Abstract.—From the mid-1970's to the mid-80's, Stellwagen Bank was an important humpback whale feeding area with sand lance (*Ammodytes* spp.) as the major prey. Between 1988 and 1994, however, the number of humpback whales we identified each year on Stellwagen declined from a high of 258 (1990) to 7 (1994), and the mean number of whales identified per day fell from 17.7 (1988) to 0.9 (1994). Adult whales decreased steadily after 1988; juveniles decreased rapidly after 1991. Echo-sounder data from Stellwagen showed that prey trace levels declined from 19.1% of the vertical water column in 1990 to 2.8% in 1992 (no readings were taken in 1988–89, or 1993–94). Simultaneously, the number of whales identified on Jeffreys Ledge, north of Stellwagen Bank, increased dramatically beginning in 1992. Sixty-four percent of the whales identified on Jeffreys in 1992–94 were seen on Stellwagen Bank in 1988 and 1989. We hypothesize that humpback whales shift their distribution in order to prey upon recovering herring populations, their primary source of food.

Manuscript accepted 21 April 1997.
Fishery Bulletin 95:826–836 (1997).

A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine

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Humpback whales, *Megaptera novaeangliae,* migrate seasonally between low-latitude breeding grounds and high-latitude feeding areas (Kellogg, 1929; Mackintosh, 1965; Katona, 1986). In the western North Atlantic, whales that winter in Caribbean waters migrate to feeding grounds in New England (the Gulf of Maine), in the Gulf of St. Lawrence, and in waters off Newfoundland, Greenland, Iceland, and Norway (Katona and Beard, 1990). The whales using each feeding area appear to consist of extended matrilines (Baker et al., 1990; Clapham et al., 1992). Within feeding areas, prey distribution has been a primary influence on the local distribution and micromovements of all baleen whales examined to date (Whitehead and Carscadden, 1985; Payne et al., 1986, 1990; Piatt et al., 1989).

Studies of humpback whale movement, ecology, demography, behavior, and social organization on their feeding grounds in the Gulf of Maine have been ongoing since the mid-1970's, (Payne et al., 1986; Clapham and Mayo, 1987, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992; Weinrich et al., 1992; Katona et al.[1]). During this period, several shifts in the distribution of humpback whales have been reported. Payne et al. (1986) showed that humpback whales in the late 1970's had moved from primary abundance on Georges Bank and in the waters of the northern Gulf of Maine to the inshore southwestern Gulf of Maine, especially Stellwagen Bank and the Great South Channel. They attributed this shift to a fishery-induced collapse of herring (*Clupea harengus*) populations (Anthony and Waring, 1980; Grosslein et al., 1980) and a corresponding increase in sand lance (*Ammodytes* spp.) (Meyer et al., 1979; Sherman et al., 1981, 1988; Sherman 1986; Sissenwine 1986). Both species are known prey for humpback whales (Mitchell, 1973; Overholtz and Nicholas, 1979; Kawamura, 1980). These fish species are potential ecological competitors (Reay, 1970; Meyer et al., 1979; Sherman et al., 1981); moreover, herring are known predators of

[1] Katona, S. K., P. Harcourt, J. S. Perkins, and S. D. Kraus. 1980. Humpback whales: a catalog of individuals identified by fluke photographs. College of the Atlantic, Bar Harbor, ME, var. pagination.

sand lance (Fogarty et al., 1991). Sightings of humpback whales off the Maine coast, where herring were the primary whale prey, decreased dramatically during the late 1970's (Payne et al., 1986; Mullane and Rivers[2]). Sand lance frequently use shallow areas with sandy bottoms, such as Stellwagen Bank in the southern Gulf of Maine (Meyer et al., 1979). This shift in distribution, and corresponding change in primary prey type, may have also led to changes in feeding behavior (Weinrich et al., 1992). Humpback whales remained abundant in the southwestern Gulf of Maine throughout the 1980's, with a brief decrease in some areas during 1986–87 (Payne et al., 1990; Cetacean Res. Unit[3]).

We documented a gradual but continuous decrease in the use of Stellwagen Bank by humpback whales during 1988–94. Our data suggest that whales have returned to a distribution similar to that documented until the late 1970's. We hypothesize that this return is due to the recovery of herring stocks in the Gulf of Maine and to a corresponding decrease in available prey for humpback whales on Stellwagen Bank and in other areas favored by sand lance in the southwestern Gulf of Maine.

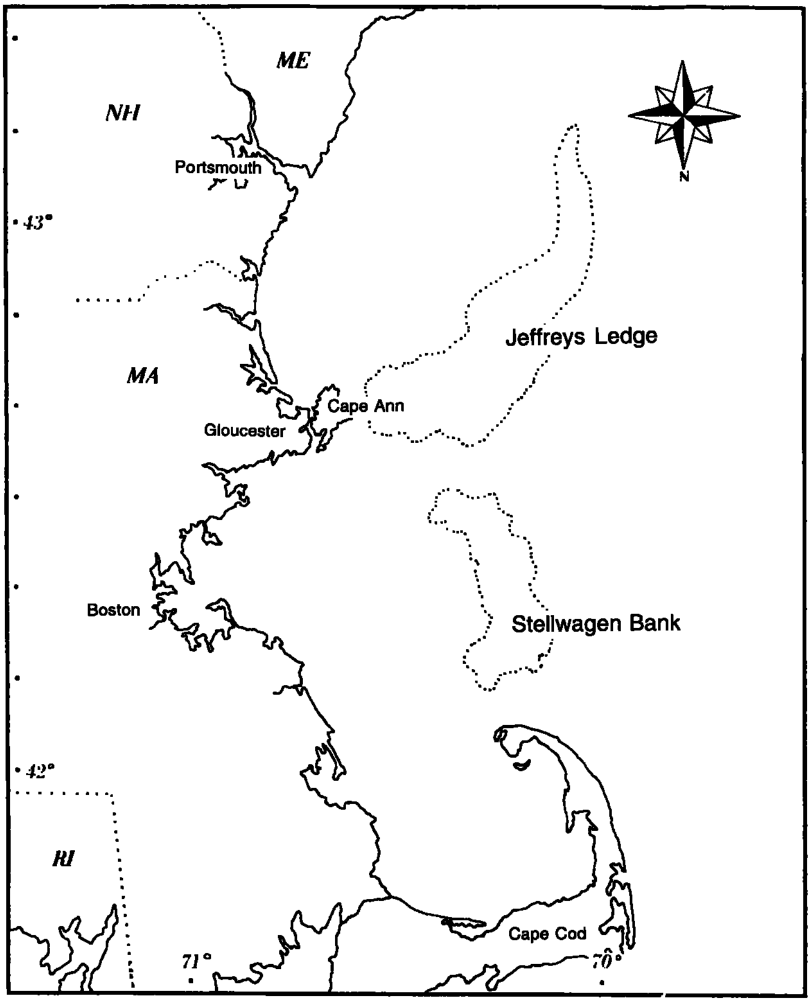

Figure 1
The study area in the Gulf of Maine.

Methods

Survey methods

From 1 May to 30 October, 1988 to 1994, daily shipboard surveys were carried out aboard commercial whale-watching boats. These departed from Gloucester and Boston, Massachusetts, and were typically 4–5 hours in duration. There were usually two cruises per vessel per day. A typical cruise included 90–120 minutes in areas where whales were often observed, as well as 2–3 hours of transit time. Whale watches usually emphasized the northern half of Stellwagen Bank. On occasion, whale watches surveyed the southern half of Jeffreys Ledge to the northeast of Cape Ann (Fig. 1). This effort is detailed in Table 1. Within each whale-watching trip, protocol and typical amount of observation time were consistent on all vessels.

Whale-watching cruises were supplemented by occasional day-long (7–13 h) excursions on research vessels. These took place 1 April to 15 November of each year, with emphasis on April and October–November, as well as during periods of significant whale concentration from May to September. During each cruise, a specific attempt was made to conduct a comprehensive photo-identification survey of a specific area (i.e. northern Stellwagen Bank, southern Jeffreys Ledge, etc.). As time allowed, coverage was devoted to a larger portion of the entire geographic feature (either Stellwagen Bank or Jeffreys Ledge). Specific areas were determined by recent sightings of whale aggregations, reliable reports of whale sightings from local boaters, or a determination that an area had not been recently surveyed. Jeffreys

[2] Mullane, S. J., and A. Rivers. 1982. Mt. Desert Rock, Maine. Annual Report, 27 p. [Available from Allied Whale, College of the Atlantic, Bar Harbor, ME.]

[3] Cetacean Research Unit. 1980–89. Cetacean Research Unit, PO Box 159, Gloucester MA 01930. Unpubl. data.

Table 1
Study effort by both number of survey days and number of survey trips for both Stellwagen Bank and Jeffreys Ledge. "JLSN days" represent the total number of survey days represented by the Jeffreys Ledge Sighting Network (JLSN), established after the 1992 season (see text for further details).

Year	Stellwagen days	Stellwagen trips	Jeffreys days	Jeffreys trips	JLSN days
1988	145	558	16	44	0
1989	151	550	17	20	0
1990	166	516	32	37	0
1991	160	460	31	36	0
1992	171	506	34	37	69
1993	106	364	48	79	119
1994	86	141	86	141	138

Ledge was the destination for just under half of the dedicated cruises from 1988 to 1992, all but four in 1993, and all but two in 1994.

Beginning in 1990, sighting and photo-identification data were also collected from a whale-watching boat operating out of Kennebunk, Maine, to obtain information from the northern end of Jeffreys Ledge. Observer coverage was for one trip per day, 3–5 days per week. Because of the unusually large number of whales first observed on our dedicated cruises to Jeffreys Ledge in 1992, a photo-identification network (consisting of three whale-watching boats working on Jeffreys Ledge for one trip per day) was formalized in fall 1992 (after the completion of field efforts), and existing 1992 data were obtained. Beginning in 1993, data collection from these vessels was standardized to be directly comparable with Stellwagen Bank whale-watching data. Because 1993 represented the first year in which Jeffreys Ledge data were collected in any kind of standardized fashion, occurrence and occupancy (defined below) were not calculated for Jeffreys Ledge humpback whale sightings.

Study areas

Stellwagen Bank, now a National Marine Sanctuary, is a sandy glacial deposit approximately 32 km long with depths from 18 to 37 m (Fig. 1). It borders the eastern margin of Massachusetts Bay and is located approximately halfway between Cape Ann and Cape Cod, Massachusetts. Jeffreys Ledge is a more complex, winding, shallow ledge, with typical depths of 45 to 61 m and with a length of approximately 54 km. Its substrate is a mixture of rocky and muddy bottoms. The southern edge of Jeffreys Ledge is 9 km northeast of Rockport, Massachusetts, whereas the northern end lies 36 km east of York, Maine. Stellwagen Bank and Jeffreys Ledge are separated by 21.6 km at their closest point.

Field methods

Individual humpback whales were identified from photographs of distinctive pigment patterns on the ventral surface of their tail flukes or from the shape of and scarring on the dorsal fin (or by both features) (Katona and Whitehead, 1981). Two observers collected data on each whale or group of whales. One observer was responsible for photographing each whale, while the second recorded the whale's location (by means of LORAN-C), group affiliations, and behavior. This observer also recorded which photographs were taken of each whale, as dictated by the photographer. Each group of whales in an area was usually observed for 1–30 minutes; most, if not all, whales in a single location (3–5 km radius) were identified during each observation period. Field methods were consistent on all vessels.

Age class and sex determination

Individuals were identified by comparing photographs with those of a catalog of humpback whales maintained at the Cetacean Research Unit (CRU), Gloucester, MA. Details on cataloging methods and contents of the catalog were given in Weinrich (1991), Weinrich and Kuhlberg (1991), and Weinrich et al. (1992) and are based on procedures outlined by Katona and Whitehead (1981). Whales were sexed by photographing them while belly up at the surface (and by noting the presence or absence of a small lobe immediately posterior to the genital slit [Glockner, 1983]), by observing a female with calf, or by using molecular techniques (Baker et al., 1991). Individuals were assigned to age classes (juvenile or adult) based on known age (first observation as a calf) or based on the consensus among all experienced CRU observers of an animal's relative size at first sighting. The accuracy of the latter technique was confirmed by estimating the age class of animals of unknown identity in the field and by finding that these estimates matched (photographically) animals of known age. No incorrect classifications were made (n=51). For the purposes of this paper, an animal was classified as an adult if it was known to be at least five years old, an age at which 50% or more of the population is mature (Chittleborough, 1965; Clapham and Mayo, 1990).

Prey density

In 1990–92, a SITEX HE-358 50-kHz echo-sounder and chart recorder aboard a whale-watching vessel were used to record prey density on Stellwagen Bank in the immediate area where whales had been observed. The echo-sounder was used for 83 days during 1990 (9 May to 20 October; 153 total hours), 98 days during 1991 (9 May to 28 September; 221 total hours), and 69 days during 1992 (24 April to 24 October; 60 total hours). Clear readings throughout the water column (i.e. with no interference present) were obtained for 69 hours in 1990, 166 hours in 1991, and 60 hours in 1992. An echo-sounder operating at this frequency is likely to detect the presence of fish but unlikely to detect plankton unless it is present in extreme densities (Dolphin[4]). The echo-sounder was started as the boat slowed to begin whale observations and turned off when the vessel left the observation area to return to port. Because echo-sounder tracings were obscured by noise when the vessel was moving at cruising speed (e.g. moving from one group of whales to the next), tracings performed at cruising speed were eliminated from analysis. A timing mark was placed simultaneously on both the echo-sounder chart and the data sheets by the second observer at 10-min intervals.

The echo-sounder chart was later sampled at 2-min intervals by interpolating between the 10-min marks. For each sampling point, prey presence was scored visually in 3.3 m (10 ft) vertical increments from the surface to the bottom, with a sliding score of zero (for no prey) to 10 (prey throughout that 3.3 m interval). From these readings mean values for vertical bait density were calculated for each quarter of the water column and the total water column. Mean depth in which readings were taken was 38.4 m (SD=15.1 m). No echo-sounder data were recorded on Jeffreys Ledge.

Although such data give an idea of the availability of prey in the immediate vicinity of whales, they do not reflect an area where whales were not present. Hence, there could have been very similar or different prey concentrations very nearby, without that information ever being recorded. However, since each year's data set came from numerous days and contained data points from several different locations (albeit within a 3–4 mile radius) within each day's observations, we feel they at least give a crude overview to overall prey densities in the vicinity of whales.

Data management and analysis

Both daily whale sighting data and prey density data were stored in PC-based computer files and analyzed with commercially available statistical software (SPSS/PC+, Kinnear and Gray, 1992). For daily sighting data, an Xbase program was written to isolate the sightings of each whale and to calculate statistics summarizing that individual's within-year sighting history (including occurrence and occupancy—see below) in each part of the study area. These values were then stored in a separate data file and analyzed with the same statistical software. Temporal trends were analyzed with least-squares regression (Snedecor and Cochran, 1967) of individual data points with the year of observation as the independent variable, although only annual means are presented in our tables for occurrence and occupancy scores. The slope of the regression line (B) and the probability value (*P*) from a test of the null hypothesis that the slope did not differ from zero are presented for each test. Calves were eliminated from these analyses because we assumed that a calf is merely following the mother in her choice of habitat.

Definitions

"Occurrence" is defined as the number of days on which an individual whale was photographed in a single year. "Occupancy" is the number of days elapsed from the first to the last recorded sighting of an individual whale within a year. These definitions are consistent with those used by Clapham et al. (1992).

Results

Stellwagen Bank

Total number of humpback whales identified per year The number of humpback whales identified in any single year on Stellwagen Bank ranged from 258 (1990) to a low of 7 (1994), with a mean of 153.6 (SD=88.4) (Fig. 2). These values show a statistically significant declining trend (B=–32.82, *P*=0.033).

When the total number of whales was broken into age class, differences in annual trends were apparent. Numbers of adult whales identified on Stellwagen ranged from 173 (1990) to 3 (1994; mean=102.8, SD=60.4). These values also showed a statistically significant declining trend (B=–0.84, *P*=0.018). Number of juveniles identified in each year varied from 85 (1990) to 4 (1994; mean=50.71, SD=29.2). These also showed a downward trend, although not statistically significant (B=–23.50, *P*=0.099). The ratio of identified adult whales to identified juveniles varied from 2.5:1 (in 1988) to 0.75:1 (in 1994). Numbers of cow-calf pairs throughout the study period

[4] Dolphin, W. F. 1994. Department of Biomechanical Engineering, Boston University, Boston, MA 02215. Personal commun.

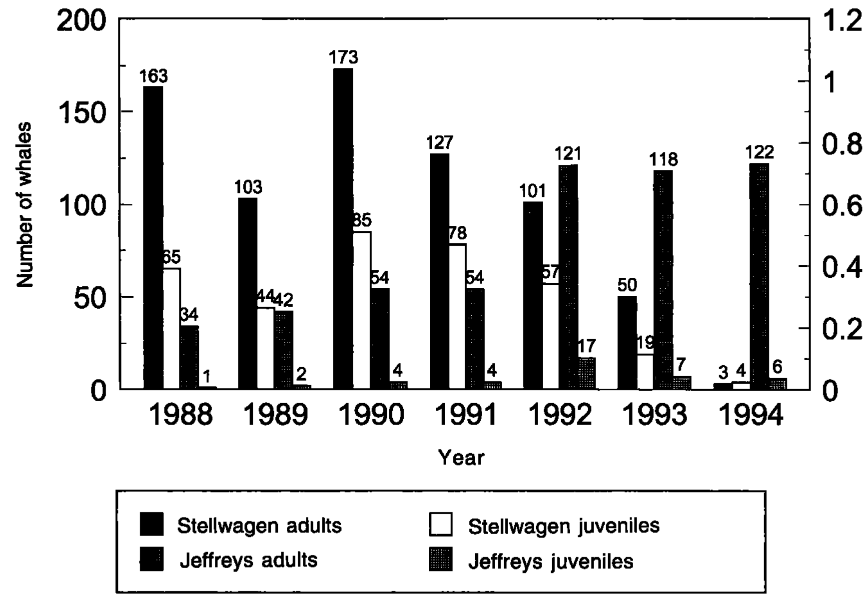

Figure 2

The number of individual humpback whale adults and juveniles identified per year on Stellwagen Bank and Jeffreys Ledge, 1988–94. Note the rapid annual decrease of adults on Stellwagen Bank starting in 1991, and the corresponding increase on Jeffreys Ledge beginning in 1992. Juveniles started a rapid decrease on Stellwagen Bank in 1992.

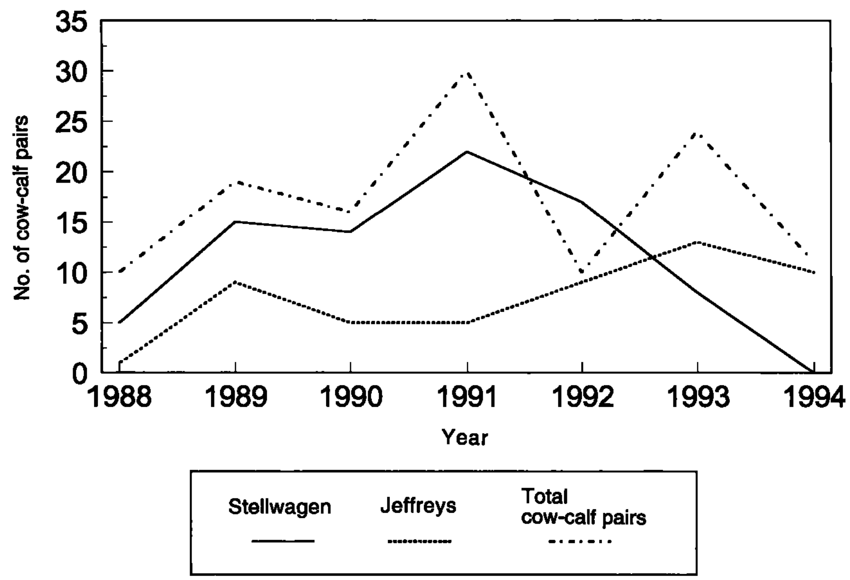

Figure 3

The number of cow-calf pairs on Stellwagen Bank, Jeffreys Ledge, and in the entire Gulf of Maine, 1988–94. The percentage of known mother-calf pairs that were sighted on Stellwagen began to decrease dramatically in 1992, the same year that the percentage mother-calf pairs began to increase on Jeffreys Ledge.

showed no significant trend in the absolute number seen on Stellwagen (B=–1.214, P=0.424). Numbers of cows and calves began in 1991 to decline sharply, especially when compared with the total number of cow-calf pairs in the Gulf of Maine. By the last year of the study no cow-calf pairs were seen (Fig. 3).

Occurrence and occupancy Mean occurrence of humpback whales on Stellwagen Bank within a single season ranged from 13.1 days (1989, n=147) to 6.6 days (1993, n=69) (Table 2; B=–0.30, P=0.501). Adults showed a within-year mean occurrence of 6.4 days (SD=4.8, n=720), with a statistically significant declining trend through the study period (B=–1.98, P<0.001). Compared with adults, juveniles showed a higher mean within-year occurrence (mean= 14.5 days, SD = 4.2, n=352), which significantly increased throughout the study period (B=1.63, P=0.030).

Occupancy of individual whales within years declined significantly from a mean of 61.8 days (1989, n=147) to 21.6 days (1994, n=7) (Table 3; B=–7.07, P=0.002). Again, age classes showed different trends. Adults had a mean occupancy period of 39.3 days (SD = 23.56, n=720) throughout the study period, with a significant declining trend (B=–10.65, P<0.001). In contrast, juveniles had a mean occupancy period of 55.0 days (SD=13.21, n=352), with no significant trend apparent (B=–2.82, P=0.296).

Although juveniles showed no significant trend in occupancy and had occurrence values that actually increased throughout the period, a comparison of median values for

Table 2

The mean occurrence (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	13.5	7.2	11.2
1989	12.2	15.2	13.1
1990	7.9	12.5	9.6
1991	6.2	17.0	10.7
1992	7.2	19.6	12.0
1993	3.1	15.7	6.6
1994	1.3	19.8	11.9

Table 3

The mean occupancy (in days) of humpback whales on Stellwagen Bank, 1988–94.

Year	Adults	Juveniles	Combined total
1988	67.9	47.1	60.4
1989	56.5	71.6	61.8
1990	52.3	55.0	51.8
1991	47.5	73.1	54.6
1992	32.4	53.3	42.2
1993	17.2	48.4	25.7
1994	1.3	36.8	21.6

each of these variables portrays a trend more similar to that seen from adults. From 1992 through 1994, prolonged residency of a few juveniles skewed occurrence and occupancy values. During 1991–93, median occurrence of juveniles fell from seven days to three, whereas median occupancy periods fell sharply, from 59.5 days to 15 days. In 1994, so few juveniles were seen (four) that the relatively high values of two individuals severely skewed the results for that year. Median values of adult occurrence and occupancy showed the same trends as those portrayed from the regression analyses.

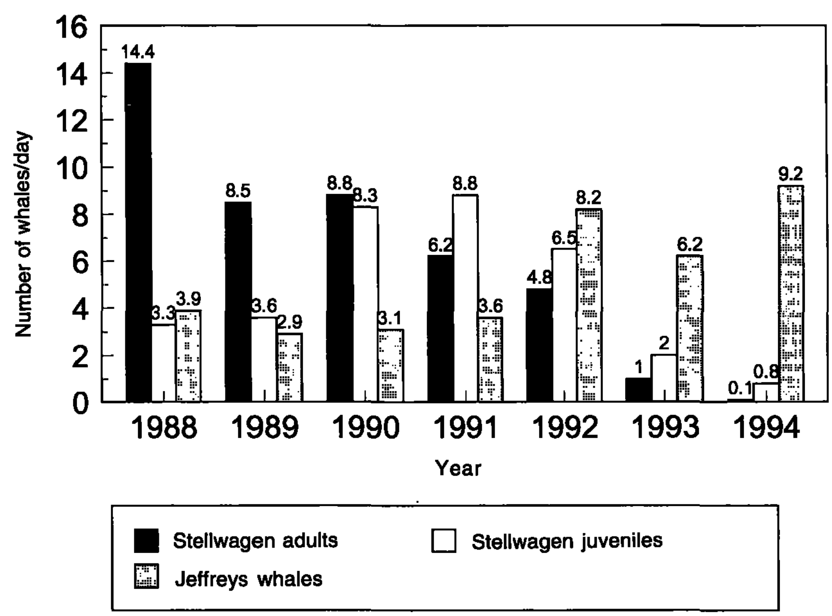

Figure 4

The mean number of whales identified per day in each age class and year on Stellwagen Bank and Jeffreys Ledge, 1988–94. Jeffreys Ledge juveniles were not included because of their low numbers. Note the rapid decrease among adults on Stellwagen Bank beginning after 1988, and the decrease among juveniles on Stellwagen beginning in 1992. Jeffreys Ledge values were highest in the final three years, after the general decrease on Stellwagen Bank.

Number of whales per day

One of the clearest indicators of habitat use is the number of identified humpback whales sighted on Stellwagen Bank each day. This measure incorporates two of the above components—the number of whales identified as well as how often they were sighted in the area. Throughout the study period, a mean of 12.7 (SD=11.31, n=1,072) whales were identified per day, ranging from an annual high of 17.7 (SD= 15.30, n=153 days) in 1988 to a low of 0.9 (SD=0.76, n=97 days) in 1994 (Fig. 4). Adults and juveniles again showed different trends. Adults per day declined steadily from 14.4 in 1988 to 0.1 in 1994 (B=–2.21, P<0.001), whereas juveniles showed no clear trend, with a high of 8.8 in 1991 and a low of 0.8 in 1994 (B=–0.44, P=0.501). Juvenile values showed a clear peak in 1990–91 as compared with other years (Fig. 4).

Vertical prey density Mean overall vertical prey density decreased from 19.1% with prey traces in 1990 to 2.8% with prey traces in 1992 (B=–0.38, P<0.001) (Table 4). Similar significant decreases were seen in each vertical quarter of the water column (Table 4).

Although it was impossible to determine prey type from traces alone, catches of groundfish (mainly Atlantic cod [*Gadus morhua*] and haddock [*Melanogrammus aeglefinus*]), and bluefish (*Pomatomus saltatrix*) in the immediate area of trace recordings

Table 4
Percentage of the water column with echo-sounder prey traces by year in each quarter. Mean depth was 38.4 meters.

	Quarter of the water column				
Year	Top 25%	2nd 25%	3rd 25%	4th 25%	Total
1990	17.2%	15.0%	16.8%	24.3%	19.1%
1991	3.1%	4.5%	7.3%	12.7%	7.9%
1992	1.4%	0.3%	0.8%	1.1%	2.8%

by party-fishing boats indicated that sand lance were the predominant fish prey in stomach contents of humpback whales; some small mackerel (*Scomber scombrus*) and herring were also observed in stomachs in much lower frequencies. Herring were more prominent in October during each field season, when only a small number of echo-sounder data points were recorded.

Jeffreys Ledge

Total number of humpback whales identified The number of humpback whales we identified on Jeffreys Ledge increased from a low of 35 (in 1988) to a high of 138 (in 1992) (B=19.57, P=0.004; Fig. 2). Although there was a generally increasing trend, there was a sudden increase from 58 in 1991 to 138 in 1992.

The increase among adult whales also showed a significant increase across years (B=17.25, P=0.003). Although juveniles increased steadily throughout the period, and suddenly from 1991 to 1992, they did not do so at a significant rate (B=1.357, P=0.201). (The same analysis without 1992 data, where there were an unusually high number of juveniles, does show a statistically significant increasing trend among juveniles [B=0.914, P=0.006]). Cow-calf pairs also showed a significantly increasing trend (B=1.429, P=0.049).

In each year, identified humpback whales on Jeffreys Ledge were biased toward adults. No more than 17 juveniles were photographed on Jeffreys Ledge in any year, and the number of juveniles photographed exceeded 10 in only a single season (1992). The ratio of adult to juvenile whales ranged from a high of 34.0:1 in 1988 to 7.1:1 in 1992, higher in all cases than the adult:juvenile ratios on Stellwagen Bank.

Number of whales per day The mean number of whales per day ranged from a low of 2.9 (SD=1.9, n=22) in 1989 to a high of 9.2 (SD=7.7, n=138) in 1994 (Fig. 4; B=0.98, P=0.022). In 1993 and 1994, the only years with coverage comparable to Stellwagen Bank levels, means of 6.2 (SD=6.9, n=116) and 9.2 (SD=7.7, n=138) whales were identified on each day of coverage, respectively.

The pattern of humpback abundance on Jeffreys Ledge showed surprising seasonal consistency throughout the study. Sightings were sporadic during May, June, and early July, with few, if any, concentrations of whales observed. In all years, concentrations increased from late July through September, with whales still abundant in three of the seven Octobers observed (1988, 1989, 1993).

Identification comparison To determine whether the whales using Jeffreys Ledge were the same as those previously inhabiting Stellwagen Bank, we examined how many of the 210 humpback whales identified on Jeffreys Ledge in 1992–94 had been previously sighted on Stellwagen Bank. Of this group, 123 (58.5%) were photographed on Stellwagen Bank during 1988–89. When the 17 animals that had not yet been born in 1988–89 were also discounted from the Jeffreys population, 63.7% of all animals were found to have been seen previously on Stellwagen. By comparison, only 35 (16.6%) of the Jeffreys Ledge whales were also seen on Stellwagen Bank during the 1992–93 period, or 16.6% of the total Jeffreys Ledge population.

Discussion

Humpback whales, especially adult and cow-calf pairs, decreased their use of Stellwagen Bank drastically between 1988 and 1994. The decreased use is reflected in decreased numbers of whales identified, decreased numbers of whales (regardless of age class) per day, and decreased adult occurrence and occupancy. The decline led to a virtual abandonment in 1994, when only seven humpback whales were seen on Stellwagen, and only two of those had occupancy periods longer than ten days. The decline in whale use corresponds with a decline in the amount of echo-sounder prey traces at the sites on Stellwagen Bank where whales were found over three years during the study. Although adults showed a clear decreasing trend on Stellwagen Bank, juvenile whales showed a less clear pattern. However, even juveniles showed a rapid decrease in use from 1991 to 1994.

The increase in juvenile whales on Stellwagen Bank during 1990–91 while adult use decreased may also be a more subtle indicator of a shift in habitat quality. Previous work has shown that juvenile humpback whales are often found in areas where prey density is lower than in areas where adults predominate (Weinrich and Kuhlberg, 1991; Belt et al.[5]), and may, therefore, be considered suboptimal habitat for the species. The vertical distribution of prey has also been reported to be different between concentration areas of the two age classes. Adults are found where prey is concentrated in the upper reaches of the water column (Belt et al.[5]) where a humpback whale's bubble and cooperative feeding strategies are most effective (Hain et al., 1982; D'Vincent et al., 1985; Weinrich et al., 1992; Weinrich et al.[6]) or where foraging is most efficient because energy expenditures associated with diving are lowest (Dolphin, 1987). Juveniles appear to concentrate more often in areas where prey are predominantly subsurface, often feeding on or near the sea floor (Swingle et al., 1993; Hain et al., 1995; Belt et al[5]; Weinrich et al.[6]). In the years where juvenile use increased while adult use decreased (1990–91), echosounder data showed that prey were most concentrated in the bottom 25% of the water column. Even within the year 1990, prey traces were found to be more common in the upper portions of the water column on days when more adult whales than juveniles were present (Belt et al.[5]).

These findings suggest that there are multiple ways of assessing habitat quality for whales. Past reports of population trends have included only the number of whales sighted per unit of effort as a guide to habitat quality (Payne et al., 1986, 1990; Piatt et al., 1989). However, indicators such as independent trends in occurrence and occupancy of individual whales, the number of individuals identified over a given time period, and even the age class of individuals, may also be important indicators of habitat quality. Although all of these measures (except the last) are factors of sightings per unit of effort, these individual components may be illuminating in detailed studies of a particular area. Prey type, for instance, could influence factors such as occurrence or occupancy (or both). In this case, a relatively nonmigratory prey species, such as sand lance (which are tied to areas of particular bottom substrate and topography) could lead to residency extremes (with whales staying in an area for prolonged periods or avoiding the area altogether), while a less habitat-restricted prey (such as herring) could lead to highly variable intraseason distribution patterns.

Although the number of whales on Stellwagen Bank showed a dramatic decrease, the number of whales photographed on Jeffreys Ledge more than doubled in the last three years of the study. The corresponding increase in observer effort during the same period no doubt had some effect on the dramatic increase in both the number of identified individuals and the mean number of whales identified per day. However, existing opportunistic data were collected following the 1992 season because of the increased use of the area suggested from our dedicated vessel surveys, where methods remained standard across years. Further, captains of whale watching boats and naturalists who had worked on Jeffreys Ledge since the mid-1980's unanimously agreed that there was a sudden, dramatic increase in daily whale sightings beginning in 1992. Therefore, we fully believe that an increase in effort is not the sole, or even the primary, cause for any increase in humpback whale numbers reported beginning in 1992.

Our data show that the sudden increase in humpback whale abundance on Jeffreys Ledge was primarily the result of whales seen on Stellwagen Bank earlier in the study relocating for much or all of their summer feeding season. What is perhaps more surprising is the relatively small number of whales that appeared in both areas during 1992 and 1993, despite the relative nearness of these areas to each other. Most of those whales photographed in both areas were seen on Stellwagen Bank for a brief period in October 1993, when herring stocks are known to migrate through the area (Fogarty and Clark[7]).

The consistent timing of whale aggregations on Jeffreys Ledge in each year (starting in early summer) corresponds with both the major influx of herring onto the Ledge and the start of their spawning season (USDC, 1991; Fogarty and Clark[7]). The biomass of the Georges Bank herring population (of which this is a segment—Stephenson and Kornfeld, 1990; Fogarty and Clark[7]) has increased dramatically over the past decade and, by 1991, was comparable to that of its preexploitation size (Stephenson and Kornfeld, 1990; Sherman, 1992; NMFS[8]). Echo-sounder data, observation of surface prey, and catches of local fishing boats all indicated that herring were common on Jeffreys Ledge at the same time and location as aggregations of

[5] Belt, C. R., M. T. Weinrich, and M. R. Schilling. 1991. Effects of prey density on humpback whale (*Megaptera novaeangliae*) distribution in the Southern Gulf of Maine. P. 6 *in* Abstracts of the 9th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Chicago, IL.

[6] Weinrich, M. T., C. R. Belt, M. R. Schilling, and M. E. Cappellino. 1985. Habitat use patterns as a function of age and reproductive status in humpback whales. Abstract *in* Abstracts of the 6th biennial conference on the biology of marine mammals. Society for Marine Mammalogy, Lawrence, KS.

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whales. The area is also a primary location for seine fishing for herring off New England. Herring seiners were observed fishing or transiting to or from areas of whale aggregation daily during summers 1992–94.

Although herring stocks were increasing, our data indicated that prey available for whales on Stellwagen showed a marked decrease, corresponding to a decrease in sand lance populations throughout the Northeast ecosystem (Sherman, 1992). This decrease in prey would be expected given the documented inverse relation between sand lance and herring or mackerel stocks, primarily due to direct predation (Fogarty et al., 1991). Although we cannot assign a definitive prey type to our echo-sounder traces from Stellwagen, the documented importance of sand lance as a prey for whales on Stellwagen Bank through observations of prey in the mouths of feeding whales (Hain et al., 1982; Weinrich et al., 1992), the direct observation of sand lance on Stellwagen Bank (Hain et al., 1995), prey in fish stomachs, and the lack of other suitable prey records throughout the years suggest that sand lance remained the predominant prey type for whales in that location.

We propose that humpback whales feeding in the Gulf of Maine ecosystem have shifted from their primary distribution of the mid-1970's through the late-1980's as a result of a shift in the abundance of available prey. Although we have considered only a small portion of the Gulf of Maine habitat, our findings correspond with other data from the same period. In the western side of the Great South Channel (an important area for whales from 1979 to 1991 where sand lance were the primary prey [Kenney and Winn, 1986; Payne et al., 1990]) humpback whale sightings were sporadic after July 1991 (Francis[9]; Clapham[10]; Mattila[11]). Off Mt. Desert Rock, Maine, where humpbacks were virtually absent throughout the 1980's, numbers of whale sightings increased to levels far above those of the mid-1970's (Fernald[12]). Surveys conducted in 1993 on Georges Bank by researchers from the YONAH (Years of the North Atlantic Humpback) project also sighted large numbers of humpbacks, including many animals photographed on Stellwagen Bank in previous years (Clapham[10]).

If a resurgence of herring is responsible for shifts in distribution and in primary prey type, it suggests that the distribution of humpback whales through the late 1970's and 1980's may have been a human-induced consequence. The "explosion" of sand lance in the mid- to late 1970's is thought to be primarily the result of the virtual elimination of herring due to overfishing. If this is true, we hypothesize that our observed distribution of whales from 1992 to 1994 should remain relatively stable over the course of a fairly long period because the current situation would be closer to a "natural" ecosystem.

Alternatively, fluctuations in primary prey may occur naturally, and may take place regardless of human interference. If this is true, we hypothesize that whale distributions will show fluctuations that may be cyclical. New England ground-fishermen have for years talked of regular cycles in sand lance abundance, although there are no scientific data to support this often-made contention.

Regardless of which hypothesis, if either, proves true, our data show a shift in both distribution and primary prey type for humpback whales in southern New England waters in recent years. Because this shift has been so complete, it will be interesting and illustrative to see whether, and how, other potentially prey-dependant humpback whale life history parameters, such as reproductive patterns, social behavior, and demographics of whales, all well-documented during a period of explosive sand lance abundance (Clapham and Mayo, 1990; Weinrich, 1991; Weinrich and Kuhlberg, 1991; Clapham et al., 1992), change in response to these ecosystem alterations.

Acknowledgments

We would like to thank Cindy Belt, Tina Laidlaw, Joy Lapseritis, Laine Gonzales, Nancy Miller, Liz Phinney, Leo Axtin, Karla Bristol, and many interns at the Cetacean Research Unit for their assistance in gathering sighting data for this study. Staff of the Center for Coastal Studies, Provincetown, MA, and the Atlantic Cetacean Research Center, Gloucester, MA, were generous in sharing data on ages and sightings of individuals, especially mother-calf pairs. Portions of this study were funded by the Bruce J. Anderson Foundation, the Sudbury Foundation, the Fund for Preservation of Wildlife and Natural Areas, the Norcross Wildlife Foundation, and the American Cetacean Society—Los Angeles Chapter. This work was conducted under Marine Mammal Research Permit no. 681.

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