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Gadids and Alewives: Structure Within Complexity in the Gulf of Maine

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Abstract

The collapse of Atlantic cod (*Gadus morhua*) along the northern 240 km of New England's historically productive coastal shelf has continued for nearly twenty years. Resident spawning groups and their subpopulations have disappeared and have yet to recover, causing local groundfish fisheries to collapse. Three additional gadid species, haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and white hake (*Urophyscus tenuis*) collapsed along the northern coastal shelf during the same period, raising concerns that their resident coastal groups were part of a metapopulation and may have also been lost. Analysis of their distribution and movements in the 1920s appeared to corroborate this. The four gadids had clusters of resident coastal groups along the coastal shelf that coexisted in the same area. Cod, white hake and pollock appeared to exhibit metapopulation characteristics, having resident and migrating components distributed along the coast in three different areas, with migrating components arriving and leaving along common migration routes fall when alewives left. The groups were centered near rivers with alewife spawning runs and disappeared from the area during the 1950s after alewives (*Alosa pseudoharengus*) declined locally. The results suggest that large, stable concentrations of young-of-the-year alewives were a factor in where resident and migrating gadid groups were located.

Introduction

Fishermen have depended on landings of Atlantic cod (*Gadus morhua*) and other gadid species, including haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), and white hake (*Urophyscus tenuis*) throughout New England's rich history of groundfishing. While the majority of these landings came from the Gulf of Maine (GOM)'s offshore banks, a significant portion of the catch came from inshore grounds along New England's coastal shelf. Landings there have varied greatly, both spatially and temporally, and while inner grounds have long been abandoned, gadids have continued to be available on grounds somewhat farther offshore. That is no longer true along New England's northern coastal shelf. Approximately 20 years ago cod and three other gadids became depleted throughout the area, raising concerns why such radical changes in their spatial distribution had occurred (NOAA 2010 and earlier reports in the series).

A Gulf of Maine-wide (GOM) tagging study for Atlantic cod completed in 2007 (Tallack, 2007) concluded that a progressive recovery was underway in some areas, but cod were recovering very slowly if at all along the northern 240 km-long coastal shelf between Casco Bay and Canada. When the results were displayed with the Androscoggin-Kennebec, Penobscot and St. Croix watersheds, the depleted area with the fewest tag returns closely fit the entire section of coastal shelf bordering the watersheds (Fig. 1). Groundfish surveys by Maine Department of Marine Resources found juveniles of cod and other gadids in this area, but very few adults were present (Sherman et al., 2004–2010), corroborating the tagging study results. The depleted area represents the northern third of New England's coastal shelf.

The purpose of this study has been to examine the historical distribution of the four gadids among fishing grounds and to track their seasonal movements by following shifts of fish concentrations (movements) among grounds in the immediate vicinity of the previous season's location. Specific issues addressed include identifying which of the four gadids had coastal groups, where those groups were located and whether there was evidence of common population structures and shared migration corridors; second, comparing the seasonal shifts of individual gadids among fishing grounds with that of other gadids and third; assessing whether their movements appeared to be linked to alewife predation. Finally, were differences in the availability of clupeid prey along the northeastern coastal shelf a factor in the continued depletion of northeastern GOM?

The study examined fishermen's observations gathered during the 1920s about the distribution and abundance of the four gadids on coastal fishing grounds during a period when gadids were more abundant (Rich, 1929).

Methodology

The study area included that part of the GOM enclosed by a line extending due east from Highland Heights, Cape Cod, MA lying north of a line extending east from Highlands Light, Cape Cod (42˚N, 70˚ W) to Wrights Swell, then to Yarmouth, N.S. (43˚50´ N, 6˚07´ W) (Fig. 2), an area similar to that used previously to determine the population structure of 1920s and 1930s Atlantic cod (Ames, 2004) and white hake (Ames, 2011). A smaller area (Fig. 2) in Midcoast Maine was used to examine gadid movement patterns for indications of predator–prey interactions near Muscongus Bay. The small 10 km-wide bay receives two secondary rivers, the Damariscotta and St. George Rivers that had documented landings of alewives during the 1920s (Hall et al., 2011; Spencer, 2006). Unlike most other rivers in New England, the Damariscotta and St. George Rivers remained open to alewives throughout the 20th century (Fig. 2).

The following definitions were used to evaluate population structure (Smedbol and Stephenson, 2001):

(a) A population is defined as 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.

(b) 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 the population.

(c) A spawning component is a segment of a population that does not differ in genetics or growth, but occupies discrete spawning areas inter-annually.

(d) A stock is an arbitrary collection of fish large enough to be essentially self-reproducing, with members of the unit exhibiting similar life history.

(e) A group of fish is a stock component that remains in a local area throughout the year (Wise, 1963).

Sources of 1920s information about cod, haddock, pollock, white hake and alewives

The study relied extensively on Rich's "Fishing Grounds of the Gulf of Maine" (Rich, 1929) and was supplemented by Ames (1997, 2004). Rich interviewed groups of experienced fishing vessel captains who related the seasonality of gadid stocks on the grounds he documented. When disagreements arose about the relative abundance or seasonality of fish on a given ground, the majority opinion was accepted. The work of Rich not only revisited the grounds described by Collins and Rathbun (1887), but included an extensive number of additional grounds mentioned during his interviews. Most of the fishermen used hook-and-line technologies to catch fish on grounds that were feeding stations. Ames conducted interviews of retired fishing vessel captains who were active from the 1920s to 1950s and in addition to employing hooks, most had used other capture methods. Supporting empirical information came from Bigelow and Schroeder (1953) and Collette and Klein-MacPhee (2002). Alewife distribution among Maine rivers was derived from Hall et al. (2011), Lotze and Milewski (2004), Bigelow and Schroeder (1953) and Atkins (1887) and the towns of Newcastle, ME and Warren, ME (Spencer, 2006). The resulting qualitative and empirical data was used to examine the historical distribution and seasonal movement patterns of the four coastal gadid species and compared with recent scientific indices.

Summary of gadid and clupeid characteristics

National marine fisheries service groundfish surveys (NMFS, 2010) noted that the fishery for cod, haddock, and pollock in western GOM appeared to be recovering, though in northeastern GOM the three gadids, plus white hake have been chronically depleted since the early 1990s (NMFS, 1978–2009).

Cod: Cod reproduce along the northeastern coastal shelf (Ames, 1997), have been found to return to natal spawning areas (Wroblewski, 1998) and migrate seasonally with adult herring and alewives (Tallack, 2007), but during the 1920s others remained in the general vicinity of their spawning grounds all year (Ames,2004). These local groups were distributed among three subpopulations along the study area's coastal shelf, with the eastern-most being cross-boundary. Each subpopulation contained multiple spawning components that migrated seasonally along separate migration pathways located in different parts of the coastal shelf between Cape Cod Bay and Bay of Fundy, reproduced on coastal shelf spawning grounds located within the subpopulation's domain and the abundance of each subpopulation varied independently from the others (Ames, 2004). The diet of cod is so varied that nearly all species of appropriate size are consumed (Bigelow and Schroeder, 1953). Among these, alewives prior to their collapse, and Atlantic herring were important prey.

Haddock: Historical haddock spawning grounds were often located near those of cod (Ames, 1997), with haddock preferring smoother, more regular areas (Bigelow and Schroeder, 1953). Unlike cod, haddock do not migrate, but remain in relatively small areas in deeper water than that preferred by cod (Collette and KleinMacPhee, 2002). Gut analyses of haddock indicate that the variety of species they prey upon is as great as cod, though haddock prefer smaller prey and while both are noted for gorging on herring spawn, haddock appear to do so more frequently than cod (Bigelow and Schroeder, 1953). Today, gut analyses show that GOM haddock consume fewer herring then those on Georges Bank (GB) and Scotian shelf (Collette and Klein-MacPhee, 2002), the difference being attributed to their gorging on the eggs of Atlantic herring, though numerous reports describe haddock gorging on small fish. The preferred bait for catching haddock during the 1880s was slivers of menhaden, a reasonable facsimile of juvenile alosids or clupeids (Goode and Collins, 1881).

White Hake: White hake inhabit muddy substrates in relatively deep water (80 m or deeper), though historically they were occasionally found in lesser depths (Rich, 1929). They are known to prey on herring, juvenile fish, and pelagic shrimp (Collette and KleinMacPhee, 2002). Historically, white hake appear to have had both resident coastal groups and migrating components (Ames, 2011), though Bigelow and Schroeder (1953) reported that they were more stationary than either cod or haddock. Hake display diurnal behavior, remaining on bottom in day and feeding at mid-depths in the night (Collette and Klein-MacPhee, 2002). Fahay and Able (1989) reported the spawning contribution of white hake within the GOM was negligible and proposed that the fishery was based on fish that originated from either the Scotian shelf stock or along the continental slope lying south and west of Georges Bank. Little reproduction is believed to occur in the GOM today.

Pollock: Pollock are the most pelagic of the GOM gadids and are considered voracious predators of small fish and small crustaceans (Collette and Klein-MacPhee, 2002). They are commonly found near hard or rocky substrates. Though pollock migrate seasonally, adults were present all year in the GOM during the 1920s and appeared to have components remaining on inshore grounds through the year (Rich, 1929). Pollock spawn in fall and winter and readily bite lures and baited hooks at various depths where they are frequently found pursuing prey.

Alewives: Adult alewives arrive at their natal rivers in spring to reproduce in lakes and ponds connected to the river. Shortly after spawning, they return to marine habitats where they remain until fall. They then leave, co-migrating with Atlantic herring to Ipswich Bay and south along the coastal shelf (Graham et al., 1984; Stone and Jessop, 1992). Alewives in the depleted northeast collapsed in the late 1860s from an estimated population of 50 million to approximately 3 million individuals, where until recently, it remained.

Young-of-the-year (YOY) alewives remain in natal lakes and ponds until plankton abundance declines in late summer, when they enter the river and migrate to the sea and gather among nearby coastal estuaries and shoals. By late fall, YOY alewives and YOY Atlantic herring are the only abundant clupeid species remaining along the northern coast. They move progressively to deeper, warmer depths in winter where they and juvenile Atlantic herring remain through the winter (Townsend et al., 1989), returning to coastal nurseries in spring.

Herring: Atlantic herring reproduce along the shoals and shores of the outer coastal islands, usually in the fall, but with smaller contingents spawning during spring and through the summer

(Collette and Klein-MacPhee, 2002; Bigelow and Schroeder, 1953). After hatching, their larvae are distributed along the coast by tides and currents. Metamorphosis from larvae to juveniles occurs from April to October in northern GOM coastal waters within 3–6 months, depending on when hatched (Sinclair and Tremblay, 1984). At the end of their first year their size varies from 9.0 cm to 12.5 cm (Collette and Klein-MacPhee, 2002).

YOY Atlantic herring are distributed along the coast by variable and comparatively unpredictable winds, currents and tide, leading to a patchy distribution of YOY and the likelihood that while certain areas receive many larvae, others may receive but few (Graham et al., 1984). In contrast to herring, YOY alewives enter the marine system at specific sites each year and historically, piscivores such as cod developed a predictable response to that repetitive event (Baird, 1872–1873). Estuaries that received the YOY of both species would continue to provide prey if alewives disappeared, but at a lower amounts. Those receiving only alewives would have been greatly affected by their loss.

Locating historical fishing grounds

Historical fishing grounds were located by following the historical navigation directions of Rich (1929) to a point using digitized NOAA nautical charts having 10 m depth contours in a GIS system. A location in the immediate vicinity of this point was selected that was consistent with the orientation, size, shape, and substrate characteristics described by fishermen of the period and agreed well with recent evaluations of the depth and substrates of grounds where each gadid species was recently found (Methratta and Link, 2006). Without this clarification, the procedure suggests a visual precision that would appear to overstate the information contained in historical navigation directions.

Estimating fish concentrations using relative abundance (RA)

Estimates of fish concentrations were derived from subjective, fishermen-based descriptions of how good fishing was on individual grounds during each season (Fishermen's ecological knowledge) by determining each fishing ground's relative abundance (RA) for each season of the year (Ames, 2004). This allowed estimating the abundance of gadids on a ground without regard to fishing methodology, size of vessel, or requiring proprietary information about actual landings. While the method provides no actual measure of landings or numbers of fish caught on a particular ground, it does provide a pragmatic measure of a selected species' availability on that particular ground during a given season.

Fishermen's ecological knowledge (FEK) gathered from historical references (Collins and Rathbun, 1887; Rich, 1929; Ames, 1997) was used to establish a colour gradient on GIS for each species and season for each ground, with the darker, more intense shade indicating the greater number of fish. RA values quantified fishermen's descriptive estimates of gadid availability by assigning the following values: absent = 0, poor = 1, fair = 2, good = 3, and very plentiful, outstanding or abundant = 4 (Table 1). Species reported to be present on a ground but lack supporting abundance estimates were assumed to have provided fishermen with fair fishing and were arbitrarily assigned a value of two. The criteria were based on how rapidly fish could be caught; that is, how rapidly a captain was able to put fish into the hold of his vessel. While this provides no actual measure of landings or numbers of individuals on the ground, it does provide a pragmatic measure of the availability of the four gadids on each ground and each season without regard to fishing methodology or size of vessel. This avoided the need for having fishermen share proprietary information about actual landings.

Maps were prepared, for example, showing the location of cod fishing grounds and its RA based on the depth of colour for each season. Those grounds reporting cod being present but lacking abundance information were assumed to have provided fishermen with fair fishing and were assigned a value of 2. When placed in sequence, fishermen's seasonal observations gave the spatial distribution of cod groups throughout the GOM study area (Fig. 2a–d). Similar maps were prepared for haddock, pollock and white hake.

Determining seasonal movements of four gadids in the GOM

The base map of fishing grounds used to determine seasonal distribution also functioned as an X–Y plot that allows concentrations of fish to be followed between seasons through the year. This approach relies on two assumptions: (a) a fishing ground recording a decrease in RA from one season to the next was assumed to have fewer fish present, while a ground recording an increase in RA was assumed to have more fish present and (b) that fish minimized the distance they moved during seasonal movements. For example, when cod moved, it was assumed they went to the nearest ground having an increase in RA. The direction the concentration of cod moved was described on GIS with an arrow extending from the ground losing fish to the ground gaining fish, with the arrow pointing in the direction of movement. This gave unambiguous results for isolated movements; however, when the movements of multiple grounds overlapped, identities were obscured.

While the movements of cod (and other gadids) could only be tracked among the grounds mapped, they were assumed to also inhabit areas with suitable habitat adjoining the grounds at times. Areas where multiple grounds had overlapping concentrations of gadids moving in a common direction were interpreted as being general seasonal movements (Fig. 3a–d), while areas having a broad, continuous RA movement in one direction involving several grounds between seasons and accompanied by a similar, opposite movement during a later seasonal change, were classified as migrations. Most gadids were found on relatively few GOM fishing grounds in winter, making it an appropriate season to start tracking the annual movements of gadid concentrations.

Results

Characterizing the movements of 1920s coastal cod, haddock, pollock and white hake in the Gulf of Maine

A total of 290 fishing grounds and 470 associated substrates (Fig. 1) were identified (Rich, 1929; Ames, 1997, 2004). Coastal concentrations of the four species occurred in patchy distributions among fishing grounds throughout the year. Most grounds on the coastal shelf were occupied for but one or two seasons, with the fewest being occupied in winter. Areas where concentrations of a given species could be found all year during the 1920s were arbitrarily called groups (Wise, 1963). Shifts between seasons of those concentrations, or groups among nearby grounds were tracked for each species and the grounds each group occupied during four consecutive seasons were encircled and described the aggregate of grounds used annually. Those groups along the shore were called resident coastal groups. The distribution of cod during each season provides an example of groups movements and the areas they occupied (Fig. 3a–d). The distribution of all four groups shows they were found throughout the study area.

Three of the species, cod, pollock and white hake had offshore groups connected to their coastal areas by a common migration corridor (Fig. 4a–d) and used them during spring and fall to travel between the two sets of grounds, and have been tentatively identified as subpopulations (Kritzer and Sale, 2006). When the three migrating species are displayed concurrently with the historical migration routes of cod (black dashed lines), they appear to share the same common migration corridors. Pollock, the most pelagic of the gadids appear to overlap with western GOM subpopulations (Fig. 4c).

When the grounds occupied seasonally by the three species were displayed on detailed benthic maps (Barnhardt et al., 1998), the three species appeared to follow along the contours of drowned river channels at the bottom of the GOM, although the three species were usually found on different substrates. White hake appeared to follow ancient muddy riverbeds, while cod moved along bordering slopes and pollock migrated along rocky outcroppings. The grounds have been described as feeding stations (Rich, 1929).

Subpopulations between Cape Cod Bay and Bay of Fundy occurred in three spatially distinct sites (Fig. 4a–d), with one in western GOM, a second in midcoast Maine, and the third in northeastern GOM. Haddock had groups distributed along the coast, but lacked a migrating component.

In the 1920s, two of the four gadids, cod and haddock were known to reproduce within the area of their subpopulations (Ames, 1997). Juvenile white hake were also common, but have no identifiable spawning grounds and are either serial spawners (Battle, 1951) or have protracted spawning seasons (Lang et al., 1994). Pollock reproduced on grounds in Cape Cod Bay and on the Shoal Ground off Gloucester (Rich, 1929), but while there were resident groups of pollock in the depleted northeast and juveniles were abundant, no spawning grounds were identified (Fig. 5).

Evaluation of alewife predation by gadids during the 1920s

A coastal site along the depleted northeastern coastal shelf, Muscongus Bay (Fig. 2, insert), was used to compare gadid movement patterns with a diadromous prey, alewives. During the 1920s, Muscongus Bay received two secondary rivers with landings records of alewives, the Damariscotta and St. George Rivers, and had resident groups of the four gadid species near the Bay's entrance.

Seasonal shifts of each species' group were mapped and examined for movements that correlated with the arrival and departure of alewives; namely, their movements from (a) winter to spring when alewives arrive to spawn, (b) summer to fall, when adult alewives migrate out of the area and their YOY are emigrating from the rivers to coastal nurseries, and (c) fall to winter as YOY alewives are moving to deeper, warmer water bordering their estuaries. Particular attention was given to their movements between summer and fall when YOY alewives were emigrating from their rivers and their adults were migrating towards their winter grounds.

All gadid groups appeared to move inshore towards grounds closer to the Bay in spring, apparently attracted by prey species migrating inshore to warmer costal waters. By summer, the offshore group of each species had mixed so thoroughly with resident coastal groups that they were indistinguishable.

As fall approached, the offshore groups disengaged and began their migration back towards their offshore winter grounds, a pattern that continues today. Simultaneously, coastal groups moved to grounds that placed them in the path of YOY alewives as they left their natal rivers and entered the Bay (Fig. 6a–d). By winter YOY alewives and coastal gadid groups moved slightly offshore to deeper water, but continued to remain in areas where the YOY alewives were likely to be located.

Discussion

Three species of gadids had metapopulation-like characteristics in coastal New England during the 1920s

Cod, pollock and white hake had concentrations of fish, or groups that remained at specific locations on the coastal shelf through the year. Their groups occurred in three clusters that were distributed between northern Cape Cod Bay and Bay of Fundy and included both resident and migrating components. Migrants arrived in spring and left in fall via a common migration corridor unique to each subpopulation. The groups appeared to remain in spatially distinct areas and their abundance appeared to vary independently. These are similar to the metapopulation-like characteristics used to classify subpopulations of cod (Ames, 2004) and now are tentatively apply to pollock and white hake.

Haddock groups were similarly distributed along the coastal shelf in the 1920s, but had no migrating components and did not have the larger, intermediate population structures that characterize the other three species. Their relative immobility may be a contributing factor to both their continued depletion in northeastern GOM and to the dramatic fluctuations in abundance frequently attributed to haddock stocks (Collette and Klein-MacPhee, 2002).

In fall, cod, pollock and white hake move offshore, while haddock move to deeper water (Collette and Klein-MacPhee, 2002). This behavior pattern continues to exist in western GOM today. If YOY alewives were important prey for Muscongus Bay gadids, instead of moving offshore, they would move close to the Bay in the fall when YOY alewives were leaving their natal rivers. All four 1920s gadid groups were found to remain inshore on grounds near Muscongus Bay where they could prey on the YOY (Fig. 6a–d).

Could there have been enough YOY alewives entering Muscongus Bay to attract the four gadid groups?

By the 1920s GOM alewife landing had declined precipitously. In Maine, there were but two rivers, the Damariscotta and St. George Rivers that still documented landings of alewives. Both emptied into Muscongus Bay. In addition, four species of gadids had resident groups bordering the Bay, suggesting that a predator–prey linkage existed. Predators are known to seek areas where their prey will be concentrated, such as when alewives are entering or leaving their natal rivers. But adult alewives and herring had already by fall and were migrating south along the coastal shelf. Only YOY alewives were left to attract the four groups of predators, and to accomplish that, their YOY had to be credibly abundant.

To evaluate their numbers, Walton (1987) calculated the sevenyear average of YOY alewives leaving the Damariscotta River per female entering, based on a seven year dataset. Using Walton’s ratio of 1500 YOY alewives per female entering for both the Damariscotta and St. George Rivers, a crude estimate of YOY alewife numbers entering the Bay in the fall has been made, based on the following equation:

$(kn)(N_f) = TN$ and $(kn)(N_f)(mass/n) = B_T$

where k = average YOY produced per female (1500), n = YOY alewife, N_f = number of females entering the river's watershed and TN = total number of YOY produced by the watershed per year. Mass/n = the estimated mass of each YOY alewife and B_T = the total biomass per year of YOY alewives, and the mass of each fingerling alewife is assumed to have a mass of 1.0 g

In 1925 the combined landings of alewives from the Damariscotta and St. George Rivers was approximately 1.5×10^6 adults (Spencer, 2006). Assuming 7.5×10^5 were female, then:

$(1.5 \times 10^3$ YOY/female$)$ $(0.75 \times 10^6$ females$) = 1.13 \times 10^9$ YOY/year

$(1.13 \times 10^3$ YOY/female$)$ $(1.0$ g/YOY$)$ $(1.0 \times 10^6) = 1.13 \times 10^9$ g, or 1130 mt YOY/year

The number of YOY alewives emigrating from the two rivers in 1925 shows the 10 km-wide Muscongus Bay had received an estimated biomass of approximately 1130 mt of YOY alewives in the fall, a biomass sufficiently large to attract nearby piscivores to a small bay.

Were there other prey species that arrived in fall that might have attracted the four gadids to Muscongus Bay until the following spring?

By fall, most migrating prey species, including alewives, herring, mackerel (*Scombrus scombrus*) and squid (*Illex illecebrosus*) have left the northeastern New England coast and northern shrimp (*Pandalus borealis*), Aesop shrimp (*P. montagui and P. propinquus*) will not arrive until winter. By fall, lobsters (*Homarus americanus*) and crabs (*Cancer borealis, Cancer irratorus*) are still available, but are moving progressively to deeper water. Other than YOY of alewives and herring, only juvenile fish and resident species such as mussels (*Mytilus edulis*) and hard shell clams (*Mercenaria mercinera*) remain inshore.

Cod disappeared after alewives collapsed, even though an abundance of other prey species, including mollusks, annelids, echinoderms and other invertebrates remained in the area. Coastal groups of cod and other gadids apparently responded to the loss of alewives by moving somewhat farther offshore to areas where Atlantic herring or other prey were plentiful. Without alewives to draw them back to the mouths of rivers in spring, or schools of YOY alewives to attract them in fall, cod and other predators had no reason to return inshore.

YOY Atlantic herring were abundant and provided similar prey for gadids. But unlike YOY alewives that enter the marine system from the same sites each year, Atlantic herring larvae are redistributed by currents and tides to various coastal nursery areas after hatching. Though they are notably abundant, the unpredictability of coastal currents and weather tends to create areas where too few herring larvae arrive to attract gadid groups, thus potentially reducing the number of locations with resident gadid groups.

What appears to have caused the depleted northeast area to be aligned with Maine's four major river systems?

Each fall herring and alewives migrate and overwinter between Ipswich Bay and Block Island. Few adults remain east of there. Finding that four groups of 1920s piscivores overwintered near Muscongus Bay where was receiving ~1130 mt of fingerling alewives each year, or that the gadids disappeared after YOY numbers dropped below some minimal threshold, suggests (a) gadid residency was a classic predator–prey response, in both their presence when alewives were abundant and their disappearance after prey abundance declined, and (b) today, there are too few gadids to form groups and too few YOY alewives to attract them in the fall.

While this does not eliminate the possibility that coastal groups were genetically unique, it does suggest that if diadromous species recover, local gadids may re-establish their metapopulation structures in northeastern New England.

How do these results fit with the collapse of cod and other gadids in northeastern GOM, but not in western GOM?

The study results suggest the following series of events: that alewives and Atlantic herring were both preferred prey of cod. Following the collapse of alewives in the late 1960s, coastal gadid groups moved somewhat offshore to join other groups preying on herring. This gadid-clupeid linkage continued along outer coastal grounds, albeit with considerable fluctuations until the 1990s, when Maine closed fishways on the St. Croix River, triggering the collapse of Maine's largest remaining population of alewives and in the same period an industrial-scale fishery for adult Atlantic herring was established in coastal New England and rapidly intensified (Joseph, 2009; Federal Register, 2011). Based primarily on the recalculation of stock assessments in

2009, northeastern GOM herring landings (Herring Management Area 1A) were reduced from 60,000 mt to 45,000 mt, and further reduced in 2011 from 45,000 mt to 25,245 mt. The large-scale removals of migrating herring in the area may have also disrupted the feeding migration of cod pursuing them in spring and fall.

The rapid reduction of adult herring may have caused the number of YOY being distributed to northeastern coastal estuaries to fall below that needed to attract gadids. In brief, northeastern GOM has too few adult cod and too few clupeid prey to establish spawning groups. The tendency of maturing cod to become piscivores and to migrate (Collette and Klein-MacPhee, 2002), suggests that cod disappearing from northeastern New England are pursuing migrating herring to the southwest in the fall and supplementing cod numbers in western GOM, rather than remaining behind in coastal nurseries. The loss of young adults, combined with too few cod remaining behind to form spawning groups may have contributed to the collapse.

The reduction in adult herring does not appear to have hindered the recovery of cod in western GOM and may possibly have been beneficial. Northeastern New England's adult herring and alewives, apparently being pursued by young adult gadids as they migrate south in the fall, significantly augmenting both prey and gadid abundance in Ipswich Bay and south.

Conclusions

Historical gadid behavior provides limited insights into coastal ecosystem dynamics in part because the system was more robust than that found today, but it is perhaps the only way remaining to evaluate such interactions. Two features of 1920s gadids in northeastern New England were particularly notable. The first was the discovery that the four different gadid species inhabited the same part of the coast, shared coastal shelf areas and migration corridors, and their groups functioned as components in a subpopulation. The second was finding that the innermost nodes of 1920s subpopulations were linked to bays having alewives, suggesting that prey, in this case alewives, played a significant role in its location.

The interactions of 1920s gadids suggest that the predator–prey interaction between alewives and gadids were a driver in the maintenance of inshore gadid groups along the northeast coastal shelf. This may have occurred in two ways: (1) the presence of YOY alewives as prey all year to provide a basis for local gadid groups and (2) juvenile gadids preyed on YOY alewives in coastal estuaries and as they were maturing and becoming piscivorous, they pursued schools of juvenile alewives. When the juvenile alewives embarked on their first fall migration, many cod (and perhaps other gadids) followed. Others remained behind with the local group and continued to prey on the newly emerging year class. This hypothesis implies that (a) migrations of local alewives may have been the mechanism that guided pursuing cod back to their natal spawning grounds and (b) when their local prey disappeared, cod did not return.

The tendency of cod and other gadids to prey on alewives and to remain in areas where they or their YOY continue to be plentiful appears to express a general behavior of gadids towards an abundant prey. The study suggests that providing alewives with access to their historical spawning areas will enhance the recovery of cod and other gadids and perhaps encourage the reformation of metapopulation components along the northeastern New England coastal shelf, assuming that gadids are allowed to reproduce and recruit to the fishery.

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Table 1

A description of relative abundance values (RA) for white hake based on observations by fishing captains for each season of the year during the 1920s. The term "very plentiful" describes several comments indicating better than "good".

Relative abundance (RA) values				
None	Poor	Fair	Good	Very plentiful
0	1	2	3	4

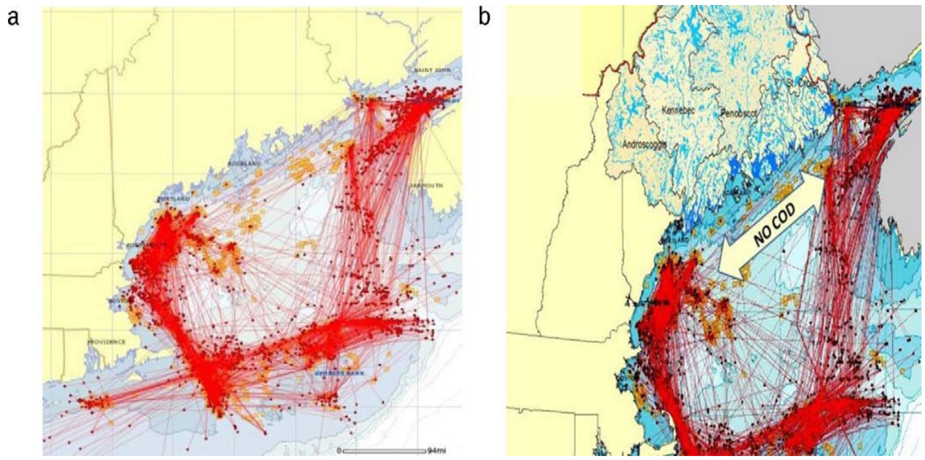

Fig. 1. (a) The results of the recently completed Gulf of Maine Research Institute Cod Tagging Study (Tallack, 2007). Tan squares are tagging sites, red dots are tag recapture sites and red lines connect the two. (b) The results of the GMRI cod tagging project in 2007 and Maine's major watersheds. Note the absence of cod between the Kennebec–Androscoggin River and the St. Croix River. Tan squares = tagging site, red dots = recapture site and red lines connect the two. The arrow stating "No Cod" has been added to identify the area having minimal tag returns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

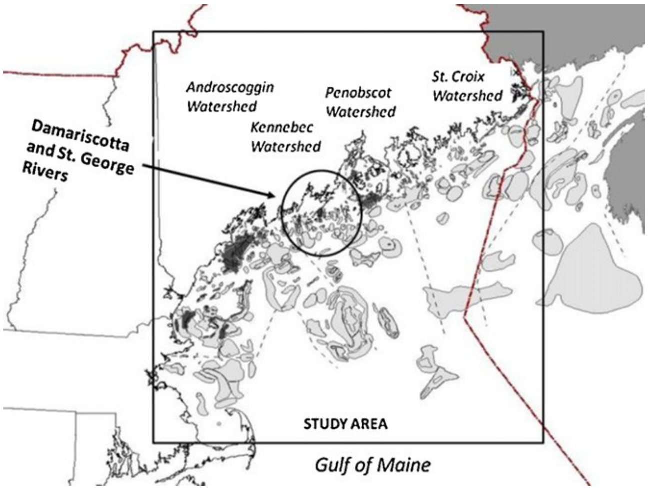

Fig. 2. The Gulf of Maine (GOM) study area. The insert shows the location of the gadid predation study at Muscongus Bay. Historical fishing grounds = grey areas, historical cod and haddock spawning areas = black. The circled area encloses the Damariscotta and St. George Rivers where predation by the four resident gadid groups was studied. Black dashed lines separate migration corridors of historical cod subpopulations (Ames, 2004).

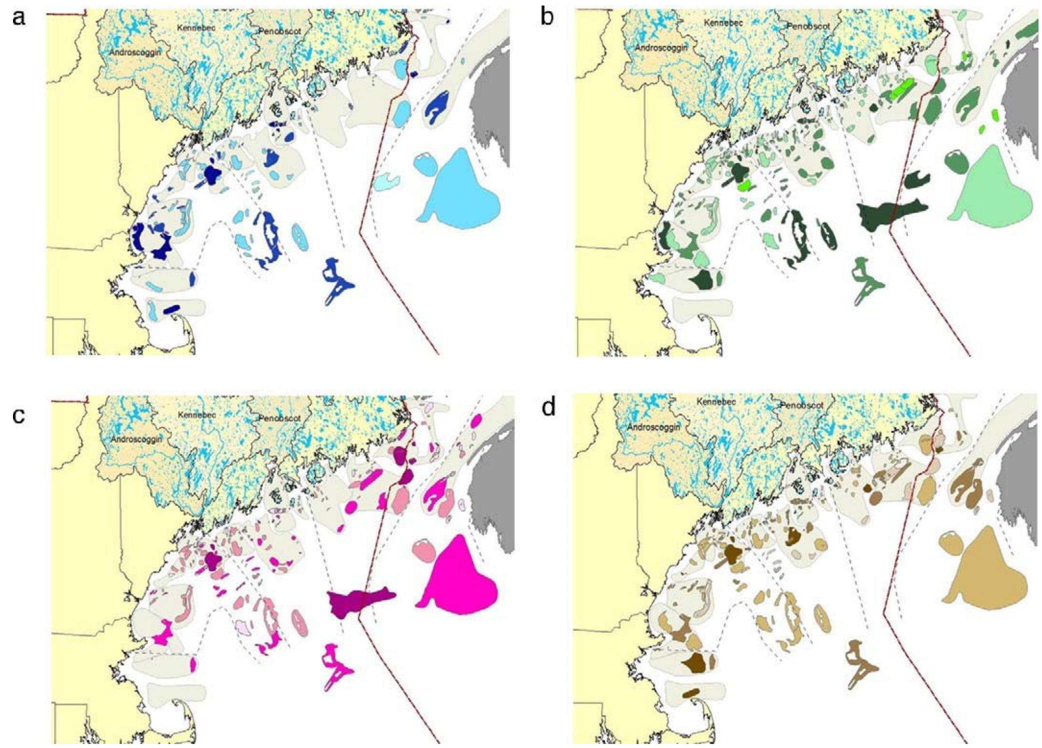

Fig. 3. (a)–(d) The seasonal distribution of 1920s Atlantic cod in the Gulf of Maine. Fishing grounds having darker shades of colour indicate larger concentrations of cod. (a) Winter cod = blue, (b) spring cod = green, (c) summer cod = red, and (d) fall cod = brown. Grey areas indicate the annual range of individual spawning components; dashed black lines separate migration corridors of cod subpopulations (Ames, 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

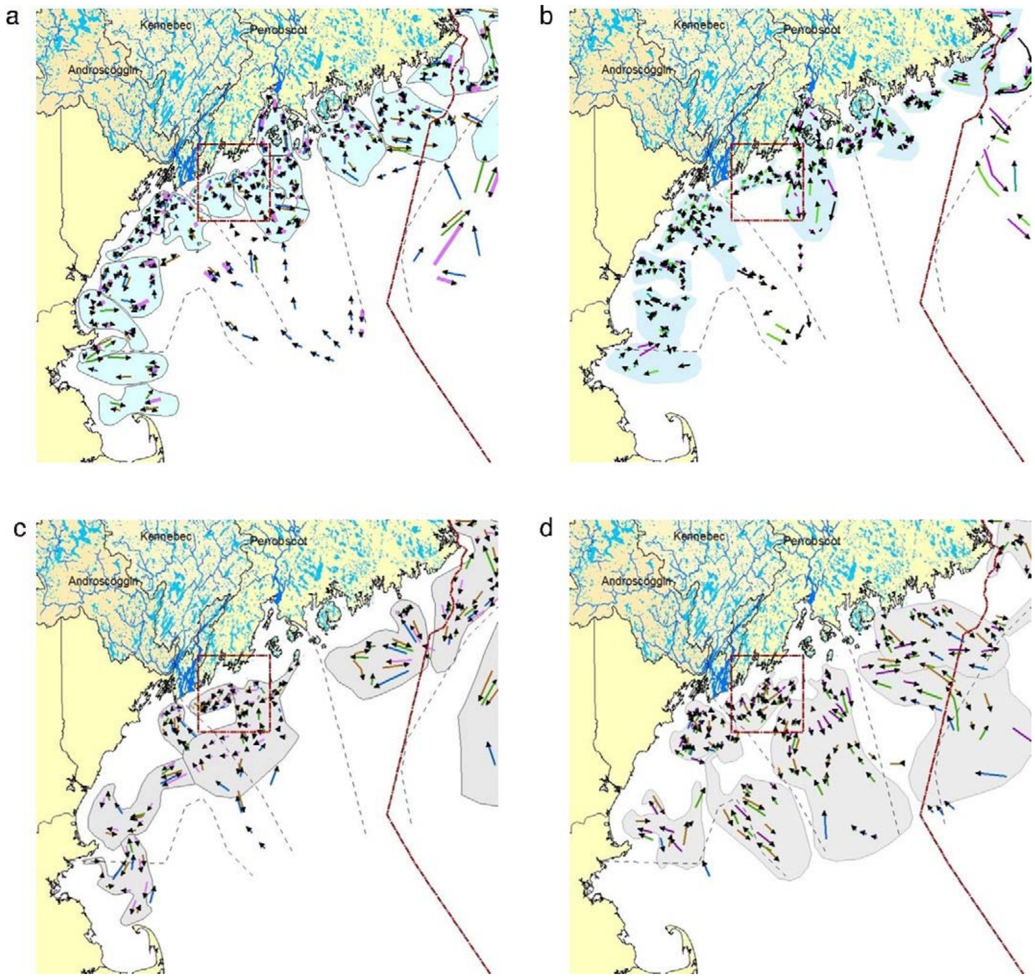

Fig. 4. (a)–(d) The distribution of four gadid spawning components and groups along coastal Gulf of Maine. (a) Cod = grey, haddock = blue; (b) white hake = light grey; (c) pollock = dark grey. Dashed black lines indicate the boundaries of cod subpopulations (Ames, 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

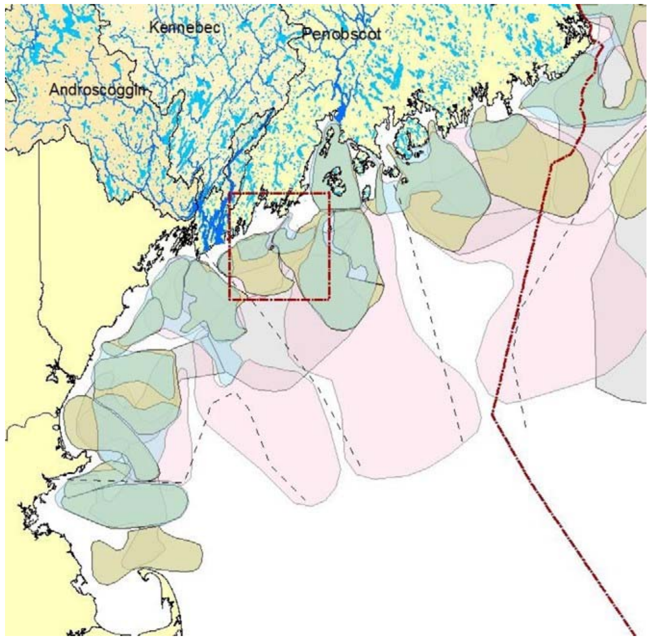

Fig. 5. (a) When the distribution of the four 1920s gadid species are simultaneously displayed near Muscongus Bay, bordering resident groups of each species can be identified. Cod = tan, haddock = blue, pollock = green diagonal lines and white hake = pink vertical lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

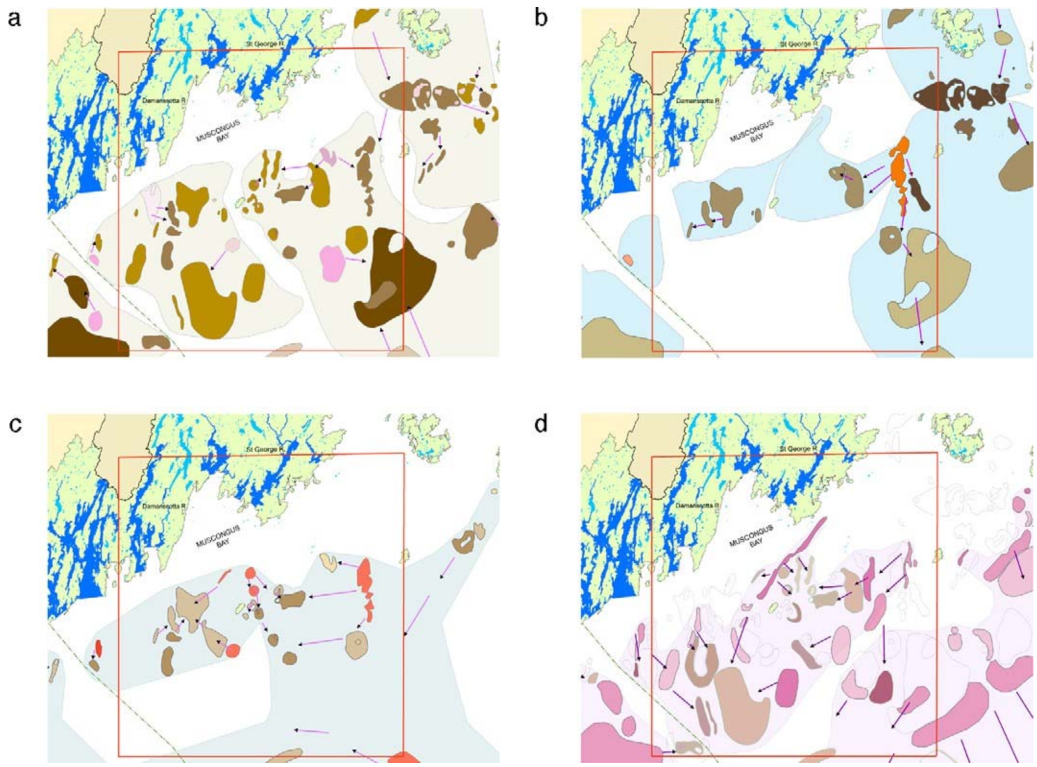

Fig. 6. (a)–(d) The distribution of each 1920s gadid group and associated movements from summer to fall among fishing grounds bordering the Damariscotta and St. George Rivers. Greater relative abundance (RA), is represented in darker shades. Summer grounds of cod (a), haddock (b) and pollock (c) are shades of orange; fall grounds, are shades of brown. The summer grounds of white hake (d) are shades of rose; fall grounds are brown. Arrows indicate the direction of their movement between seasons. Grounds with no arrows indicate the gadid remained on the same ground during both seasons. Note the four piscivores move to the same general area in the fall. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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