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# White hake (*Urophycis tenuis*) in the Gulf of Maine: Population structure insights from the 1920s

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### ABSTRACT

White hake (*Urophycis tenuis*) provides an important fishery in the Gulf of Maine (GOM) that is currently depleted. Even though several year classes are present, there is little evidence of white hake reproduction occurring along the northern coastal shelf. Based on survey indices of early life history stages, researchers concluded that they reproduced at one of the two population centers located either from the Scotian Shelf area in eastern GOM or from the Georges Bank-Mid Atlantic Bight area. White hake have been absent from large areas of the GOM for more than 15 years and this suggests substantive changes may have occurred in their distribution since the 1920s. Various factors may have contributed to this observation, including the loss of spawning aggregations. This study examined the historical population structure of white hake in the Gulf during the 1920s, a period when stocks were more abundant. Their seasonal distribution, movement patterns and the behavior of individual population components were derived from relevant scientific literature and surveys of fishermen gathered during the period. The study identified several resident groups of white hake near the coastal shelf that displayed cyclic movement patterns to fishing grounds that have been abandoned for decades. The comparison of historical distribution patterns to recent white hake surveys revealed the loss of resident white hake groups from grounds bordering the northern GOM coastal shelf that apparently were undetected spawning components. Significance of the predator–prey linkage with alewives is discussed.

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## 1. Introduction

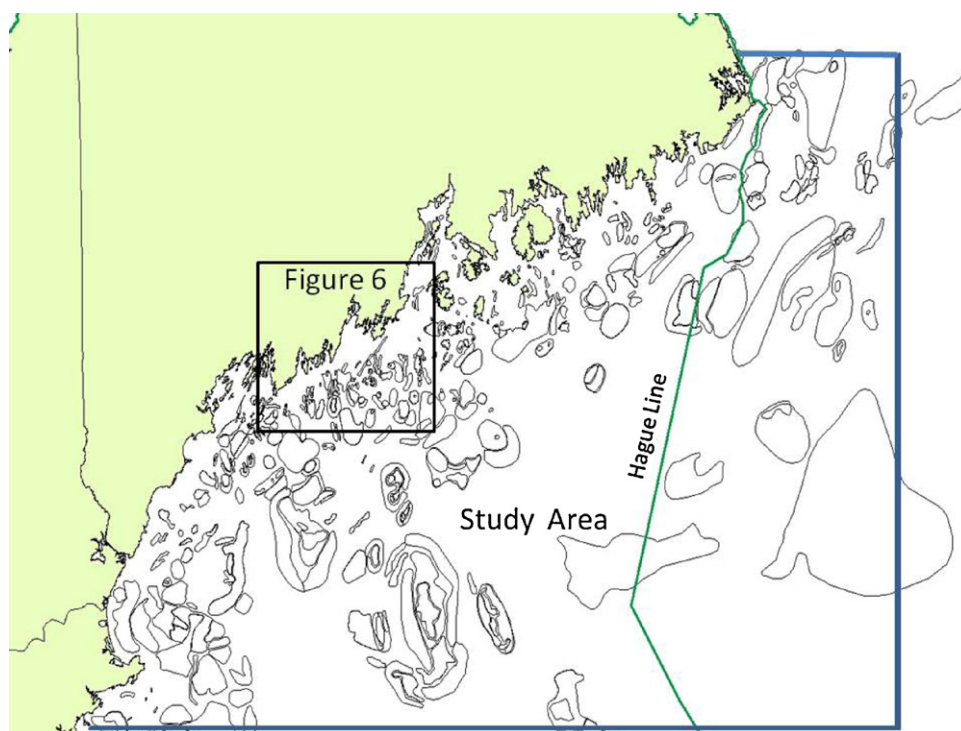
White hake (*Urophycis tenuis*) have been an important part of New England's Groundfish fishery for centuries. Survey data from 1955 to 1961 (Fritz, 1965) show that white hake were much more abundant than either cod or haddock in autumn and were concentrated in two general areas; one being the grounds along the northern coastal shelf from Gloucester, MA to Yarmouth, N.S., and the other being the grounds along the northern and eastern boundaries of Georges Bank (GB). However, white hake abundance in the GOM has fluctuated considerably since passage of the Magnuson Act (Magnuson-Stevenson Act, 1976). White hake landings varied from 4000 to 9600 mt/year from 1974 to 1998 (Collette and Klein-MacPhee, 2002), but by 2006 stocks in the GOM had declined to less than 2000 mt (Sosebee, 1998). These large fluctuations suggest that single species management efforts may not be the best way to achieve BMSY and have led to concerns that a better understanding of population structure and their interactions with other

species may be valuable in developing more effective management strategies.

The purpose of the study has been to determine whether white hake population structure in the GOM was previously more complex than is found today and if so, to identify any outstanding factor(s) linked to those changes. This research addressed the following specific issues: Is there historical evidence that a resident population of white hake existed in the GOM; second, if a resident population existed in the GOM, is there evidence to suggest that local spawning occurred and third, is there evidence indicating their contribution to the fishery was significant? Finally, was there evidence suggesting why coastal white hake stocks may have disappeared?

The research evaluates historical information from the 1920s and 1930s relating to the distribution and dynamics of white hake in the GOM, a period when commercial stocks were robust and their habitats were comparatively undisturbed. The primary source of fishermen's ecological knowledge (FEK) used for the study came from Rich (1929), with supplemental information from Ames (1997, 2004). The primary source of empirical data was derived from Bigelow and Schroeder (1953). The resulting combination of qualitative and empirical data from historical sources was then compared with recent quantitative scientific indices.

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**Fig. 1.** The study area includes those Gulf of Maine waters and fishing grounds lying north of a line drawn from the Highlands Light on outer Cape Cod to Yarmouth, N.S.

## 2. Methods

The historical distribution and dynamics of white hake was evaluated in the Gulf of Maine (GOM) during the 1920s. The study area includes all the GOM lying north of a line extending east from the Highlands Light, Cape Cod ( $42^{\circ}\text{N } 70^{\circ}\text{W}$ ) to Wrights Swell, M.A. and then to Yarmouth, N.S. ( $43^{\circ}50'\text{N}, 66^{\circ}07'\text{W}$ ) and was similar to that used to determine the population structure of 1920s and 1930s Atlantic cod (Ames, 2004) (Fig. 1).

The following definitions were used to evaluate population structure:

- 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.
- 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.
- 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.
- A group of fish is a stock component that remains in a local area throughout the year (Weis, 1951).

### 2.1. Sources of 1920s white hake fishing ground information.

The database relied extensively on Rich's "Fishing Grounds of the Gulf of Maine" (Rich, 1929) and was supplemented by additional inshore grounds identified by Ames (2004, 1997). Rich interviewed groups of vessel fishing captains with considerable experience on the grounds he documented. In cases of disagreement, the majority opinion about the seasonality or relative abundance of fish on

a ground was accepted. His study revisited the grounds described earlier by Goode (Goode, 1887) and included additional grounds discussed by fishermen during his interviews. All fishermen were actively employed in the fishery and most used hook-and-line methods to catch white hake on grounds that were feeding stations. Ames conducted individual interviews with retired vessel captains who described the grounds between Gloucester, MA and Cutler, Maine (2004, 1995). While all had fished commercially using hook-and-line methods, most had also used other capture methods. Supporting information came from "Fishes of the Gulf of Maine" (Bigelow and Schroeder, 1953; Collette and Klein-MacPhee, 2002).

### 2.2. Locating historical white hake fishing grounds.

White hake are noted for inhabiting muddy substrates in relatively deep water (80 m or deeper), though historically they were occasionally found in lesser depths (Rich, 1929). They are described as being more stationary than either cod or haddock (Goode, 1887; Bigelow and Schroeder, 1953) and display diurnal behavior, remaining on bottom in day and feeding at mid-depth in the night (Collette and Klein-MacPhee, 2002; Bigelow and Schroeder, 1953). White hake are known to prey on herring, juvenile fish, and pelagic shrimp (Collette and Klein-MacPhee, 2002). The primary fishing method used to catch white hake during the 1920s period was with baited hooks (NFC historical article, 2011); a technology that required site-specific coordinates to locate the grounds fished.

Historical fishing grounds were located by following cited historical navigation directions to a point using digitized NOAA nautical charts with 10m depth contours in a GIS system. A location from 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. These locations were in agreement with the depth and substrates of grounds where white hake are currently found. This procedure implies a visual precision that without this clarification, would appear to overstate the information contained in the historical navigation directions.

The resulting information was used to create a base map of fishing grounds and their substrates.

### 2.3. Determining seasonal distributions of white hake in the GOM using relative abundance (RA)

The procedure of Ames (2004) was used to follow seasonal shifts in the abundance of white hake. This approach is based on subjective fishermen-descriptions on specific fishing grounds for each season and was used to establish a color gradient on GIS for each ground. Interviews by Collins and Rathbun (1887) and Rich (1929) were the primary sources of seasonal information about when white hake were on each fishing grounds. The procedure allowed estimating the relative abundance (RA) of hake on a ground without regard to fishing methodology or size of vessel and avoided fishermen having to share proprietary information about actual landings.

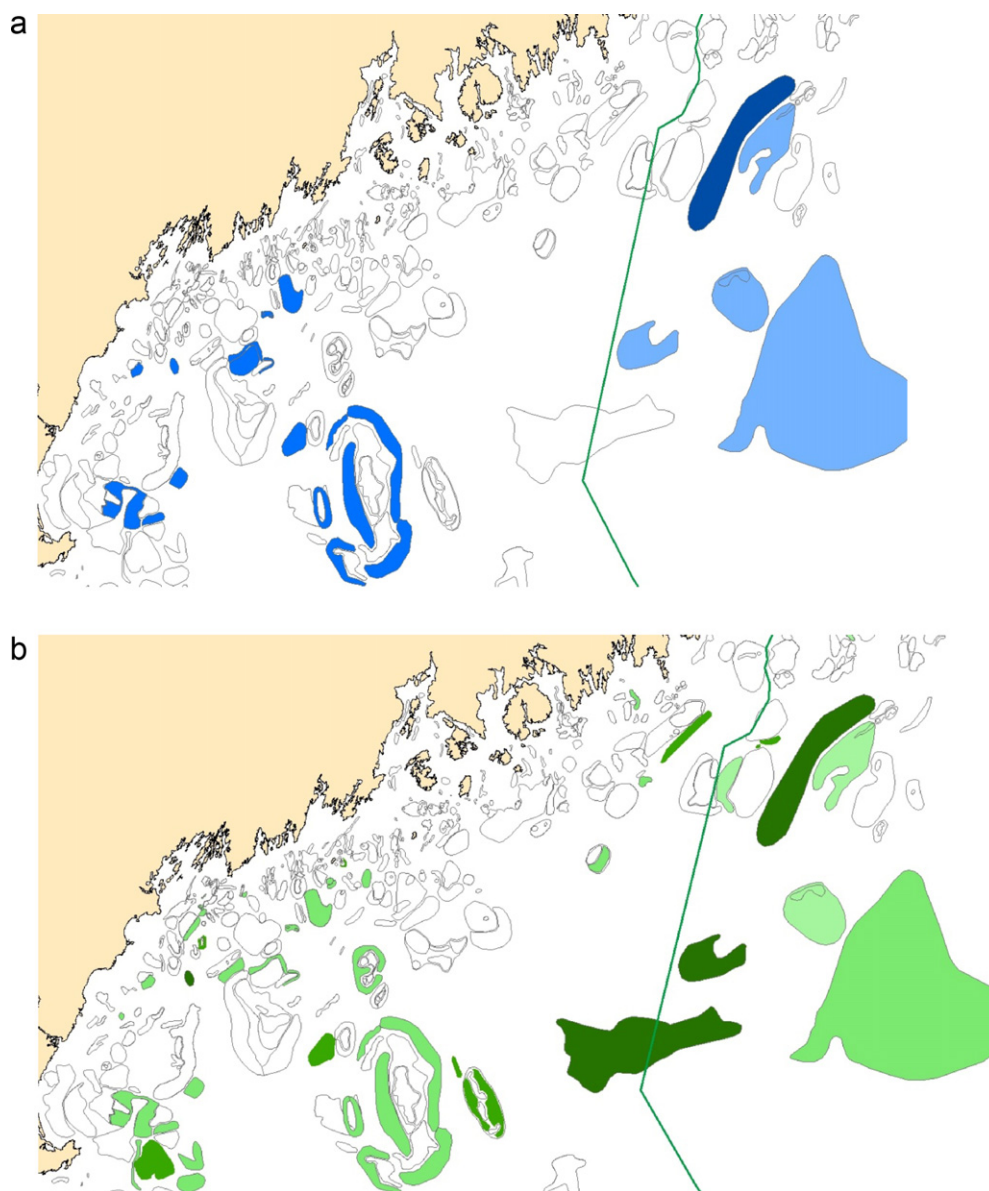
RA quantified the fishermen-estimates of white hake availability on fishing grounds by assigning values to five descriptive

**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              |

parameters describing the availability of fish. They are; absent, poor, fair, good, and very plentiful. These were given values ranging from 0 to 4 (Table 1). These 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 white hake on a ground during a given season. Maps were prepared that show the location of white hake fishing grounds and its RA based on the depth of color for each season. Those grounds reporting white



**Fig. 2.** The sequential distribution and relative abundance (RA) of 1920s white hake was plotted for each ground and for each season of the year. Darker colors indicate a higher relative abundance (RA) value for white hake on a fishing ground. (a) Winter distribution. (b) Spring distribution. (c) Summer distribution. (d) Fall distribution.



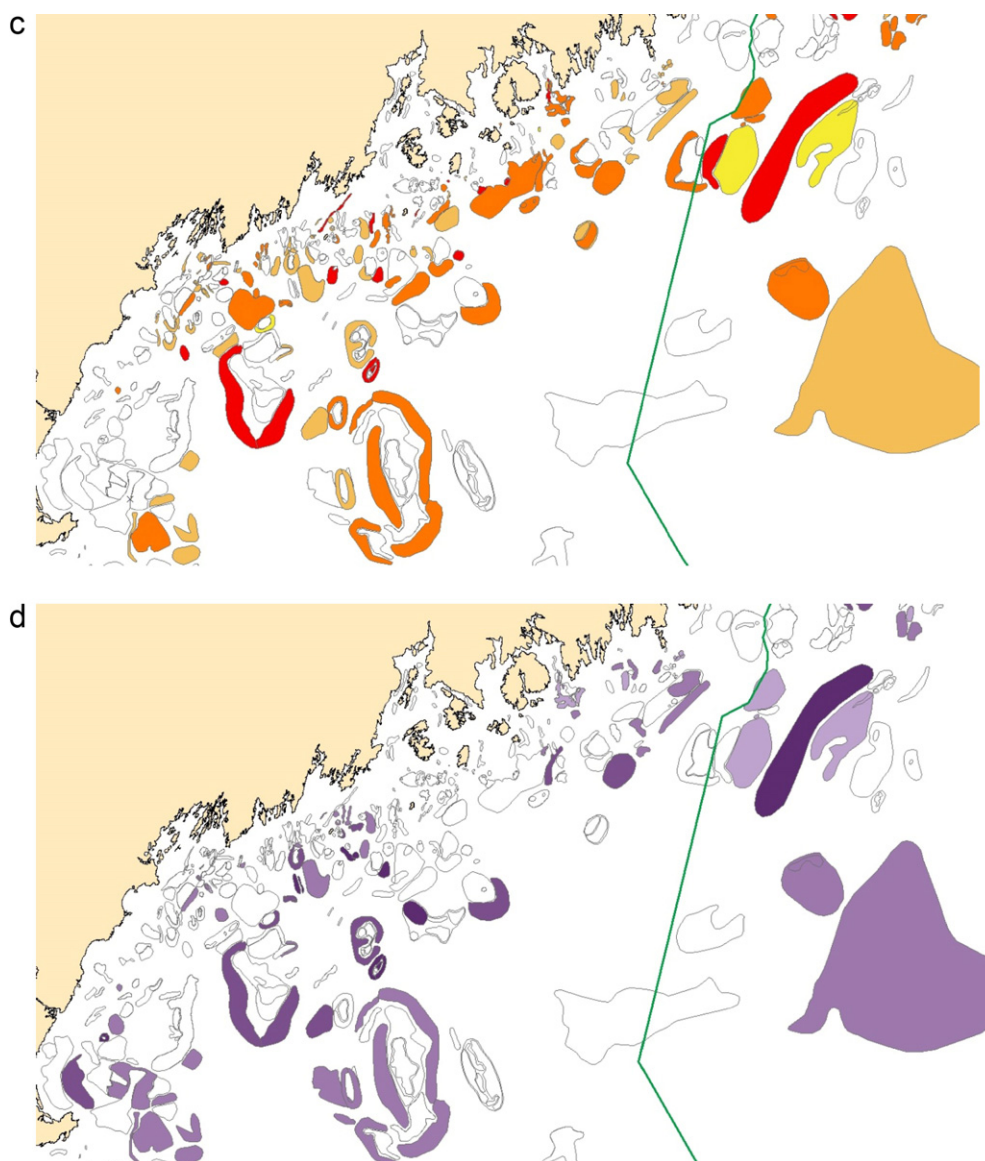


Fig. 2. (Continued)

hake being present but lacking information about their abundance were assumed to have provided fishermen with fair fishing an assigned a value of 2. When placed in sequence, fishermen's seasonal observations allowed the spatial and temporal distribution of white hake concentrations to be plotted throughout the GOM (Fig. 2a–d).

#### 2.4. Determining seasonal movements of white hake in the GOM

The base map of fishing grounds used to determine seasonal distribution can also be used to create an X–Y plot that allows the movement of white hake concentrations to be followed between seasons through the year. This approach relies on two assumptions; (a) that, a fishing ground recording a decrease in RA from one season to the next was assumed to have fewer white hake present, while a ground recording an increase in RA was assumed to have more white hake present and (b) that white hake minimized the distance they moved during seasonal movements. That is, when white hake moved, it was assumed they went to the nearest ground with an increase in RA.

The direction of movement between grounds 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 white hake could only be tracked among the grounds mapped, they were assumed to also inhabit areas with suitable habitat adjoining the grounds at times and overlaps of movement were interpreted to be general seasonal movements (Fig. 3a–d). Areas having a broad, continuous RA movement in one direction that involved several grounds during a season and accompanied by a similar, opposite movement during a later seasonal change were classified as migrations. White hake were found on relatively few GOM fishing grounds in winter, making it an appropriate starting season for tracking their annual movements.

### 3. Results

#### 3.1. Characterizing historical Gulf of Maine white hake fishing grounds

A total of 290 fishing grounds and 470 associated substrates were identified from interviews, logs and references (Rich, 1929;

Ames, 1997, 2004) (Fig. 1). White hake fishing grounds and migration corridors appeared to follow the muddy channels, gullies and basins penetrating the coastal shelf that are the geological vestiges of the Gulf's drowned river system. Substrates in these areas were consistently muddy with occasional patches of larger particle sizes interspersed on a muddy bottom. Depths on the grounds varied from approximately 40 m on inshore grounds to more than 200 m offshore. During the 1920s, large numbers of white hake were landed along the entire GOM coastal shelf, including the lower slopes of Stellwagen Bank, Jeffrey's Bank, off Penobscot Bay, Frenchman's Bay, the eastern side of the Bay of Fundy entrance and the area between Machias Bay and Mt Desert Island (Bigelow and Schroeder, 1953).

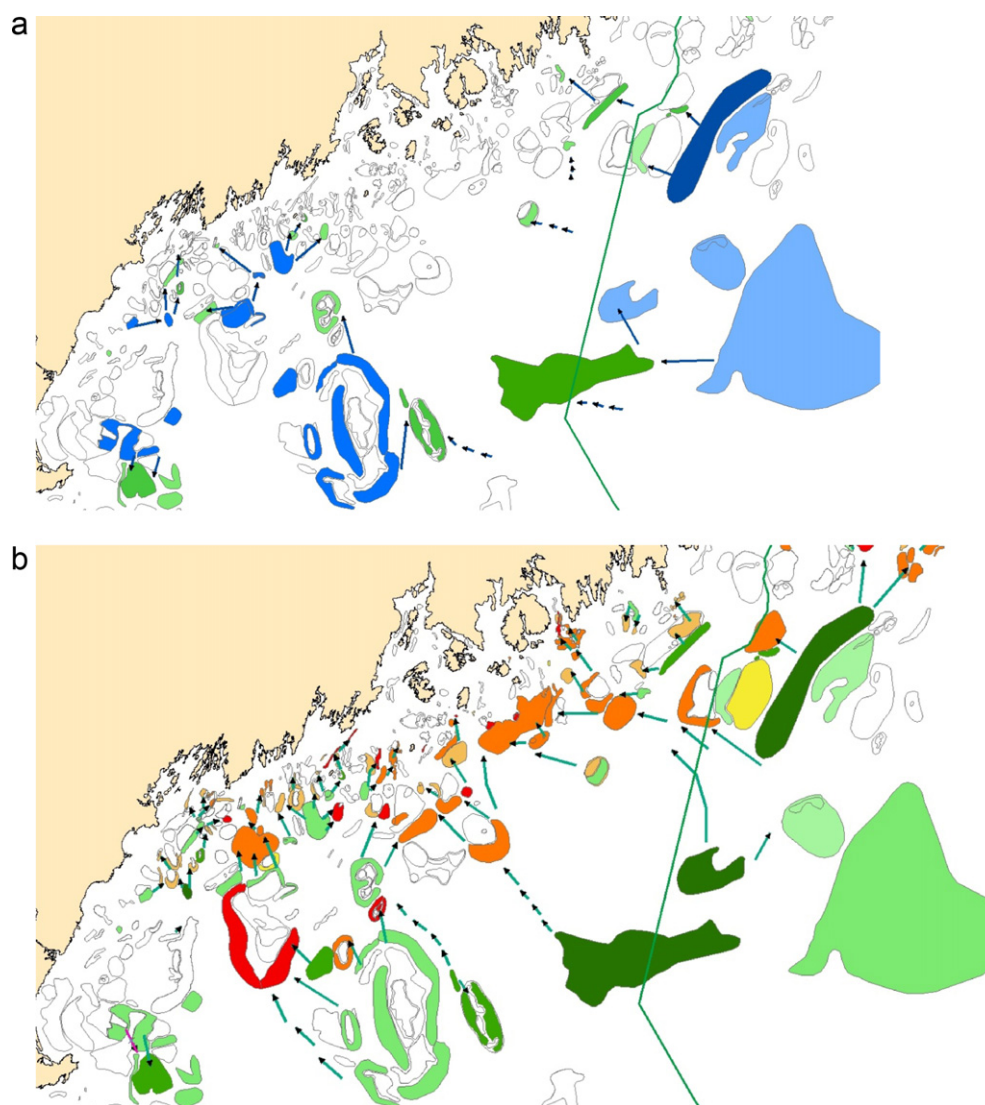
The white hake fishing grounds listed by Goode (1887) were still active during the 1920s, though many of them reported reduced landings. By 1967, landings from most of the inshore grounds were markedly reduced or collapsed and by 1995 the white hake fishery had disappeared from the northern third of New England's coastal shelf. The species is still depleted there (NOAA, 2009).

Most white hake grounds were occupied for brief periods (one or two seasons). In winter, there were but 16 GOM fishing grounds distributed in six widely separated areas that reported landings of

white hake. Of these, all but one, the Mistaken Ground, reported landings throughout the year. However, the only winter hake ground that reported abundance information was the very productive WNW Rips in the eastern entrance to the Bay of Fundy (BOF). In spring, 58 grounds reported white hake present with 15 grounds (26%) reporting good fishing or better, and in summer the number of grounds reporting landings increased to 195 grounds with 87 grounds (45%) reporting good or better fishing. Fall reports show that white hake had withdrawn from the innermost grounds but still remained on 108 grounds with 31 grounds (29%) providing good fishing or better.

### 3.2. An overview of white hake seasonal movements

To clarify the terminology used, seasonal movements refer only to changes in location occurring between two seasons. Migrations refer to the cyclic movement pattern that occurs when four consecutive seasonal movements return a group of hake to a common point. White hake migrations involved inshore movements in spring and a corresponding offshore movement in fall, a pattern repeated throughout the GOM. These movements were obvious for all seasons except spring-to-summer, where the number of



**Fig. 3.** Views summarizing the sequential movement of 1920s white hake between seasons, starting with movements from their winter grounds in spring and ending with movements in fall to return back to their winter grounds. Darker colored fishing grounds have higher relative abundance (RA) of white hake. (a) Winter to spring movements. (b) Spring to summer movements. (c) Summer to fall movements. (d) Fall to winter movements.

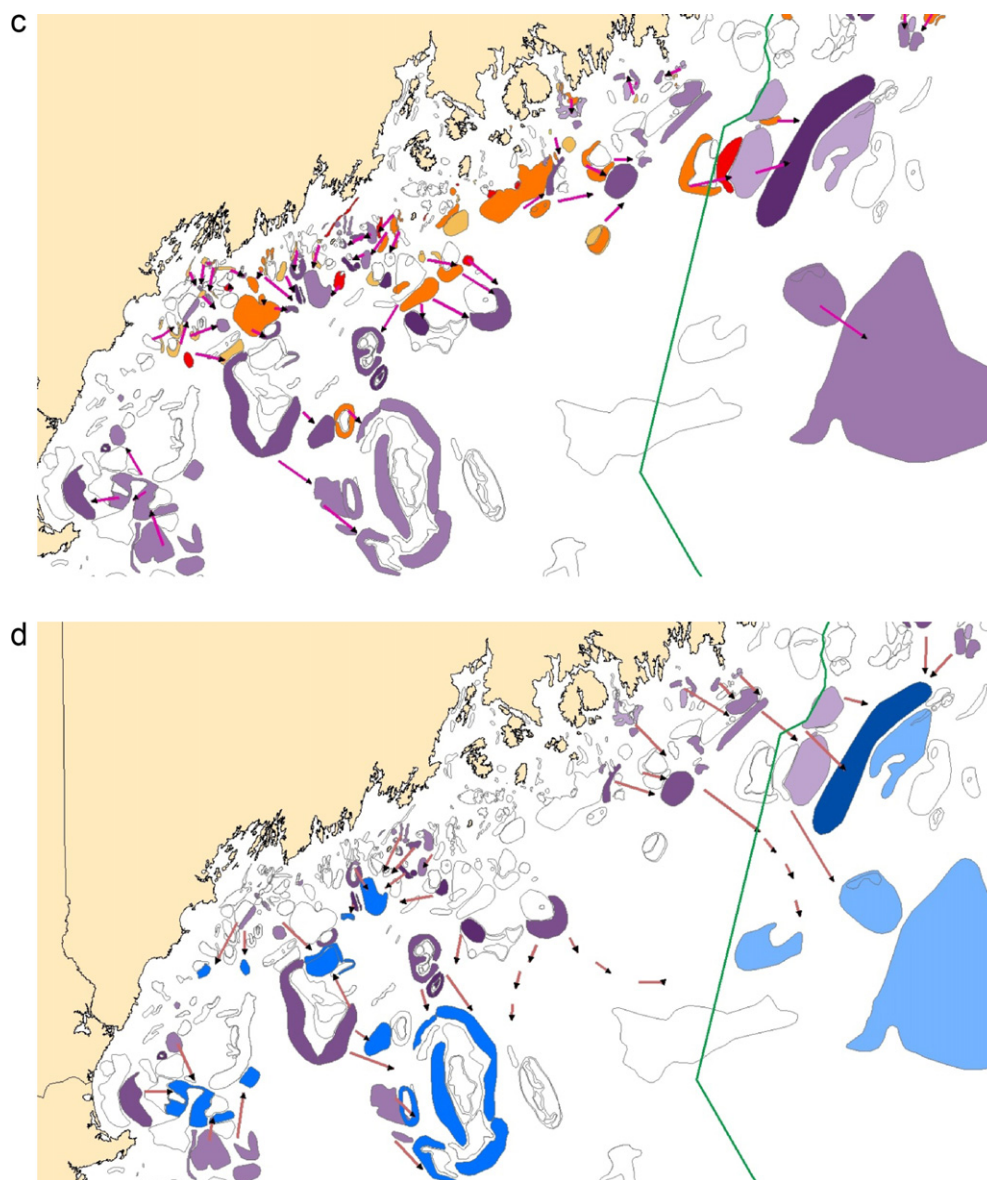


Fig. 3. (Continued)

grounds with fish mushroomed from 58 grounds to 195 grounds, making interpretation more difficult. Fig. 3a–d summarizes these movements.

In winter, white hake were reported in six different areas along the GOM coastal shelf. The four widely separated inner complexes of grounds had depths of 160–200 m and were located approximately 24–36 km from shore. The two outer complexes the muddy areas surrounding Cashes Ledge and below the WSW Rips located near the eastern entrance to the Bay of Fundy were about 90 km from shore with depths of approximately 200 m.

In spring, white hake moved a short distance inshore from most of their winter grounds. Numbers of white hake also appeared on Davis and Truxton Swells, though it is unclear whether these were lateral movements of hake from Cashes Ledge, the Seal Island Ground, N.S., or from outside the study area.

By summer the occupants of the inner spring grounds had moved to numerous inner grounds. Meanwhile outer hake groups from western Cashes Ledge, Davis Swell and Truxton Swell appeared to move to northern Wilkinson and Jordan Basins grounds bordering Platt's Bank, Newfound Bank, ME, Bank Comfort and Outer Schoodic Ridge.

By fall, all groups had left their innermost grounds for grounds closer to their winter grounds. However, no fall landings of white hake were reported from either Davis Swell or Truxton Swell, suggesting that their arrival in spring may have originated from Cashes and/or the Seal Island Ground, N.S., rather than from outside the study area.

The western-most coastal group of white hake overwintered along the western edge of Wilkinson basin mud bordering SE Jeffrey's Ledge, West Jeffries and Tillie's Bank. In spring, white hake moved inshore to muddy areas near Tillie's Bank, eastern West Jeffries, and the eastern slope of Stellwagon Bank, where they remained through the fall. By summer, some moved further inshore to the muddy bottom lying outside Ipswich Bay and Isle of Shoals where they remained through the fall. In winter, these white hake returned to their winter sites east of West Jeffrey's and Tillie's. These may also have been part of the larger GB-South Channel hake group noted by Lang et al. (1994).

The Casco Bay group wintered on and around the mud of Mistaken Ground and Cod Ridge and by spring had moved shoreward to the muddy areas of Doggett's, Trinidad and White Head grounds lying outside the Cod Ledges in Casco Bay. By summer this group



appeared to move to numerous inner grounds ranging from Mark Island Gully to the Kettles and Hill grounds lying south of Cape Small. By fall the Casco Bay group had moved to grounds part way back to their winter sites near Mistaken Ground. A second, outer group wintering on the Maurice Lubee and Sigsbee Grounds NW of Cashes Basin appeared to move to the southern and eastern muddy edges of Platt's Bank where they remained through the fall. By winter, both groups were at their winter sites.

The inner Midcoast group movements displayed similar complexity. White hake left the Peterson and Harris grounds in spring for nearby inshore grounds closer to Monhegan and western Penobscot Bay. Simultaneously, other hake left the muddy bottom north and east of Cashes and moved a few miles inshore to Toothacres Ridge. Hake also appeared on Davis and Truxton Swells along the southern rim of Jordan Basin, originating either from the Cashes Ledge and Seal Island Ground, N.S., mud or from a third migration outside the study area. Spring was the only season white hake were reported on these two grounds.

By summer the Midcoast group had moved to numerous inshore grounds from the Sheepscot area to Penobscot Bay and Skate Bank.

The hake on Davis Swell moved north along the western rim of Jordan Basin and by midsummer they overlapped with coastal groups on Newfound Ground, ME, eastern Penobscot Bay and the Isle au Haut Hake Ground. The hake on Truxton Swell moved north along the eastern side of Jordan Basin and by summer had overlapped with BOF hake on outer grounds stretching from Mt. Desert Rock to the eastern entrance to the BOF.

By fall the movement pattern reversed. The inner Midcoast white hake moved laterally from western Penobscot Bay to a band of grounds midway to the Harris ground area. By winter they were back on the Peterson and Harris grounds. The Cashes Ledge group withdrew from eastern and southern Penobscot Bay to grounds stretching between Toothacres and Newfound, ME. By winter they had returned to the Cashes mud. Neither Truxton nor Davis Swells had fall landings of white hake during the 1920s, leaving it unclear whether they were also there in the fall but unfished, or whether they had simply returned to grounds near Cashes Ledge and/or the Seal Island Ground, N.S.

A fourth coastal white hake group that wintered outside the WNW Rips near the deep, muddy eastern entrance to the Bay of Fundy (BOF). Another group near the Seal Island Ground, N.S., may have been part of this group.

In spring a cross boundary component (the Eastern Coastal Group) moved from the WNW Rips to muddy grounds lying outside Moosebec Ridges, Outer Schoodic Ridge and SE of Bank Comfort.

By summer the Eastern Coastal Group had moved further west to various coastal hake grounds from Jonesport, M.E. to Frenchman's Bay and possibly as far as the Isle au Haut hake ground. A second group moved north from the WNW Rips hake ground to various inner BOF grounds where they remained until returning to the Rips in the fall. Hake on Truxton Swell appeared to move north along the eastern edge of Jordan Basin and by summer were occupying numerous outer grounds as far west as Mt. Desert Rock, including and possibly overlapping with cross boundary components from WNW Rips grounds.

By fall the cross-boundary group left their inshore grounds moved east to grounds located midway to their winter grounds below the WNW Rips. BOF hake had partially withdrawn from the eastern part by fall, but continued to stay on grounds in western BOF and Grand Manan Channel. Hake from Truxton Swell appeared to gather on the mud bottom near outer Schoodic Ridge and Bank Comfort.

By winter, both the cross-boundary and BOF components had returned to their winter grounds below the Rips. Without hake landings from Truxton Swell or Davis Swell one cannot tell whether they overwintered near the Seal Island Ground, or that fishermen

simply ignored the area in winter when more profitable species (cod and haddock) were available closer to shore. This does, however, suggest that white hake participated in extensive seasonal migrations to the northern coastal shelf that originated at least as far as lower Jordan Basin and eastern Wilkinson Basin.

#### 4. Discussion

##### 4.1. 1920s White Hake localized population structure appeared to be related to prey availability

Initial assessments assumed the population of white hake in U.S. waters was a single stock inhabiting the waters of the GOM south to the mid-Atlantic Bight (Burnett et al., 1984). However, Fahay and Able (1989) reported the existence of two reproductively isolated stocks in the northwest Atlantic as revealed by their spawning seasonality. One, a northern white hake stock that spawns in the relatively shallow waters of the Scotian Shelf and southern Gulf of St. Lawrence in summer, while the other spawns in early spring along the continental slope lying south of Georges Bank and off southern New England in deep water. They concluded that these were the major spawning sites of white hake in the GOM and that the spawning contribution within the GOM was negligible. Collections gathered from the GOM in 1992 indicated there were either two successful spawning periods or one very protracted spawning period because two size classes of juvenile hake were found, but there was no evidence that indicated a summer spawning Scotian Shelf stock (Lang et al., 1994).

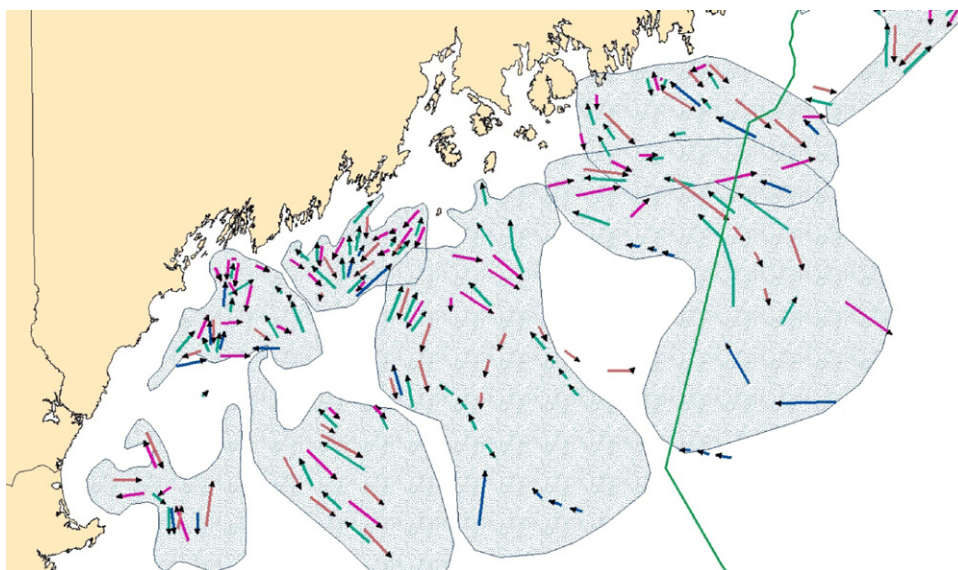
No spawning migrations of white hake have been documented by the results of NMFS trawl surveys or within the scientific literature. However, early research suggests white hake may be serial spawners (Battley, 1951) or have one protracted spawning period (Lang et al., 1994), making it likely that GOM coastal groups reproduced within the areas they occupied during the course of the year.

Based on otolith analysis and the evaluation of ocean circulation patterns show that juvenile hake spawned from the Georges Bank group also recruited northward into coastal GOM estuaries (Lang et al., 1994). The results of a recent North Atlantic estuarine species surveys (Jury et al., 1994) reported that red hake juveniles were abundant in estuaries from Casco Bay, ME and west, while white hake juveniles were abundant from Passamaquoddy Bay, ME to the Sheepscot River, ME, several years after coastal groups of white hake had disappeared.

Bigelow and Schroeder (1953) noted that adult white hake had relatively limited movements when compared to cod, did not participate in spawning migrations, but reported no evidence of significant reproduction in the GOM.

Resident white hake populations of 1920s existed in the GOM. The current study found evidence that substantial numbers of 1920s white hake were present in the GOM throughout the year. There were six resident groups distributed throughout the study area and their relatively limited seasonal movements allowed them to be tracked (Fig. 3a–d). Four of the locations bordered the U.S. coastal shelf, with one in mid-GOM, and another near the Scotian Shelf in eastern GOM. White hake displayed independent, sequential seasonal movements at each location to numerous fishing grounds that began and ended with their respective winter grounds. The rather limited movement patterns of coastal white hake groups support the observations of Bigelow and Schroeder (1953) that they tended to migrate less than cod. This observation, however, was not true for the two offshore groups.

While Fahay and Able's study (1989) found no evidence of significant spawning contributions originating with GOM white hake, Lang et al. (1994) reported that white hake either had an unusually prolonged spawning season, or multiple spawning events each



**Fig. 4.** View of the areas occupied white hake groups during the 1920s based on their seasonal movements. Each enclosure encompasses all the fishing grounds occupied by white hake from a specific group. Colored arrows indicate seasonal movements: blue = winter–spring, green = spring–summer, red = summer–fall, and brown = fall–winter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

year, and an earlier study by [Battle \(1951\)](#) found evidence of serial spawning. Their research, combined with the discovery of numerous groups of white hake would appear to make local spawning events by local groups inevitable. One must conclude that 1920s white hake groups in the GOM reproduced locally.

Ideally, their reproductive capacity could be approximated by determining the number of vacant fishing grounds that appeared to be linked to the also-abandoned 1920s white hake winter grounds ([Fig. 4](#)). Today, of the 131 white hake fishing grounds in the study area identified by Rich, fully 75 of them (56%) were located between Penobscot Bay and Casco Bay and none of them support a fishery today. The concurrent disappearance of white hake from their 1920s coastal shelf grounds, including their known winter grounds, argues that their reproductive contributions to the 1920s coastal white hake fishery must have been significant.

Yet the depletion observed today does not appear to be from lack of juveniles. In spite of the collapse of the area's coastal white hake fishery, juveniles were abundant from the Sheepscot River estuary to Passamaquoddy Bay in the early 1990s ([Jury et al., 1994](#)). Clearly, other factors have affected the recovery of white hake on those grounds.

Evidence suggests that in addition to overfishing, the loss of coastal white hake in northern GOM may have been related to the loss of certain prey species. This analysis does not diminish the consequence of overfishing, but instead examines another important factor affecting the distribution of white hake in northern GOM. That white hake abandoned their inshore grounds, even though juveniles were still abundant in bordering estuaries confirms that many juveniles migrated there, but perhaps equally important, the observed behavior of coastal white hake reflected only the behavior of adults. This suggests their departure from coastal grounds may have been related to other factors, including the loss of certain prey species.

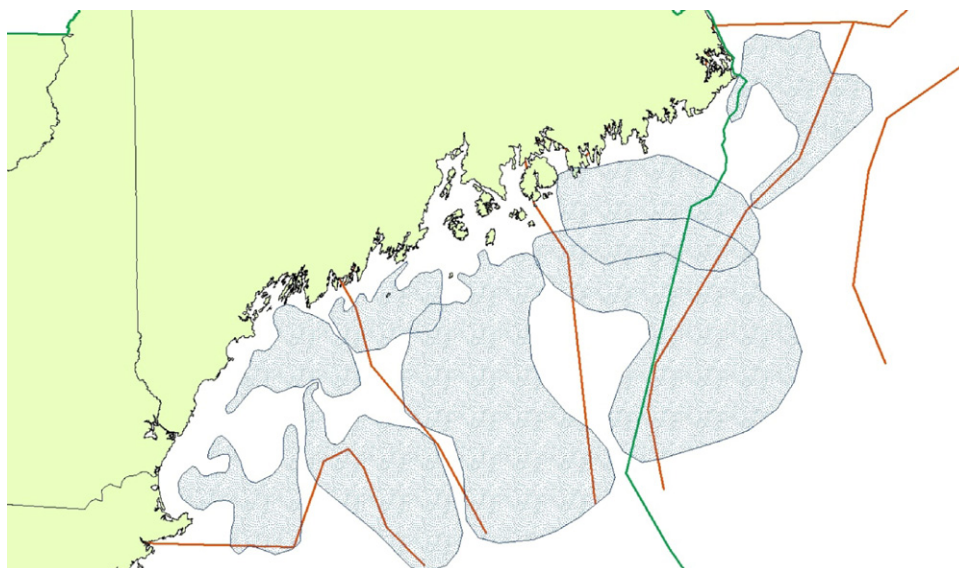
An area having suitable habitat with an abundance of prey throughout the year would logically tend to attract predators that also remained in the area, particularly if it were a species exhibiting the sedentary behavior ascribed to adult white hake ([Bigelow and Schroeder, 1953](#)). As juveniles from local nurseries matured, they would tend to remain nearby and eventually the number of residents would increase until enough were present to coalesce

into resident groups. It seems equally probable that white hake would abandon such an area once the concentrations of preferred prey disappeared from the area. This classic predator–prey behavior describes how coastal cod responded to the collapse of alewives ([Baird, 1883](#)) and it appears that white hake have responded in much the same way. However, evaluating predator–prey linkages in a marine system where the behavior, interactions, and movement patterns of multiple species function within a dynamic system that lacks obvious boundaries is especially difficult. It was the arrival of cod pursuing alewives up to the river's mouth that created the fixed barrier that allowed Baird to identify their relationship. The interface between river and coastal ecosystems also facilitated the 1920s study of alewife predation by white hake.

While the white hake's seasonal movements along the coastal shelf suggested that they were preying on alewives near various rivers, few rivers in the study area had documented alewife landings during the 1920s. However, two secondary rivers in Maine located only a few km apart with landings records during the 1920s, the Damariscotta and St. George Rivers provided an exceptional opportunity to evaluate white hake behavior near a known alewife river ([Hall et al., 2011](#)). Historical records show the nearest resident group approached the rivers' entrance in spring, remained in the area through summer and fall, and moved somewhat farther offshore in winter, but always remained close to where YOY alewives were likely to be ([Fig. 4](#)).

Adult alewives leave northern GOM in fall, co-migrating with adult herring south and west along the coastal shelf while being pursued by cod and other predators. However, their YOY do not migrate until the following year. After leaving the river in late summer, the YOY alewives gather to feed in nearby coastal nurseries. But as the days shorten, coastal waters cool and the plankton bloom fades. By fall, the young alewives were moving to nearby deeper water. Meanwhile, instead of moving directly offshore with other white hake groups, resident white hake moved laterally to occupy inshore fishing grounds where YOY alewives were likely to pass ([Fig. 6](#)). That white hake bordering the two alewife rivers remained inshore in the fall, rather than moving directly offshore as other hake were doing and as white hake normally do today is notable and appears to be linked to the migration of YOY alewives moving to deeper water.





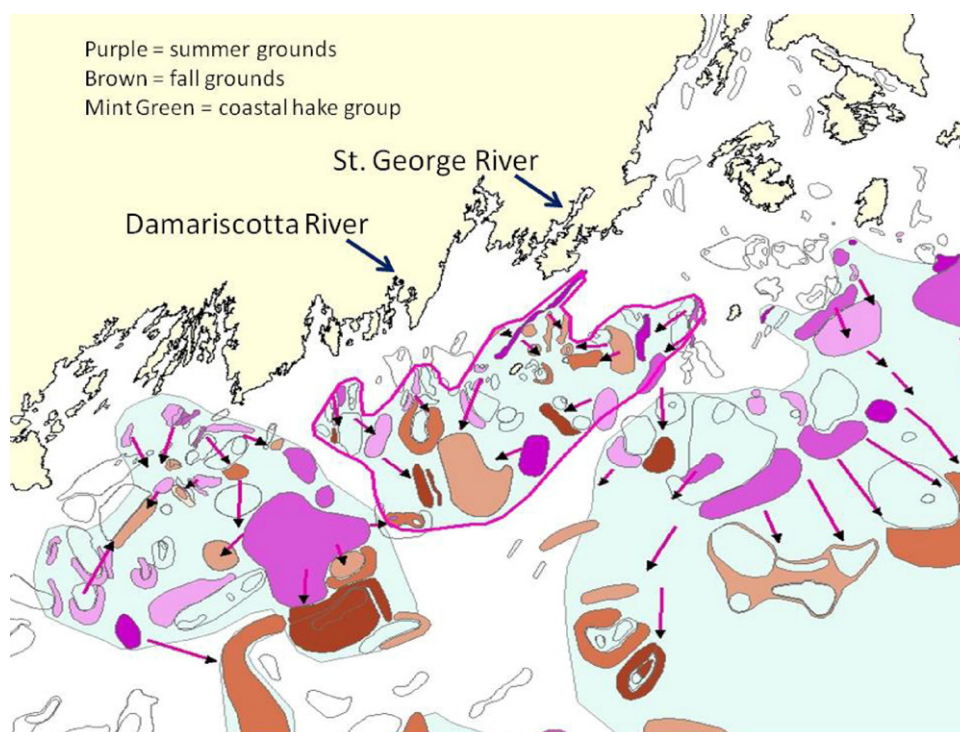
**Fig. 5.** When 1920s white hake group boundaries (purple) are placed over the subpopulation boundaries of GOM Atlantic cod (yellow), most white hake appear to stay within the boundaries of their respective cod subpopulation. For example, the white hake group bordering Jeffrey's Ledge stayed within the boundaries of the western GOM cod subpopulation, etc. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

#### 4.1.1. Observations relating to white hake and Atlantic cod during the 1920s

In addition to white hake, there was a resident cod spawning component near the two rivers that exhibited similar movement patterns (Ames, 2004), suggesting that both gadids shared a well established predator–prey linkage that included YOY alewives (Fig. 5). Comparing the behavior of white hake with that of cod provides three relevant observations: first, both species had local groups near the two alewife rivers and both appeared to coordinate their movements with alewives, particularly in the fall when YOY

were moving to deeper water. White hake predation appeared to be more episodic than cod, whose grounds were in locations where YOY alewives would be found throughout the year. The loss of YOY alewives as local prey in fall and winter appears to have been linked to the disappearance of inshore groups of white hake and cod along the northern coastal shelf.

Second, during the 1920s white hake remained in the vicinity of the two rivers all year as did Atlantic cod; that is, the annual movements of both species near the river were similar. One possible explanation for this behavior may have been that their distribution



**Fig. 6.** From summer to fall, resident white hake near the Damariscotta and St. George Rivers move laterally to occupy inshore fishing grounds where YOY alewives will pass. Other hake in the area move directly offshore.

reflected the winter distribution pattern of YOY alewives from the two rivers (Fig. 5). Additional research will be needed if such issues are to be resolved.

Third, a significant ecological problem continues to exist along the northern third of New England's coastal shelf. For more than fifteen years, white hake and cod in the northern 8000 km<sup>2</sup> section of the U.S. GOM continue to be depleted. There are few signs of recovery among stocks of white hake, cod, haddock, winter flounder and other groundfish species and the area's groundfish fishery has ceased to exist.

The recent collapse of northern GOM groundfish coincided with the closure of fishways on the St. Croix, causing a rapid decline in the area's alewife stocks and an accompanying rapid decline in adult Atlantic herring stocks from an intensified industrial fishery (Cieri et al., 2008; Overholtz, 2006). The significant reduction of overwintering prey in northern GOM, followed by the loss of predators such as white hake and cod would appear to parallel the loss of alewives and precipitous decline in coastal cod noted by Baird (1883) and raises the likelihood that the collapse of coastal white hake and related groundfish stocks in northern GOM was a predator–prey response to the rapid reduction of alewives and herring. It seems equally probable that restoring anadromous fish would enhance the recovery of white hake and related species, but further research on the linkage between alewives and the formation of coastal groups of white hake and cod will continue to be needed.

This study concludes that the disappearance of 1920s coastal white hake groups in northern GOM was linked to alewives and suggests that their recovery inshore may require the restoration of alewives.

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