggest high spawning site fidelity in subsequent spawning seasons (93%).

Table A2. Recaptures of Atlantic cod (*Gadus morhua*) from the Schroeder logs of cod tagged during the spawning season (February-May) off midcoast Maine (512) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)												(proportion by area)									
	461	463	465	466	467	511	512	513	514	562	?	Sum	461	463	465	466	467	511	512	513	514	562
512						1	15					16	0	0	0	0	0	0.06	0.94	0	0	0

Post-Spawning Season

	461	463	465	466	467	511	512	513	514	562	?	Sum	461	463	465	466	467	511	512	513	514	562
512	1	1	2	1	1	4	349	2	8		2	371	0.00	0.00	0.01	0.00	0.00	0.01	0.95	0.01	0.02	0

Subsequent Spawning Seasons

	461	463	465	466	467	511	512	513	514	562	?	Sum	461	463	465	466	467	511	512	513	514	562
512			1	1			50		1	1		54	0	0	0.02	0.02	0	0	0.93	0	0.02	0.02

Historical spawning in the Cape Cod area was described by Bigelow and Schroeder (1953):

> The broken bottom of Nantucket Shoals, east and south of Nantucket Island, has long been known as a center of abundance for ripe cod fish in late autumn and early winter. . . On Nantucket Shoals, ripening fish are caught from late October on, with the cod spawning there in early November to mid-February, and occasionally until April.

There were no tag releases in Schroeder's logs in February, so the same spawning season (October-January) was assumed as for the more recent studies. Results suggest relatively low (32%) spawning site fidelity in subsequent spawning seasons, and substantial movement (45%) to southern New England/Mid-Atlantic regions (Table A3).

Table A3. Recaptures of Atlantic cod (*Gadus morhua*) from the Schroeder logs of cod tagged during the spawning season (October-January) in the Cape Cod area (521) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)														(proportion by area)												
Rel.	512	514	521	562	526	537	539	611	612	613	614	615	621	?	Sum	512	514	521	562	526	537	539	611	612	613	614	615	621
521		1	5		1		2		25	4	6		1	3	48	0	0.02	0.11	0	0.02	0	0.04	0	0.56	0.09	0.13	0	0.02

Post-Spawning Season

Rel.	512	514	521	562	526	537	539	611	612	613	614	615	621	?	Sum	512	514	521	562	526	537	539	611	612	613	614	615	621
521		8	34	2	6	2	2	2	5	3	8	2		3	77	0	0.11	0.46	0.03	0.08	0.03	0.03	0.03	0.07	0.04	0.11	0.03	0.00

Subsequent Spawning Seasons

Rel.	512	514	521	562	526	537	539	611	612	613	614	615	621	?	Sum	512	514	521	562	526	537	539	611	612	613	614	615	621
521	1		7		2		1	2	4	1	1		1	2	22	0.1	0	0.35	0	0.10	0	0.05	0.10	0.20	0.05	0.05	0	0.05

Supplemental Materials B. 1994-1996 Canadian Tagging Data

The 1994 tagging reported by Hunt et al. (1999) included 5,067 releases in March, primarily on eastern Georges Bank (551, 552, 562), with some releases in the Bay of Fundy, Scotian Shelf, and southern New England. There were 217 reported recaptures with recapture position, with some reported recaptures up to 5 years. There was 61% regional residence on Georges Bank (522, 551, 552, 561, 562), with 36% movement to Scotian Shelf and Bay of Fundy (461, 462, 463, 464, 465, 466; Table B1a).

Table B1a. All recaptures of Atlantic cod (*Gadus morhua*) from Canada Department of Fisheries and Oceans 1994 cod tagging by statistical area of release (Rel.) and recapture. Colors indicate geographic regions (dark blue: Scotian Shelf; light blue: Bay of Fundy; orange: Georges Bank; pink: S. New England/Mid-Atlantic), and outlines indicate regional residence.

	Recapture Area																	
Rel.	461	462	463	464	465	466	511	514	515	521	522	551	552	561	562	526	?	Sum
463			4		1												1	6
465			1	2	4												0	7
467						2											0	2
551					2							3					2	7
552	3	8	20	14	18	4	2	1	1	1	2	77	23	3			38	215
562				3						2		8	5		2		4	24
526																1	0	1
Sum	3	8	25	19	25	6	2	1	1	3	2	88	28	3	2	1	45	262

Residence and movement from statistical areas indicate >50% residence in the western Scotian Shelf (463), southern Bay of Fundy (465), and the northeast peak of Georges Bank (551; Table B1b).

Table B1b. All recaptures of Atlantic cod (*Gadus morhua*) from Canada Department of Fisheries and Oceans 1994 cod tagging by statistical area of release (Rel.) and recapture, expressed as the proportion of known-area recaptures from each release area. Outlines indicate residence in each area.

	Recapture Area															
Rel.	461	462	463	464	465	466	511	514	515	521	522	551	552	561	562	526
463	0	0	0.8	0	0.2	0	0	0	0	0	0	0	0	0	0	0
465	0	0	0.14	0.29	0.57	0	0	0	0	0	0	0	0	0	0	0
467	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
551	0	0	0	0	0.4	0	0	0	0	0	0	0.6	0	0	0	0
552	0.02	0.05	0.11	0.08	0.10	0.02	0.01	0.01	0.01	0.01	0.01	0.44	0.13	0.02	0	0
562	0	0	0	0.15	0	0	0	0	0	0.10	0	0.40	0.25	0	0.10	0
526	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Seasonal patterns of recaptures demonstrated high spawning site fidelity and dispersal in the post-spawning season (Table B2). There were few recaptures (n = 6) with reported recapture locations during the release season. During the post-spawning season (179 recaptures with locations), there was 66% residence on Georges Bank (522, 551, 552, 561, 562) and 32% movement to the Scotian Shelf and the Bay of Fundy. During subsequent spawning seasons (119 recaptures with locations), there was 53% residence on Georges Bank and 45% movement to the Scotian Shelf and the Bay of Fundy.

Table B2. Recaptures of Atlantic cod (*Gadus morhua*) from Canada Department of Fisheries and Oceans 1994 cod tagged during the spawning season (December-May) on Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in each area.

Recapture Area (# recaptures)

Season of Release

Rel.	461	462	463	464	465	466	511	514	515	521	522	551	552	561	562	?	Sum
552				2				1		1		1		1		4	10

Post-Spawning Season

551					1							3				1	5
552	3	8	19	8	13	4	2		1		2	74	23	1		31	189
562				1						1		8	5		2	4	21
Sum	3	8	19	9	14	4	2		1	1	2	85	28	1	2	36	215

Subsequent Spawning Seasons

551					1							2				1	4
552	3	8	17	7	12	4	2					42	8	1		25	129
562				1						1		7	1		2	4	16
Sum	3	8	17	8	13	4	2			1		51	9	1	2	30	149

(proportion by area)

Season of Release

Rel.	461	462	463	464	465	466	511	514	515	521	522	551	552	561	562
552	0	0	0	0.33	0	0	0	0.17	0	0.17	0	0.17	0	0.17	0

Post-Spawning Season

551	0	0	0	0	0.25	0	0	0	0	0	0	0.75	0	0	0
552	0.02	0.05	0.12	0.05	0.08	0.03	0.01	0	0.01	0	0.01	0.47	0.15	0.01	0
562	0	0	0	0.06	0	0	0	0	0	0.06	0	0.47	0.29	0	0.12

Subsequent Spawning Seasons

551	0	0	0	0	0.33	0	0	0	0	0	0	0.67	0	0	0
552	0.03	0.08	0.16	0.07	0.12	0.04	0.02	0	0	0	0	0.40	0.08	0.01	0
562	0	0	0	0.08	0	0	0	0	0	0.08	0	0.58	0.08	0	0.17

Supplemental Materials C. Northeast Regional Cod Tagging Program

From the 2002-2004 Northeast Regional Cod Tagging Program, there were 6,784 reported recaptures, and 6,166 were reported with recapture positions, some at large for up to 4.5 years. Regional residence was generally high, but there was also some substantial movement between regions (Table C1a). Regional residence was 92% in the Scotian Shelf and the Bay of Fundy, 92% in the Gulf of Maine (95% in the western Gulf of Maine, but only 43% residence in the eastern Gulf of Maine), 71% in the Great South Channel, 79% on Georges Bank, and 71% in southern New England. Substantial regional movements (>10%) were from the Great South Channel to the western Gulf of Maine (16%), from Georges Bank to Scotian Shelf and Bay of Fundy (16%), and from southern New England to the Great South Channel (20%).

Table C1a. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program by statistical area of release (Rel.) and recapture. Colors indicate geographic regions (blue: Bay of Fundy; green: Gulf of Maine; dark green: western Gulf of Maine; white: Great South Channel; orange: Georges Bank; red: S. New England/Mid-Atlantic Bight), and outlines indicate regional residence.

	Recapture Area																											
Rel.	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	561	562	526	537	538	539	611	612	613	615	616	621	?	Sum
466	1		9	19	172	224	6		3				4		9	1											1	17	466
467		1	22	28	133	203	16	3	8	3		1	4	1	11													18	452
511			17	30	10	7	40		2	2			1		8	4												11	132
512				1				1	10	4	1		1																18
513			3	1	2	1			1291	287	19	31	14		3		1	1										150	1804
514									22	70	1	4																11	108
515			5	1		1		1	16	11	76	6	14	1	1	1												8	142
521			3	1	2	1			33	314	3	1526	95	39	20	12	6	39	20	3	24	2	5	7	2	1	2	314	2474
522	1		35	4	2	7	3		1	2		10	71	5	106	16	11	2										25	301
525			2						1			2	2	3	17	2	1											2	32
551				2		1						1			1														5
552				1																								1	2
561	1	8	52	9	4	10	2	1	5			22	74	13	167	154	31											42	595
562	1		16	3	1	6							16	6	53	24	41											19	186
526									1	1		9		1				1			1								14
537												2			1				9		7								19
539																			8		14	1							23
?					2	8			1																				11
Sum	4	9	164	100	328	469	67	6	1394	694	100	1614	296	69	397	214	91	43	37	3	46	3	5	7	2	1	3	618	6784

Residence and movement from statistical areas indicate >50% residence in the northwest Bay of Fundy (467), southern ME-NH (513), southwest Gulf of Maine (514), central Gulf of Maine (515), Great South Channel (521), offshore S. New England (537), and RI Sound (539). Substantial movement (>50%) was from the northeast Bay of Fundy (466) to the northwest Bay of Fundy (467), from midcoast ME (512) to southern ME-NH (513), from southwest Georges Bank (525) to northeast Georges Bank (551), and from Nantucket Shoals (526) to Great South Channel (521).

Table C1b. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program by statistical area of release (Rel.) and recapture, expressed as the proportion of recaptures from each release area. Outlines indicate residence in each area.

	Recapture Area																									
Rel.	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	561	562	526	537	538	539	611	612	613	615	616	621
466	0	0	0	0	0.4	0.5	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
467	0	0	0.1	0.1	0.3	0.5	0	0	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
511	0	0	0.1	0.2	0.1	0.1	0.3	0	0.02	0.02	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0
512	0	0	0	0.1	0	0	0	0.1	0.56	0.22	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
513	0	0	0	0	0	0	0	0	0.78	0.17	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
514	0	0	0	0	0	0	0	0	0.23	0.72	0	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
515	0	0	0	0	0	0	0	0	0.12	0.08	0.6	0.04	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
521	0	0	0	0	0	0	0	0	0.02	0.15	0	0.71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
522	0	0	0.1	0	0	0	0	0	0	0.01	0	0.04	0.3	0	0.4	0.1	0	0	0	0	0	0	0	0	0	0	0
525	0	0	0.1	0	0	0	0	0	0.03	0	0	0.07	0.1	0.1	0.6	0.1	0	0	0	0	0	0	0	0	0	0	0
551	0	0	0	0.4	0	0.2	0	0	0	0	0	0.2	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
552	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
561	0	0.01	0.1	0	0	0	0	0	0.01	0	0	0.04	0.1	0	0.3	0.3	0.1	0	0	0	0	0	0	0	0	0	0
562	0.01	0	0.1	0	0	0	0	0	0	0	0	0	0.1	0	0.3	0.1	0.2	0	0	0	0	0	0	0	0	0	0
526	0	0	0	0	0	0	0	0	0.07	0.07	0	0.64	0	0.1	0	0	0	0.1	0	0	0.1	0	0	0	0	0	0
537	0	0	0	0	0	0	0	0	0	0	0	0.11	0	0	0.1	0	0	0	0.5	0	0.4	0	0	0	0	0	0
539	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	0.6	0	0	0	0	0	0

There were only 17 recaptures of spawning cod tagged in southern New England (3 in season of release, 5 in post-spawning season, 6 in subsequent spawning season), with 76% of recaptures in the spawning area (537-539), 2 recaptures in 521 (Great South Channel), and single recaptures in 551 (eastern Georges Bank) and 611 (Long Island Sound).

Western Gulf of Maine winter spawners demonstrated strong spawning site fidelity (Table C2). All recaptures during the same release season (41 with reported recapture location) were recaptured in the spawning area (513-514, western Gulf of Maine). Of the 159 recaptures in the post-spawning period, 93% were in the spawning area, and 1-3% moved to Browns Bank (464), central Gulf of Maine (515), Great South Channel (521), and Georges Bank (522, 562). In subsequent spawning seasons there was 100% residence in the Gulf of Maine, 96% residence in spawning area, and 4% movement to central Gulf of Maine (515).

Table C2. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the winter-spawning season (October-January) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of release

	Recapture Area (# recaptures)									(proportion by area)						
Rel.	464	513	514	515	521	522	562	?	Sum	464	513	514	515	521	522	562
513		28	11					2	41	0	0.72	0.28	0	0	0	0
514			2					2	4	0	0	1	0	0	0	0
Sum		28	13					4	45							

Post-Spawning Season

Rel.	464	513	514	515	521	522	562	?	Sum	464	513	514	515	521	522	562
513	1	114	27	2	4	3	1	10	162	0.01	0.75	0.18	0.01	0.03	0.02	0.01
514			7					2	9	0	0	1	0	0	0	0
Sum	1	114	34	2	4	3	1	12	171							

Subsequent Spawning Seasons

Rel.	464	513	514	515	521	522	562	?	Sum	464	513	514	515	521	522	562
513		14	5	1				2	22	0	0.70	0.25	0.05	0	0	0
514			5						5	0	0	1	0	0	0	0
Sum		14	10	1				2	27							

Western Gulf of Maine spring spawners also demonstrated high spawning site fidelity (Table C3). Of the 491 recaptures during the same release season, there was 99% residence in spawning area (513-514, western Gulf of Maine) and <1% movement to the Great South Channel (521) and Georges Bank (522, 551). There were 679 recaptures with reported recapture locations during the post-spawning season, with 94% residence in spawning area, 3% movement to the Great South Channel (521), 1% to central Gulf of Maine (515), 1% to Georges Bank (522, 551), and 1% to Scotian Shelf/Bay of Fundy (464, 465, 466, 467), and <1% to offshore southern New England (526). Similar to the results reported by Loehrke (2014) and Zemeckis et al. (2017), the 318 recaptured in subsequent spawning seasons with location information had 96% residence in spawning the area, 1% movement central Gulf of Maine (515; 98% residence in the Gulf of Maine), 1% to Great South Channel (521), 1% to central Gulf of Maine (515), and 2% to Georges Bank (522, 551).

Table C3. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spring-spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)													(proportion by area)										
Rel.	464	465	466	467	513	514	515	521	522	551	526	?	Sum	464	465	466	467	513	514	515	521	522	551	526
513					453	18		2	1	1		18	493	0	0	0	0	0.95	0.04	0	0.00	0.00	0.00	0
514					9	5		2					16	0	0	0	0	0.56	0.31	0	0.13	0	0	0
Sum	0	0	0	0	462	23	0	4	1	1	0	18	509											

Post-Spawning Season

Rel.	464	465	466	467	513	514	515	521	522	551	526	?	Sum	464	465	466	467	513	514	515	521	522	551	526
513	2	1	1	1	397	196	10	19	5	1	1	85	719	0.00	0.00	0.00	0.00	0.63	0.31	0.02	0.03	0.01	0.00	0.00
514					10	33		2				7	52	0	0	0	0	0.22	0.73	0	0.04	0	0	0
Sum	2	1	1	1	407	229	10	21	5	1	1	92	771											

Subsequent Spawning Seasons

Rel.	464	465	466	467	513	514	515	521	522	551	526	?	Sum	464	465	466	467	513	514	515	521	522	551	526
513					260	27	3	2	5	1		25	323	0	0	0	0	0.87	0.09	0.01	0.01	0.02	0.00	0
514					3	16	1					1	21	0	0	0	0	0.15	0.8	0.05	0	0	0	0
Sum	0	0	0	0	263	43	4	2	5	1	0	26	344											

Cape Cod spawners demonstrated less residence and greater dispersal (Table C4). During the release season (57 recaptures with locations), there was 84% residence in the spawning area (521-526, Great South Channel/Nantucket Shoals), 7% movement to southwestern Gulf of Maine (514), 7% to Georges Bank (522, 551, 561), and 2% movement to the Mid-Atlantic Bight (616, Hudson Canyon). During the post-spawning season (348 recaptures with locations), there was 65% residence in spawning area, 20% movement to the Gulf of Maine (513, 514, 515), 11% to Georges Bank (522, 525, 551, 561), 3% to southern New England (537, 538, 539), and 1% to the Mid-Atlantic Bight (612, 613, off Long Island). During subsequent spawning seasons (68 recaptures with locations) there was 57% residence in the spawning area, 30% movement to the western Gulf of Maine (513, 514), 6% to Georges Bank (522, 525, 551), 4% to southern New England (537, 538, 539), 1% to the Mid-Atlantic Bight (612 off Long Island), and 1% to Browns Bank (464).

Table C4. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (October-January) in the Cape Cod area (521) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)																	
Rel.	464	513	514	515	521	526	522	525	551	561	537	538	539	612	613	616	621	?	Sum
521			3		45	1	2		1	1						1		1	55
526			1		1	1													3
Sum	0	0	4	0	46	2	2	0	1	1	0	0	0	0	0	1	0	1	58
Post-Spawning Season																			
521		9	62	1	215	6	24	8	4	2	3	2	4	1	1		1	49	392
526					4								1						5
Sum	0	9	62	1	219	6	24	8	4	2	3	2	5	1	1	0	1	49	397
Subsequent Spawning Seasons																			
521	1	2	17		39	1	2	1	1		1	1	1	1				11	79
526																			0
Sum	1	2	17	0	39	1	2	1	1	0	1	1	1	1	0	0	0	11	79

Table C4, Continued. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (October-January) in the Cape Cod area (521) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

(proportion by area)

Rel.	464	513	514	515	521	526	522	525	551	561	537	538	539	612	613	616	621
521	0	0	0.06	0	0.83	0.02	0.04	0	0.02	0.02	0	0	0	0	0	0.02	0
526	0	0	0.33	0	0.33	0.33	0	0	0	0	0	0	0	0	0	0	0

Post-Spawning Season

Rel.	464	513	514	515	521	526	522	525	551	561	537	538	539	612	613	616	621
521	0	0	0.18	0	0.63	0.02	0.07	0.02	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0	0.00
526	0	0	0	0	0.80	0	0	0	0	0	0	0	0.20	0	0	0	0

Subsequent Spawning Seasons

Rel.	464	513	514	515	521	526	522	525	551	561	537	538	539	612	613	616	621
521	0.01	0.03	0.25	0.00	0.57	0.01	0.03	0.01	0.01	0	0.01	0.01	0.01	0.01	0	0	0
526																	

Georges Bank spawners demonstrated high spawning site fidelity and dispersal in the post-spawning season (Table C5). During the release season (177 recaptures with locations), there was 98% residence on Georges Bank (522, 525, 551, 552, 561, 562), 1% movement to the western Scotian Shelf (465), 1% movement to the western Gulf of Maine (513), and 1% to the Great South Channel (521). During the post-spawning season (567 recaptures with locations), there was 71% residence on Georges Bank (522, 525, 551, 552, 561, 562), 24% movement to the Scotian Shelf/Bay of Fundy (462, 463, 464, 465, 466, 467), 3% movement to the Great South Channel (521), and 2% movement to the Gulf of Maine (511, 512, 513, 514). During subsequent spawning seasons (155 recaptures with locations), there was 87% residence on Georges Bank, 5% movement to the western Scotian Shelf and Browns Bank (463, 464), 5% movement to the Great South Channel (521), and 2% movement to the Gulf of Maine (511, 514). There was no documented movement to southern New England or the Mid-Atlantic Bight.

Table C5. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (December-May) on Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release																		
	Recapture Area (# recaptures)																	
Rel.	462	463	464	465	466	467	511	512	513	514	521	522	525	551	561	562	526	?	Sum
522											1	18	2		1			1	23
551																			0
552																			0
561				1					1			5	5		112	20		10	154
562													3			8			11
Sum	0	0	0	1	0	0	0	0	1	0	1	23	10	0	113	28	0	11	188
Post-Spawning Season																			
522	1		34	4	2	7	3		1	1	3	32		100	3	5		15	211
551				2		1					1			1					5
552				1														1	2
561	1	5	37	7	2	9		1	3		14	28	1	139	3	5		15	270
562	1		14	3	1	6						9		50	14	12		7	117
Sum	3	5	85	17	5	23	3	1	4	1	18	69	1	290	20	22	0	38	605
Subsequent Spawning Seasons																			
522			1							1	4	21	3	6	12	6	2	9	65
551																			0
552																			0
561		1	3				2				4	28	5	3	5	2		12	65
562			2									7	3	3	10	21		11	57
Sum	0	1	6	0	0	0	2	0	0	1	8	56	11	12	27	29	2	32	187

Table C5., continued. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (December-May) on Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

(proportion by area)

Rel.	462	463	464	465	466	467	511	512	513	514	521	522	525	551	561	562	526
522	0	0	0	0	0	0	0	0	0	0	0.05	0.82	0.09	0	0.05	0	0
551																	
552																	
561	0	0	0	0.01	0	0	0	0	0.01	0	0	0.03	0.03	0	0.78	0.14	0
562	0	0	0	0	0	0	0	0	0	0	0	0	0.27	0	0	0.73	0
Post-Spawning Season																	
522	0.01	0	0.17	0.02	0.01	0.04	0.02	0	0.01	0.01	0.02	0.16	0	0.51	0.02	0.03	0
551	0	0	0	0.40	0	0.20	0	0	0	0	0.20	0	0	0.20	0	0	0
552	0	0	0	1.00	0	0	0	0	0	0	0	0	0	0	0	0	0
561	0.00	0.02	0.15	0.03	0.01	0.04	0	0.00	0.01	0	0.05	0.11	0.00	0.55	0.01	0.02	0
562	0.01	0	0.13	0.03	0.01	0.05	0	0	0	0	0	0.08	0.00	0.45	0.13	0.11	0
Subsequent Spawning Seasons																	
522	0	0	0.02	0	0	0	0	0	0	0.02	0.07	0.38	0.05	0.11	0.21	0.11	0.04
551																	
552																	
561	0	0.02	0.06	0	0	0	0.04	0	0	0	0.08	0.53	0.09	0.06	0.09	0.04	0
562	0	0	0.04	0	0	0	0.00	0	0	0	0	0.15	0.07	0.07	0.22	0.46	0

Bay of Fundy spawners demonstrated high spawning site fidelity (Table C6). There was 100% residence in the spawning area (Bay of Fundy; 466, 467) during the release season (126 recaptures with locations). During the post-spawning season (503 recaptures with locations), there was 94% residence in the spawning area (466, 467), 4% movement to Georges Bank (522, 551), and 3% movement to the Gulf of Maine (511, 513). During subsequent spawning seasons 128 recaptures with locations, there was 94% residence in the spawning area, 3% movement to the Gulf of Maine (511, 513), 2% to Georges Bank (522, 551, 561), and 1% to the Mid-Atlantic Bight (621, off DE-MD).

Table C6. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (January-May) in the Bay of Fundy (466-467) and recaptured during the same spawning season, the post-spawning season (June-December), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)												
Rel.	462	463	464	465	466	467	511	513	522	551	561	621	?	Sum
466					44	16								60
467					32	34							1	67
Sum	0	0	0	0	76	50	0	0	0	0	0	0	1	127
Post-Spawning Season														
466				8	97	179	5	2	3	9			12	315
467		1	5	3	60	119	5	1	1	5			5	205
Sum	0	1	5	11	157	298	10	3	4	14	0	0	17	520
Subsequent Spawning Seasons														
466	1		9	11	31	29	1	1	1		1	1	4	90
467			6	10	14	9	1	1		1			5	47
Sum	1	0	15	21	45	38	2	2	1	1	1	1	9	137

Table C6, continued. Recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program of cod tagged during the spawning season (January-May) in the Bay of Fundy (466-467) and recaptured during the same spawning season, the post-spawning season (June-December), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

(proportion by area)

Rel.	462	463	464	465	466	467	511	513	522	551	561	621
466	0	0	0	0	0.73	0.27	0	0	0	0	0	0
467	0	0	0	0	0.48	0.52	0	0	0	0	0	0
Post-Spawning Season												
466	0	0	0	0	0	1	0.02	0.01	0.01	0.03	0	0
467	0	0.01	0.03	0.02	0.3	0.60	0.03	0.01	0.01	0.03	0	0
Subsequent Spawning Seasons												
466	0.01	0	0.10	0.13	0.36	0.34	0.01	0.01	0.01	0	0.01	0.01
467	0	0	0.14	0.24	0.33	0.21	0.02	0.02	0	0.02	0	0

Supplemental Materials D. Massachusetts Marine Fisheries Institute

There were 1,814 reported recaptures with recapture position from the Massachusetts Marine Fisheries Institute tagging in 2000-2014 and some at liberty for up to 10 years. Regional residence was generally high, but there were also some substantial movements between regions (Table D1a). Regional residence was 91% in the western Gulf of Maine, 50% in the Great South Channel, 66% on Georges Bank, 92% in southern New England, and 100% in the Mid-Atlantic Bight. Substantial regional movements were from the Great South Channel to the western Gulf of Maine (34%) and to southern New England (12%) and also from Georges Bank to the Great South Channel (16%) and to the Scotian Shelf (9%).

Table D1a. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Massachusetts Marine Fisheries Institute by statistical area of release (Rel.) and recapture. Colors indicate geographic regions (green: western Gulf of Maine; white: Great South Channel; orange: Georges Bank; red: S. New England/Mid-Atlantic Bight), and outlines indicate regional residence.

								Release Area																
Rel.	463	464	512	513	514	515	521	522	525	551	561	562	526	537	538	539	611	612	613	614	621	626	?	Sum
513				22	13		1				1				1									38
514			2	107	1104	1	74	2	6					1	32								3	1332
521				7	35		62	5					3	1	2	9		1						125
522							1	1		1	1													4
525							1																	1
561	1	2				1	3	3	1	10	3	1			2									27
526													5	1	1									7
537				1			6							67		103	1	1	2					181
539							7	1						27	1	33		1	1					71
621																					18	2		20
625																				1	2			3
626																					3	2		5
?					1																			1
Sum	1	2	2	137	1153	2	155	12	7	11	5	1	8	97	39	145	1	3	3	1	23	4	3	1815

Substantial residence (Table D1b) was in southern ME-NH (513), southwest Gulf of Maine (514), Great South Channel (521), Nantucket Shoals (526), and off Delaware Bay (621). Substantial movement (>50%) was from offshore southern New England (537) to RI Sound (539) and from off MD (525, 526) to off DE (621).

Table D1b. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Massachusetts Marine Fisheries Institute by statistical area of release (Rel.) and recapture, expressed as the proportion of known-area recaptures from each release area. Outlines indicate residence in each area.

Release Area

Rel.	463	464	512	513	514	515	521	522	525	551	561	562	526	537	538	539	611	612	613	614	621	626
513	0	0	0	0.58	0.34	0	0.03	0	0	0	0.03	0	0	0	0.03	0	0	0	0	0	0	0
514	0	0	0.00	0.08	0.83	0.00	0.06	0.00	0.00	0	0	0	0	0.00	0.02	0	0	0	0	0	0	0
521	0	0	0	0.06	0.28	0	0.50	0.04	0	0	0	0	0.02	0.01	0.02	0.07	0	0.01	0	0	0	0
522	0	0	0	0	0	0	0.25	0.25	0	0.25	0.25	0	0	0	0	0	0	0	0	0	0	0
525	0	0	0	0	0	0	1.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
561	0.04	0.07	0	0	0	0.04	0.11	0.11	0.04	0.37	0.11	0	0	0	0.07	0	0	0	0	0	0	0
526	0	0	0	0	0	0	0	0	0	0	0	0	0.71	0.14	0.14	0	0	0	0	0	0	0
537	0	0	0	0.01	0	0	0.03	0	0	0	0	0	0	0.37	0	0.57	0.01	0.01	0.01	0	0	0
539	0	0	0	0	0	0	0.10	0.01	0	0	0	0	0	0.38	0.01	0.46	0	0.01	0.01	0	0	0
621	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.90	0.10
625	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0.67	0
626	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.60	0.40

Western Gulf of Maine winter spawners demonstrated strong spawning site fidelity (Table D2). Of the 54 recaptures during the same release season, 98% were recaptured in the spawning area (514, western Gulf of Maine), with some movement (2%) to the central Gulf of Maine (515). Of the 132 recaptures in the post-spawning period, 92% were in western Gulf of Maine (513-514), 2% moved to the Great South Channel (521), and 4% moved to southern New England. In subsequent spawning seasons, there was 89% residence in the spawning area, 5% movement to the Great South Channel (521), and 5% movement to southern New England (538).

Table D2. Recaptures of Atlantic cod (*Gadus morhua*) from the Massachusetts Marine Fisheries Institute of cod tagged during the winter-spawning season (October-January) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

	Recapture Area (# recaptures)									(proportion by area)						
Rel.	513	514	515	521	522	537	538	?	Sum	513	514	515	521	522	537	538
Season of Release																
514		53	1						54	0	0.98	0.02	0	0	0	0
Post-Spawning Season																
514	7	114		3	1	1	5	1	132	0.05	0.87	0	0.02	0.01	0.01	0.04
Subsequent Spawning Seasons																
514	2	30		2			2		36	0.06	0.83	0	0.06	0	0	0.06

Western Gulf of Maine spring spawners also demonstrated high spawning site fidelity (Table D3). Of the 389 recaptures during the same release season, 96% were recaptured in the spawning area (513-514, western Gulf of Maine), with some movement (8%) to the Great South Channel (521). Of the 411 recaptures in the post-spawning period, 88% were in the spawning area, 8% moved to the Great South Channel (521), and 4% moved to southern New England. In subsequent spawning seasons, there was 92% residence in the spawning area and 5% movement to the Great South Channel (521).

Table D3. Recaptures of Atlantic cod (*Gadus morhua*) from the Massachusetts Marine Fisheries Institute of cod tagged during the spring spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

	Recapture Area (# recaptures)									(proportion by area)						
Season of Release																
Rel.	512	513	514	521	525	538	561	?	Sum	512	513	514	521	525	538	561
513		9	3						12	0	0.75	0.25	0	0	0	0
514	1	19	342	10		5			377	0.00	0.05	0.91	0.03	0	0.01	0
Sum	1	28	345	10		5			389							
Post-Spawning Seasons																
513		8	9	1		1			19	0	0.42	0.47	0.05	0	0.05	0
514		53	290	31	2	16		1	393	0	0.14	0.74	0.08	0.01	0.04	0
Sum		61	299	32	2	17		1	412							
Subsequent Spawning Seasons																
513		5	1				1		7	0	0.71	0.14	0	0	0	0.14
514		14	124	8	1	2		1	150	0	0.09	0.83	0.05	0.01	0.01	0
Sum		19	125	8	1	2	1	1	157							

Southern New England spawners demonstrated high spawning site fidelity (Table D4). During the release season (139 recaptures), there was 99% residence in the spawning area (537, 538, 539), with some movement to the Mid-Atlantic Bight (611, 613). During the post-spawning season (42 recaptures), there was 74% residence in southern New England, 19% movement to the Great South Channel (521), and 5% movement to the Mid-Atlantic Bight (612, 613). During subsequent spawning seasons (19 recaptures), there was 95% residence in southern New England and 5% movement to the Great South Channel (521).

Table D4. Recaptures of Atlantic cod (*Gadus morhua*) from the Massachusetts Marine Fisheries Institute of cod tagged during the spawning season (December-May) off southern New England (537, 539) and recaptured during the same spawning season, the post-spawning season (November-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)									(proportion by area)							
Rel.	513	521	537	538	539	611	612	613	Sum	513	521	537	538	539	611	612	613
537			52		82	1		1	136	0	0	0.39	0	0.61	0.01	0	0.01
539					3				3	0	0	0	0	1.00	0	0	0
Sum			52		85	1		1	139								

Post-Spawning Season

Rel.	513	521	537	538	539	611	612	613	Sum	513	521	537	538	539	611	612	613
537	1	6	8		14		1	1	31	0.03	0.20	0.27	0	0.47	0	0.03	0.03
539		2	3	1	6				12	0	0.17	0.25	0.08	0.50	0	0	0
Sum	1	8	11	1	20		1	1	43								

Subsequent Spawning Seasons

Rel.	513	521	537	538	539	611	612	613	Sum	513	521	537	538	539	611	612	613
537			7		7				14	0	0	0.50	0	0.50	0	0	0
539		1			4				5	0	0.20	0	0	0.80	0	0	0
Sum		1	7		11				19								

From the Massachusetts Marine Fisheries Institute cod tagging, only 43 Cape Cod spawners tagged during the spawning season were recaptured, and 49% were recaptured in the spawning area (521). Only one cod tagged on Georges Bank during the spawning season was recaptured.

Supplemental Materials E. Fisheries and Oceans Canada (DFO) 2001-2004 Tagging Data

Canada DFO tagged approximately 10,000 cod on the Scotian Shelf in 2001-2004 that are not included in the Northeast Regional Cod Tagging Program database. There were 472 recaptures reported, and 445 were reported with recapture position, some at liberty for up to 5 years. Residence was 95% on the Scotian Shelf and Bay of Fundy (Table E1a-b). Within the region, there was 84% residence on the western Scotian Shelf (462, 463), with 7% movement to Browns Bank (464), 4% to the Bay of Fundy (465, 466, 467), 3% to Georges Bank (525, 551, 561, 562), and 2% movement to the east (461). There was 68% residence on Browns Bank with some movement to the Scotian Shelf, Bay of Fundy, and Georges Bank. There was low residence in the Bay of Fundy (41% in 465 and 466), with 47% movement to Browns Bank and the Scotian Shelf and 12% movement to Georges Bank.

Table E1a. All tag recaptures of Atlantic cod (*Gadus morhua*) from Canada DFO 2001-2004 by statistical area of release (Rel.) and recapture.

	Recapture Area												
Rel.	461	462	463	464	465	466	467	511	525	551	561	562	?	Sum
462		91	11	2	2					1		1	9	117
463	6	35	144	22	8	2	1	1	1	5	1	2	12	240
464	1	3	2	28	3	2				2			3	44
465		2	18	12	24	4				4	3	1	3	71
Sum	7	131	175	64	37	8	1	1	1	12	4	4	27	472

Table E1b. All tag recaptures of Atlantic cod (*Gadus morhua*) from Canada DFO 2001-2004 by statistical area of release (Rel.) and recapture, expressed as the proportion of recaptures from each release area. Outlines indicate residence in each area.

	Recapture Area											
Rel.	461	462	463	464	465	466	467	511	525	551	561	562
462	0	0.84	0.10	0.02	0.02	0	0	0	0	0.01	0	0.01
463	0.03	0.15	0.63	0.10	0.04	0.01	0.00	0.00	0.00	0.02	0.00	0.01
464	0.02	0.07	0.05	0.68	0.07	0.05	0	0	0	0.05	0	0
465	0	0.03	0.26	0.18	0.35	0.06	0	0	0	0.06	0.04	0.01

Cod tagged during the spawning season (January-May) had 84% fidelity to the Scotian Shelf/Bay of Fundy region in subsequent spawning seasons, with 16% movement to Georges Bank during subsequent spawning seasons and 4% movement to the east (461; Table E2).

Table E2. Recaptures of Atlantic cod (*Gadus morhua*) from Fisheries and Oceans Canada (DFO) 2001-2004 cod tagged during the spawning season (January-May) on the western Scotian Shelf (463, 465) and recaptured during the same spawning season, the post-spawning season (April-December), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release																				
	Recapture Area (# recaptures)																			
Rel.	461	462	463	464	465	466	551	561	562	?	Sum	461	462	463	464	465	466	551	561	562
463			8		1					0	9	0	0	0.9	0	0.1	0	0	0	0
465			3		6	1				0	10	0	0	0.3	0	0.6	0.1	0	0	0
Sum			11		7	1				0	19									
Post-Spawning Season																				
463	3	1	41	5	3	1	1			3	58	0.05	0.02	0.75	0.09	0.05	0.02	0.02	0	0
464	1			4	1					2	8	0.17	0	0	0.67	0.17	0	0	0	0
465		1	14	5	10	2	3		1	3	39	0	0	0.39	0.14	0.28	0.06	0.08	0	0
Sum	4	2	55	14	14	3	4		1	8	105									
Subsequent Spawning Seasons																				
463		1	3	5				1		0	10	0	0.1	0.3	0.5	0	0	0	0.1	0
464		1		1						0	2	0	0.5	0	0.5	0	0	0	0	0
465		1	1	6	6	1	1	3		0	19	0	0.05	0.05	0.32	0.32	0.05	0.05	0.16	0
Sum		3	4	12	6	1	1	4		0	31									

Supplemental Materials F. Massachusetts Bay Spring Cod Conservation Zone

There were 155 reported recaptures from the Massachusetts Spring Cod Conservation Zone (514) tagging during 2010-2013, with some at liberty for up to 2 years. Residence in the western Gulf of Maine (513, 514) was high (92%), with 7% movement to the Great South Channel (521; Table F1). Western Gulf of Maine spring spawners also demonstrated high spawning site fidelity. Of the 48 recaptures during the same release season, 94% were recaptured in the spawning area, with 4% movement to the Great South Channel. Of the 76 recaptures in the post-spawning period, 89% were in the spawning area, and 11% moved to the Great South Channel. In subsequent spawning seasons, there was 96% residence in the spawning area, and 4% movement to the Great South Channel.

Table F1. Recaptures of Atlantic cod (*Gadus morhua*) tagged in the Massachusetts Spring Cod Conservation Zone during the spring spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

	Recapture Area (# recaps)					(proportion by area)			
All Recaptures									
Rel.	512	513	514	521	Sum	512	513	514	521
513			1		1	0	0	1.00	0
514	1	32	111	11	155	0.01	0.21	0.72	0.07
Sum	1	32	112	11	156				
Season of Release									
514	1	8	37	2	48	0.02	0.17	0.77	0.04
Post-Spawnign Season									
513			1		1	0	0	1.00	0
514		19	48	8	75	0	0.25	0.64	0.11
Sum		19	49	8	76				
Subsequent Spawning Seasons									
514		4	22	1	27	0	0.15	0.81	0.04

Supplemental Materials G. Combined Tagging Data

Tagging data from Fisheries and Oceans Canada (DFO) 1994 tagging, Northeast Regional Cod Tagging Program, the Massachusetts Marine Fisheries Institute, and the Massachusetts Spring Cod Conservation Zone were combined for aggregate and seasonal analyses. There were 8,351 reported recaptures with recapture position. Regional residence was generally high, but there were also some substantial regional movements (Table G1a). Regional residence was 88% in the Bay of Fundy, 92% in the Gulf of Maine, 69% in the Great South Channel, 76% on Georges Bank, 88% in southern New England, and 100% in the Mid-Atlantic Bight. Substantial regional movements (>10%) were from the Great South Channel to the Gulf of Maine (17%), and from Georges Bank to the Scotian Shelf and the Bay of Fundy (22%).

Table G1a. All tag recaptures of Atlantic cod (*Gadus morhua*) from Fisheries and Oceans Canada (DFO) 1994 tagging, the Northeast Regional Cod Tagging Program, the Massachusetts Marine Fisheries Institute, and the Massachusetts Spring Cod Conservation Zone by statistical area of release (Rel.) and recapture. Colors indicate geographic regions (dark blue: Scotian Shelf; light blue: Bay of Fundy; green: Gulf of Maine; dark green: western Gulf of Maine; white: Cape Cod; orange: Georges Bank; red: southern New England/Mid-Atlantic Bight), and outlines indicate regional residence.

Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526	537	538	539	611	612	613	614	615	616	621	626	Sum
462	0	91	11	2	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	108
463	6	35	148	22	9	2	1	1	0	0	0	0	0	0	1	5	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	233
464	1	3	2	28	3	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
465	0	2	19	14	28	4	0	0	0	0	0	0	0	0	0	4	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	75
466	0	1	0	9	19	172	224	6	0	3	0	0	0	4	0	9	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	449
467	0	0	1	22	28	135	203	16	3	8	3	0	1	4	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	436
511	0	0	0	17	30	10	7	40	0	2	2	0	0	1	0	8	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	121
512	0	0	0	0	1	0	0	0	1	10	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
513	0	0	0	3	1	2	1	0	0	1313	301	19	32	14	0	3	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1693
514	0	0	0	0	0	0	0	0	3	161	1285	13	78	2	6	0	0	0	0	0	1	32	0	0	0	0	0	0	0	0	0	1581
515	0	0	0	5	1	0	1	0	1	16	11	76	6	14	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	134
521	0	0	0	3	1	2	1	0	0	40	349	3	1588	100	39	20	0	12	6	42	21	5	33	2	6	7	0	2	1	2	0	2285
522	0	1	0	35	4	2	7	3	0	1	2	0	11	72	5	107	0	17	11	2	0	0	0	0	0	0	0	0	0	0	0	280
525	0	0	0	2	0	0	0	0	0	1	0	0	3	2	3	17	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	31
551	0	0	0	0	4	0	1	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
552	3	8	20	14	19	4	0	2	0	0	1	1	1	2	0	77	23	3	0	0	0	0	0	0	0	0	0	0	0	0	0	178
561	0	1	9	54	9	4	10	2	1	5	0	1	25	77	14	177	0	157	32	0	0	2	0	0	0	0	0	0	0	0	0	580
562	0	1	0	19	3	1	6	0	0	0	0	0	2	16	6	61	5	24	43	0	0	0	0	0	0	0	0	0	0	0	0	187
526	0	0	0	0	0	0	0	0	0	1	1	0	9	0	1	0	0	0	0	7	1	1	1	0	0	0	0	0	0	0	0	22
537	0	0	0	0	0	0	0	0	0	1	0	0	8	0	0	1	0	0	0	0	76	0	110	1	1	2	0	0	0	0	0	200
539	0	0	0	0	0	0	0	0	0	0	0	0	7	1	0	0	0	0	0	0	35	1	47	1	1	1	0	0	0	0	0	94
621	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	2	20
625	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	3
626	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	5
Sum	3	12	35	185	125	334	469	69	9	1563	1960	114	1772	310	76	496	28	222	94	52	134	42	191	4	8	10	1	2	1	26	4	8351

Residence and movement from statistical areas (Table G1b) indicate >50% residence on the western Scotian Shelf (463), the southern Bay of Fundy (465), southern ME-NH (513), southwest Gulf of Maine (514), central Gulf of Maine (515), Great South Channel (521), RI Sound (539), and off DE (621). Substantial movement (>50%) was from the northeast Bay of Fundy (466) to the northwest Bay of Fundy (467), from midcoast ME (512) to southern ME-NH (513), from southwest Georges Bank (525) to northeast Georges Bank (551), from offshore southern New England (537) to RI Sound (539), and from off MD (625, 626) to off DE (621).

Table G1b. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program, Fisheries and Oceans Canada, Massachusetts Marine Fisheries Institute, and MA Spring Cod Conservation Zone by statistical area of release (Rel.) and recapture, expressed as the proportion of known-area recaptures from each release area. Outlines indicate residence in each area.

	Recapture Area																													
Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526	537	538	539	611	612	613	614	615	616	621	626
462	0	0.84	0.1	0.02	0.02	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
463	0.03	0.15	0.64	0.09	0.04	0.01	0	0	0	0	0	0	0	0	0	0.02	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0
464	0.02	0.07	0.05	0.68	0.07	0.05	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
465	0	0.03	0.25	0.19	0.37	0.05	0	0	0	0	0	0	0	0	0	0.05	0	0.04	0.01	0	0	0	0	0	0	0	0	0	0	0	0
466	0	0.00	0	0.02	0.04	0.38	0.50	0.01	0	0.01	0	0	0	0.01	0	0.02	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0.00	0
467	0	0	0.00	0.05	0.06	0.31	0.47	0.04	0.01	0.02	0.01	0	0.00	0.01	0.00	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
511	0	0	0	0.14	0.25	0.08	0.06	0.33	0.00	0.02	0.02	0	0	0.0	0	0.07	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
512	0	0	0	0	0.06	0	0	0	0.06	0.56	0.22	0.06	0	0.06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
513	0	0	0	0.00	0.00	0.00	0.00	0	0	0.78	0.18	0.01	0.02	0.01	0	0.00	0	0.00	0.00	0.00	0	0.00	0	0	0	0	0	0	0	0	0
514	0	0	0	0	0	0	0	0	0.00	0.10	0.81	0.01	0.05	0.00	0.00	0	0	0	0	0	0.00	0.02	0	0	0	0	0	0	0	0	0
515	0	0	0	0.04	0.01	0	0.01	0	0.01	0.12	0.08	0.57	0.04	0.10	0.01	0.01	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0
521	0	0	0	0.00	0.00	0.00	0.00	0	0	0.02	0.15	0.00	0.69	0.04	0.02	0.01	0.00	0.01	0.00	0.02	0.01	0.00	0.01	0.00	0.00	0.00	0	0.00	0.00	0.00	0
522	0	0.00	0	0.13	0.01	0.01	0.03	0.01	0	0.00	0.01	0	0.04	0.26	0.02	0.38	0.00	0.06	0.04	0.01	0	0	0	0	0	0	0	0	0	0	0
525	0	0	0	0.06	0	0	0	0	0	0.03	0	0	0.10	0.06	0.10	0.55	0.00	0.06	0.03	0	0	0	0	0	0	0	0	0	0	0	0
551	0	0	0	0	0.40	0	0.10	0	0	0	0	0	0.10	0	0	0.40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
552	0.02	0.04	0.11	0.08	0.11	0.02	0	0.01	0	0	0.01	0.01	0.01	0.01	0.00	0.43	0.13	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
561	0	0.00	0.02	0.09	0.02	0.01	0.02	0.00	0.00	0.01	0	0.00	0.04	0.13	0.02	0.31	0.00	0.27	0.06	0	0	0.00	0	0	0	0	0	0	0	0	0
562	0	0.01	0	0.10	0.02	0.01	0.03	0	0	0	0	0	0.01	0.09	0.03	0.33	0.03	0.13	0.23	0	0	0	0	0	0	0	0	0	0	0	0
526	0	0	0	0	0	0	0	0	0	0.05	0.05	0	0.41	0	0.05	0	0	0	0	0.32	0.05	0.05	0.05	0	0	0	0	0	0	0	0
537	0	0	0	0	0	0	0	0	0	0.01	0	0	0.04	0	0	0.01	0	0	0	0	0.38	0	0.55	0.01	0.01	0.01	0	0	0	0	0
539	0	0	0	0	0	0	0	0	0	0	0	0	0.07	0.01	0	0	0	0	0	0	0.37	0.01	0.50	0.01	0.01	0.01	0	0	0	0	0
621	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	0.1
625	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0.67	0
626	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.4

Major patterns of residence and movement (Figure G1) show high residence in most areas, with greatest residence on the Scotian Shelf and in the western Gulf of Maine, substantial movement (from the Bay of Fundy to eastern Gulf of Maine, from the Scotian Shelf to Georges Bank, and from southern New England to the Great South Channel), and mixing within Georges Bank (recaptures on the northeast peak of Georges Bank, 551, from all Georges Bank release areas) and within the Mid-Atlantic Bight.

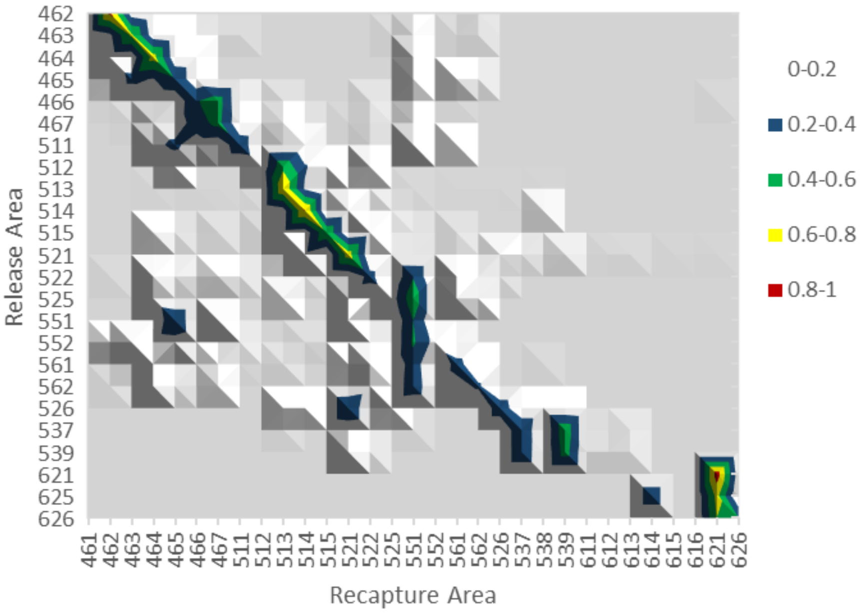

Figure G1. All tag recaptures of Atlantic cod (*Gadus morhua*) from the Northeast Regional Cod Tagging Program, Fisheries and Oceans Canada, Massachusetts Marine Fisheries Institute, and MA Spring Cod Conservation Zone by statistical area of release and recapture, expressed as the proportion of known-area recaptures from each release area.

Western Gulf of Maine winter spawners (NERCTP + MFI) demonstrated strong spawning site fidelity (Table G2). Nearly all (99%) of recaptures during the same release season (95 with reported recapture location) were recaptured in the spawning area (513-514, western Gulf of Maine). Of the 290 recaptures with known recapture position in the post-spawning period, 93% were in the spawning area, and 6% moved to the Great South Channel (521), Georges Bank (522, 562), and southern New England (537, 538). In subsequent spawning seasons, there was 93% residence in the Gulf of Maine, 92% residence in spawning area, 2% movement to central Gulf of Maine (515), and 6% movement to the Great South Channel and Georges Bank.

Table G2. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Tallack 2011; Loehrke 2014) of cod tagged during the winter spawning season (October-January) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (February-September), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release	Recapture Area (# recaptures)											(proportion by area)								
Rel.	464	513	514	515	521	522	562	537	538	?	Sum	464	513	514	515	521	522	537	538	562
513	0	28	11	0	0	0	0	0	0	2	41	0	0.72	0.28	0	0	0	0	0	0
514	0	0	55	1	0	0	0	0	0	2	58	0	0	0.98	0.02	0	0	0	0	0
Sum	0	28	66	1	0	0	0	0	0	4	99									
Post-Spawning Season																				
513	1	114	27	2	4	3	1	0	0	10	162	0.01	0.75	0.18	0.01	0.03	0.02	0.01	0	0
514	0	7	121	0	3	1	0	1	5	3	141	0	0.05	0.88	0	0.02	0.01	0	0.01	0.04
Sum	1	121	148	2	7	4	1	1	5	13	303									
Subsequent Spawning Seasons																				
513	0	14	5	1	0	0	0	0	0	2	22	0	0.70	0.25	0.05	0	0	0	0	0
514	0	2	35	0	2	0	0	0	2	0	41	0	0.05	0.85	0	0.05	0	0	0	0.05
Sum	0	16	40	1	2	0	0	0	2	2	63									

Western Gulf of Maine spring spawners (NERCTP + MFI + MSCCZ) also demonstrated high spawning site fidelity (Table G3). Of the 1,036 recaptures during the same release season with known recapture location, there was 97% residence in spawning area (513-514, western Gulf of Maine), and 2% movement to Great South Channel (521). There were 1,138 recaptures with reported recapture location during the post-spawning season, with 91% residence in spawning area, 5% movement to the Great South Channel (521), 1% to central Gulf of Maine (515), 1% to Georges Bank (522, 525, 551, 561), and 2% to southern New England (526, 538). Similar to the results reported by Loehrke (2014) and Zemeckis et al. (2017), the 501 recaptured in subsequent spawning seasons with location information had 95% residence in spawning the area, 1% movement central Gulf of Maine (515; 96% residence in the Gulf of Maine), 2% to the Great South Channel (521), and 2% to Georges Bank (522, 525, 551, 561).

Table G3. Recaptures of Atlantic cod (*Gadus morhua*) from combined studies (Tallack 2011; Loehrke 2014; Zemeckis et al. 2017) of cod tagged during the spring spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

Recapture Area (# recaptures)

Rel.	464	465	466	467	512	513	514	515	521	522	525	551	561	526	538	?	Sum
513	0	0	0	0	0	462	22	0	2	1	0	1	0	0	0	18	506
514	0	0	0	0	2	60	458	0	23	0	0	0	0	0	5	0	548
Sum	0	0	0	0	2	522	480	0	25	1	0	1	0	0	5	18	1054
Post-Spawning Season																	
513	2	1	1	1	0	405	205	10	20	5	0	1	0	1	1	85	738
514	0	0	0	0	1	71	360	0	35	0	2	0	0	0	16	8	493
Sum	2	1	1	1	1	476	565	10	55	5	2	1	0	1	17	93	1231
Subsequent Spawning Seasons																	
513	0	0	0	0	0	265	28	3	2	5	0	1	1	0	0	25	330
514	0	0	0	0	0	21	162	1	9	0	1	0	0	0	2	2	198
Sum	0	0	0	0	0	286	190	4	11	5	1	1	1	0	2	27	528

Table G3, continued. Recaptures of Atlantic cod (*Gadus morhua*) from combined studies (Tallack 2011; Loehrke 2014; Zemeckis et al. 2017) of cod tagged during the spring spawning season (April-July) in the western Gulf of Maine (513-514) and recaptured during the same spawning season, the post-spawning season (August-March), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

Recapture Area (proportion by area)

Rel.	464	465	466	467	512	513	514	515	521	522	525	551	561	526	538
513	0	0	0	0	0	0.95	0.05	0	0	0	0	0	0	0	0
514	0	0	0	0	0	0.11	0.84	0	0.04	0	0	0	0	0	0.01
Post-Spawning Season															
513	0	0	0	0	0	0.62	0.31	0.02	0.03	0.01	0	0	0	0	0
514	0	0	0	0	0	0.15	0.74	0	0.07	0	0	0	0	0	0.03
Subsequent Spawning Seasons															
513	0	0	0	0	0	0.87	0.09	0.01	0.01	0.02	0	0	0	0	0
514	0	0	0	0	0	0.11	0.83	0.01	0.05	0	0.01	0	0	0	0.01

Georges Bank spawners (NERCTP + DFO 1994) demonstrated high spawning site fidelity and dispersal in the post-spawning season (Table G4). During the release season (183 recaptures with locations), there was 96% residence on Georges Bank (522, 525, 551, 552, 561, 562), 2% movement to the western Scotian Shelf and Browns Bank (464, 465), 1% movement to the western Gulf of Maine (513, 514), and 1% to the Great South Channel (521). During the post-spawning season (746 recaptures with locations), there was 70% residence on Georges Bank (522, 525, 551, 552, 561, 562), 26% movement to the Scotian Shelf/Bay of Fundy (461, 462, 463, 464, 465, 466, 467), 3% movement to the Great South Channel (521), and 2% movement to the Gulf of Maine (511, 512, 513, 514, 515). During subsequent spawning seasons (274 recaptures with locations), there was 72% residence on Georges Bank, 5% movement to the Scotian Shelf/Bay of Fundy (461, 462, 463, 464, 465, 466), 3% movement to the Great South Channel (521), 2% movement to the Gulf of Maine (511, 514), and 2% movement to Nantucket Shoals (526).

Table G4. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Hunt et al. 1999; Tallack 2011) of cod tagged during the spawning season (December-May) on Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

Recapture Area (# recaptures)

Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526	?	Sum
522	0	0	0	0	0	0	0	0	0	0	0	0	1	18	2	0	0	1	0	0	1	23
552	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	4	10
561	0	0	0	0	1	0	0	0	0	1	0	0	0	5	5	0	0	112	20	0	10	154
562	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	8	0	0	11
Sum	0	0	0	2	1	0	0	0	0	1	1	0	2	23	10	1	0	114	28	0	15	198
Post-Spawning Season																						
522	0	1	0	34	4	2	7	3	0	1	1	0	3	32	0	100	0	3	5	0	15	211
551	0	0	0	0	3	0	1	0	0	0	0	0	1	0	0	4	0	0	0	0	1	10
552	3	8	19	8	14	4	0	2	0	0	0	1	0	2	0	74	23	1	0	0	32	191
561	0	1	5	37	7	2	9	0	1	3	0	0	14	28	1	139	0	3	5	0	15	270
562	0	1	0	15	3	1	6	0	0	0	0	0	1	9	0	58	5	14	14	0	11	138
Sum	3	11	24	94	31	9	23	5	1	4	1	1	19	71	1	375	28	21	24	0	74	820
Subsequent Spawning Seasons																						
522	0	0	0	1	0	0	0	0	0	0	1	0	4	21	3	6	0	12	6	2	9	65
551	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	4
552	3	8	17	7	12	4	0	2	0	0	0	0	0	0	0	42	8	1	0	0	25	129
561	0	0	1	3	0	0	0	2	0	0	0	0	4	28	5	3	0	5	2	0	12	65
562	0	0	0	3	0	0	0	0	0	0	0	0	1	7	3	10	1	10	23	0	15	73
Sum	3	8	18	14	13	4	0	4	0	0	1	0	9	56	11	63	9	28	31	2	62	336

Table G4, continued. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Hunt et al. 1999; Tallack 2011) of cod tagged during the spawning season (December-May) on Georges Bank (522, 551, 552, 561, 562) and recaptured during the same spawning season, the post-spawning season (June-November), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

Recapture Area (proportion by area)

Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526
522	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.82	0.09	0	0	0.05	0	0
552	0	0	0	0.33	0	0	0	0	0	0	0.17	0	0.17	0	0	0.17	0	0.17	0	0
561	0	0	0	0	0.01	0	0	0	0	0.01	0	0	0	0.03	0.03	0	0	0.78	0.14	0
562	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.27	0	0	0	0.73	0

Post-Spawning Season

Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526
522	0	0.01	0	0.17	0.02	0.01	0.04	0.02	0	0.01	0.01	0	0.02	0.16	0	0.51	0	0.02	0.03	0
551	0	0	0	0	0.33	0	0.11	0	0	0	0	0	0.11	0	0	0.44	0	0	0	0
552	0.02	0.05	0.12	0.05	0.09	0.03	0	0.01	0	0	0	0.01	0	0.01	0	0.47	0.14	0.01	0	0
561	0	0.00	0.02	0.15	0.03	0.01	0.04	0	0.00	0.01	0	0	0.05	0.11	0.00	0.55	0	0.01	0.02	0
562	0	0.01	0	0.12	0.02	0.01	0.05	0	0	0	0	0	0.01	0.07	0	0.46	0.04	0.11	0.11	0

Subsequent Spawning Seasons

Rel.	461	462	463	464	465	466	467	511	512	513	514	515	521	522	525	551	552	561	562	526
522	0	0	0	0.02	0	0	0	0	0	0	0.02	0	0.07	0.38	0.05	0.11	0	0.21	0.11	0.04
551	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0.67	0	0	0	0
552	0.03	0.08	0.16	0.07	0.12	0.04	0.00	0.02	0	0	0	0	0	0	0	0.40	0.08	0.01	0	0
561	0	0	0.02	0.06	0	0	0	0.04	0	0	0	0	0.08	0.53	0.09	0.06	0	0.09	0.04	0
562	0	0	0	0.05	0	0	0	0	0	0	0	0	0.02	0.12	0.05	0.17	0.02	0.17	0.40	0

Western Scotian Shelf-Bay of Fundy spawners (NERCTP + Canada DFO 2001-2004) demonstrated high spawning site fidelity (Table G5). There was 100% residence in the spawning area (463, 464, 465, 466, 467) during the release season (146 recaptures with locations), as well as 100% residence in the Bay of Fundy (466, 467). During the post-spawning season (503 recaptures with locations), there was 94% residence in the spawning area, 4% movement to Georges Bank (522, 551), and 2% movement to the Gulf of Maine (511, 513). During subsequent spawning seasons (168 recaptures with locations), there was 92% residence in the spawning area, 5% movement to Georges Bank (522, 551, 561), 3% movement to the Gulf of Maine (511, 513), and 1% to the Mid-Atlantic Bight (621, off DE-MD).

Table G5. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Clark and Emberley 2010; Tallack 2011) of cod tagged during the spawning season (January-May) in the Bay of Fundy (466-467) and recaptured during the same spawning season, the post-spawning season (June-December), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release																
	Recapture Area (# recaptures)															
Rel.	461	462	463	464	465	466	467	511	513	522	551	561	562	621	?	Sum
463			8		1										0	9
465			3		6	1									0	10
466						44	16									60
467						32	34								1	67
Sum	0	0	11	0	7	77	50	0	0	0	0	0	0	0	1	146
Post-Spawning Season																
463	3	1	41	5	3	1					1				3	58
464	1			4	1										2	8
465		1	14	5	10	2					3		1		3	39
466					8	97	179	5	2	3	9				12	315
467			1	5	3	60	119	5	1	1	5				5	205
Sum	4	2	56	19	25	160	298	10	3	4	18	0	1	0	25	625
Subsequent Spawning Seasons																
463		1	3	5								1			0	10
464		1		1											0	2
465		1	1	6	6	1					1	3			0	19
466		1		9	11	31	29	1	1	1		1		1	4	90
467				6	10	14	9	1	1		1				5	47
Sum	0	4	4	27	27	46	38	2	2	1	2	5	0	1	9	168

Table G5, continued. Recaptures of Atlantic cod (*Gadus morhua*) from combined tagging studies (Clark and Emberley 2010; Tallack 2011) of cod tagged during the spawning season (January-May) in the Bay of Fundy (466-467) and recaptured during the same spawning season, the post-spawning season (June-December), and subsequent spawning seasons. Colors indicate relative proportions, and outlines indicate residence in the area of release.

Season of Release

	Recapture Area (# recaptures)													
Rel.	461	462	463	464	465	466	467	511	513	522	551	561	562	621
463	0	0	0.89	0	0.11	0	0	0	0	0	0	0	0	0
465	0	0	0.3	0	0.6	0.1	0	0	0	0	0	0	0	0
466	0	0	0	0	0	0.73	0.27	0	0	0	0	0	0	0
467	0	0	0	0	0	0.48	0.52	0	0	0	0	0	0	0

Post-Spawning Season

Rel.	461	462	463	464	465	466	467	511	513	522	551	561	562	621
463	0.05	0.02	0.75	0.09	0.05	0.02	0	0	0	0	0.02	0	0	0
464	0.17	0	0	0.67	0.17	0	0	0	0	0	0	0	0	0
465	0	0.03	0.39	0.14	0.28	0.06	0	0	0	0	0.08	0	0.03	0
466	0	0	0	0	0.03	0.32	0.59	0.02	0.01	0.01	0.03	0	0	0
467	0	0	0.01	0.03	0.02	0.3	0.6	0.03	0.01	0.01	0.03	0	0	0

Subsequent Spawning Seasons

Rel.	461	462	463	464	465	466	467	511	513	522	551	561	562	621
463	0	0.1	0.3	0.5	0	0	0	0	0	0	0	0.1	0	0
464	0	0.5	0	0.5	0	0	0	0	0	0	0	0	0	0
465	0	0.05	0.05	0.32	0.32	0.05	0	0	0	0	0.05	0.16	0	0
466	0	0.01	0	0.1	0.13	0.36	0.34	0.01	0.01	0.01	0	0.01	0	0.01
467	0	0	0	0.14	0.24	0.33	0.21	0.02	0.02	0	0.02	0	0	0

8. FISHERMEN'S ECOLOGICAL KNOWLEDGE

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Abstract

Fishermen's Ecological Knowledge (FEK) related to the spawning behavior and population structure of Atlantic cod (Gadus morhua) in US waters was collected and synthesized through semistructured interviews. Fifty fishermen, with homeports ranging from New York to Nova Scotia were interviewed as part of this project. Collectively, these fishermen had 2,000 years of experience targeting groundfish, including 1,700 years of directed fishing experience for cod in the Gulf of Maine and on Georges Bank. The fishermen had a detailed understanding of cod movement patterns, which spanned a range of spatial and temporal scales. The fishermen also had fine-scale knowledge of the spatial and temporal distribution of spawning activity, and their knowledge was used to produce a detailed map of cod spawning grounds on Georges Bank, Nantucket Shoals, the Great South Channel, and the western Gulf of Maine. The fishermen observed that spawning on western Georges Bank (Nantucket Shoals and Great South Channel) peaks in November and December, while spawning activity across eastern Georges Bank primarily occurs from January through April. In the western Gulf of Maine, fishermen identified 2 peaks in spawning activity, corresponding to the winter and spring spawning events, and identified 22 spawning grounds, many of which have been previously documented in the scientific literature. Many of the fishermen perceived that cod on eastern Georges Bank are likely distinct from cod in the Great South Channel and Nantucket Shoals, as noted through differences in fish size, diet, fillet quality, geographic distribution, and seasonal movements. Fishermen also remarked that cod on Nantucket Shoals and the Great South Channel are connected to groups in the western Gulf of Maine. The information collected through this study reaffirms that FEK is a valuable supplement to traditional scientific information, and that FEK can help inform multidisciplinary stock identification studies.

Introduction

Fishermen's Ecological Knowledge (FEK) can be defined as the experiential knowledge that fishermen accumulate as they interact with the marine environment over an extended period of time (Hind 2015). Fishermen share information in real time while at sea and also acquire knowledge from their predecessors, and these sources allow them to accumulate a knowledge base that spans a range of temporal and spatial scales (Johannes et al. 2000; Bergmann et al. 2004). For example, fishermen often understand how fish move seasonally across large geographic areas for feeding or spawning. At the same time, fishermen also recognize that abundance and distribution of fish can vary at fine spatial scales, and they are aware of fine-scale habitat features (e.g., habitat edges, boulder piles) that influence fish distribution. Following years of observation, fishermen are cognizant of long-term trends in fish abundance and changes in size structure (Pederson and Hall-Arber 1999; Macdonald et al. 2014). In addition, fishermen also understand how the distribution and abundance of target species can change across tidal, diel, lunar, and seasonal scales (Berkes et al. 2000; Johannes et al. 2000).

There is increasing recognition that FEK can serve as a valuable supplement to information collected with traditional scientific approaches (Murray et al. 2008a; Hind 2015), and that FEK should routinely be considered as part of the best available information (Stephenson et al. 2016). Combining FEK with scientific data allows for a deeper understanding of biological and ecological issues that are important for sustainable management (Hedeholm et al. 2016). Further, the solicitation of FEK provides an avenue for fishermen to actively contribute to the scientific information that informs resource management (Macdonald et al. 2014; Yates 2014), which can lead to increased credibility and trust in subsequent management actions (Bergmann et al. 2004; Stephenson et al. 2016).

The scientific literature abounds with case studies where FEK has been used to better understand the life history of commercially important fish stocks. For example, FEK has been used throughout the world to identify the timing and location of spawning activity (e.g., Neis 1999a; Johannes et al. 2000; Silvano et al. 2006), and fishermen often identified spawning locations that had not been previously detected with traditional scientific approaches (e.g., Neis 1998; Maurstad 2002). Additionally, FEK has been used to document the extirpation of spawning components, which provides critical insights into long-term changes in productivity, recruitment, and population structure (Neis 1998; Pederson and Hall-Arber 1999; Ames 2004).

Because Atlantic cod (Gadus morhua) is an important target species throughout much of its range, FEK has proven to be a valuable source of information to better understand the life history and behavior of cod populations. In New England, historical research (e.g., Goode 1887; Rich 1929; Bigelow and Schroeder 1953) related to the seasonal movements, habitat preferences, and diets of cod relied extensively on information provided by fishermen. In Newfoundland, where fishermen could readily differentiate between cod from different groups by their body shape, color, filet quality, diet, and behavior, FEK has been collected and analyzed in conjunction with scientific information to provide a more holistic understanding of the spawning dynamics and stock structure of cod (Neis 1998; Neis et al. 1999a, 1999b; Murray et al. 2008a). Maurstad (2002) solicited FEK to document cod spawning grounds off the coast of Norway, including many locations that were previously unknown to scientists. Figus et al. (2017) used questionnaires and semi-structured interviews to collect FEK related to long-term changes in the abundance, distribution, and condition of cod in the Baltic Sea.

The overarching goal of this chapter is to collect and synthesize FEK related to the stock structure and spawning behavior of cod in US waters. This report includes the findings from DeCelles et al. (2017a) which collected and synthesized FEK related to cod spawning on Georges Bank, Nantucket Shoals, and the Great South Channel. The specific research objectives of this chapter are as follows:

1. Collect FEK to better understand the spatial and temporal distribution of cod spawning activity in the western Gulf of Maine, on Nantucket Shoals, in the Great South Channel, and on eastern Georges Bank.
2. Gather FEK related to morphometric variation amongst cod spawning groups.
3. Collect FEK related to connectivity amongst cod spawning components.
4. Synthesize the FEK collected during objectives 1-3, to serve as a complement to our traditional scientific knowledge to inform cod stock structure in the region.

Interested readers are encouraged to refer to the previous research of Ames (1998, 2004) which used FEK to investigate the spawning grounds and stock structure of cod in the eastern Gulf of Maine.

Methods and Materials

Georges Bank and Western Gulf of Maine

Semi-structured interviews were completed with active and retired commercial fishermen who have experience fishing for cod in the Gulf of Maine, on Georges Bank, on Nantucket Shoals or the Great South Channel. Fifty fishermen were interviewed in total. Forty interviews were conducted as part of the DeCelles et al. (2017a, b) study, and the geographic focus of those interviews was Georges Bank, the Great South Channel, and Nantucket Shoals. An additional ten fishermen were interviewed in 2018 to collect FEK related to Atlantic cod in the western Gulf of Maine. Each interview began with a series of demographic questions designed to document the fishermen's experience fishing for groundfish, and their experience specifically targeting cod on Georges Bank or in the Gulf of Maine (Part 1 of Table 8.1). Fishermen were also asked to identify times and locations where they had captured spawning cod, and a common series of questions was asked related to each spawning ground identified by the fishermen (Part 2 of Table 8.1). NOAA nautical charts, which are familiar to the fishermen, were used to help identify and delineate the spawning grounds. Many fishermen also voluntarily provided spatial information from their own logbooks, paper charts, and electronic plotters. We asked the fishermen to specifically indicate the criteria they used to classify an area as a cod spawning ground. US fishermen typically dress their catch at sea, giving them a chance to examine the stomach contents and maturity stage of their catch. When fishermen indicated that they were basing their reports on observed cod maturity stages, a photo guide provided by Dr. Richard McBride (NOAA Fisheries/Northeast Fisheries Science Center) was shown to them in an attempt to identify specific maturity stages that they remembered seeing in the catch. The visual guide often helped to delineate spawning grounds from feeding grounds. The final part of the interview (Part 3 of Table 8.1) included questions related to the stock structure of cod in the region.

The spawning grounds identified by each fisherman were digitally mapped with ArcGIS, and a unique shapefile was produced for each spawning ground. Monthly maps were created by grouping all of the spawning grounds that were identified to be active in each month. For the spawning grounds identified on Georges Bank, Nantucket Shoals, and the Great South Channel, ArcGIS geoprocessing tools (shapefiles) were used to quantify the spatial overlap amongst spawning grounds in order to quantify the number of fishermen that independently identified spawning activity at a given location. Spawning grounds that were independently identified by 3 or more fishermen were classified as "consensus spawning grounds."

Table 8.1. List of questions that asked during the semi-structured interviews.

Part 1: Demograhic Questions

1) How old are you?
2) How many total years of experience do you have commercial fishing?
3) How many years of experience do you have commercial fishing for groundfish in the Gulf of Maine?
4) How many years of experience do you have fishing specifically for cod in the Gulf of Maine?
5) Of the total years you have spent fishing for groundfish in the Gulf of Maine, how many years were you a deckhand, a mate, and a captain?
6) What types of gear did you use when fishing for cod?

Part 2: Questions Specific To Each Spawning Ground

1) What was the name of the spawning ground?
2) What months did spawning occur here?
3) How were you able to determine this area was a cod spawning ground?
4) What maturity stages did you see at this spawning ground?
5) At what depths did you find spawning cod at this location?
6) How would you describe the magnitude of cod spawning at this site?
7) What was the predictability or consistency of this spawning ground from year to year?
8) What size were the majority of cod you encountered at this spawning ground?
9) How would you describe the habitat at this spawning ground?
10) Is this spawning ground still active?
10a) If the spawning ground is still active, what is the magnitude of spawning now, compared to past levels?
10b) If the spawning ground is no longer active, what year did it cease to be active, and why do you think spawning stopped at this location?

Part 3: Secondary Questions That Were Asked As Time Allowed

1) Is there connectivity between the spawning sites you identified?
2) Was there anything unique about the shape of the cod at any of the spawning grounds?
3) Was there anything unique about the color of the cod at any of the spawning grounds?
4) Is there anything else that you think is important for us to know?

Eastern Gulf of Maine

Fishermen's Ecological Knowledge for the eastern Gulf of Maine was collected from interviews with 27 retired highliner fishermen known locally for their expertise in catching cod and haddock (Melanogrammus aeglefinus). For a detailed description of the methods please refer to Ames (1998). The historical spawning grounds were later used as fixed points of origin in order to link historical spawning areas with the seasonal movement patterns of cod, based on interviews of fishermen during the 1920s (Rich 1929). This provided insights into the western Nova Scotia population structure of cod from Ipswich Bay to the Lurcher Shoal in, which is detailed in Ames (2004). Cod from the midcoast subpopulation formerly occupied grounds in NAFO statistical area

511, while cod in the eastern subpopulation occupied statistical area 512 (See Figure 1.1 for map of statistical areas).

Results

Temporal and Spatial Distribution of Spawning Cod – Georges Bank and Western Gulf of Maine

Fifty fishermen were interviewed in total, and collectively these individuals had 2,000 years of fishing experience, including 1,700 years of experience specifically targeting cod on Georges Bank and in the Gulf of Maine. With the exception of one individual, all of the fishermen had been captains for the majority of their careers. At the time of the interviews, the captains had an average of 34.7 years of experience targeting cod on Georges Bank and/or the Gulf of Maine (range = 12 to 66 years). The majority of fishermen (n = 45) used an otter trawl to target cod, while others used gillnets (n = 10), longline (n = 8), and rod and reel (n = 4). Some fishermen used multiple gear types during their careers. The captains we interviewed fished from New Bedford, MA (n = 21), Chatham, MA (n = 7), Hyannis, MA (n = 1), Gloucester, MA (n = 6), Newburyport, MA (n = 1), Nantucket, MA (n = 1), Scituate, MA (n = 1), Boston, MA (n = 2), Montauk, NY (n = 1), Hampton, NH (n = 2), Portland, ME (n = 1), Pubnico, Nova Scotia (n = 3), Yarmouth, Nova Scotia (n = 2), and Lunenburg, Nova Scotia (n = 1).

It was evident during the interviews that captains were attentive to the reproductive condition of the cod they had caught. American fishermen would observe the reproductive condition of the fish when they gutted them, and often observed large amounts of milt or eggs on the deck when they encountered spawning cod. However, Canadian fishermen do not dress their fish at sea, and instead land them round. Therefore, Canadian fishermen typically could not tell that they caught spawning cod unless they observed milt or eggs freely flowing from the fish. Fishermen also described high catch rates associated with targeting spawning aggregations, and some noted they could identify cod spawning aggregations based on the images appearing on their sounders.

During the DeCelles et al. (2017a, b) study, 40 fishermen identified 210 cod spawning grounds in total on Nantucket Shoals and Georges Bank, although the same spawning grounds were often identified independently by multiple fishermen (Figure 8.1). Twenty-six consensus spawning grounds were documented during the interviews, (Figure 8.2), many of which were discrete and associated with specific bathymetric features such as channels between shoals, edge habitats adjacent to shoals, complex rocky bottom, or areas with steep bathymetric contours.

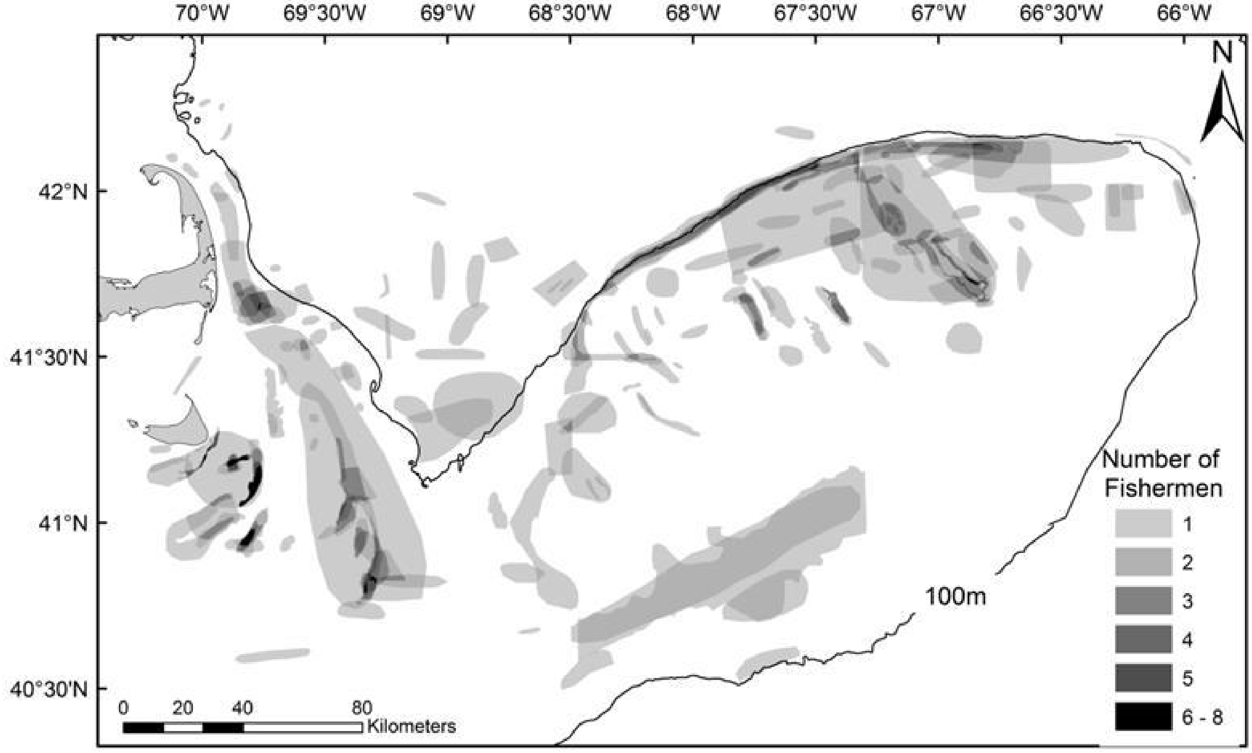


Figure 8.1. Atlantic cod (*Gadus morhua*) spawning grounds on Nantucket Shoals, the Great South Channel, and Georges Bank that were identified by fishermen during the DeCelles et al. (2017a, b) study (n = 210). Each shaded area represents a spawning ground that was identified by a single fisherman. The shading is used to identify areas where cod spawning activity was independently identified by multiple fishermen.

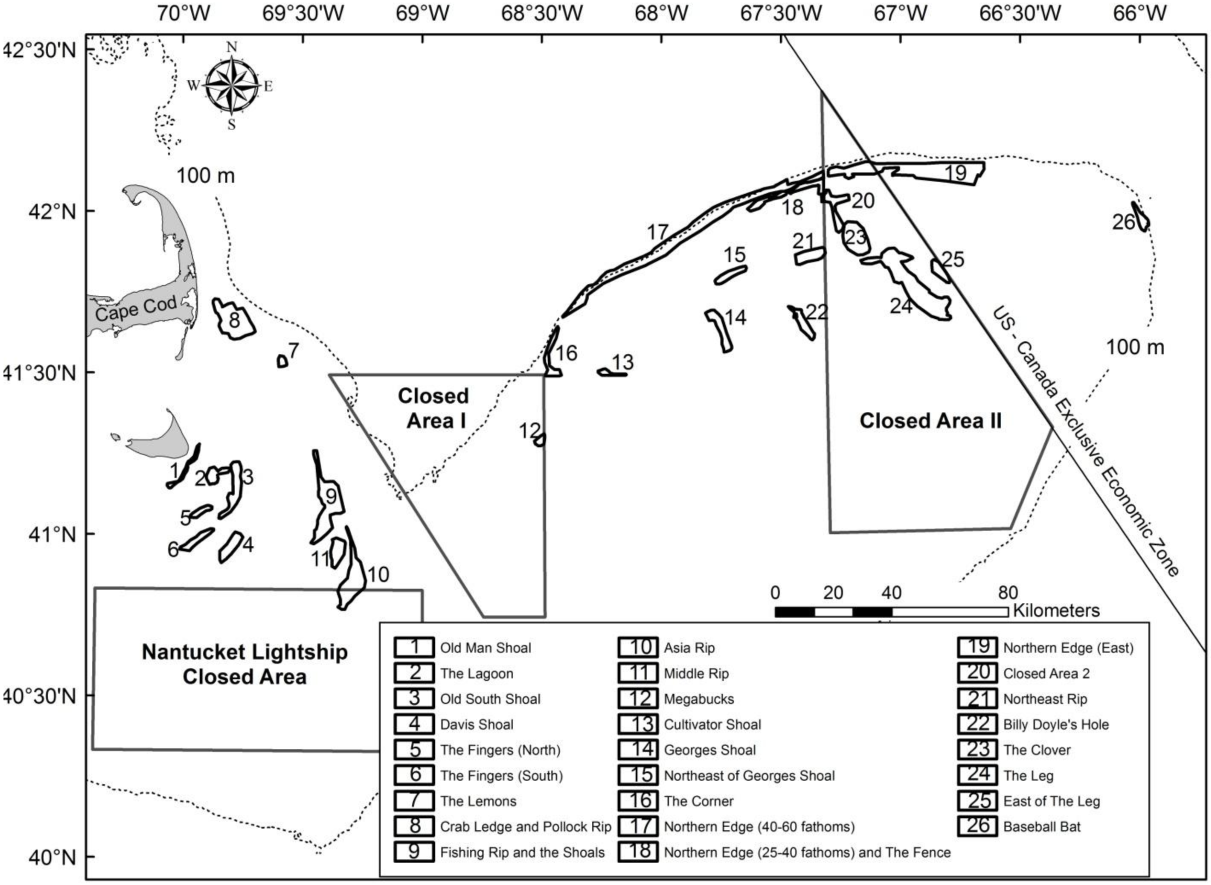


Figure 8.2. Consensus Atlantic cod (*Gadus morhua*) spawning grounds on Georges Bank, in the Great South Channel, and on Nantucket Shoals that were identified independently by at least 3 fishermen during the DeCelles et al (2017a, b) study.

The 40 fishermen interviewed during the DeCelles et al. (2017a, b) study had detailed knowledge about the timing of cod spawning across Georges Bank and the seasonal availability of cod on the fishing grounds. Fishermen reported that cod spawning is relatively rare on Georges Bank between July and September and that cod spawning activity increases from October to December (Figure 8.3). Over half of the participating fishermen reported cod spawning locations that were active in January, February, and March. Fishermen noted that cod spawning activity declined from relatively high levels in April to lesser amounts in May and June.

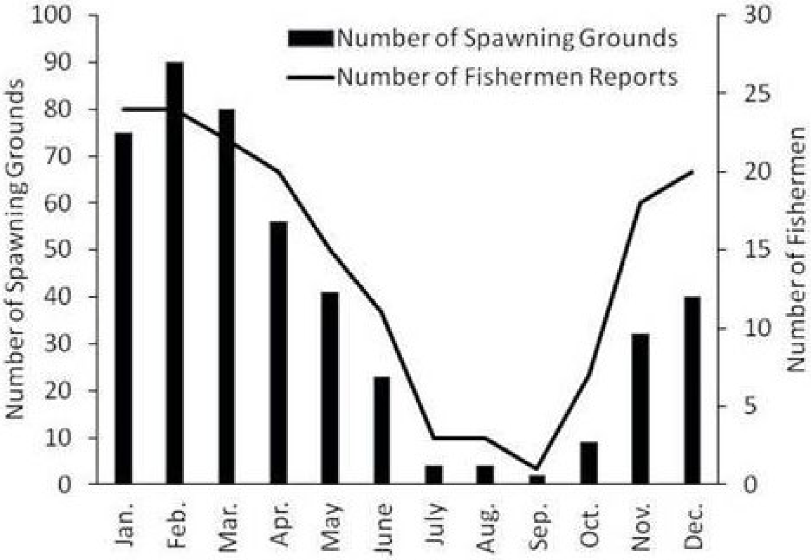
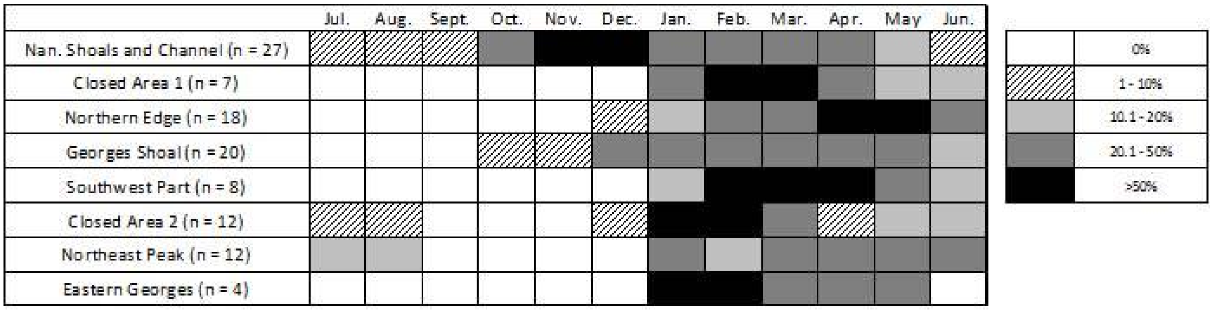


Figure 8.3. The number of Atlantic cod (*Gadus morhua*) spawning grounds, and the number of fishermen that identified spawning activity in each month on Georges Bank, in the Great South Channel, and on Nantucket Shoals. Figure taken from DeCelles et al. (2017a, b).

Fishermen reported that the timing of spawning activity varied across the different regions of Georges Bank. Most fishermen described the spawning period on western Georges Bank (Nantucket Shoals and the Great South Channel) as occurring from October to April, with peak spawning in November and December, although at least 1 fisherman described spawning activity in the region in each month (Figure 8.4). Based on fishermen's reports, it appears that peak spawning occurs earlier on Nantucket Shoals and the Great South Channel than elsewhere on Georges Bank. On Georges Shoal, the spawning season was described as lasting from October through June, with the majority of spawning observed between December and May. Peak spawning in the relatively deep waters of the Northern Flank was reported in April and May.



	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
Nan. Shoals and Channel (n = 27)	▨	▨	▨	▓	■	■	▓	▓	▓	▓	░	▨
Closed Area 1 (n = 7)	□	□	□	□	□	□	▓	■	■	▓	░	░
Northern Edge (n = 18)	□	□	□	□	□	▨	░	▓	▓	■	■	▓
Georges Shoal (n = 20)	□	□	□	▨	▨	▓	▓	▓	▓	▓	▓	░
Southwest Part (n = 8)	□	□	□	□	□	□	░	■	■	■	▓	░
Closed Area 2 (n = 12)	▨	▨	□	□	□	▨	■	■	▓	▨	░	░
Northeast Peak (n = 12)	░	░	□	□	□	□	▓	░	▓	▓	▓	▓
Eastern Georges (n = 4)	□	□	□	□	□	□	■	■	▓	▓	▓	□

□	0%
▨	1 - 10%
░	10.1 - 20%
▓	20.1 - 50%
■	>50%

Figure 8.4. Proportion of fishermen that reported Atlantic cod (*Gadus morhua*) spawning activity in a given month for each of the 8 regions of Georges Bank. The number of fishermen that identified spawning is shown in parenthesis. Figure taken from DeCelles et al. (2017a, b).

Fishermen reported that cod spawn across a wide range of depths on Georges Bank, the Great South Channel, and on Nantucket Shoals (Figure 8.5A; see Figure 2.1 for place names). Although the majority of spawning activity was reported to occur in depths ranging from 20 to 91 meters, fishermen also reported that cod also spawn in shallow water on Nantucket Shoals (≤ 20m) and in relatively deep water (≥ 165m) off the Northern Edge of Georges Bank.

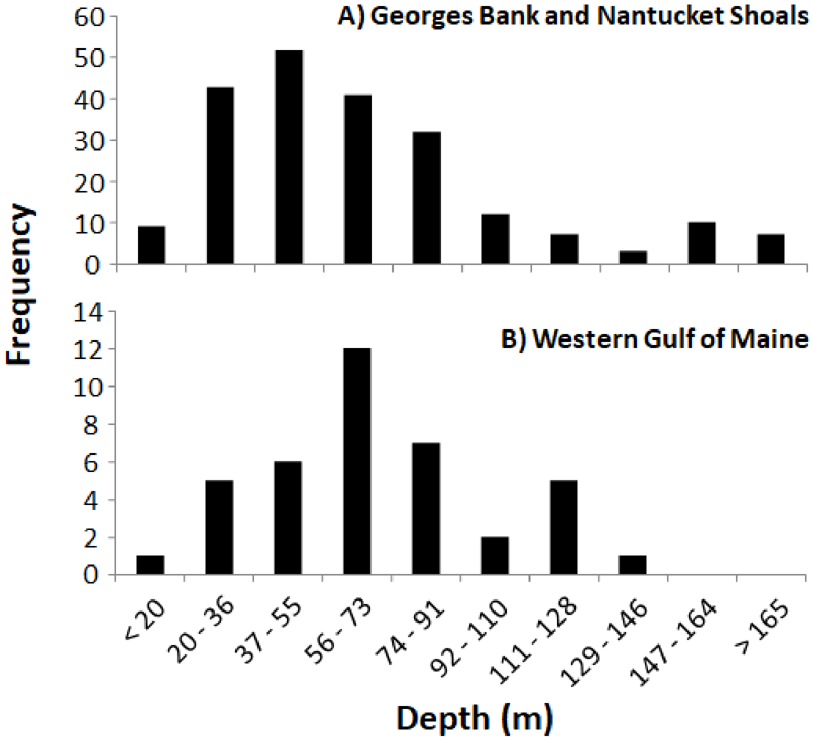


Figure 8.5. The depth ranges of the Atlantic cod (*Gadus morhua*) spawning grounds that were reported by fishermen on Georges Bank and Nantucket Shoals (A) and in the western Gulf of Maine (B).

Fishermen typically identified one or more habitat characteristics associated with each cod spawning ground, and these habitat characteristics included both abiotic and biotic attributes. On Georges Bank, cod spawning grounds were most commonly characterized as occurring in areas with sandy substrates, and fishermen often described sand "lumps" as the preferred spawning habitat, particularly the spawning grounds identified on Nantucket Shoals and Georges Shoals (Table 8.2). The fishermen also reported that the cod spawning grounds on Nantucket Shoals and Georges Shoals often contained high concentrations of shellfish, including surf clams, quahogs, and mussels. Rocky, hard bottom habitats and areas with gravel substrate were also identified as important for cod spawning activity and were the most common habitat type associated with cod spawning activity in the Gulf of Maine. The fishermen often observed that cod spawning grounds were in areas with complex bathymetric features such as ridges, valleys, and deep holes. Fishing in these complex habitats is difficult, particularly with mobile gear, and requires a priori knowledge that the fishermen acquire through direct experience and information sharing. In some instances, cod spawning aggregations were reported to be associated with areas that held high concentrations of forage fish, such as herring, mackerel, or sand lance.

Table 8.2. Frequency of biotic and abiotic habitat characteristics that fishermen associated with Atlantic cod (*Gadus morhua*) spawning grounds in the Gulf of Maine and on Georges Bank.

Georges Bank and Nantucket Shoals				Western Gulf of Maine	
Abiotic Habitat Attributes		Biotic Habitat Attributes		Abiotic Habitat Attributes	
Sand or sand lumps	105	Shellfish	50	Rocks and "hard" bottom	15
Rocks and "hard" bottom	67	Herring	9	Mud	9
Gravel	36	Mackerel	3	Gravel	4
Pebble and cobble	11	Sand lance	8	Edges	4
Mud	9	Macroalgae	5	Sand	3
Shipwrecks	7	Crabs	1		
Strong tides and currents	9	Worms	2		
"Broken" bottom	3	Squid	1		
		Silver hake	1		
		Sponges	1		
		Sea Stars	3		
		Small haddock	1		

In the western Gulf of Maine, the 10 fishermen interviewed as part of the Atlantic Cod Stock Structure Working Group project identified 22 spawning grounds, and some of these spawning grounds were recognized independently by multiple fishermen (Figure 8.6). The reported cod spawning sites spanned the western Gulf of Maine, including locations in Cape Cod Bay, Massachusetts Bay, Ipswich Bay, and on Jeffreys Ledge. Many of these spawning locations had been previously identified. For example, several fishermen identified spawning activity in the "Whaleback" area, which has been well documented (e.g., Bigelow and Schroeder 1953; Howell et al. 2008; Howell 2009). Winter spawning activity identified in Massachusetts Bay (Area 1C; Figure 8.6) was described by Bigelow and Schroeder (1953) and recently confirmed with acoustic telemetry (Zemeckis et al. 2019). The fishermen reported cod spawning activity across a wide range of depths in the western Gulf of Maine (Figure 8.5B).

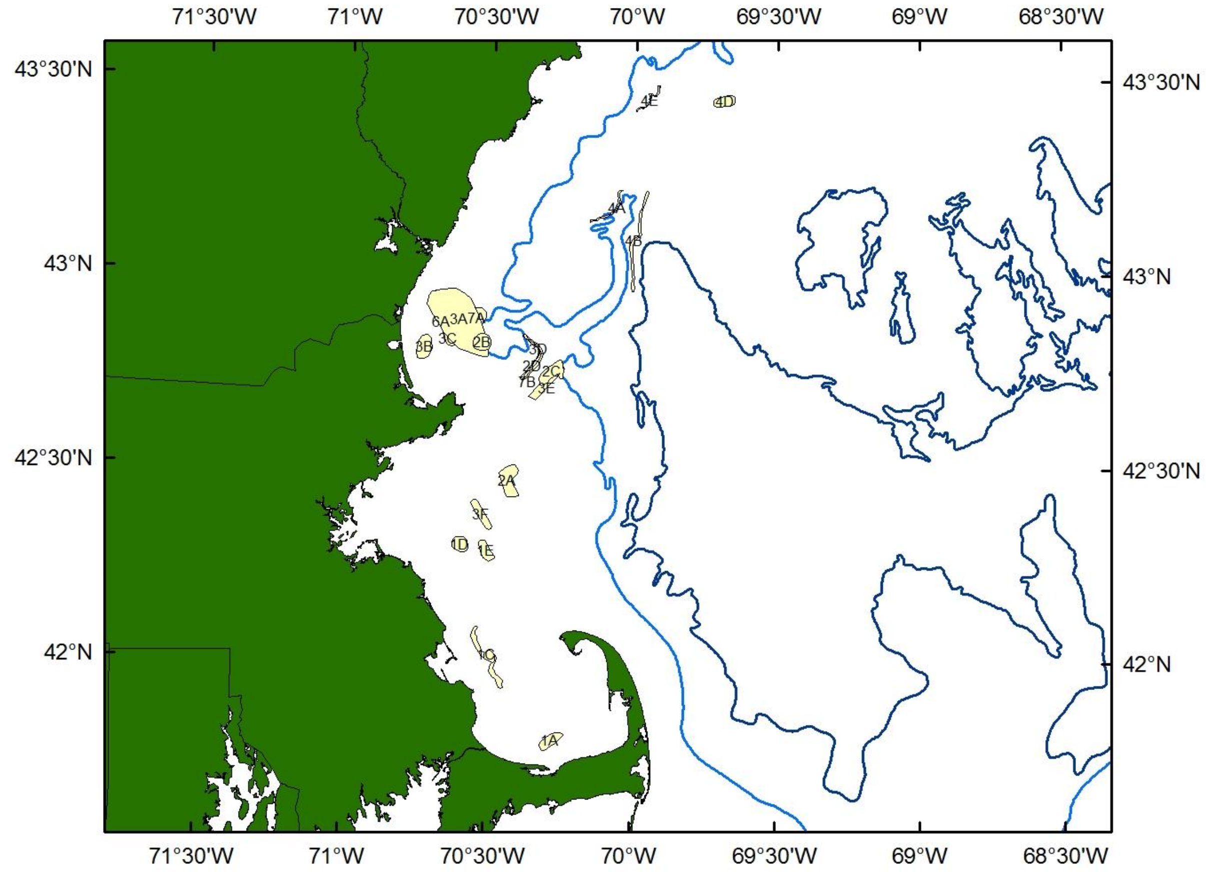


Figure 8.6. Map of the 22 Atlantic cod (*Gadus morhua*) spawning grounds that were identified in the Gulf of Maine. Individual sites are labeled with an alphanumeric key referencing back to individual interviews.

While the fishermen identified cod spawning activity in the western Gulf of Maine throughout the year, seasonal peaks in spawning activity were evident in May and June and again in November and December (Figure 8.7). The fishermen commonly referred to 2 spawning groups of cod in the western Gulf of Maine ("spring" and "winter" spawners), which is consistent with the available scientific information (Chapters 3 and 4, both this volume).

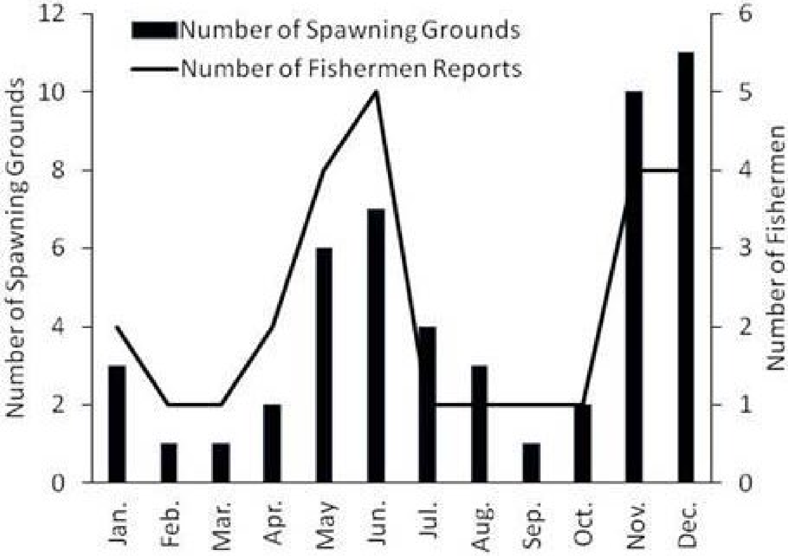


Figure 8.7. The number of Atlantic cod (*Gadus morhua*) spawning grounds, and the number of fishermen that identified spawning activity in each month in the western Gulf of Maine.

Temporal and Spatial Distribution of Spawning Cod – Eastern Gulf of Maine

The 27 fishermen interviewed identified 14,594 hectares of historical inshore cod spawning grounds from Ipswich Bay to Grand Manan Channel (Ames 1998). These grounds were either channels or basins with gravel or gravel and sand substrates bordering muddy bottoms. Depths varied from 30 to 100 meters, with some less than 30 meters and usually proximate with rocky bottom.

The cod in eastern Gulf of Maine —NAFO statistical areas 511 and 512— collapsed in the mid-1990s. An extensive cod tagging project confirmed this (Tallack 2011), and the area continues to show few signs of recovery. Cod in the eastern Gulf of Maine formerly included population components of the Gulf of Maine cod metapopulation that occupied grounds along the Maine coastal shelf from eastern Muscongus Bay to Grand Manan Channel in western Bay of Fundy. First-year and second-year cod are occasionally encountered, but age-3 and older cod are uncommon in the Maine Center for Coastal Fisheries Sentinel Survey (Chen et al. 2016). Cod no longer return to the area seasonally, nor are they known to reproduce there, though vestigial numbers of a cross-boundary cod group persists near Grand Manan Channel in eastern statistical area 511, as evidenced by catches in the Maine - New Hampshire Inshore Trawl Survey (e.g., Sherman et al. 2004).

Evidence associated with statistical area 512 indicated that at least 2 substocks of cod were formerly present in Penobscot Bay: the first was a resident stock of large fish that arrived inshore in spring, and the second substock had reproduced elsewhere and arrived in June to feed. In the eastern Gulf of Maine, cod movements were persistent, following numerous deep channels towards shore in spring and moving further offshore along the same channels by fall, with resident fish remaining in adjacent deep water. The consensus of interviewees was that young juvenile cod were found close to shore and were relatively stationary, while older juveniles and young adults were more mobile and wide ranging; large cod remained inshore in deep water and were more sedentary.

Cod were found to occupy 4 relatively discrete subunits of the Gulf of Maine metapopulation north of Cape Ann. Each subunit utilized separate migration corridors, and their abundance varied independently from its neighbors. Prior to collapse, historical movement patterns indicated that many cod remained on grounds in the collapsed area all year and reproduced in or near coastal estuaries. Others migrated from the area in fall and returned in spring (Perkins et al. 1996; Ames 2004). Each subpopulation was characterized by having multiple spawning sites where local reproduction occurred. The 2 cod subpopulation collapses in eastern Gulf of Maine coincided with the loss of local cod spawning events.

Fishermen's Observations of Stock Structure and Connectivity

The fishermen we interviewed during these projects had several observations related to the broad scale movements of Atlantic cod in the Gulf of Maine and on Georges Bank, and several common themes emerged during the discussions. Fishermen often expressed their concern that the current management units for cod in US waters do not match the biological population structure of the resource. For example, 5 fishermen observed that they would commonly "follow" a body of cod from the waters east of Cape Cod into the western Gulf of Maine during their annual migration. They explained that they would begin to target cod off of Chatham in the early spring (March and April) and would follow the fish to the fishing grounds off Nauset in April and May, and finally to Stellwagen Bank in May and June. The fishermen remarked that this group of cod typically fed on sand lance. Similar observations were made during an outreach workshop in June 2018, organized by New Hampshire Sea Grant, as part of the Atlantic Cod Stock Structure Working Group's deliberations. Another fisherman remarked that when fishing under Days at Sea with differential trip limits (i.e., higher daily catch allowance for the Georges Bank stock) they used to refer to the 42°N line as a "joke," because the cod were continuously distributed on either side of the stock boundary. Similarly, during the Georges Bank cod spawning interviews, 10 fishermen remarked that there is connectivity between cod in the western Gulf of Maine and the Great South Channel and Nantucket Shoals. These fishermen thought that cod would make regular seasonal migrations from the western Gulf of Maine to Nantucket Shoals and the Great South Channel, and that these movements were related to foraging behavior.

During the prior study (DeCelles et al. 2017a) 15 fishermen remarked that they believe cod on eastern Georges Bank are distinct from those on Nantucket Shoals and the Great South Channel, and their conclusions were based on several observations. Many fishermen remarked on the discontinuous distribution of cod across Georges Bank. Fishermen often noted that cod on eastern Georges Bank often attained larger sizes than those taken inshore. Fishermen also consistently described differences in the color, shape, and fillet quality of cod between the 2 areas, and posited that the disparities in fillet qualities were related to the distinct diets of cod in these 2 regions. The geographic differences in the timing of spawning also reinforce these observations that cod on eastern and western Georges Bank are discrete groups. Many fishermen identified a longitudinal divide that they believe separate the 2 groups of cod on eastern and western Georges Bank cod, and most suggested a boundary line of either 68ºW or 69ºW, with others suggesting that the Great South Channel acts as a boundary between eastern Georges Bank cod and western cod groups.

In the western Gulf of Maine, some fishermen noted finer-scale differences between the cod groups on Stellwagen Bank and Jeffreys Ledge. In particular, fishermen noted that the 2 groups of cod typically have different diets, with cod on Stellwagen Bank feeding primarily on sand lance, while those on Jeffreys Ledge mainly feed on herring and shrimp. The fishermen also commented that there are "localized groups" of cod in Ipswich Bay, which they can follow predictably during their seasonal migrations to the Whaleback spawning ground. However, further discussions are needed to better capture the details associated with this fine-scale structure.

A few fishermen with extensive experience fishing on Nantucket Shoals, primarily during the 1970s and 1980s, provided detailed descriptions of their understanding of cod movements. The fishermen recalled seeing "different runs of cod" on Nantucket Shoals throughout the year. The fishermen described a group of fish they called "groundskeepers," which were resident cod that would remain on Nantucket Shoals throughout the year. The resident cod were joined seasonally on Nantucket Shoals by migrating fish. During the fall, migratory cod would move from the deeper waters of the Great South Channel, and perhaps from the western Gulf of Maine, towards Nantucket Shoals. The fishermen felt that these inshore movements may have been coincident with the first major winter storm (i.e., nor'easter). The migratory cod would first arrive on the eastern portion of Nantucket Shoals (e.g., Davis South Shoal and Johnson Shoal), and would move westerly across Nantucket Shoals as the winter progressed. Some of the migratory fish would remain on Nantucket Shoals to spawn, while others would migrate further westward to Nomans Land and Cox Ledge, presumably to spawn there. The migratory fish would complete their return migration to the east in the summer and early fall. These seasonal observations of cod distribution and behavior around Nantucket Shoals are largely consistent with observations provided by early scientific studies (Smith 1902; Schreoder 1930; Wise 1958).

Fishermen's Observations of Cod Morphology and Color

Fishermen were observant of differences in the size and shape of cod between spawning groups. Two fishermen in the Gulf of Maine remarked that the spring spawning cod were generally "meatier" (i.e., higher yield) than those that spawned in the winter. One fisherman remarked that he regularly caught "whale cod" (i.e., very large) in the spring spawning aggregations, while whale cod were relatively rare in the winter spawning aggregations. Several fishermen remarked that the cod on eastern Georges Bank were generally larger than those taken on Nantucket Shoals or the Great South Channel and that the largest cod they encountered were on eastern Georges Bank.

The fishermen reported that red cod were common throughout the Gulf of Maine, and that they were often captured in close proximity to areas with hard bottom habitat (e.g., rock piles). They reported red cod in multiple locations, ranging from areas close to shore off of New Hampshire and Massachusetts, to depths of 70 fathoms in Ipswich Bay. The fishermen remarked that red cod and olive cod were often caught together in feeding aggregations and that red cod generally composed a small proportion (e.g., <5%) of the total cod catch. Interestingly, the fishermen reported that they did not recall catching red cod in spawning condition, and that red cod were only captured in feeding aggregations. One fisherman remarked that the red cod he captured were generally smaller than the olive cod.

Other Recurrent Topics of Interest Related to Cod Biology

Several fishermen commented that they have observed truncation of the size structure of cod over the course of their careers, both in the Gulf of Maine and on Georges Bank. Some fishermen expressed concern that the loss of older and larger spawners had an effect on the cod behavior, and reduced the spatial stability of the spawning aggregations. One fisherman commented, "The younger cod have no one to lead them home," while another lamented that intense fishing on Nantucket Shoals had "wiped the genetic memory out of the fish." A few fishermen also remarked that they observed declines in the size at maturity for cod during their careers.

Unsurprisingly, climate change and water temperature were recurrent topics during the interviews. The majority of fishermen noted that they have observed long-term changes in water temperature, and they expressed concern that warming waters were deleterious to the productivity of cod. Many fishermen felt that cod were especially sensitive to water temperature and observed that the distribution of spawning activity changes in response to temperature. For example, several fishermen commented that spawning activity has shifted to deeper waters in Ipswich Bay in recent years and implicated climate change as the likely driver. Others noted that the exact location of spawning will change from year to year, dependent upon temperature, with cod often seeking out the coldest available habitats to spawn.

Discussion

Insights into Cod Population Structure from FEK

This case study provides a valuable example of how FEK can serve as a complement to enhance our understanding of stock structure. Fishermen's observations related to the timing and location of cod spawning on Georges Bank were well supported by the existing scientific information and by previous reports that synthesized fishermen's ecological knowledge in the late 1800s and early 1900s (see detailed reviews in DeCelles et al. 2017a, 2017b). The fishermen also identified some cod spawning grounds that were not previously described in scientific reports. Further, many fishermen possessed a detailed understanding of cod movement patterns and geographic variation in cod morphology, diet, and coloration. Traditional scientific data collection approaches cannot easily produce the same level of spatial resolution that FEK can provide.

Several fishermen remarked that there was connectivity between cod in the western Gulf of Maine and cod on Nantucket Shoals and in the Great South Channel. Their observations are well aligned with the tagging results from Wise (1963), who found that 15% of cod tagged off of Chatham in March and April were later recaptured in the Gulf of Maine. Loehrke (2013) noted that cod tagged east of Cape Cod (off Chatham and in the Great South Channel) exhibited dispersive movements and observed that the interpretation of the movement patterns was dependent upon whether the recaptures were weighted by geographic differences in fishing effort. While cod released east of Cape Cod were observed to disperse to southern New England, Georges Bank, and the Gulf of Maine, the principal direction of movement was northwest, into the western Gulf of Maine. Tallack (2011) observed that sublegal cod tagged east of Cape Cod exhibited 2 major movement patterns, with some individuals migrating eastward towards Georges Bank and others moving northwards into the western Gulf of Maine. Trawl survey data demonstrate that cod are continuously distributed from the western Gulf of Maine to the east of Cape Cod and into the Great South Channel (Begg et al. 1999; McBride et al., this TM). Using a suite of genetic markers, Kovach et al. (2010) identified a "southern complex" of cod, which included winter spawning cod in Massachusetts Bay and Ipswich Bay and winter spawning cod on Cox Ledge and Nantucket Shoals.

Many fishermen expressed their opinion that cod on eastern Georges Bank are distinct from those on Nantucket Shoals and in the Great South Channel. Their observations are congruent the results of with several tagging studies. Schroeder (1930) reported that cod tagged on Nantucket Shoals were rarely recaptured on Georges Bank east of 68°W. Wise (1963) reported that few cod tagged off Chatham were later recaptured on eastern Georges Bank, and that no cod tagged on eastern Georges Bank were recaptured in the Great South Channel or Nantucket Shoals. Many fishermen suggested that the longitudinal division between cod on eastern and western Georges Bank was either 69°W or 68°W, and Wise (1963) similarly suggested the population division occurs at 68°W. Similarly, Hunt et al. (1999) noted that very few cod tagged on eastern Georges Bank were recaptured in the Great South Channel, and that none were recaptured on Nantucket Shoals. Tallack (2011) reported that cod tagged on eastern Georges Bank made extensive movements to the Scotian Shelf but rarely moved to Nantucket Shoals or the Great South Channel. Based on bottom trawl survey data, Begg et al. (1999) also documented a discontinuous distribution of cod between eastern and western Georges Bank, which was most pronounced during the fall survey, particularly between 1989 and 1997. However, the fishermen's observations that cod on eastern Georges Bank were larger than those on western Georges Bank did not match the von Bertalanffy growth parameters reported by Begg et al. (1999), which consistently estimated a larger L_∞ for cod on western Georges Bank. Several studies have indicated that genetic differences exist between cod on eastern Georges Bank and those on Nantucket Shoals (Lage et al. 2004; Wirgin et al. 2007; Kovach et al. 2010).

How Fisheries Management Influences FEK

Fishermen's observations related to the timing and location of cod spawning activity are undoubtedly influenced by fishery management and regulations. Under Days-at-Sea management, many fishermen targeted cod aggregations because they could maximize their catch per unit effort and revenue and make trips close to shore that would allow them "to beat the clock." Since the transition to sector management in 2010 and the quotas cuts that followed, the majority of active fishermen reported that they no longer target cod because of the low allocations and high lease prices, in recent years. Spatial regulations have also had a substantial influence over when and where fishermen can target cod. Closed areas that were implemented in US waters to reduce fishing mortality (e.g., Closed Areas I and II [Georges Bank], Cashes Ledge [Gulf of Maine]), or to protect habitat (e.g., Nantucket Shoals habitat closure) have prohibited fishing in many of the areas where the US fleet used to target spawning cod. In addition to the year-round closed areas, a number of seasonal closures have been implemented in the Gulf of Maine to protect cod spawning activity (e.g., Whaleback, Winter Cod Conservation Zone), and "rolling" closures have been used to limit fishing mortality on cod and other groundfish. Many of these closures have been altered over time as new information has become available and management priorities have changed. American fishermen have been banned from fishing on eastern Georges Bank since the Hague Line was established in 1984. On the Canadian portion of eastern Georges Bank, the Canadian trawl fleet is required to use selective fishing gear (e.g., haddock separator trawl) which is designed to reduce cod bycatch, and fishing is typically prohibited from early February through May to protect spawning cod (Wang et al. 2015). In addition, fishermen from the Gulf of Maine and Cape Cod have noted that the quantity of lobster traps has increased substantially in the last decade and that the spatial footprint of the lobster fishery has expanded further offshore and into deeper water. As a result, many of areas where trawl fishermen formerly targeted cod are no longer available to them, which further limits their ability to understand cod movements and spawning behavior. In combination, these factors make it difficult for fishermen to assess the current spatial and temporal extent of cod spawning on Georges Bank and in the Gulf of Maine. Unfortunately, in many cases these limitations also make it difficult to understand whether historical spawning grounds have been extirpated. Therefore, it is important to recognize that FEK can only provide a partial picture of cod spawning behavior and stock structure and that the greatest utility of FEK will be realized when it is considered in conjunction with traditional scientific information.

Fishery regulations, particularly the fear of additional regulations, may also influence whether fishermen will choose to share their knowledge (Pederson and Hall-Arber 1999; Maurstad

2002; Bergmann et al. 2004). We contacted 52 fishermen to discuss Georges Bank conditions, and 40 agreed to complete an interview. The high participation rates were likely due to several factors (see DeCelles et al. 2017b), and many of the fishermen we collaborated with were retired, which may have increased their willingness to share information. However, some fishermen in the western Gulf of Maine were more guarded in providing their information. Several refused to complete an interview, and others who did complete an interview were sometimes unwilling to share spatial information related to cod spawning. Therefore, the spawning grounds identified in the western Gulf of Maine are not exhaustive. However, based on the discussion during the interviews, it is evident that fishermen in the western Gulf of Maine have a detailed understanding of cod distribution, morphometrics, and spawning activity, and further research and outreach would be valuable to investigate fine-scale population structure in the Gulf of Maine. Nevertheless, the insights that fishermen shared during the interviews can provide valuable information when considering the biological structure of regional cod populations.

Conclusion

Fishermen in the Gulf of Maine and Georges Bank have a detailed understanding cod behavior, including their seasonal movement patterns and spawning locations. This knowledge can provide critical insights into the population structure of cod in US waters and should be given formal consideration as part of a multidisciplinary stock identification study. The observations of fishermen collected during the semi-structured interviews largely supports the emerging view that cod on eastern Georges Bank are largely distinct from groups on Nantucket Shoals and the Great South Channel.

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9. SYNTHESIS

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Previous chapters reviewed different 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 that 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 or 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, then identify mismatches between these units and the biological evidence, and finally evaluate alternative stock hypotheses.

The Current Management Unit Framework

As outlined in the Introduction (Chapter 1), the initial process of 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 Northwest Atlantic Fisheries Organization (NAFO) divisions, which are composed of statistical areas used for reporting fishery catch (Chapter 2). Cod distributed in division 5, with statistical areas in the 500s, are considered in US waters, with the exceptions outlined in Fig. 9.1.

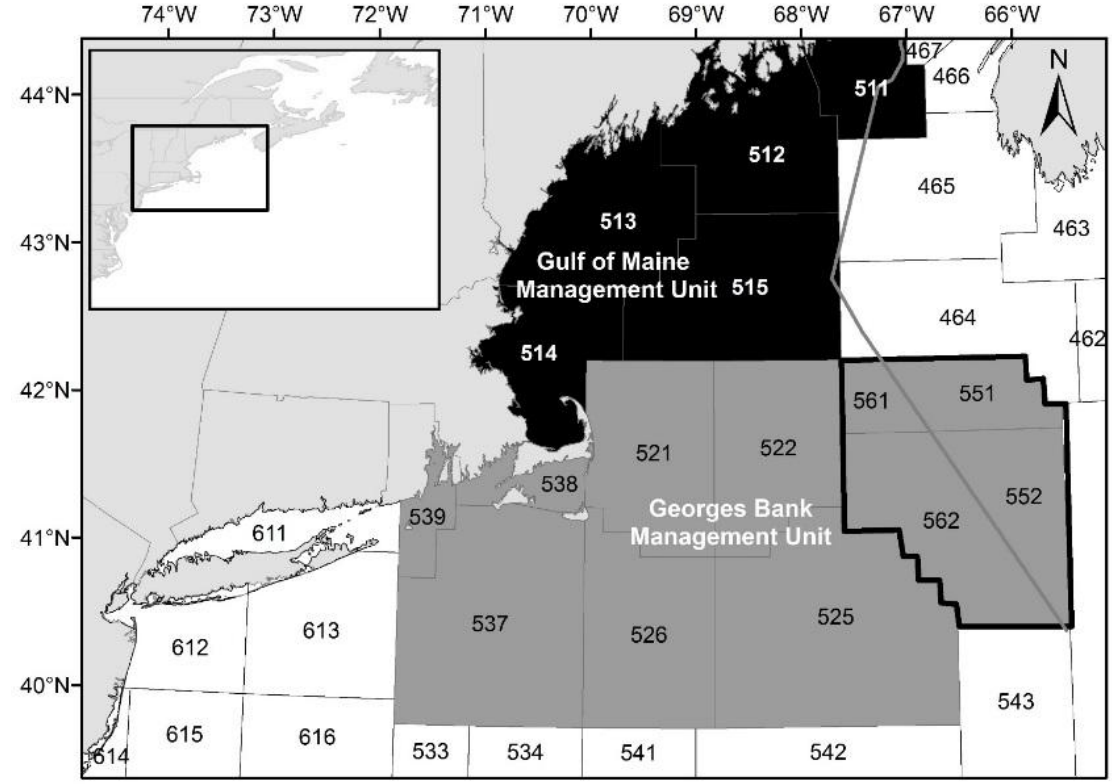


Figure 9.1. Current boundaries for the 2 US Atlantic cod (*Gadus morhua*) management units – Gulf of Maine (black polygons) and Georges Bank (gray polygons) – both within the Northwest Atlantic Fisheries Organization (NAFO) division 5. The individual polygons are "statistical areas" used to aggregate 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 4 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.

The NAFO statistical area framework is foundational for aggregating fishery monitoring data. The ACSSWG accepts this framework 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. The ACSSWG also considered 10’ squares of latitude-longitude as an alternative spatial framework, but not all fishery monitoring data support this scale. Furthermore, this finer scale is less likely to be adopted by end users because many regions of division 5 do not have data relevant for stock identity at this spatial scale.

Mismatches Between Current Management Units and Biological Stock Structure

We outline 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 in Fig. 9.1 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 (Chapters 3 and 8), growth rates (Chapter 5), and morphometrics (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).

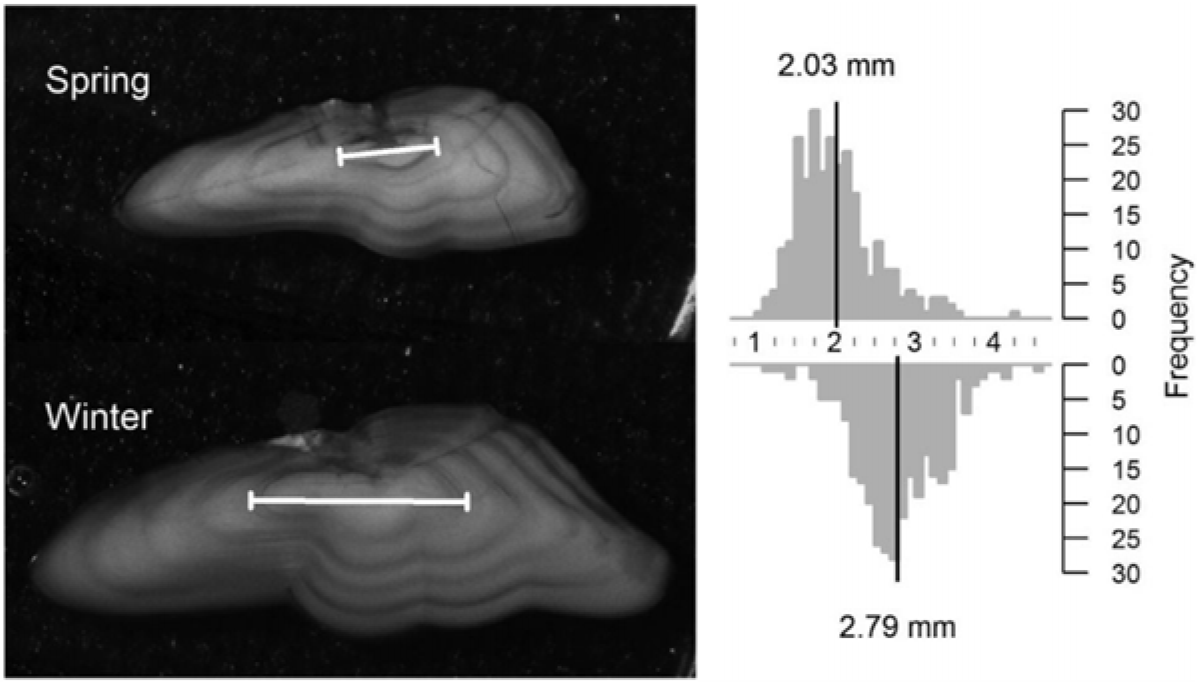


Figure 9.2 Winter and spring spawning cod (*Gadus morhua*) from the same management unit [Gulf of Maine] have different mean diameter measures of the first annulus. [Left] Otolith cross-sections from 2 age-4 cod, both captured in spawning condition. The one at top was captured in May, while the one at bottom was captured in December. The diameter of the first annulus (A1) 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 management units as well as heterogeneity within the current management units (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 from 2 genetically distinct populations with different reproductive phenologies (i.e., winter and 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 (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).

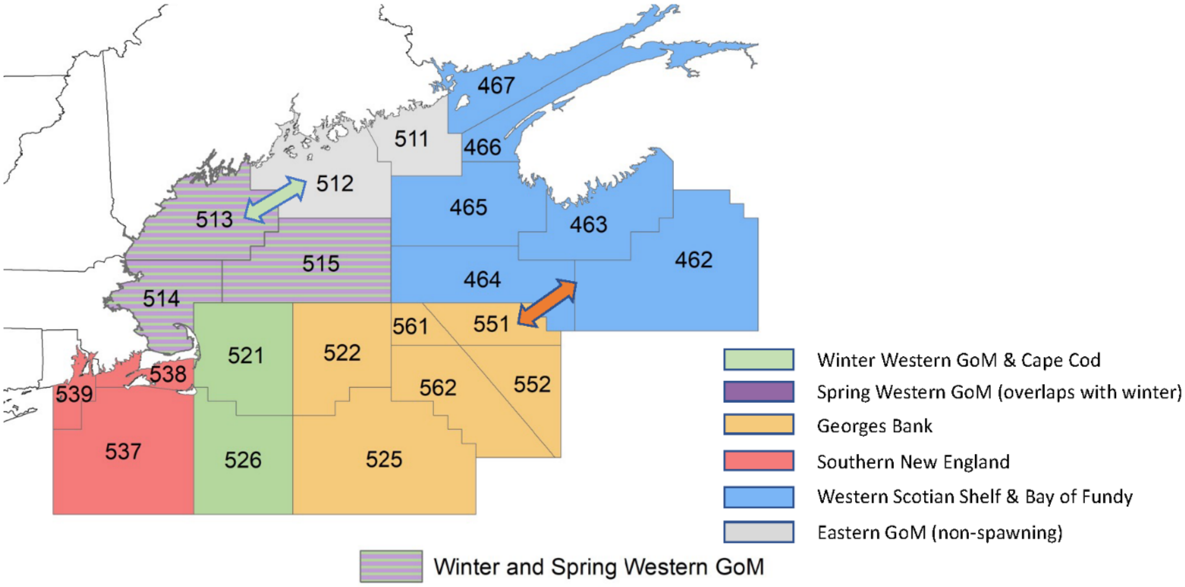


Figure 9.3. Population genetic structure of Atlantic cod (*Gadus morhua*) in Northwest Atlantic Fisheries Organization (NAFO) divisions 5 and 4X, based on synthesis of all available data. Five US genetic populations and 1 Canadian genetic population are depicted, including 2 US populations that overlap, 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 nonspawning cod in area 512, where a green arrow suggests connectivity between there and the western Gulf of Maine (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 (Fig. 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. Historically, cod in northeastern Gulf of Maine (e.g., 511) have 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 side of 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 indicate 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.

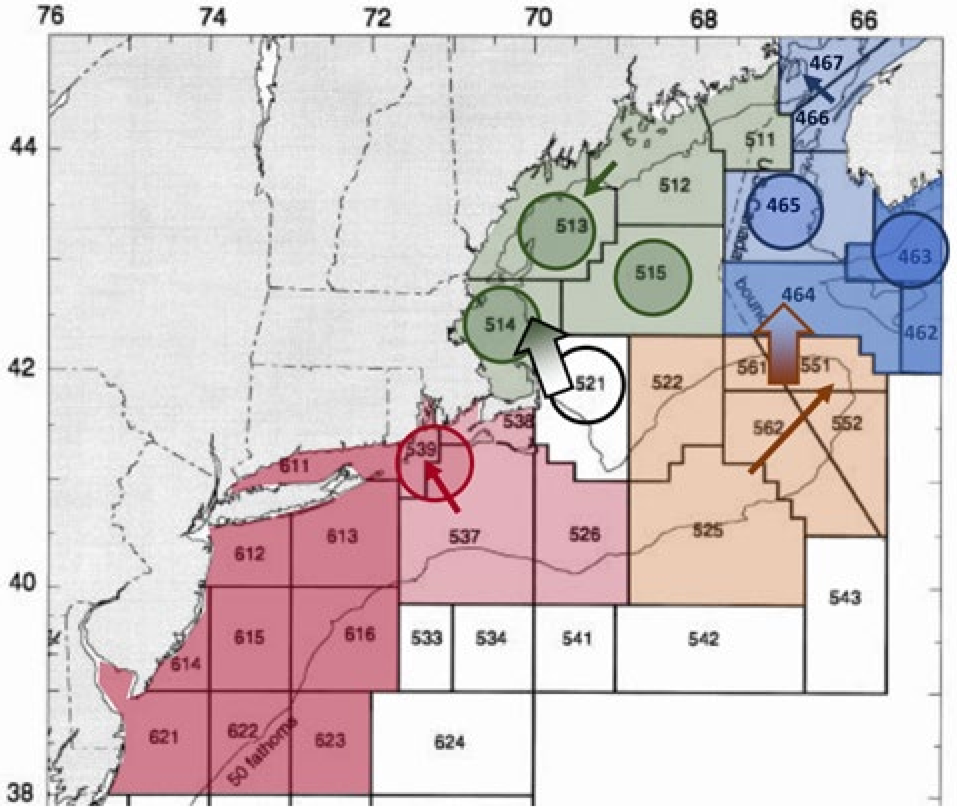
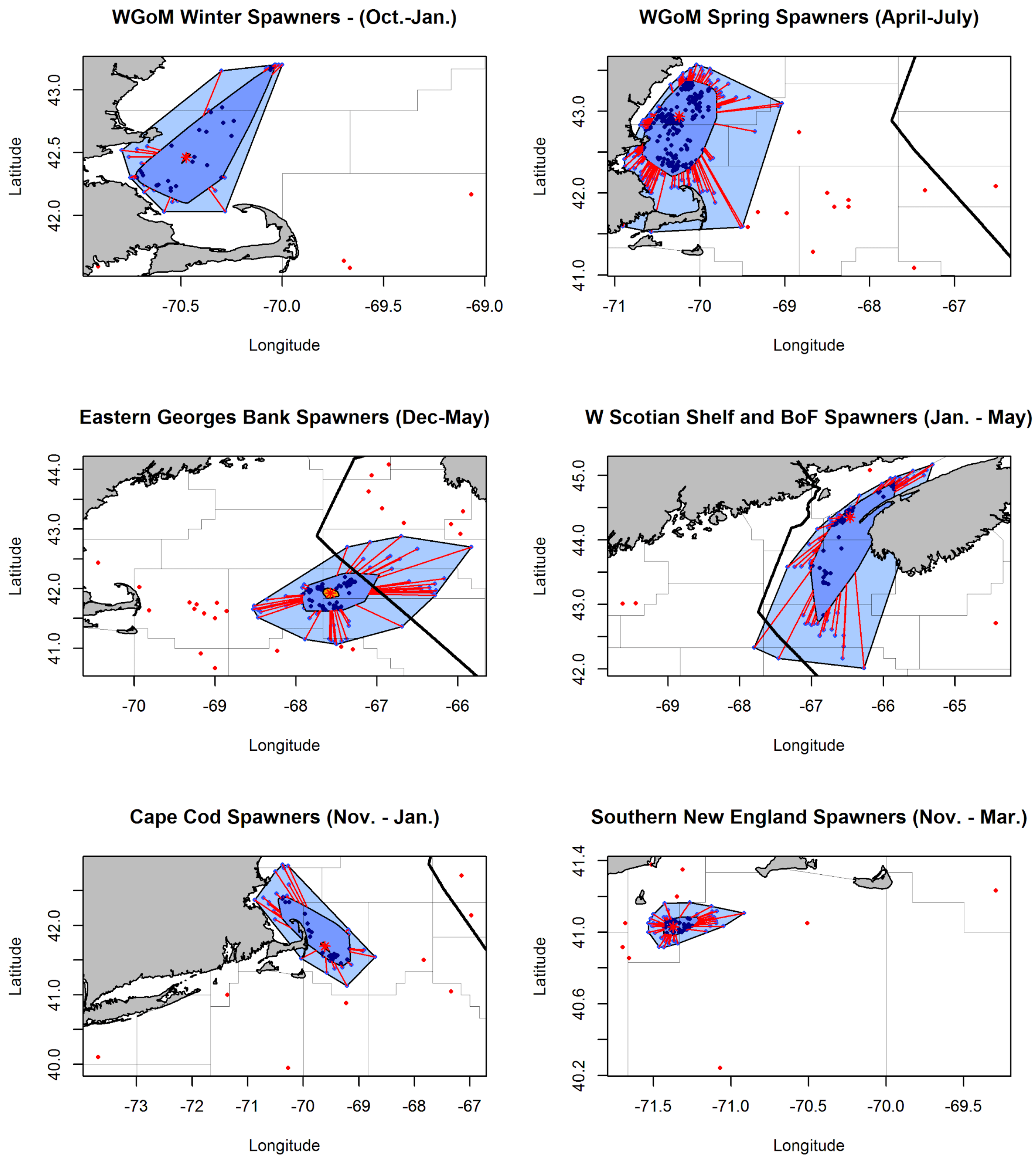


Figure 9.4. Major patterns of Atlantic cod (*Gadus morhua*) movements among regions (multicolor arrows: >10% movement), movement within regions (solid colored arrows: >50% movement from statistical area), and residence within statistical areas (circles: >50% residence in statistical area) from combined 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 nonspawning seasons varies (Fig. 9.5, 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.



WGoM Winter Spawners - (Oct.-Jan.)

WGoM Spring Spawners (April-July)

Eastern Georges Bank Spawners (Dec-May)

W Scotian Shelf and BoF Spawners (Jan. - May)

Cape Cod Spawners (Nov. - Jan.)

Southern New England Spawners (Nov. - Mar.)

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: western Gulf of Maine (WGoM), western Scotian Shelf (W Scotian Shelf), and Bay of Fundy (BoF).

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

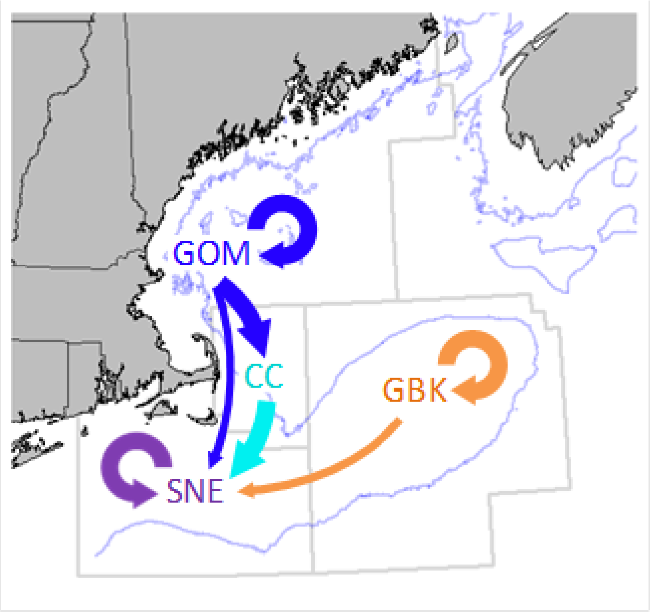


Figure 9.6. [left] Summary of the early life connectivity between spawning groups and settlement areas for Atlantic cod (Gadus morhua) in US waters. An uppercase "C" indicates major connectivity; a lowercase "c" indicates minor connectivity; an "X" indicates unlikely connectivity. The Gulf of Maine (GOM) stratum is defined by statistical areas 511-515 and includes 2 spawning groups: spring (S) and winter (W); 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, so it is 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 suggest 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 nonspawning 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. Likewise, it does not account for the considerable connectivity of larvae and movements by adults between these management units around Cape Cod, or the existence of 2 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 acknowledge biological complexity.

As proposed by Zemeckis et al. (2014), an alternative, yet still simple 2-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). 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 2 management units. For example, in Canada, the northern cod stock (2J3KL) has inshore and offshore spawning components, with complex annual spawning and feeding migrations and genetic differences; however, it is assessed and managed as 1 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, anticyclonic 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°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°W, 69°W, or the Great South Channel (Chapter 8). As recently as a few years ago, Zemeckis et al. (2014) stated that 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).

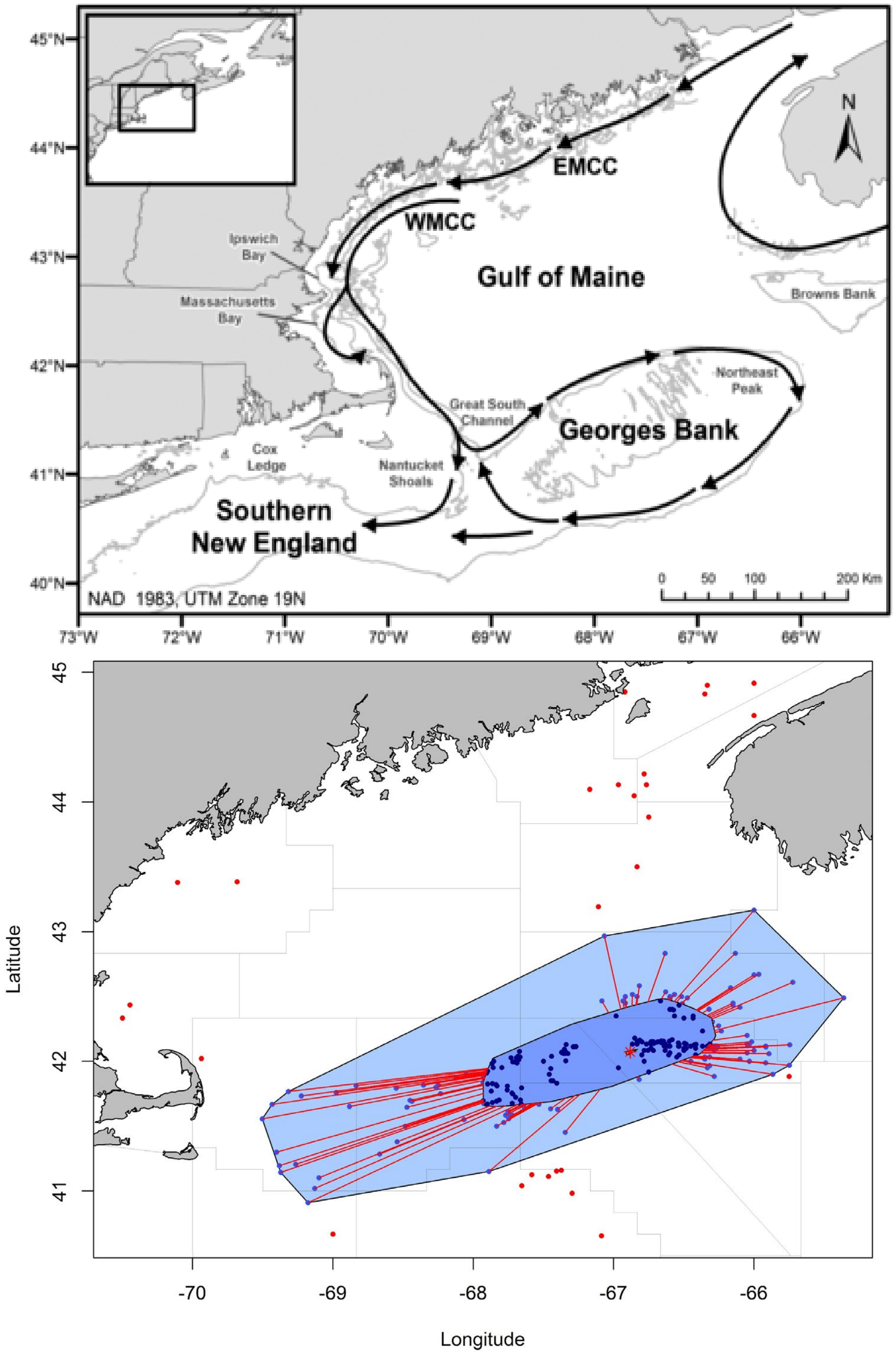


Figure 9.7. (above) Oceanographic delineation of Georges Bank as an anticyclonic (clockwise) gyre from the Great South Channel to the Northeast Peak (from Zemeckis et al. 2014; EM = eastern Maine, WM = western Maine, CC = coastal current); (below) A bagplot of 311 Atlantic cod (Gadus morhua) recaptures from fish released in statistical 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 [see Chapter 7, Glossary]). 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 2 units (1 inshore and the other offshore) 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, there is considerable evidence that cod in the central part of 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 3 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 overlap results in fish from these 2 spawning groups being caught by the fishery as mixed compositions in these areas, as well as in adjacent feeding areas, such as area 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. In fact spawning patterns may be complex, because Ames (1997) notes that both winter and spring spawning occurred there in the past. The genetic data available at this time do not clarify the stock identity of cod from northern Gulf of Maine because fish have not spawned there in recent decades, and best practices for identifying genetic stock structure is to collect spawning fish on their spawning grounds in the spawning season.

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).

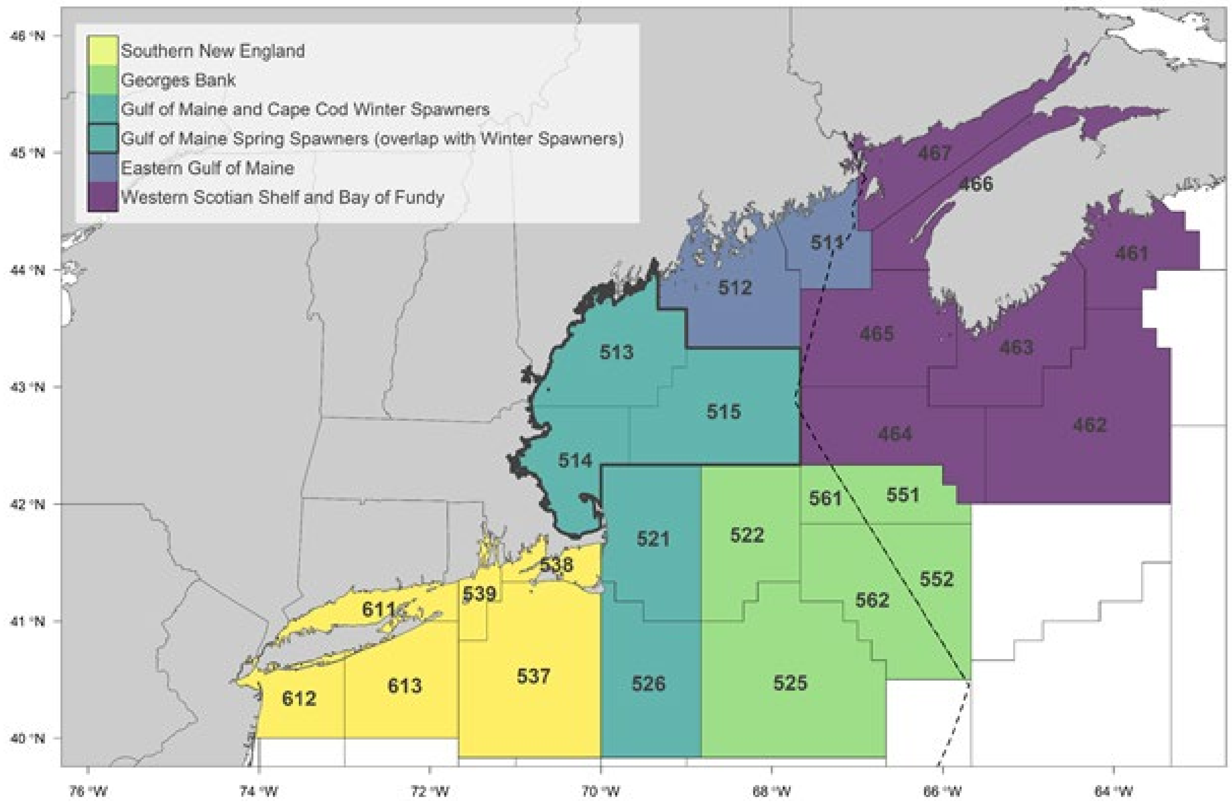


Figure 9.8. Proposed biological stock structure of Atlantic cod (*Gadus morhua*) in Northwest Atlantic Fisheries Organization (NAFO) division 5 and adjacent division 4X.

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 to the southern New England parts of this management unit. Genetic markers confirm strong genetic differentiation. As discussed above, there 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 to set 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 1 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 Mid-Atlantic seaboard, and tag returns since the 1980s suggest much less connectivity of 537-9 with 521. 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 even more for area 526 where there is potential for mixing with the newly redefined 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 of Maine group. Larval modeling suggest self-replenishment is possible in 511-512 and outside sources are less likely which hints at the source-sink dynamics between the eastern Gulf of Maine 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 the 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 2 management units as an accurate representation of the biological stock structure of cod in US waters. Major issues were:

1. numerous instances of both phenotypic and genetic variability indicate that cod are not well mixed within each management unit,

2. adult cod in some areas exhibit extensive movements, including swimming between current US-US and US-Canada management units,
3. cod larvae are dispersed 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. mix-stock fisheries are apparent from interdisciplinary evidence of sympatric winter- and spring-spawning cod in the southwestern Gulf of Maine and around Cape Cod.

Our consensus proposal expands the number of biological cod stocks from 2 to 5 in US waters (NAFO division 5). Inferences by the ACSSWG are, however, based on a diminished biological resource relative to the historical biomass and productivity of cod. If there had been a larger breadth of information on stock conditions, a review may have reached different conclusions about stock structure. The working group recommends continued evaluations to monitor if extirpated spawning grounds become recolonized in Downeast Maine or Nantucket Shoals and to be aware of any broadly based changes in productivity to the region that affect cod.

Recommendations for Additional Work

Our recommendations for additional work are presented in 2 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, which they organized by putative cod stock.

Recommendations from the ACSSWG

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

High priority or short term recommendations

- Simulate alternative management procedures' ability to meet fishery management objectives. The operating models should reflect the most likely scenarios of population structure and alternative management procedures, including the current stock boundaries, alternative stock boundaries, and intermediate approaches (e.g., spawning closures, stock composition monitoring). This simulation will ideally occur before the 2023 research track assessment of cod.

- Conduct 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 of Maine 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

- Identify 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, which would provide valuable early life history information for these areas of uncertainty with respect to stock structure.

- Collect more samples to clarify the connectivity between Cape Cod and the western Georges Bank (the area east of the Great South Channel) and 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°W or 69°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 process, 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.

- Promote additional use of natural markers because of previously successful applications in documenting spatial variation, particularly if done cooperatively with the fishing fleets to optimize low cost and large sampling scale.

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

- Integrate 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: "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 2 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, several 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 reactivation of spawning grounds; to investigate natural markers, especially genetic markers, for stock identification and possibly for mixed stock analysis; and to 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 examined 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 US 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 necessitates additional studies with natural markers in areas with high catches/abundance of nonspawning 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 5 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: The age at which a fish has a 50% probability of being sexually immature or mature and ready for spawning.

ACSSWG: US and Canadian scientists in government, universities, and nonprofit organizations formed the Atlantic Cod Stock Structure Working Group in early 2018 to inventory and summarize all relevant peer-reviewed information about stock structure of Atlantic cod in an international and interdisciplinary effort that brings together the existing data, studies, and knowledge about cod stock components.

Adaptive genetic variation: Changes resulting from natural selection found between the genomes of individuals that have evolved to help an organism to increase its fitness.

AIC: Akaike's information criterion is an estimator of prediction error that evaluates the relevance of one model against another, given a set of data. Simply put, AIC penalizes a model with more independent (predictor) variables, so AIC identifies the best-fit model as the one that explains the greatest amount of variation by using the fewest possible independent variables.

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

Annulus (plural: annuli): An annual growth increment shaped like a ring and observable in a mineralized part of a marine organism, such as the ear stone (otolith). Each annulus represents a year's growth, so by counting the annuli, it is possible to estimate the fish's age, similar to rings in the trunk of a tree.

Anticyclonic: A clockwise flow of air or water 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.

Assignment test: The use of individual genotypes to assign individuals to populations or clusters.

Benthic: Associated with or occurring on the bottom of the ocean or other body of water.

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

Biological population: A group of organisms of one species that interbreed and live in the same place at the same time.

Candidate gene: a gene whose chromosomal location is associated with a particular phenotype, trait, 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 because of incompatibility while pairing during meiosis.

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

Cyclonic: A counter-clockwise flow of air or water in the northern hemisphere, as driven by the Coriolis effect.

DFO: Fisheries and Oceans Canada is a department of the government of Canada responsible for developing and implementing policies and programs in support of Canada's economic, ecological, and scientific interests in oceans and inland waters.

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 by using tracking technologies (e.g., acoustic transmitters)

Extirpation: When a species ceases to exist in a chosen geographic area of study, though it still exists elsewhere (i.e., a local extinction).

Fishermen's Ecological Knowledge: Encompasses information on biology of species and climatic and oceanographic changes, related to schools of fish and their capture. Local fishermen can contribute their knowledge to the evaluation of living marine resources.

Fishing Statistical Area: See Statistical Area.

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

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

Genetic drift: Changes in gene frequencies within a population owing to random chance disappearance of particular genes.

Genetic marker: a gene or DNA sequence with a known location on a chromosome that can be used to identify individuals, populations, or species. This genetic variation is an observable, heritable indicator in a specific location on a chromosome. useful for identifying individuals or populations.

Genome: The complete set of genes or genetic material present in an organism (RNA and DNA, coding and noncoding).

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 US and Canadian fishing waters.

Interdisciplinary (holistic) approach: Collection, review, and synthesis of data from multiple disciplines (e.g., life history, natural markers, fishermen's ecological knowledge), 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 (countable) characteristics in various species of fish. The most commonly observed relationship is that fin ray, vertebrae, or scale numbers increase with decreasing temperature.

L_{50}, Median length at maturity. See A_{50}. The length at which a fish has a 50% probability of being sexually immature or mature and ready for spawning.

Life history: The pattern of distribution, abundance, survival, and reproduction events during the life of an organism. Life history traits between populations include maximum body size, longevity, age at maturity, and fecundity.

Linkage disequilibrium: Nonrandom association of alleles at 2 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: All of the genes and markers on a single chromosome that are frequently inherited together 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.

Local adaptation: A population becomes well suited to the particular environmental features of its location through evolution and the associated gene frequency changes (see **adaptive genetic variation)**. For local adaptation to occur between populations, they each experience and respond to different selective pressures from the environmental.

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

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.

MA MFI: Massachusetts Marine Fisheries Institute is a cooperative venture between UMass Dartmouth's School for Marine Science and Technology (SMAST) and the Massachusetts Division of Marine Fisheries. It promotes sustainable fisheries by providing timely information needed to protect, conserve, and manage Massachusetts marine and coastal resources and fostering a cooperative working relationship among scientists, government, fishermen, and environmentalists.

MARMAP: The Marine Resources Monitoring, Assessment, and Prediction was an ecosystem monitoring program from 1977 through 1988, when the program collected biological and environmental information from periodic surveys of northeastern US continental shelf waters. The program integrated field data on seasonal and annual variability with fine-scale process-oriented field studies and laboratory research.

Meristics: Countable physical features of fishes such as fin spines and rays, gill rakers, lateral line scales, and vertebrae.

Metapopulation: A group of spatially separated populations of the same species which interact at some level.

Microsatellite markers: A tract of repetitive DNA in which certain DNA motifs are repeated, typically 5–50 times. Microsatellites occur at thousands of locations within an organism's genome. They have a higher mutation rate than other areas of DNA leading to high genetic diversity.

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 broadscale differences among deep evolutionary lineages and is 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.

NAFO: Northwest Atlantic Fisheries Organization is an intergovernmental organization with a mandate to provide scientific advice and management of fisheries in the northwestern part of the Atlantic Ocean, to ensure long term conservation and sustainable use of the fishery resources, and to safeguard the marine ecosystems in which these resources are found.

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 adjacent to US waters are delineated as division 4, particularly 4X, which encompasses the Bay of Fundy, the Scotian shelf, and offshore banks such as Browns Bank.

Natal homing: A return migration of sexually mature individuals to spawn upon the grounds where they were spawned.

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.

NEFMC: New England Fishery Management Council is one of eight regional councils established by federal legislation in 1976, is charged with conserving and managing fishery resources from three to 200 miles off the coasts of Maine, New Hampshire, Massachusetts, Rhode Island, and Connecticut.

NERCTP: Northeast Regional Cod Tagging Program was initiated to study cod movements using a standardized technique on a region-wide scale, whilst simultaneously achieving international collaboration between fishermen and scientists.

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: Genomic locations (or markers or base pairs) that show behavior or patterns of variation that are extremely divergent from the rest of the genome. These are often diagnosed as having statistically higher differentiation than expected under neutrality and are interpreted as 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: The set of observable characteristics of an individual, such as its size or shape, rate of growth, behavior, resulting from the interaction of its genotype with the environment.

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 procedure is sometimes conducted with 2 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.

SCCZ (Spring Cod Conservation Zone): A seasonal spawning closure in northern Massachusetts Bay in the western Gulf of Maine.

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).

SNP, Single nucleotide polymorphism: Single base differences at any position in the genome, occurring as the result of point mutations; one type of 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.

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 different areas throughout the year. For example, 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 primary scientific and technical advisory body to the fishery management councils and is made up of scientists who are independent of the councils.

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.

Stock: 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.

Subpopulation: A single, mostly self-sustaining unit within a metapopulation.

Sympatric: Biological populations that overlap geographically.

TMGC: Transboundary Management Guidance Committee enhances coordination among fishery management partners concerning process-related issues, data needs, and stock assessments; or serve as mechanisms to facilitate management negotiations. Council members, NOAA Fisheries representatives, and Canadian officials who serve on the TMGC negotiate the allocations annually based on the historic proportions of fishery landings caught by US and Canadian fishermen, and resource distribution.

TRAC: Transboundary Resources Assessment Committee: the scientific arm of the US-Canada Transboundary Resources Steering Committee. This group ensures discussion between the United States and Canada on transboundary integrated ecosystem management issues associated with the Gulf of Maine and Georges Bank marine environment.

Transboundary: Crossing over national boundary lines. 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.

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