THE DISTRIBUTION OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, ON GEORGES BANK AND IN THE GULF OF MAINE IN RELATION TO DENSITIES OF THE SAND EEL, *AMMODYTES AMERICANUS*

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ABSTRACT

The distribution of the humpback whale, *Megaptera novaeangliae*, (based on shipboard sighting data) is significantly correlated (r = 0.81, df = 13) with the number of sand eel, *Ammodytes americanus*, per standardized tow (based on NMFS/NEFC groundfish surveys) by strata within the Gulf of Maine. A demonstrated increase in the number of humpback whale sightings in the southwest Gulf of Maine since 1978 concurrent with an increase in the number of sand eel in the same area supports the hypothesis that within the Gulf of Maine the present distribution of humpback whales is due to the distribution of their apparent principal prey, the sand eel. A similar correlation between humpback whale sightings and sand eel abundance on Georges Bank was not significant (r = 0.24, df = 18) despite dense patches of sand eel in that region. Therefore, within the combined Gulf of Maine-Georges Bank regions, factors other than simply prey availability must influence the feeding distribution of the humpback whale. We argue that the bottom topography of the Gulf of Maine and the foraging behavior of the whales are critical factors influencing their present feeding distribution.

In the northwest Atlantic, the major summer concentrations of humpback whales, *Megaptera novaeangliae*, occur off the coasts of Newfoundland-Labrador and off the coast of New England in the Gulf of Maine which includes Georges Bank (Katona et al. 1980; Whitehead et al. 1982). During this period feeding is their principal activity. The major winter concentrations in the western North Atlantic occur along the Antillean Chain in the West Indies, principally on Silver and Navidad Banks which lie north of the Dominican Republic (Winn et al. 1975; Balcomb and Nichols 1978; Whitehead and Moore 1982). During this season conception and calving are their primary activities; food does not seem to be an important determinant of the humpbacks in these areas (Whitehead and Moore 1982).

Humpbacks have been generally considered coastal animals (Mackintosh 1965). However, their migratory routes between regions of winter breeding and summer feeding in the northwest Atlantic (based on sighting data) occur in deeper, slope waters off the continental shelf (Hain et al. 1981; Kenney et al. 1981; Payne et al. 1984). Several possible offshore routes between winter and summer grounds suggest reasonably distinct stocks (Katona et al. 1980). Kenney et al. (1981) suggested that for the Gulf of Maine stock, the Great South Channel (Fig. 1) is the major exit-entry between the Gulf of Maine feeding area and the deeper, offshore migration route.

Humpback whales have been described as generalists in their feeding habits (Mitchell 1974). The reported prey of humpbacks in the Gulf of Maine are Atlantic herring, *Clupea harengus*; Atlantic mackerel, *Scomber scombrus*; pollock, *Pollachius virens*; and the American sand eel, *Ammodytes americanus* (Gaskin 1976; Katona et al. 1977; Watkins and Schevill 1979; Kraus and Prescott 1981). In recent years, observations of feeding humpbacks indicate that sand eels have become an increasingly important prey item in the Gulf of Maine (Overholtz and Nicolas 1979; Hain et al. 1982; Mayo 1982).

Kenney et al. (1981) hypothesized that the observed distribution of the Gulf of Maine humpback stock was due to the distribution of sand eel, their apparent principal prey species. However, the present distribution of the humpback whale in the Gulf of Maine and throughout the remaining shelf waters of the northeastern United States is not so clearly related to the distribution of sand eel as was suggested. Although we recognize an important predator-prey interaction between humpbacks and sand eel, we hypothesize that behavior and bottom

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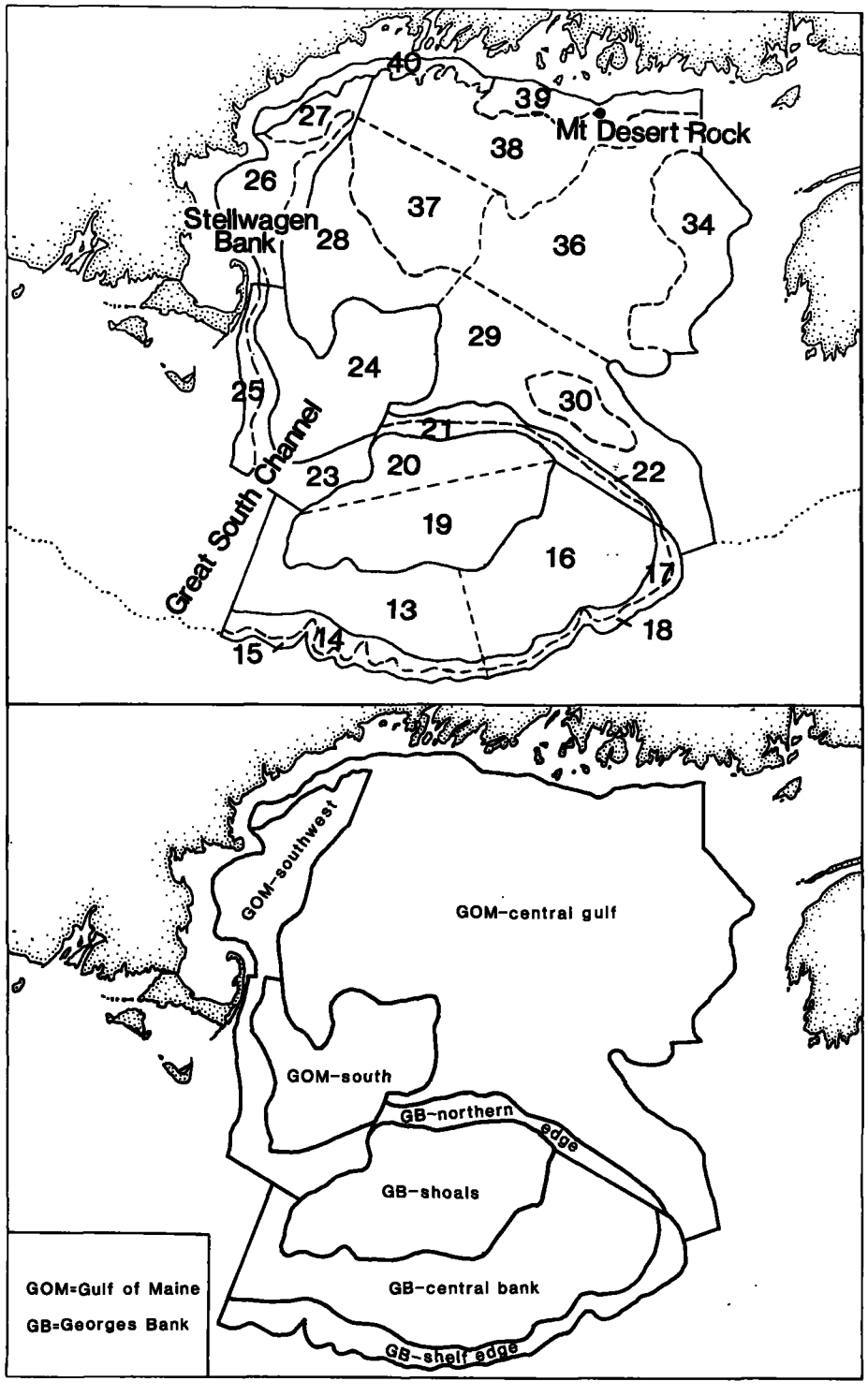

FIGURE 1.—The geographical areas and NMFS/NEFC bottom-trawl survey strata in the study area (upper) and the combined strata into regions (lower) referred to throughout the text.

topography are also critical factors in the foraging strategy of humpbacks, hence the present distribution of these whales. We base this hypothesis on observed sightings of humpbacks throughout the shelf waters of the northeastern United States in relation to sand eel abundance, and on an apparent shift in the center of feeding areas used by humpbacks in the Gulf of Maine since the mid-1970's.

METHODS

The collection of fisheries data used in these analyses was carried out by National Marine Fisheries Service/Northeast Fisheries Center (NMFS/NEFC) scientists and technicians on domestic research vessels during standardized spring bottom-trawl surveys. These surveys measure trends in finfish population abundance and have been used to monitor changes in the size and composition of finfish biomass (Clark and Brown 1977; Grosslein et al. 1980).

Meyer et al. (1979) found that spring (March-May) bottom-trawl surveys accurately reflect trends in sand eel abundance. Therefore, the fisheries data we examined were from these surveys, 1978-82. The stratified mean catch per tow of sand eel was calculated for each region and considered proportional to the population size within each region. We transformed the mean catch into logarithmic values; then, using a two-way analysis of variance (F-statistic), we compared sand eel population size by region and year.

The survey area includes shelf waters from Cape Hatteras north to Nova Scotia and has been spatially stratified by the NMFS/NEFC, based principally on depth and latitude (Grosslein 1969). Sampling stations are randomly assigned within a stratum and the number of stations allocated to strata approximately in proportion to the area of each stratum (Grosslein 1969). In this study, individual stratum have been combined into regions (Fig. 1), in a manner consistent with NMFS/NEFC management units. The two important regions emphasized are the Gulf of Maine and Georges Bank.

Sightings of humpback whales were recorded by observers from the Manomet Bird Observatory (MBO) on NMFS/NEFC research vessels conducting standardized surveys. Observations were recorded continuously along the predetermined cruise path between the sampling stations (following Payne et al. (1984)) in 15-min periods where each period represents a transect. Thus, the duration of each observation period was constant, but the linear km surveyed within each 15-min period depended upon vessel speed. The location (latitude-longitude) of each 15-min observation and the location and number of humpback whales observed were recorded and assigned to appropriate regions to facilitate direct comparisons between the observed number of humpbacks per linear km (humpbacks/effort) and potential prey densities.

Humpback whales are generally present in the study area from spring through fall (March-November) and absent during the winter (CETAP 1982). Therefore, sighting data and effort for winter months were excluded from the analyses. We also examined sighting data collected only during optimum sea conditions less than Beaufort (Kenney et al. 1981) (<16 nmi/h). Difference between the number of humpbacks/effort sighted by region and year were also compared by a two-way analysis of variance (F-statistic).

A coefficient of correlation (r) from the linear regression between the stratified mean catch of sand eel (log) and the number of humpbacks/effort was used to determine whether concentrations of humpback whales co-occurred with patches of sand eel within regions of the Gulf of Maine and Georges Bank.

A $P < 0.05$ was considered statistically significant.

RESULTS

Distribution of Sand Eel

The stratified mean number of sand eel varied significantly between regions on Georges Bank ($F = 14.14$, $df = 3, 12$) and in the Gulf of Maine ($F = 16.90$, $df = 2, 8$). On Georges Bank, sand eel were very abundant on the shoals with catches ranging from 1.117 sand eel/tow (log value) in 1978 to 2.846 (log value) in 1982 (Table 1). Sand eel were absent from most tows along the northern and shelf edges. Sand eel were also abundant in the southwest Gulf of Maine ranging from 0.670 sand eel/tow (log value) in 1978 to 2.422 in 1981 (Table 1). Sand eel were not abundant in the deeper, central Gulf of Maine. This patchy distribution reflects a known preference of the sand eel for sand-bottom substrates (Bigelow and Schroeder 1953) characteristic of submarine banks and shoals. No significant differences were found between the stratified mean catch per tow (log value) by year.

Distribution of Humpback Whales

Since 1978, the observed number of humpbacks/effort in the Gulf of Maine has steadily increased

TABLE 1.—Stratified mean number of sand eel per tow ± SE (in parentheses) and the number of sampling tows (lower number) by region and year.

Region	1978	1979	1980	1981	1982
Georges Bank					
shoals	1.117	1.200	2.752	1.850	2.846
	(0.233)	(0.305)	(0.590)	(0.499)	(0.691)
	15	30	15	15	15
northern edge	0.000	0.256	0.000	0.747	0.000
	—	(0.211)	—	(0.464)	—
	9	16	8	8	8
shelf edge	0.100	0.000	0.000	0.000	0.000
	(0.707)	—	—	—	—
	15	14	14	10	14
central bank	0.941	0.410	0.236	0.654	0.034
	(0.182)	(0.202)	(0.132)	(0.396)	(0.341)
	21	38	18	19	19
Gulf of Maine					
central gulf	0.000	0.012	0.141	0.055	0.000
	—	(0.012)	(0.101)	(0.545)	—
	64	61	47	45	47
southern	0.000	0.625	0.116	1.077	0.116
	—	(0.422)	(0.115)	(0.617)	(0.115)
	9	12	6	6	6
southwest	0.670	1.286	1.240	2.422	0.860
	(0.371)	(0.289)	(0.384)	(0.756)	(0.318)
	20	34	16	18	21

(Table 2). Over 90% of the humpbacks/effort observed each year in the combined Georges Bank-Gulf of Maine waters were seen in the Gulf of Maine. The increased number of humpbacks/effort observed was significantly different between regions in the Gulf of Maine ($F = 7.098$, $df = 2, 8$). The greatest concentrations of humpbacks in the Gulf of Maine are located in the southwest region (Table 2). Between 1978 and 1982, 82% of the total humpbacks/effort in the Gulf of Maine were observed in the southwest region. The importance of this region for feeding humpbacks has been previously reported (Kenney et al. 1981; Hain et al. 1982).

Although there were no significant differences between the number of humpbacks/effort seen by year ($F = 0.824$, $df = 4, 12$) or region ($F = 0.609$, $df = 3, 12$) on Georges Bank, the number of humpbacks/effort observed on the bank has steadily declined since 1978. Sixty percent of the humpbacks/effort observed on Georges Bank between 1978 and 1982 occurred during 1978 (Table 2).

We examined the apparent increase in the southwest Gulf of Maine more thoroughly by dividing it into two smaller components (Table 3), a southern which extends from the Great South Channel north along the outside of Cape Cod (NMFS/NEFC strata 23, 25, from Figure 1) and a northern which centers on Stellwagen Bank (NMFS/NEFC strata 26, 27, from Figure 1). The number of humpbacks/effort observed within the southwest Gulf of Maine-northern segment steadily increased by an order of magnitude from 1.86×10^{-2} whales/effort in 1978 to 29.01×10^{-2} whales/effort in 1982. Therefore, the observed increase in the number of humpbacks/effort in the southwest Gulf of Maine since 1978 has occurred primarily in the northern half of this region (NMFS/NEFC strata 26, 27).

TABLE 2.—The number of humpback whales per linear km $\times 10^{-2}$ (humpbacks/effort) seen during shipboard observations and the total number of linear km surveyed (in parentheses) by region and year.

Region	1978	1979	1980	1981	1982
Georges Bank					
shoals	—	0.189	—	—	—
	(480.9)	(529.0)	(190.0)	(342.6)	(744.5)
northern edge	1.500	—	—	—	—
	(200.0)	(176.8)	(66.5)	(89.8)	(222.7)
shelf edge	—	—	—	—	0.225
	(230.0)	(213.6)	(115.6)	(207.0)	(198.6)
central bank	0.168	0.285	0.299	—	0.116
	(593.6)	(701.9)	(334.4)	(895.9)	(863.5)
Gulf of Maine					
central gulf	0.750	0.119	—	0.855	—
	(933.1)	(841.7)	(966.0)	(467.6)	(1,172.8)
southern	2.449	0.828	—	0.393	1.662
	(489.8)	(482.8)	(267.6)	(254.2)	(223.5)
southwest	1.174	2.817	7.679	11.172	6.814
	(681.2)	(745.4)	(547.0)	(454.9)	(692.5)

TABLE 3.—The number of humpback whales per linear km $\times 10^{-2}$ (humpbacks/effort) seen during shipboard observations and the total number of linear km surveyed (in parentheses) within the partitioned southwest Gulf of Maine.

Region	1978	1979	1980	1981	1982
Northern	1.864	2.655	10.794	22.469	29.014
(strata 26, 27)	(34.9)	(263.6)	(333.5)	(252.6)	(299.6)
Southern	0.556	3.113	2.811	1.987	3.308
(strata 23, 25)	(359.3)	(481.8)	(213.5)	(202.3)	(392.9)

Correlation Between Humpback Whale Distribution and Sand Eel Abundance

A significant correlation ($r = 0.81$, $df = 13$) exists between the observed number of humpbacks/effort and the log-mean number of sand eel/tow by region within the Gulf of Maine (Fig. 2). This indicates that within the Gulf of Maine the distribution of humpback whales do co-occur with dense patches of sand eel in that region. The greatest densities of sand eel in the Gulf of Maine and the greatest observed numbers of humpbacks/effort have both occurred in the southwest Gulf of Maine since 1978. This supports the hypothesis by Kenney et al. (1981) that within the Gulf of Maine, the

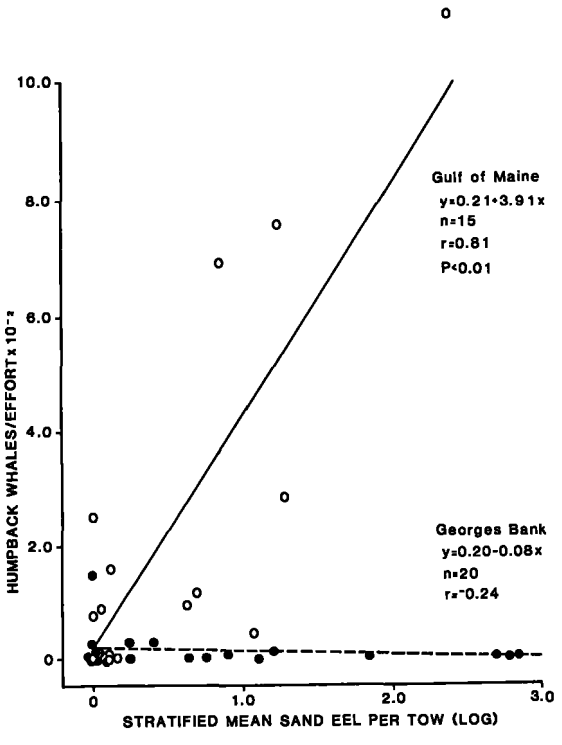

FIGURE 2.—The regression and correlation coefficient (r) between the stratified mean number of sand eel/tow (log value) and the number of humpback whales/effort × 10^{-2} by region and year on Georges Bank (closed circles) and in the Gulf of Maine (open circles).

observed distribution of the humpback whale was due to the distribution of sand eel.

However, the correlation between the observed number of humpbacks/effort and the log mean number of sand eel/tow by region on Georges Bank (Fig. 2) was not significant (r = 0.24, df = 18). The mean number of sand eel/tow (log value) on Georges Bank was greatest on the shallow shoals. Only one humpback whale was observed on the shoals between 1978 and 1982. Our data does not support any co-occurrance between humpback whale distribution and sand eel abundance on Georges Bank despite dense patches of sand eel in that region.

DISCUSSION

Our data suggest that the distribution of humpback whales in the Gulf of Maine-Georges Bank region is presently centered in the southwest Gulf of Maine. This distribution is correlated with dense concentrations of sand eel, a principal prey item, which has dramatically increased throughout shelf waters of the eastern United States including the southwest Gulf of Maine since the mid-1970's (Meyer et al. 1979; Sherman et al. 1981). This increase in sand eel followed a decline of Atlantic herring stocks from the mid-1960's to the mid-1970's (Anthony and Waring 1980; Grosslein et al. 1980), and possible replacement by sand eel of depleted fish stocks in the northwest Atlantic (Sherman et al. 1981). The correlations between the humpback distribution in the Gulf of Maine and sand eel abundance supports the theory by Kenney et al. (1981) that the present distribution of the whales in that region is due to the distribution of sand eel. A demonstrated shift in the humpback distribution since the mid-1970's from the upper Gulf of Maine-lower Bay of Fundy southward into the southwest Gulf of Maine also supports this theory.

A 10-yr summary of observations from Mt. Desert Rock, ME (MDR, Fig. 1) in the northern Gulf of Maine shows a dramatic decrease in the number of humpback sightings/observer hour since 1977 (Mullane and Rivers 1982). The maximum number of humpbacks observed in that summary occurred in 1975 (98 whale sightings, 0.123 humpbacks/observer hour). Only 10 humpbacks were seen from 1978 to 1982, and the maximum number of humpbacks/effort since 1975 has been 0.005/observer hour in 1982. This decline in the number of humpbacks at MDR coincides with the increased numbers of humpbacks observed in the southwest Gulf of Maine. Twelve of the 17 humpbacks photo-identified from 1975 to 1977 at MDR have subsequently been seen in the southwest Gulf of Maine, principally on Stellwagen Bank. At least three of these whales have been observed during three different years on Stellwagen Bank since they were first identified at MDR (Mullane and Rivers 1982). In comparison, only one whale identified at MDR has consistently returned to the coastal waters of eastern Maine and New Brunswick. Katona et al. (1977) also listed the Grand Manan Banks, Briers Island-St. Mary's Bay, Nova Scotia, and the lower Bay of Fundy as areas of humpback congregations. However, humpbacks were not common in the Bay of Fundy during 1981 and 1982 (Kraus and Prescott 1981, 1982).

Shifts in the distribution of humpbacks caused by changes in the distribution and density of prey species have been shown elsewhere (Lien and Merdsoy 1979; Whitehead et al. 1980). We believe that the correlations between humpbacks/effort and mean sand eel catches in the southwest Gulf of Maine, and the demonstrated decline of humpbacks throughout the upper Gulf of Maine-lower Bay of Fundy concurrent with an increase in the numbers

of humpbacks in the southwest Gulf of Maine reasonably explains the present distribution of humpbacks within the Gulf of Maine. However, it does not adequately explain the paucity of humpbacks on Georges Bank (Table 2) and throughout the remaining shelf waters of the northeastern United States (Hain et al. 1981; Kenney et al. 1981; Payne et al. 1984), areas where sand eel have also increased since 1975. The nonsignificant correlation between humpbacks/effort and the log-mean catches of sand eel/tow on Georges Bank suggests that factors other than simply food concentrations, perhaps behavioral or environmental, may influence the humpback's feeding strategy and location.

Sutcliffe and Brodie (1977) reported that humpbacks are led into ecological or oceanographic boundaries (i.e., isopleths or shelf-edges) and feed in patchy areas of dense prey aggregations along these boundaries. A change in depth on the shelf is often accompanied by a concentration of near-surface zooplankton; in general, the more abrupt the change, the greater the concentration (Sutcliffe and Brodie 1977). Concentrations are especially noticeable along the edge of banks where the availability of prey is most affected (Jaansgard 1974). Reay (1970) found that sand eel concentrations are greatest on the edges of sandy banks where currents and prey (zooplankton) are optimum; thus the whales, in seeking the highest concentrations of prey, feed most frequently along the edges of the banks (Sutcliffe and Brodie 1977; Brodie et al. 1978). Observations of feeding humpbacks in the Gulf of Maine have occurred primarily along the edge of submarine banks or canyons (Hain et al. 1982; CETAP 1982).

If bottom topography influences feeding behavior of humpbacks (by concentrating prey), then the paucity of humpbacks on Georges Banks and throughout the mid-Atlantic Bight regions becomes more understandable. The floor of the broad mid-Atlantic Bight is gently sloping continental shelf with no relief until it steepens sharply at the shelf break, at about 200 m depth, to form the continental slope. Since the feeding behaviors for humpbacks described by Hain et al. (1982) occur principally over a shelf-floor with rugged relief, the strategies used by humpbacks seem most efficient in these waters. This also explains the present lack of sightings in the mid-Atlantic shelf waters and the offshore migration route between calving and feeding areas. It seems energetically advantageous for the humpback, a relatively slow-moving whale, to migrate over deep water with little apparent feeding, then feed on the densely concentrated prey along the bottom profiles of the Gulf of Maine.

We maintain that humpbacks are merely utilizing the first concentrations of prey available to them in spring, after they reach shelf-waters from their offshore migration route between winter-calving and summer-feeding grounds. The humpbacks seem to use the Great South Channel as an entry-exit into the Gulf of Maine (as hypothesized by Kenney et al. (1981)), and follow the bottom profile northward, using this profile to their feeding advantage until they reach the dense concentrations of sand eel available within the southwest Gulf of Maine. The quantities of sand eel available to humpbacks at this location have allowed the whales to remain throughout the feeding season; therefore, the recent paucity of sightings in the northern Gulf of Maine.

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