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Atlantic Cod Stock Structure in the Gulf of Maine

ABSTRACT

Atlantic cod (*Gadus morhua*) in the Gulf of Maine provide an important but depleted fishery that needs to be made sustainable. However, restoring and maintaining robust population components to achieve sustainability is made difficult when their distribution and character is unknown. This study clarifies the structure of the Gulf of Maine cod grouping by deriving the distribution, movements, and behavior of population components from 1920s data and surveys of retired fishermen. These derivations are consistent with current cod populations and with the existence of localized spawning components. Nearly half the coastal spawning grounds of 50 to 70 years ago are abandoned today and their spawning components have disappeared, suggesting depletion, undetected by system-wide assessments, may have been well advanced by the 1980s.

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The Gulf of Maine (GOM) fishery for Atlantic cod (*Gadus morhua*), a mainstay for New England and Canadian fishermen (Rich 1929; O'Leary 1981), has remained relatively productive and resilient to fishing pressure until recently, even though the stock biomass has been declining for a number of years. In 1998, National Marine Fisheries Service (NMFS) reported Atlantic cod stocks in the Gulf of Maine were overexploited and at extremely low biomass levels (Mayo et al. 1998). Historical studies describe the decline of some Atlantic cod stocks as long-term processes that vary greatly in the short term and are related to human interaction (Hutchings and Meyers 1995). They imply that if such fisheries were to be restored, more effective management would have to be developed. Implicit to improved management, however, is the need to identify the population components of Atlantic cod found in areas like the Gulf of Maine and to better understand how those structures relate to diversity within and among species (Smedbol and Stephenson 2001).

In the present article, I evaluated the distribution and dynamics of Atlantic cod in the Gulf of Maine (GOM) during the 1920s, a period when cod were abundant (Rich 1929; Ames 1997). Subpopulations and spawning components were tentatively identified; their distribution and spawning areas were compared to recent tagging studies and cod egg distribution surveys. The study area included the GOM lying north of a line from northern Massachusetts Bay (42 30'N) to Wrights Swell (42 30'N, 68W), thence northeast to Yarmouth, N. S. (43 50'N, 66 7'W) (Figure 1).

A Review of Atlantic Cod Population Structure and Dynamics in the Gulf of Maine. To clarify the terms used to describe population structure, the following definitions were used: a population is a self-reproducing group of conspecific individuals that inhabit the same range at the same time, are affected by similar environmental factors, and are reproductively isolated from other populations. A subpopulation is a semi-independent, self-reproducing group of individuals within a larger population that undergoes some measurable but limited exchange of individuals with other areas within a population. A spawning component is a segment of a population that does not differ in genetics or growth, but occupies discrete spawning areas inter-annually. A stock is an arbitrary collection of fish large enough to be essentially self-reproducing, with members of the unit exhibiting similar life history, and a local stock is a stock that remains in a local area throughout the year (Smedbol and Stephenson 2001).

The GOM Atlantic cod stock is described as being one of three or possibly four groupings of cod found in northeast U. S. waters (Serchuk and Wigley 1993). Groupings were reported to have limited exchange with others (Wise 1963; Serchuk et al. 1994), but the issue of genetic separation remains unclear. The GOM grouping was identified by length-frequency differences (Wise and Murray 1957, 1958, 1959), parasite studies (Sherman and Wise 1961), and meristic studies (Schmidt 1930), and was reported to contain many subdivisions (Wise 1963).

Reproduction, based on the maximum average abundance of cod eggs in the Gulf of Maine, occurs in March (Berrien and Sibunka 1999). In the study area, however, coastal spawning areas exhibit a bimodal pattern with peak spawning in spring and fall. Spring spawning occurs in some areas of the Bay of Fundy (Neilsen and Perley 1996) and on the inner historical spawning ground locations along the New England coast (Berrien and Sibunka 1999). Fall spawning generally occurs at the outer spawning locations and in coastal areas of the Bay of Fundy (McKenzie 1934). Recent studies indicate cod return to natal spawning areas (Perkins et al. 1997; Wroblewski 1998; Green and Wroblewski 2000). Gulf of Maine Atlantic cod spawning grounds and juvenile habitats are on the coastal shelf and within approximately 37 km of the shore (Bigelow and Schroeder 1953; Ames 1997; Berrien and Sibunka 1999).

With the approach of spawning season cod start migrating towards their respective spawning grounds, often appearing to move sequentially closer (Perkins et al. 1997). Spawning migrations close to the shore and rivers of the Gulf of Maine historically involved large fish, but during the 1920s, the average size of cod on most other spawning grounds was smaller (Bigelow and Schroeder 1953).

After arriving at their spawning area, Atlantic cod often gather into large schools (Earll 1880; Smedbol 1997). Being broadcast spawners, older adults release small quantities of eggs into the water column over a period of time until spent. Depending on salinity, cod eggs usually float to the surface and are gradually dispersed by winds and currents. Eggs hatch in two or more weeks, depending on water temperature, and in another month or more, the resulting larvae metamorphose to juveniles and settle to the bottom. Predation is very high on young juveniles during this phase unless they quickly find shelter within interstices of the proper size among substrate particles (Gotceitas and Brown 1993).

Once spawning is completed, Atlantic cod leave their spawning areas to pursue forage stocks in various feeding areas and initiate the next annual cycle.

Methods

Sources of 1880s Fishing and Spawning Ground Information: The 1880s database of cod grounds relied heavily on descriptions and maps found in Collins and Rathbun (1887) and Earll (1880). Collins and Rathbun gathered their information from interviews with fishing captains of the

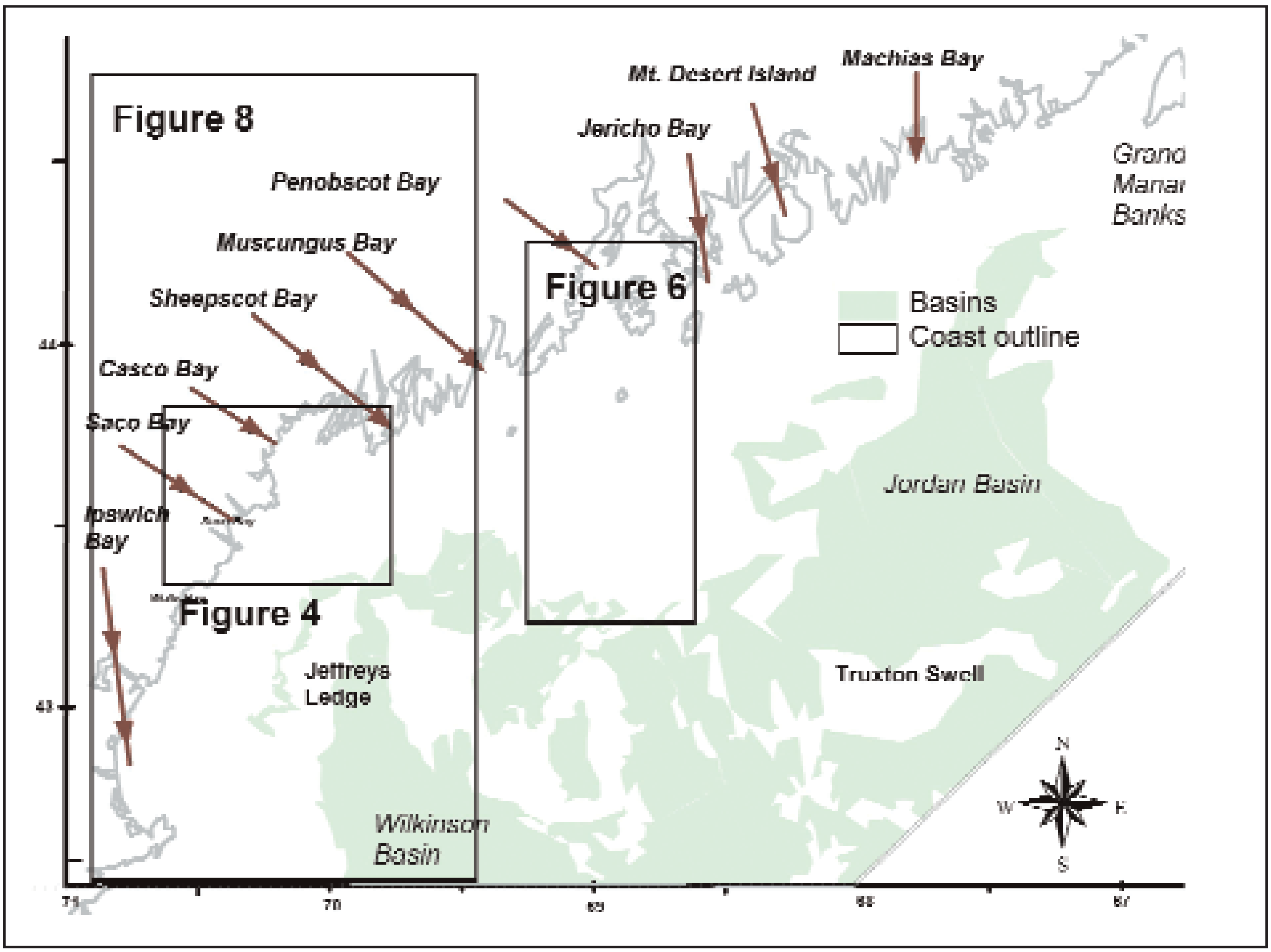


Figure 1. A map of the study area shows the location of figures used in the study.

period, while Earll focused on cod spawning activity in Ipswich Bay. The limited number of appropriate records used to construct the 1880s database restricted its use to evaluation of the persistence of cod on particular fishing grounds.

Sources of 1920s Fishing and Spawning Ground Information: The 1920s database formed the basis for the current study. The cod fishing grounds of Rich (1929), supplemented by Bigelow and Schroeder (1953) and Ames (1997), provided historical fishing ground information. Rich gathered his data from direct interviews with "a large number of fishing captains of long experience upon these grounds" and "in cases of conflict of their opinion, the greatest agreement as to the facts has been accepted." His interviews were conducted during the 1920s and included "a large number of grounds described earlier by G. Browne Goode" (Collins and Rathbun 1887). Most interviews were with experienced captains using hook-and-line techniques. Additional grounds came from Ames (1997), who collected fishers' ecological knowledge (FEK) from 28 interviews with retired fishing captains, many of whom operated otter trawlers from 1930-1960, and the classic work by Bigelow and Schroeder (1953) that summarized 1920s and 1930s fisheries research from U.S. Bureau of Commercial Fisheries.

Cod spawning areas of the period identified by Ames (1997) were supplemented by additional grounds from Bigelow and Schroeder (1953) and Coon (1998), who had gathered FEK in the Bay of Fundy area about where ripe Atlantic cod were caught. Cod egg distribution studies by McKenzie (1934) were used to confirm locations identified by Coon (1998). Cod spawning area criteria (Ames 1997) required that spawning areas have two or more independent reports of ripe cod being caught on site during spawning season, with depths of 10 m to 100 m, and that the substrate was sand, muddy sand, muddy gravel, or a muddy basin grading to sand along its edges. Much of this information came from otter trawlers of the period. Spawning areas were often depressions of muddy gravel and sand bordering cod feeding grounds. Bigelow and Schroeder did not discuss spawning area substrates, but NOAA charts indicated the areas identified had appropriate depths and substrates.

Gulf of Maine spawning seasons for cod were obtained from historical reports (Earll 1880; McKenzie 1934; Bigelow and Schroeder 1953) and recent cod egg distribution surveys (Nielsen and Perley 1996; Berrien and Sibunka 1999). Cod spawning peaked between September and December in the GOM and continued at moderate levels from January through May. Several areas had two or more spawning events in the same year. Cod eggs continue to be reported at many Gulf of Maine locations each year, but recent spawning events east of Casco Bay have been intermittent and small (Berrien and Sibunka 1999).

Locating Historical GOM Fishing and Spawning Grounds. Historical fishing and spawning grounds were compiled in a GIS system by following historical navigation instructions with a navigation program using digitized NOAA nautical charts (Ames 2001). Single or multiple point bearings were extrapolated to a point near the ground. From the immediate vicinity of this point, a location was selected that had the appropriate scale, orientation, and benthic characteristics consistent with that described by fishermen (Figure 2a). In the case of spawning areas, these characteristics were in agreement with the depth and substrates of other known spawning habitats of Atlantic cod, e.g., muddy depressions of sand or gravel or hard mud bottom surrounded by cobble or gravel. This procedure imparts a visual precision to the figures that, absent this clarification, would appear to overstate the information contained in the historical navigation instructions.

Determining Seasonal Distributions of Atlantic Cod Using Relative Availability (RA). Maps were prepared for each season of the year showing distribution based on fishermen's estimates of Atlantic cod concentrations on cod grounds (Rich 1929). Fishermen normally estimated the availability of cod by describing fishing as good, fair, poor, etc. It provided a convenient way to share information with each other, regardless of the size of the vessel, or type of gear being used, and avoided the need to share vessel landings which were proprietary information and often unavailable. When placed in appropriate spatial and temporal context, their observations of cod concentrations allowed their knowledge to be applied to tracking historical cod shifts in cod availability.

Relative availability (RA) quantified those estimates for each season on each specific fishing ground. It provides no actual measure of tonnage landed, but refers to which season fishermen deemed best, average, or poorest for catching cod on a particular ground. High RA values occurred when large seasonal concentrations were present and described optimal conditions for cod to gather on a particular fishing ground. RA values ranging from 0-4 (Table 1) were used to establish color gradients on GIS displays of fishing grounds to visualize seasonal spatial distributions of cod availabilities (Figures 3a,b,c,d).

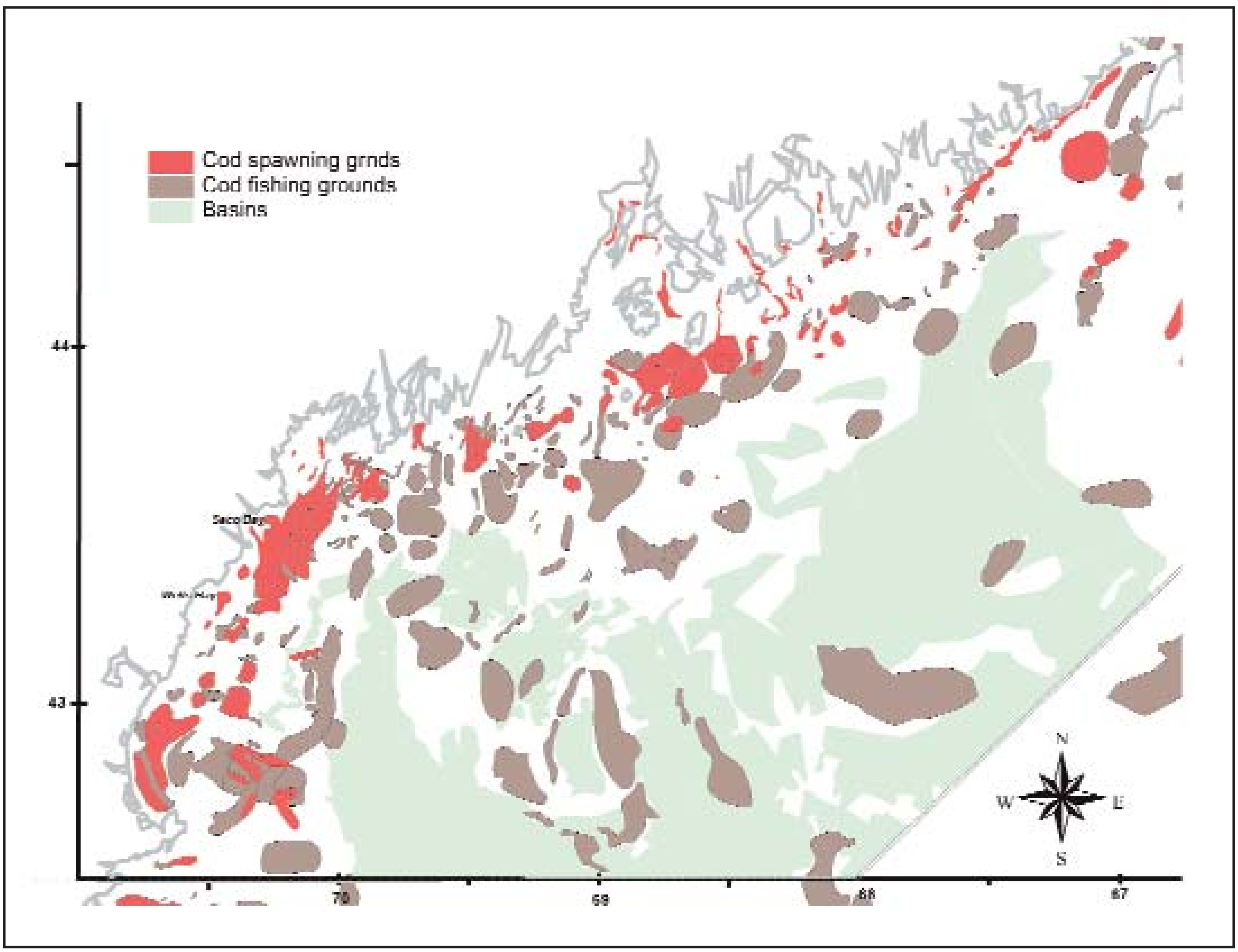
Determining Historical Movements of Atlantic Cod with RA values. In addition to determining seasonal distribution, RA values were used to track 1920s cod movements and migrations between seasons. Grounds recording an increase in RA during a seasonal change were assumed to have received additional cod from the nearest bordering fishing ground reporting a lower RA value. In other words, it was assumed that cod minimize the distance traveled in migration. One could imagine river-like topographies where fish had to pass one site in order to reach others, but, with some exceptions, this is not the case in the GOM.

The direction of RA movement between bordering grounds was described on GIS with an arrow drawn between the two bordering grounds. This procedure yielded unambiguous results when tracking local movement patterns of isolated cod concentrations that linked the winter locations of subpopulations with historical spawning areas (Figure 4). However, the identities were obscured when two or more cod concentrations overlapped. Cod movements could only be tracked along the grounds mapped, but cod were assumed to also inhabit areas surrounding the grounds at times and overlaps of movement were interpreted to be general seasonal movements (Figures 5a,b).

Regions having a broad-based, continuous direction of RA movement involving several grounds one season and accompanied by a similar, opposite movement during a later seasonal change, were tentatively classified as migration corridors (Figure 6). These areas showed migration patterns similar to recent tagging studies in eastern GOM (Hunt et al. 1998) and western GOM (Perkins et al. 1997).

Identifying Historical Spawning Components. Spawning components were identified by tracking seasonal RA values through an annual cycle. A given cod concentration on a ground experiencing a seasonal decrease in RA value was assumed to have moved to the nearest ground showing an increase in RA. Concentrations were tracked only where cod were present all

Figure 2a. Historical fishing grounds and spawning areas of Atlantic cod in the Gulf of Maine were used to create an X-Y plot for tracking Atlantic cod movements.



year and their shifts were obvious. Cod concentrations that were present all year and demonstrated cyclic RA movement patterns between their winter grounds and a specific historical spawning area that was occupied during spawning season were tentatively identified as spawning components. Many of these historical spawning sites are still active while others are abandoned and their spawning components have disappeared (Ames 1997; Berrien and Sibunka 1999).

These mapping procedures produce patterns that are strongly consistent with the existence of local populations and were distributed along the entire length of the northern GOM coastline.

Experimental Design: Edge Effects. Seasonal migrations and movements of cod concentrations were tracked on an X–Y grid of fishing grounds. This strategy worked well as long as the movement remained within the grid. However, when fish movement occurred at the edge of the grid (for instance, movements during the summer in Penobscot Bay) they were arbitrarily assumed to move in the same direction as other cod in the immediate area.

Table 1. Fishermens' descriptions of cod fishing were standardized into relative availability (RA) values.

Descriptive comments	Atlantic cod concentrations
Not mentioned or absent	0
Poor fishing	1
Fair or present with no estimate	2
Good or abundant	3
Excellent or very abundant, etc.	4

Results

Characterizing the Gulf of Maine's Historical Atlantic Cod Grounds. In all, approximately 260 fishing grounds (Rich 1929; Ames 1997) and 91 spawning grounds (Bigelow and Schroeder 1953; Ames 1997; Coon 1998) were distributed between Cape Ann in western GOM and the Lurcher Shoal in eastern GOM (Figure 2a). Inshore cod feeding grounds were generally areas of rocky bottom along the 100-m depth contour on the coastal shelf and bordered deeper coastal depressions and channels that were used as spawning areas in some locations. Depths on the grounds ranged from a few meters to more than 200 m. Atlantic cod grounds further offshore included the banks, ridges, and swells that lie between the major basins of the gulf. Most historical fishing grounds were located on the shelf within 45 km of land.

Coastal spawning grounds of Atlantic cod were either contiguous with, or when in the vicinity of major bays, often closer to shore than fishing grounds of the period. Spawning occurred in channels and basins bordering the rocky, shallow historical fishing grounds described by Rich and generally had bottoms of muddy gravel, sand, or mud with borders of gravel and varied in depth from less than 10 m to 100 m.

Identifying Essential Fish Habitats of Atlantic Cod in the Gulf of Maine. The selectivity of otter trawling and hook fishing, the two major fishing technologies of the 1920s, lend insight into the seasonality of different habitats by Atlantic cod. During the 1920s, Atlantic cod in the GOM were most commonly caught on baited hooks, a technology selective for foraging fish. Decades of directed fishing with hooks on the Atlantic cod's historical fishing grounds had established those grounds as preferred foraging habitats for Atlantic cod in the GOM at certain times of year. Even though the particular forage species that once attracted cod to feed at these locations remains unclear, the location of the cod's feeding areas and the seasons they were present allows thousands of square kilometers of Atlantic cod habitat to be identified.

In similar fashion, captains of early otter trawlers discovered that cod gathered along the margins of basins and channels bordering historical fishing grounds when not feeding, and in some locations, used the channels and basins as spawning areas.

Determining the Long-term Productivity of Cod on Historical Atlantic Cod Fishing Grounds. Of the 260 fishing grounds from the 1920s used in the study (Rich 1929, Ames 1997), 92 were being fished prior to 1880 (Collins and Rathbun 1887). All of the 1880s grounds continued to be productive in the 1920s, though several had reduced landings. By the 1980s, 64 of the 1880s grounds were still producing cod, while 26 inner grounds of the 1880s reported no cod.

The safety and effectiveness of motor-driven technologies rapidly displaced coastal fishing vessels relying on sail. Their development made inner grounds very accessible in winter and by the 1930s, they had become the favored fishing grounds of two new fishing technologies, otter trawlers and coastal gillnetters (Alexander 1914; Ames 1997). Their introduction, combined with the cumulative depletion of anadromous forage stocks caused by dams and coastal industrialization (Baird 1883), were major factors in the demise of the coastal cod fishery.

Evaluation of 1920s Seasonal Distribution. In spite of their wide distribution, Atlantic cod were present on most 1920s fishing grounds for only a few months of the year. Of the 260 grounds surveyed during the 1920s, only 60 were year-round fishing grounds (Figure 2b). All but

17 were deeper, offshore grounds with no reported spawning activity. Most of the remaining 200 grounds were cod grounds for two seasons of the year or less.

Of the 88 grounds reporting cod in winter and 161 grounds reporting in spring, 54% had very good cod fishing. It seems likely that the Gulf of Maine's fall and spring spawning seasons may have influenced these results. Fishermen found fewer grounds with good fishing (RA=3) in summer and fall (38% and 41% respectively), suggesting that Atlantic cod were more dispersed after spawning. The total number of cod fishing grounds and number of grounds with good fishing were summarized for each season (Table 2).

Identifying the Seasonal Movements of 1920s Atlantic Cod. Migrations and local movements were based on seasonal shifts of 1920s cod concentrations among fishing grounds. These occurred on both sides of the Gulf of Maine (Figure 6a) and agreed well with recent tagging studies (Perkins et al. 1997; Hunt et al. 1998). To avoid confusion in the current article, movements refer to cyclic movement patterns between the winter grounds of one of four large concentrations of cod and historical spawning areas lying nearby while migrations refer to large-scale RA movement patterns that extend beyond the winter grounds.

Winter, the Winter Buffer Zone, and the Separation of Inshore and Offshore Populations. In winter a continuous band of fishing grounds, sandwiched between the coast and Cashes Ledge and extending from north of Jeffreys Ledge to Grand Manan Bank, was abandoned by Atlantic cod. This appears as a zone separating inshore and offshore populations (Figure 3d). The 1920s buffer zone included more than 14 cod fishing grounds that were productive for much of the year, but had no cod landings in winter. At the same time, good winter cod fishing was reported on either side of the buffer zone.

The 1920s winter buffer zone is significant because it provides evidence of a separation between coastal cod and offshore cod precisely at the time of year when many Atlantic cod are found close to their spawning grounds and suggests that fishing grounds in the winter buffer zone were seasonal feeding areas that had been abandoned as spawning season approached.

Historical Atlantic Cod Migrations in the Gulf of Maine. When movement patterns between bordering fishing grounds in the GOM are viewed as a whole, the direction of historical migrations are evident. Offshore concentrations of 1920s Atlantic cod in the GOM generally migrated north in spring and south in fall, while inner coastal shelf cod generally had inshore-offshore movement patterns (Figure 6a).

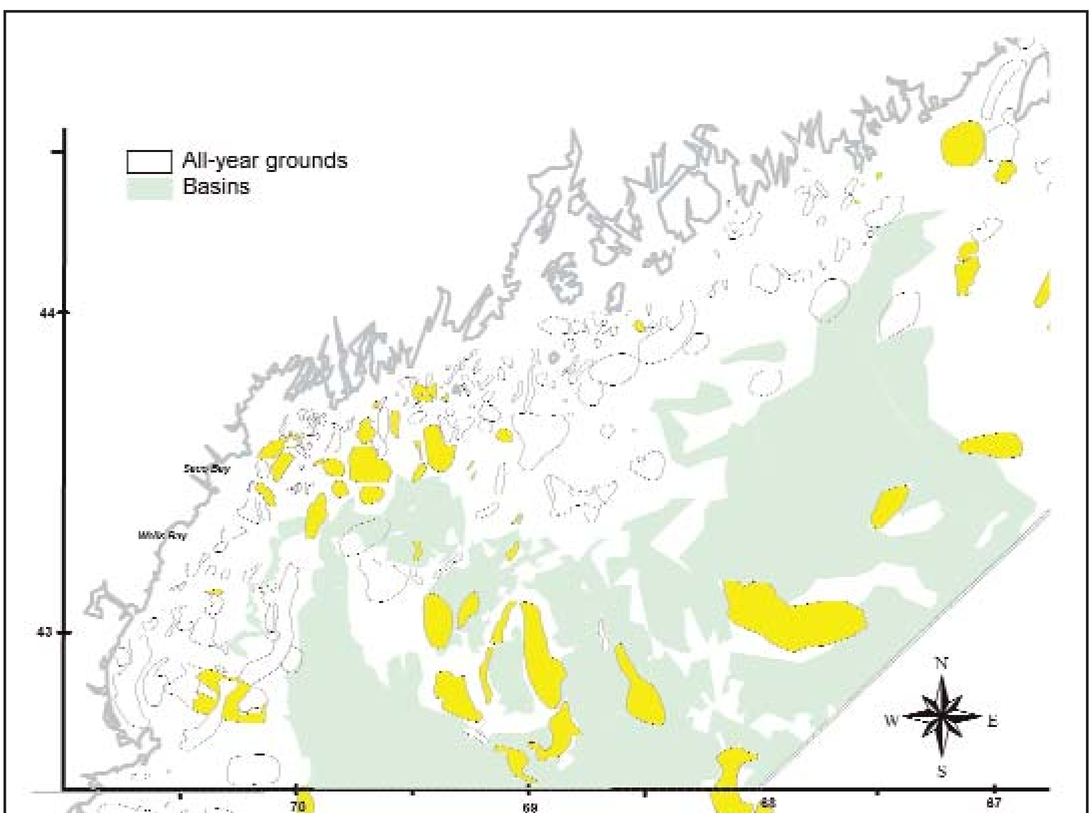


Figure 2b. Year-round Atlantic cod grounds located offshore had no spawning activity.

Movements and migrations among historical fishing grounds were in agreement with recent tagging studies (Perkins et al. 1997; Hunt et al. 1998).

Discussion

Determining Spatial Features of 1920s Atlantic Cod Stock Structure: Gulf-wide overviews were constructed to track seasonal shifts in cod availability (RA) in an effort to evaluate fine-scale population structures in the Gulf of Maine grouping. The overviews revealed how various parts of the 1920s grouping functioned as a system when the stock was robust. This allowed the interactions of various parts of the system to be studied in detail.

Wise (1963), during his characterization of the Gulf of Maine grouping, detected smaller population components that he described as subdivisions. The four large winter concentrations of Atlantic cod distributed along the coastal shelf were assumed to be those subdivisions inhabiting the study area. Further examination showed that some cod concentrations in the subdivision migrated seasonally and returned to the same spawning areas annually, while others stayed nearby. Local shifts of non-migrating cod in each subdivision between the winter grounds and specific local spawning grounds revealed several areas where cod behaved like spawning components and local stocks (Smedbol and Stephenson 2001).

Subpopulations: Each subdivision had discrete migration corridors, local cyclic movements to and from spawning grounds, nursery areas, and was partially isolated by bathymetry. The four subdivisions identified in the study were composed of clusters of spawning components or local stocks. That is, they functioned as subpopulations (Table 3).

This classification was further supported by the area-specific nature of their depletion, the co-extinction of several 1920s coastal spawning components associated with the loss of anadromous forage stocks such as alewives, the demonstration of local, long-term reproductive capacity from correlation of 1920s spawning sites with 1977-1987 cod egg distribution patterns, and validation of 1920s historical migrations and movements from two recent tagging studies in eastern and western Gulf of Maine.

Several features were common to Gulf of Maine subpopulations. In winter, cod gathered into major concentrations (Figure 3d) via separate movement patterns (Figure 6b). Each subdivision occupied a relatively distinct region on the coastal shelf that appeared to be partially separated from the others by deeper basins. subpopulations had several spawning grounds (Figure 2a), nursery areas, and a seasonal migration corridor abutting its winter grounds. Migration corridors led away from the winter grounds following local bathymetry and in some instances, involved the ridges and swells separating the major basins (Figure 6).

Significant numbers of Atlantic cod also remain offshore during spawning season. They are found in large numbers all year on the Cashes Ledge complex and the rises and swells rimming the

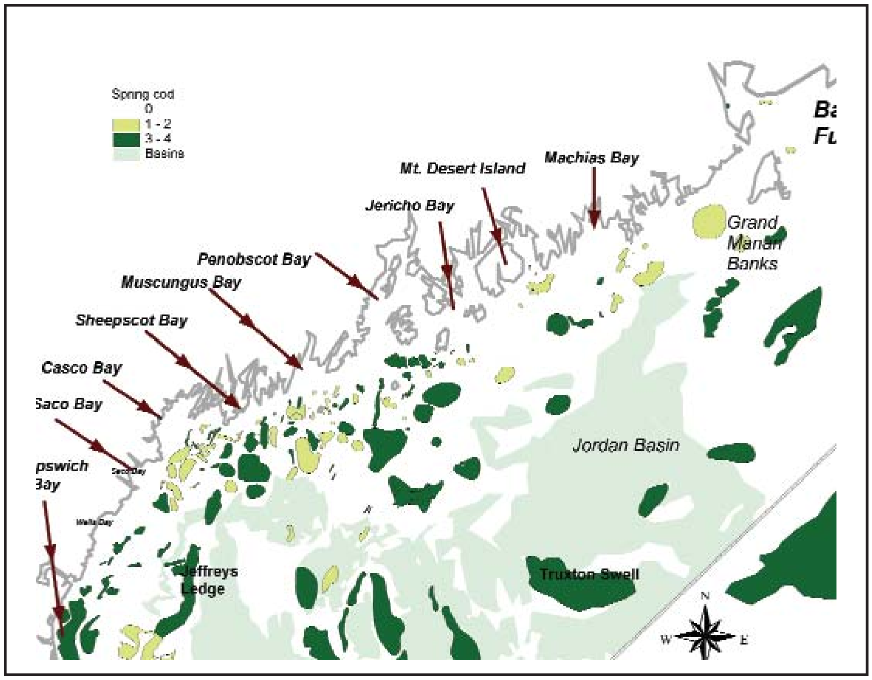
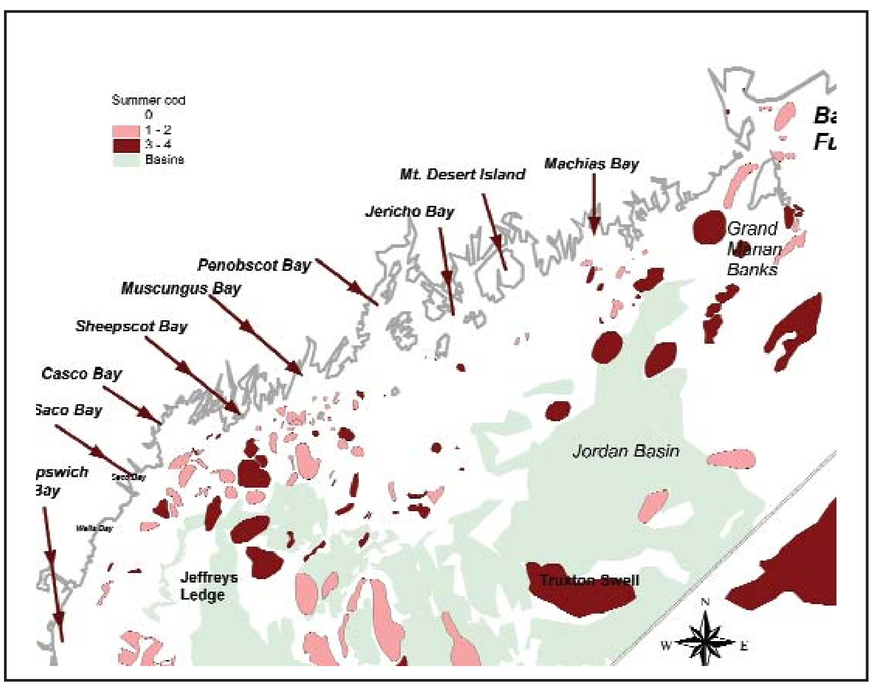


Figure 3a. The distribution of Atlantic cod and relative size of their concentrations in spring is displayed as a color gradient of fishing grounds.

Figure 3b. The distribution of Atlantic cod and relative size of their concentrations as relative availability (RA) values in summer is displayed as a color gradient of fishing grounds.



Gulf's major basins, making them very productive fishing grounds (Figure 2b). Rich (1929) described these areas as being migration conduits and feeding areas for Atlantic cod. No historical reports of ripe cod were found for the offshore areas and the 11-year cod egg survey by Berrien and Sibunka (1999) found but a single isolated spawning event near the ridge south of Fippinies. Movement patterns support their function as feeding areas for reproductively resting cod from bordering subpopulations.

Spawning Components / Local Populations. Using a list of criteria from available 1920s data (Table 4), 16 historical spawning components were tentatively identified among the 4 subpopulations. Identification was limited to areas where Atlantic cod concentrations remained in the subpopulation's area all year and seasonal shifts between winter fishing grounds and a spawning ground were obvious. This provided evidence that Atlantic cod were using specific spawning areas in each subdivision. All are described as spawning components, even though many spawning grounds in the eastern GOM once active in spring are now inactive and may have involved local populations that are now extinct.

The territory and movement patterns of two typical historical spawning components from the Midcoast subpopulation are shown; an extinct, inner western Penobscot Bay component that spawned in spring and disappeared in the 1940s, and a recently active spawning component of outer eastern Penobscot Bay that spawned in the fall (Figure 5).

Concentrations of eastern Penobscot Bay Atlantic cod returned from their offshore summer grounds in the fall to spawn on Bowdies and Gravelly (south of Matinicus Seal Island) where they remained through spring. Simultaneously, the inner western Penobscot Bay spawning component moved via Green Island Ridge, to grounds north of Matinicus and Seal Island where they remained until spawning in late winter/early spring. By summer, both components left the Penobscot Bay area for their summer grounds where they remained until fall.

The GOM demonstrates a remarkable variation in spawning times of Atlantic cod, with spawning occurring all year except midsummer. From 1977-1987, the winter grounds of historical subpopulations were usually spawning sites in the fall (Berrien and Sibunka 1999). Additional spawning components used inner spawning areas in spring.

The Interactions of Historical GOM Subpopulations and Spawning Components. Recent studies have given insight into ways historical subpopulations and spawning components interacted during seasonal migrations. The western GOM subpopulation, for example, is the most robust of the Atlantic cod subpopulations (Figure 8) and is dominated by Ipswich Bay's historical winter fishery for spawning Atlantic cod (Earll 1880; Bigelow and Schroeder 1953). With large concentrations of cod appearing in Ipswich Bay to spawn, it has always seemed logical to assume that other coastal spawning areas were not significant to either the fisheries of western GOM or Ipswich Bay (Bigelow and Schroeder 1953). Historical migration corri-

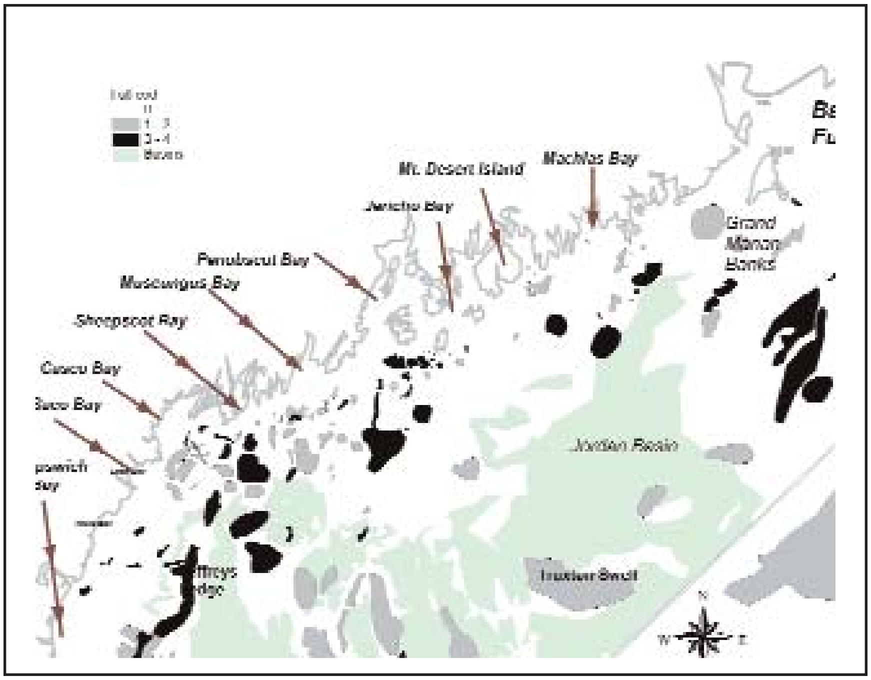
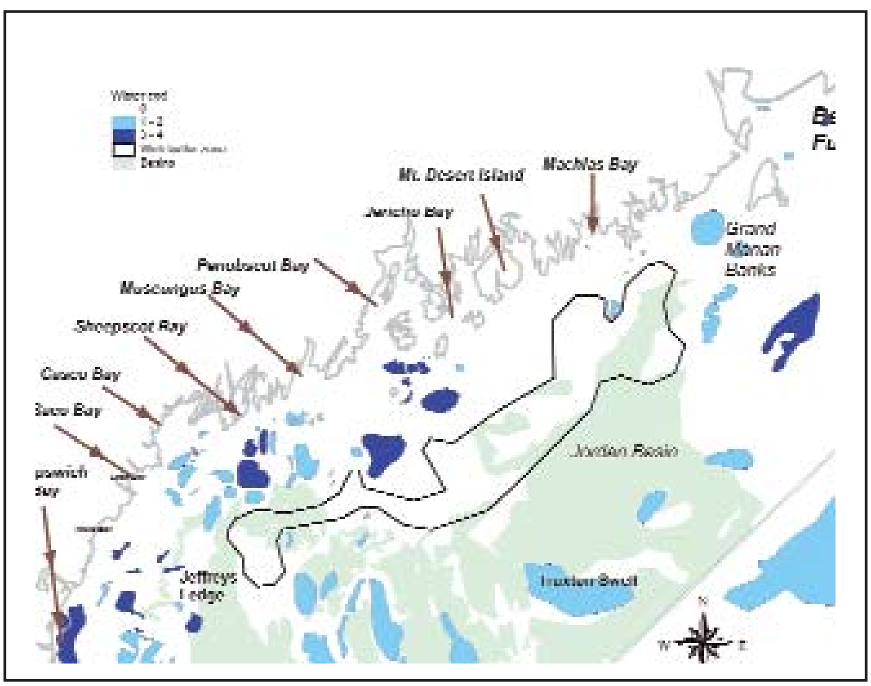


Figure 3c. The distribution of Atlantic cod and relative size of their concentrations as relative availability (RA) values in fall is displayed as a color gradient of fishing grounds.

Figure 3d. The distribution of Atlantic cod concentrations in winter and relative size of their concentrations is displayed as a color gradient of fishing grounds. The unoccupied cod grounds in the Winter Buffer Zone are also identified.



dors appeared to be simple transport corridors moving pre-spawning and spent fish to and from the two major spawning areas. However, that explanation no longer seems adequate.

Atlantic cod migrations to Ipswich Bay appear to be much more than simple spawning migrations. In fall, Atlantic cod tagged in the Sheepscot Bay region (Perkins et al. 1997) were shown to migrate progressively closer to Ipswich Bay, where they were caught during winter. They subsequently left Ipswich Bay in spring and returned to the Sheepscot area. The Perkins study showed that Sheepscot Bay cod contributed substantially to Ipswich Bay's winter cod fishery, though the reverse has not been established. This would have made Ipswich Bay landings in winter appear misleadingly large.

Berrien and Sibunka (1999) reported that spawning events in the Sheepscot area were common in May and November and in Ipswich Bay, in March-April, confirming historical observations (Earll 1880; Bigelow and Schroeder 1953). Spring spawning occurs in Sheepscot Bay spawning areas as Atlantic cod arrive from Ipswich Bay (Perkins et al. 1997). Spawning also occurs in late fall on outer Sheepscot spawning areas after the spring-spawning cod have migrated, and indicates two spawning components coexisted in the Sheepscot area.

By spring, Ipswich Bay cod had finished spawning and were leaving the Ipswich area, dispersing northward as part of a feeding migration (Bigelow and Schroeder 1953). Yet, Sheepscot Bay cod returning from Ipswich Bay were on their spring spawning migration to Sheepscot Bay (Perkins et al. 1997). The migration pattern is exactly opposite that of Ipswich Bay cod and describes the mixing of spawning components in the western subpopulation.

However, their seasonal migrations coincide with seasonal migrations of Atlantic herring (Clupea harengus) (Rich 1929; Bigelow and Schroeder 1953), raising the possibility that the pursuit of migrating forage stocks are involved in the reverse migration of Sheepscot Bay. Cod are

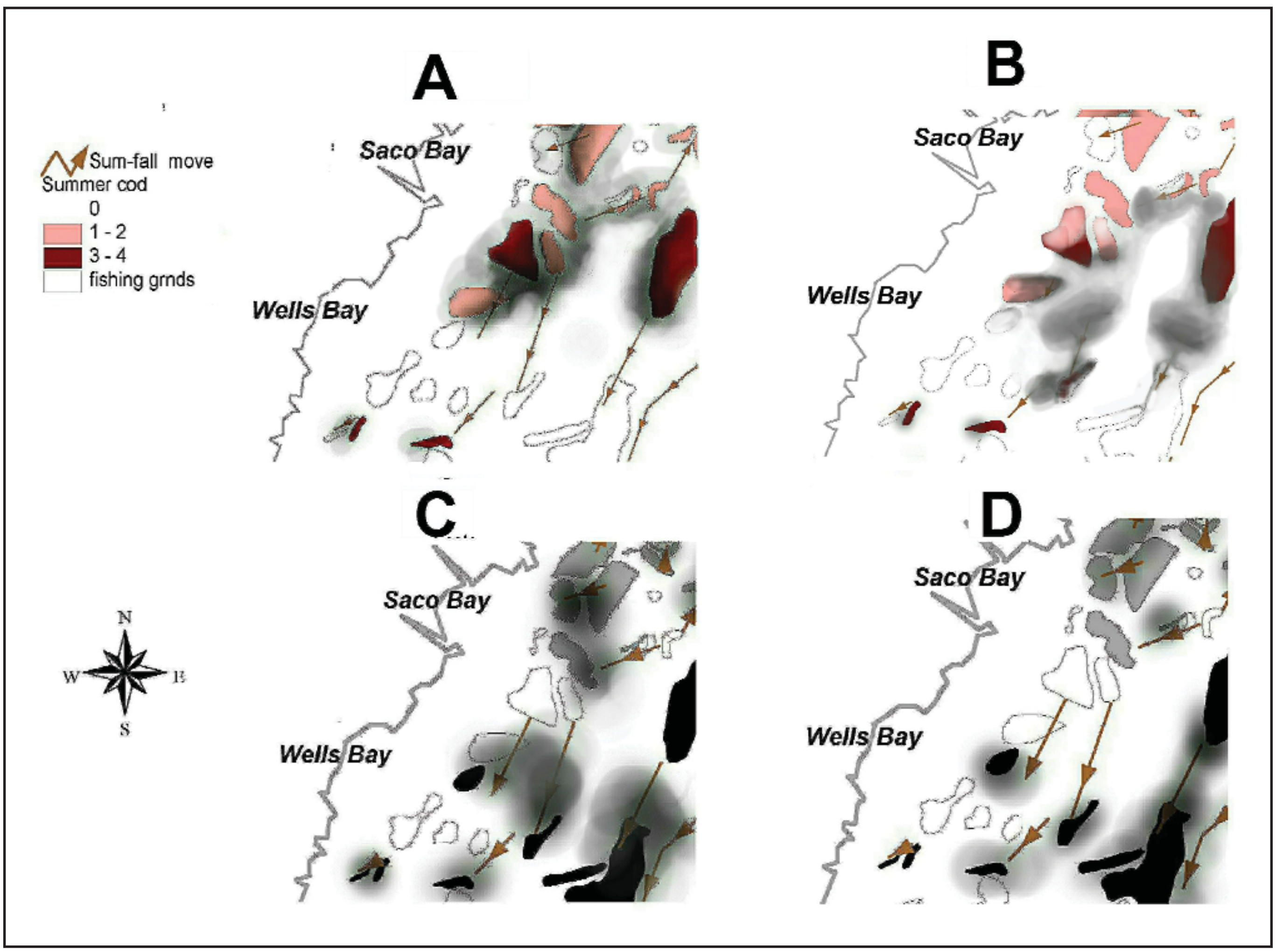


Figure 4. Sequential movements of Atlantic cod concentrations in the Wells Bay area are shown as they move from summer fishing grounds to those used in fall.

one of the three major predators of Atlantic herring (Collete and MacPhee 2002) and during the 1920s, both species overwintered in Ipswich Bay (Rich 1929; Bigelow and Schroeder 1953). Both spawning components migrated with herring in spring and fall, resulting in one spawning component being on a spawning migration while the other was on a feeding migration.

This would not be unusual. Coastal Atlantic cod also used to co-migrate in spring with alewives (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) as they returned to spawn in natal rivers and streams (Baird 1883). Baird reported that the loss of these forage stocks had triggered the collapse of the coastal cod fishery (Baird 1883) and the abandoning of spawning grounds lying close to rivers.

Such a pattern suggests that Atlantic herring and similar forage stocks may provide the impetus for Atlantic cod migrations and opens the possibility that cod are "programmed" to arrive at their spawning areas via their pursuit of a particular forage stock sharing a common migration corridor. The disappearance of local anadromous forage stocks and the disappearance of nearby Atlantic cod spawning components was a coincidence that occurred in several areas (Figure 9), suggesting that the traditional movement patterns and arrival times of Atlantic cod may have been disrupted at their inner spawning grounds when the forage stock disappeared. If so, the restoration of coastal populations of Atlantic herring, alewives, and river herring may also be important to restoration of coastal Atlantic cod fisheries.

Further Issues

While the study has demonstrated a relationship between historical and recent stock components, several issues challenge the relationship's validity and must be addressed.

Should inferred movements of cod stocks be used to make conclusions about stock structure? The study was based on the hypothesis that if Gulf of Maine cod concentrations could be tracked

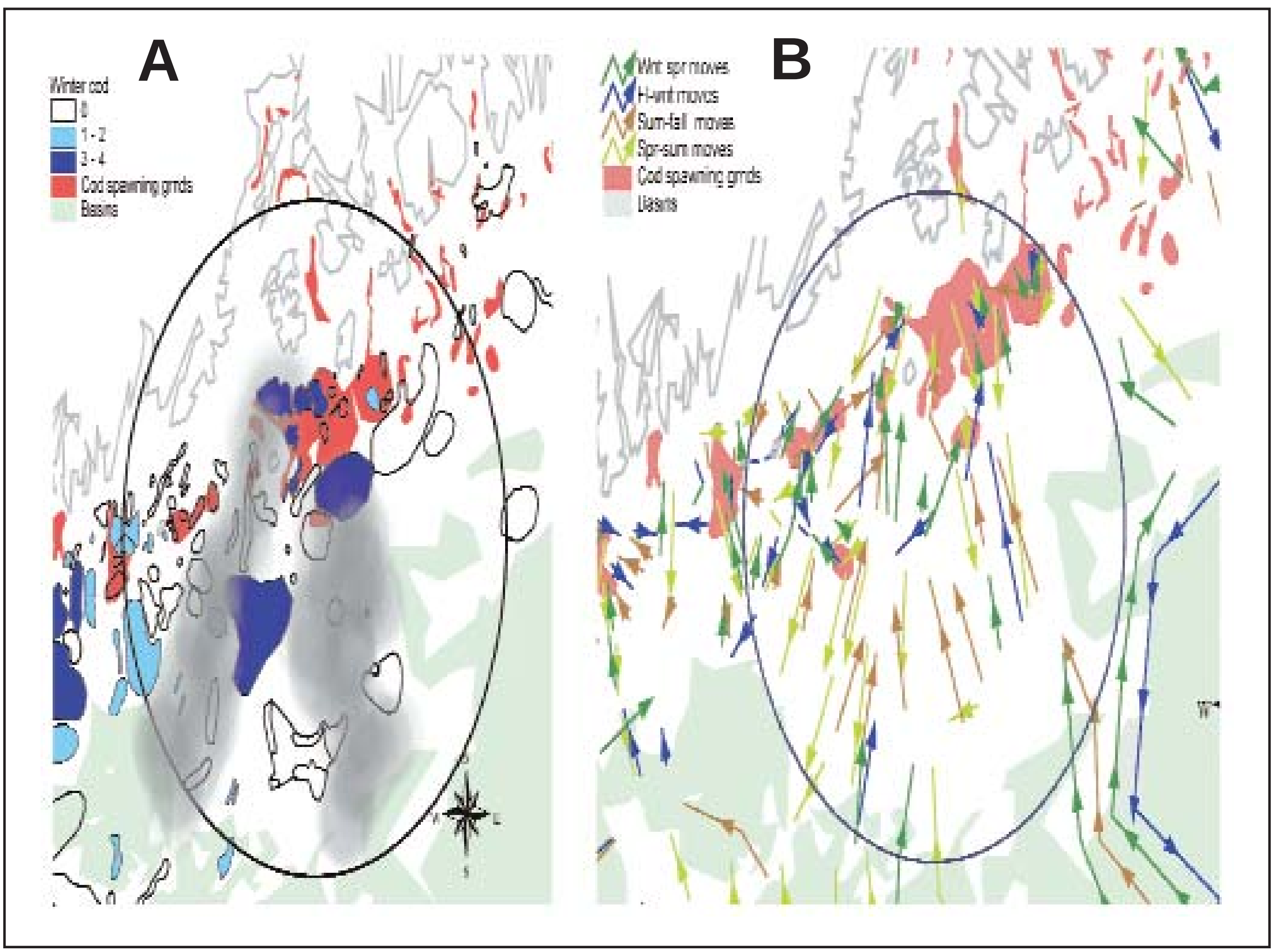


Figure 5. Local movement patterns of Atlantic cod of the two Penobscot Bay spawning components moved along different corridors, occupied different spawning grounds, and spawned at different times of year. Cashes Ledge lies slightly south (bottom) of the figure.

through the year, the location of population components in the grouping could be identified from their behavior and movements. Using the Atlantic cod's tendency to home to specific spawning areas, spawning grounds of the period were used as points of origin for identifying and tracking cod concentrations.

The protocol for tracking concentrations of Atlantic cod infers that they move conservatively; that is, they move from one fishing ground to the nearest bordering fishing ground offering appropriate conditions and habitat. These sequential movements along fishing grounds have long been recognized and exploited by New England fishermen, particularly in western Gulf of Maine. In fact, the inferred historical movements agreed with the results of the Perkins tagging study (1997) and the Hunt tagging study (1998) confirming the methodology used to identify movement patterns.

Table 2. The number of 1920 fishing grounds with landings of Atlantic cod.

	Winter	Spring	Summer	Fall	Year-round
# Grounds with cod:	88	161	117	134	58
Good fishing or better:	54%	54%	38%	41%	22%

Table 3. Gulf of Maine Subpopulations of Atlantic cod*.

1. The Western subpopulation occupied the coastal shelf from northern Massachusetts Bay and Ipswich Bay to the vicinity of Sheepscot Bay and included six spawning components.
2. The Midcoast subpopulation in the Penobscot Bay area occupied the coastal shelf from Muscongus Bay to Jericho Bay and included four spawning components.
3. The Downeast subpopulation in the Mt. Desert Island area had three spawning components distributed from Mt. Desert Rock to Petit Manan.
4. The Bay of Fundy sub-population had three spawning components and included cod from Passamaquoddy Bay to the WNW Rips and possibly German Bank.

* Similar behavior was noted outside the study area, particularly in Massachusetts Bay. However, seasonal movement patterns in Massachusetts Bay showed that cod concentrations moved east and south of Stellwagen Bank and outside the study area. Only two small spawning areas along its northern edge appeared to have cod that moved northeast in spring and returned from the north in fall.

Table 4. Criteria for identifying historical spawning components of Atlantic cod in the GOM*.

1. Winter grounds were proximal to coastal spawning areas.
2. Spawning areas bordered deeper channels or basins.
3. Atlantic cod concentrations were present in the general area all year.
4. Cod concentrations could be tracked between a specific historical spawning ground and local winter grounds during spawning season.
5. Ripe Atlantic cod were confirmed to have been present in the spawning area during spawning season by two or more independent observers.
6. Spawning grounds had appropriate depths and substrates.

* The above criteria were derived from parameters available from 1920s data and are not intended to replace today's more rigorous criteria defining cod populations.

Should subdivisions of Atlantic cod in the Gulf of Maine grouping be described as subpopulations? The four large concentrations of 1920s cod distributed in different sections of the study area were identified as the subdivisions mentioned in Wise's characterization of the Gulf of Maine grouping (1963). Depletion patterns indicated that the number of cod in a subdivision did not vary with reductions in other subdivisions and bathymetric charts show the subdivisions to be partially isolated from each other by deeper basins. Each area contained spawning grounds, nursery areas, and separate migration corridors. These features are not characteristic of migrating, pandemic populations, but are quite typical of discrete population units. They are, in fact, characteristic of semi-independent, self-reproducing groups within a larger population that undergo limited exchanges within a population (Smedbol and Stephenson 2001).

Closer examination revealed the subdivisions were composed of several bodies of cod that demonstrated separate circular movement patterns linking local winter grounds to specific local spawning areas; that is, they functioned as an assemblage of spawning components using separate spawning grounds in the area of a given subdivision. Berrien and Sibunka (1999) have reported recent spawning activity on many of these areas, indicating their continued activity. While it may be that subdivisions are but single spawning components among one or more local stocks, their behavior within the grouping is best describes as that of subpopulations (Smedbol and Stephenson 2001). In the absence of objective studies that differentiate between bordering spawning components, the evidence seems persuasive that subdivisions are subpopulations of the Gulf of Maine grouping.

Accuracy of charts and navigation techniques of the period. Much of the data used in the study predated electronic navigation. Prior to its development, fishermen located fishing grounds using sextant or compass bearings and distances from known landmarks. They were able to come close to a given fishing ground using either method, but to confirm their location fishermen had to sample the substrate and depth in the area with a sounding lead until they found the right spot. Grease stuck on the bottom of the lead provided them with a sample of the ocean bottom around the fishing ground.

Period fishermen repeatedly returned to the same fishing ground by following the same navigation instructions and correlating bottom characteristics with known bathymetric descriptions of the ground. While most fishing grounds identified in the study could be readily found, the precise location of some grounds was limited by the accuracy of bathymetric information on modern NOAA charts.

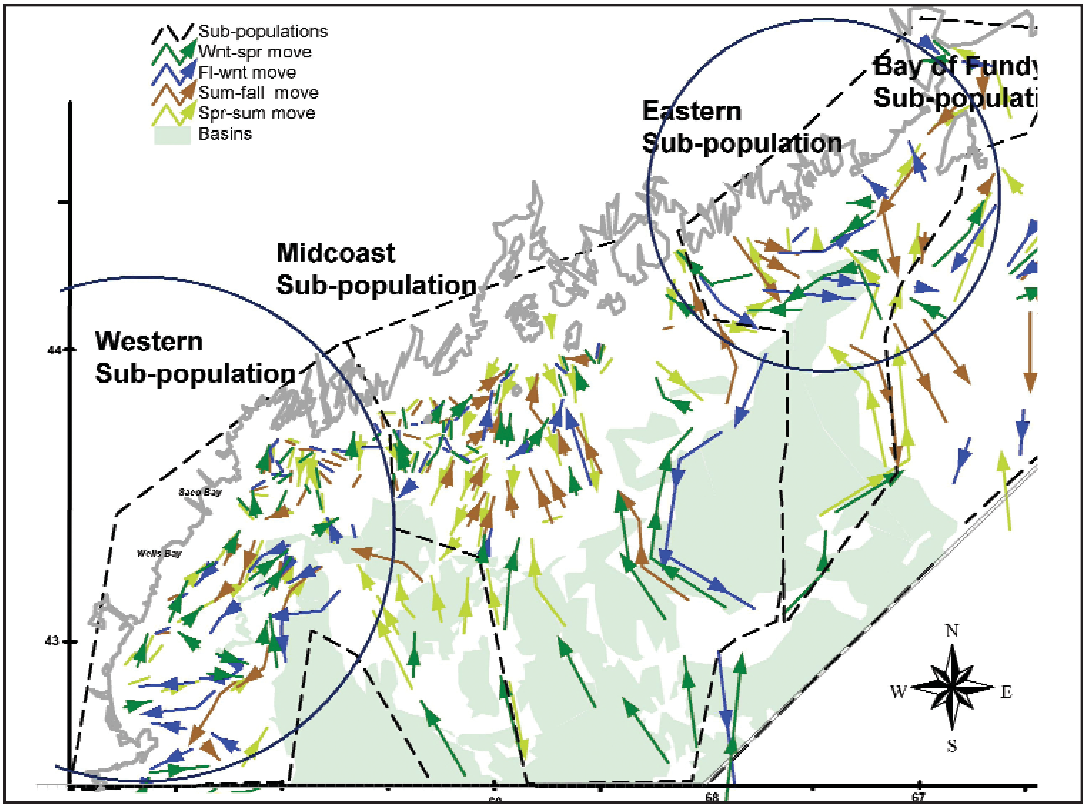
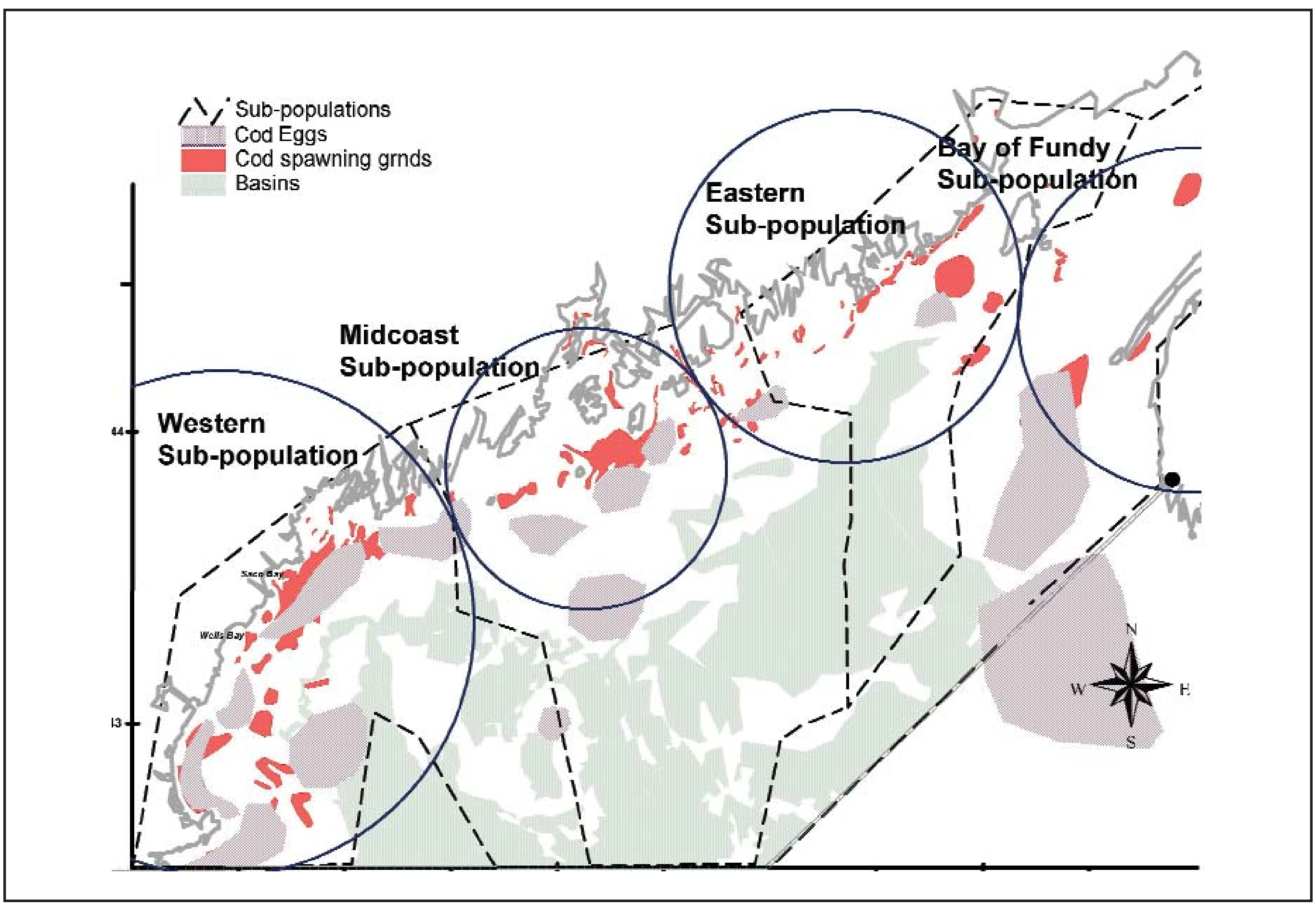


Figure 6a. Historical migration patterns of Atlantic cod in the Gulf of Maine followed contours of the coastal shelf and deeper offshore ridges and shoals. Recent tagging studies (circled areas) agreed with historical movements.
Figure 6b. Historical spawning grounds (circled areas) were at the terminus of migration corridors used by specific sub-populations of Atlantic cod.

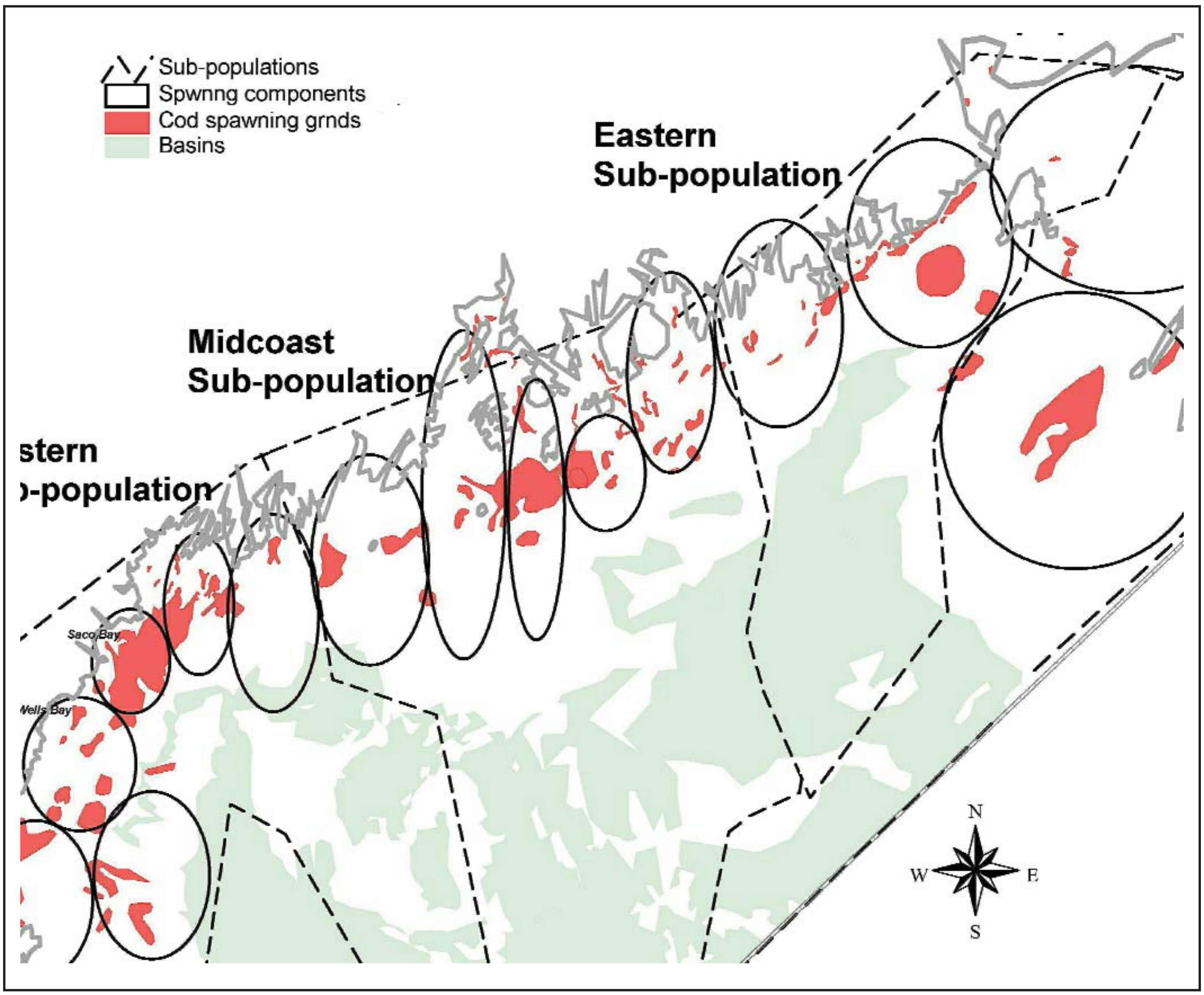


Bias and Historical Fishery Information. Different fishing methodologies generate different types of information, making it important to evaluate data carefully. For example, the prevailing technology prior to 1930 was still hook and line in coastal Gulf of Maine, which caught only foraging Atlantic cod. When fish refused to bite baited hooks, fishermen could only assume there were no cod in the area, for they had no other way to confirm their absence. However, this unintentional bias has provided a convenient way to locate the major forage habitats of Atlantic cod and identify the times of year Atlantic cod were foraging on each site.

By contrast, information about spawning Atlantic cod, which are less inclined to feed, generally came from fishing methods not relying on feeding behavior. Predictably, most spawning ground information came from interviews with inshore otter trawler fishermen of the 1930s, 1940s, and 1950s that had once targeted coastal cod spawning aggregations. The advent of the otter trawl was the first time cod spawning aggregations had been vulnerable to fishing gear on such a large scale. Early otter trawlers generally towed their nets on smoother bottom than that used by hook fishermen and because they were mobile, often could not tell exactly where they caught fish, even though cleaning the catch allowed them to identify when fish were feeding, fasting, or spawning. The rapid collapse of coastal cod stocks exposed to otter trawling may have demonstrated the great susceptibility of inshore Atlantic cod to that technology (Ames et al. 2000).

Migration patterns of the 1920s may have been transient events. Fishermen often refer to migrations and local movements of Atlantic cod and while tagging studies have clarified cod movements in some areas (Perkins et al. 1997; Hunt et al. 1998), the persistence and fine-scale details of cod movements in the Gulf of Maine have been poorly

Figure 7. Recent cod egg surveys confirm that many spawning components of historical Gulf of Maine subpopulations are still active.



understood. It is possible that historical movement patterns may only be valid for brief periods, making a comparison with recent movement patterns unjustified. To test this hypothesis, 1920s seasonal migration patterns of Atlantic cod (Figure 6) were compared to the results of recent tagging studies (Perkins et al. 1997; Hunt and Neilson 1993; Hunt et al. 1998).

The comparison showed that historical migrations of Atlantic cod occurred in the same areas, during the same seasons, and with fish moving in the same direction as in recent migrations. The test confirmed that the same migration routes have been followed for more than a century and reflect long-term responses of Atlantic cod to underlying ecological factors. This refutes the argument that Atlantic cod migrations were transient events that varied significantly in time and place. To the point, historical movement patterns may be useful in identifying the movements of today's Atlantic cod populations when they occur in the same area.

Concern exists that coastal spawning components of Atlantic cod have disappeared and may be extinct, making historical comparisons moot. If the historical coastal stocks of Atlantic cod no longer exist, comparisons of their behavior patterns with the behavior found in today's spawning components would be irrelevant.

To test this, the following extinction hypothesis was developed: because spawning components of subpopulations return to the same spawning ground each year to reproduce, no ripe fish or early stage cod eggs would be found around historical spawning areas where they were extinct. If they still exist, ripe adults and cod eggs would be found on the spawning areas during spawning season. By correlating historical spawning grounds and/or pre-spawning aggregations with recent cod egg surveys, grounds having high densities of cod eggs would indicate a continued presence of Atlantic cod populations and also give supporting evidence that homing by Atlantic cod occurs in the Gulf of Maine.

Recent GOM cod egg distribution patterns (Berrien and Sibunka 1999) were plotted on GIS and their locations were compared with the locations of historical Atlantic cod spawning grounds (Figure 7). The comparison showed that 1980s GOM areas with high-densities of cod eggs in the fall were the historical subpopulation winter grounds. In spring, several historical spawning grounds also were active, confirming the presence of continued spawning activity by some historical spawning components. However, most spawning events were small and infrequent, indicating their depleted condition.

Approximately 40 of the 90 historical spawning grounds had neither commercial landings nor evidence of spawning during the 11-year study of Berrien and Sibunka (1999) and appear to be extinct. This represents a significant reduction in the GOM's reproductive capacity and coincides with a gradual, long-term depletion

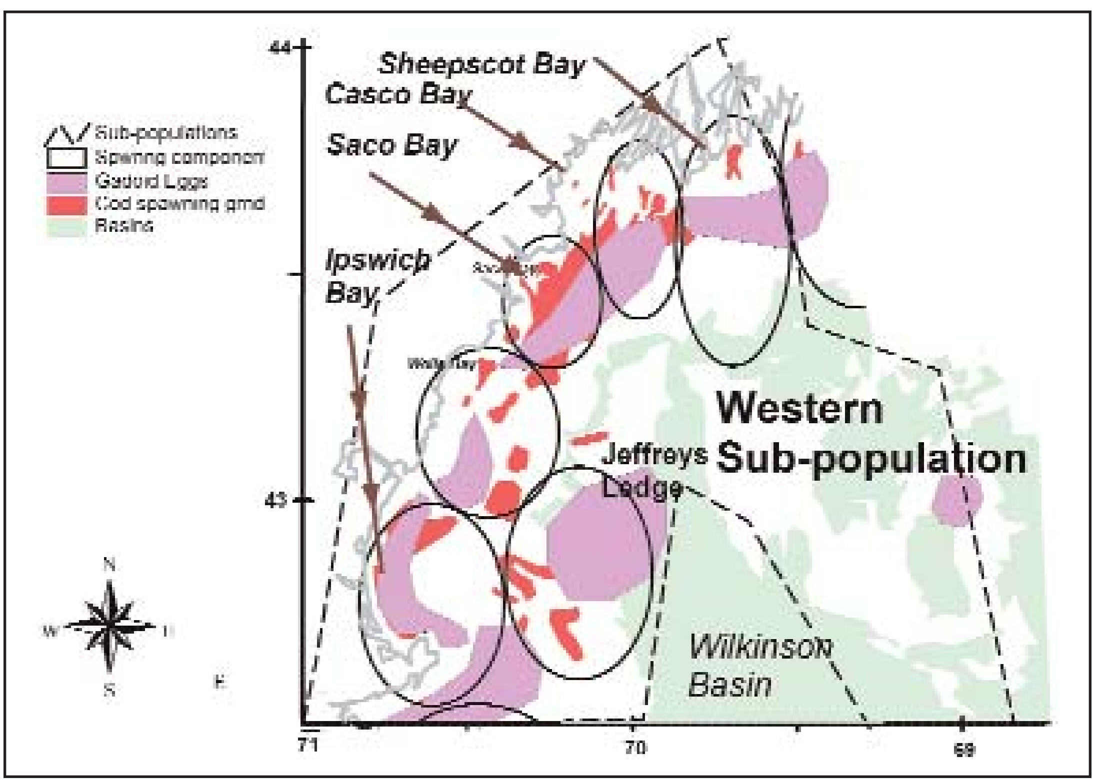


Figure 8. Displaying cod egg distribution and historical spawning grounds identifies the location of active spawning components in the Western subpopulation.

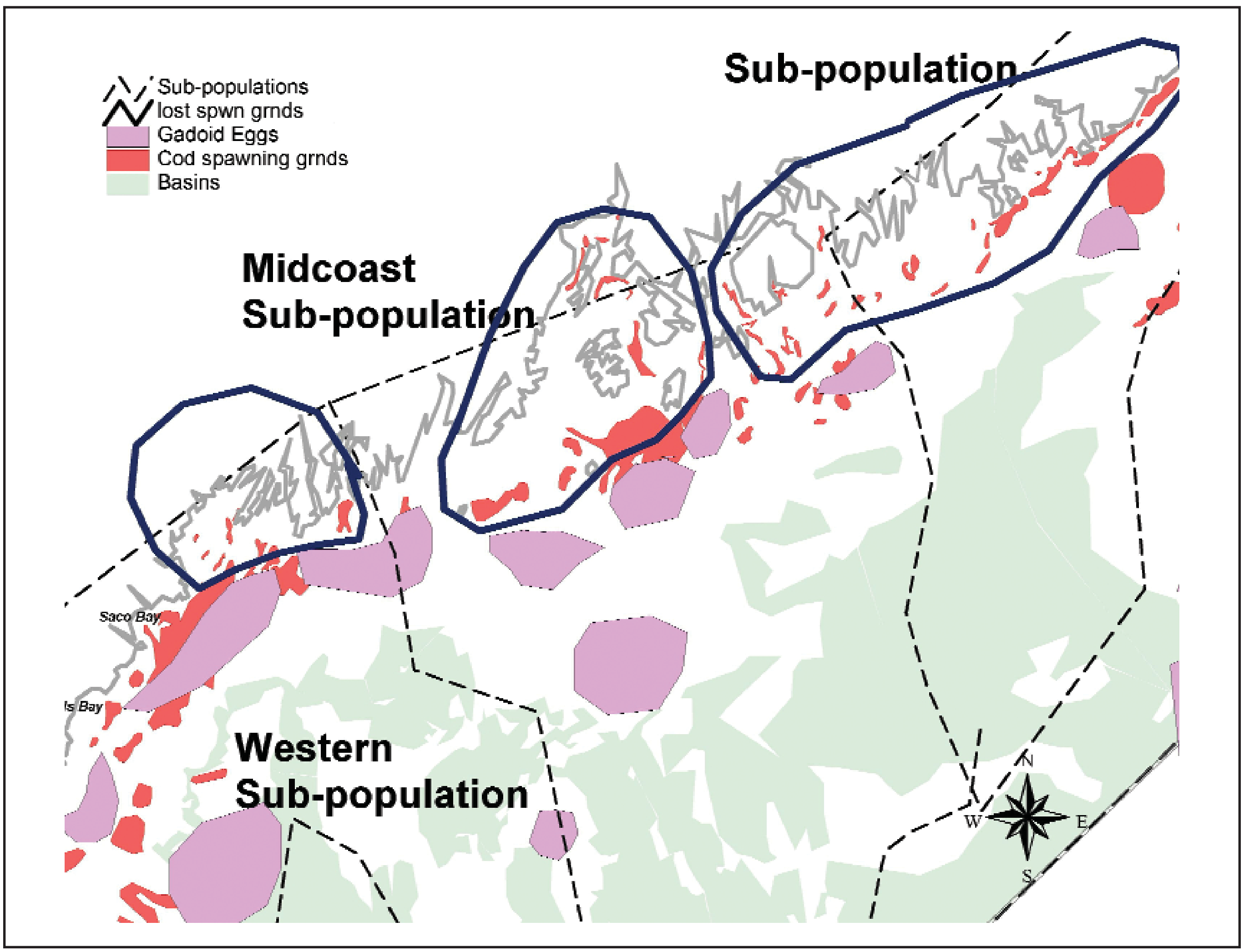
marked by large fluctuations in landings of the fishery, particularly in eastern GOM.

Depletion and recovery patterns of spawning components. By the late 1940s, coastal subpopulations were depleted or collapsed (Maine Dept. Sea and Shore 1947). Most of the spawning grounds abandoned during this period were found in coastal waters between Casco Bay and the Bay of Fundy. Many 1920s spawning components characterized in the present study were associated with these inactive spawning grounds (Figure 9). Active spawning sites are defined as those that are spatially coincidental with the egg distribution studies of Berrien and Sibunka (1999).

Spatial complexity in Atlantic cod, the distribution of spawning components, has been hypothesized to be a function of oceanographic processes during egg and larval stages (Sinclair 1988) and results in several different populations with separate spawning areas and discrete egg and larval distributions. In a review of within-species diversity, Smedbol and Stephenson (2001) observed that cod and herring have complex population structures in the Northwest Atlantic with multiple subpopulations and that managers have often failed to prevent the loss of spawning components in these heavily exploited fisheries. They concluded that spatial population structure and dynamics may be important to the maintenance of such fisheries and recommended that fine-scale population structure be preserved until "the weight of evidence suggests that it is not of ecological significance." Frank et al. (1994) attributed the collapse of the Sable-Western Bank subpopulation to a dramatic increase in exploitation and concluded the targeting of spawning aggregations resulted in lost reproductive capacity that led to the subpopulation's collapse.

At least three human-induced factors contributed to the collapse of Atlantic cod spawning components in the GOM—the increased effort

Figure 9. The absence of cod eggs on historical spawning grounds reveal the location of abandoned spawning grounds and lost spawning components. Circled areas identify inactive spawning areas.



from the introduction of otter trawling and gillnetting in coastal waters, the pollution of coastal nursery grounds, and the destruction of anadromous forage stocks by the construction of dams.

Foremost among these factors may have been the targeting of Atlantic cod spawning aggregations as they gathered in coastal basins and channels in winter by coastal otter trawlers and gillnetters after their introduction during the 1930s and 1940s. Few fishermen of the period are still alive, but the brief fishing bonanzas described in different coastal areas were predictably similar (Ames 1997). More recent collapses of subpopulations were concurrent with refinements in fishing electronics and technology that allowed greater exploitation of bottom habitats.

RODNEY ROUNDTREE

A second factor may have been the widespread degradation of coastal nursery grounds and estuaries by industrial pollution from rivers and streams in areas such as Penobscot Bay (Ames 1997). Though restoration efforts have improved water quality, cod and other commercial species have not repopulated their abandoned areas, leaving open the possibility that extinct spawning components may have been discrete populations adapted to those localities.

MARIA RECCHIA

Forage stocks such as alewives and bluebacks were lost when dams were built to power New England's factories, and caused the cod that pursued them to the mouths of rivers and streams to disappear, triggering the collapse of the coastal cod fishery (Baird 1883).

A joint collaborative cod tagging study coordinated by the Gulf of Maine Research Institute and involving Canadian and American fishermen, Canada's Department of Fisheries, and National Marine Fisheries Service is currently under way. Tag returns in the next several years are expected to reveal more details about cod population structure and movement patterns.

The combination of lost forage stocks, degradation of nursery habitats, and directed fishing on coastal spawning aggregations of Atlantic cod appears to have overwhelmed subpopulations and caused several coastal spawning components to disappear. Maintenance of remaining Atlantic cod spawning components, spawning areas, and nursery grounds seems critical to recovery if a robust, sustainable fishery is to be re-established.

MARIA RECCHIA

Management Perspectives. In spite of peaks in productivity, the gradual decline and collapse of the coastal cod fishery in mid-coast and eastern GOM has been concurrent with the disappearance of inshore spawning components and the extinction of historical coastal spawning grounds. Active spawning grounds in the study area fell from 90 in the 1920s to no more than 46 in the 1980s, with many of the remaining grounds exhibiting only sporadic activity (Figure 9). Most losses occurred in the three eastern subpopulations.

HUNT HOWELL

Similar losses in reproductive capacity from collapsed spawning components were noted in the collapse of the heavily exploited Sable/Western Bank subpopulation (Frank 1994). However, unlike the Sable/Western Bank subpopulation, depletion of coastal GOM escaped detection because system-wide assessments, the basis for current management strategies, cannot detect the gradual erosion of spawning components. If, for example, one assumes cod abundance to be equivalent among the four subpopulations, each would produce about 25% of the annual GOM landings. The collapse of a single subpopulation would cause a comparable reduction in landings. Since the confidence limits of typical groundfish assessments are also in the range of 25%, it is probable that the collapse of a single subpopulation would be undetected. However, if two or more subpopulations collapsed, annual landings would be reduced by more than half (Midcoast, Eastern, and Bay of Fundy subpopulations were recently depleted).

This simple calculation identifies the geographical character of subpopulations and spawning components as a pivotal factor in rebuilding and maintaining GOM stocks at high, sustainable levels. It also points out the consequences on a fishery when management relies primarily on system-wide assessments. Smedbol and Stephenson (2001) have suggested that managing subpopulations and spawning components on the basis of their geographical character would address such losses. A sound approach perhaps lies in the direction proposed by Wilson (1997), who stated that decentralized, hierarchical management units equivalent to the scale of the Atlantic cod's population structure would be more effective. He concluded that (1) organizing a decentralized fisheries management system and (2) creating individual incentives that are consistent with the goal of sustainability is best achieved through local authority over ecological events whose impacts are strictly local. The present study suggests that subpopulations are an appropriate management unit to minimize further losses of spawning components while rebuilding the fishery.

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