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### Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine

PHILLIP J. CLAPHAM

Cetacean Research Program, Center for Coastal Studies, Provincetown, MA 02657, U.S.A.

and

Department of Zoology, University of Aberdeen, Aberdeen AB9 2TN, Scotland

LISA S. BARAFF

Cetacean Research Program, Center for Coastal Studies, Provincetown, MA 02657, U.S.A.

CAROLE A. CARLSON

Cetacean Research Program, Center for Coastal Studies, Provincetown, MA 02657, U.S.A.

and

Department of Biology, Dalhousie University, Halifax, N.S., Canada B3H 4J1

AND

MARGARET A. CHRISTIAN, DAVID K. MATTILA, CHARLES A. MAYO, MARGARET A. MURPHY,  
AND SHARON PITTMAN

Cetacean Research Program, Center for Coastal Studies, Provincetown, MA 02657, U.S.A.

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A study of 518 individually identified humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine between 1979 and 1988 showed high rates of both within-season occurrence and annual return. On average, 77.3% of whales were resighted on more than 1 day during the year (maximum 83 days), with occupancies ranging from 1 to 324 days (mean 88.1 days). The mean rate of return of individuals in consecutive years was 73.2% (range 59.1–87.4%), and the majority of whales were still being resighted up to 10 years later. Only 13 humpbacks were recorded during 50 midwinter surveys. Variation in the occurrence of individuals appears to be related to variability in the abundance of prey and perhaps to regional preferences.

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L'étude de 518 Rorquals à bosse (*Megaptera novaeangliae*) dans la partie sud du golfe du Maine, de 1979 à 1988, a démontré un fort pourcentage de retours, aussi bien au cours de la même saison qu'au cours d'une autre année. En moyenne, 77,3% des rorquals ont été aperçus de nouveau à plusieurs reprises au cours de l'année (maximum 83 jours), et la durée de l'occupation variait de 1 à 324 jours (moyenne 88,1 jours). Le taux moyen de retour des individus au cours d'années consécutives a été évalué à 73,2% (59,1–87,4%) et la majorité des rorquals étaient parfois revus jusqu'à 10 ans plus tard. Seulement 13 rorquals ont été dénombrés au cours de 50 inventaires effectués au milieu de l'hiver. La variation enregistrée dans la position des rorquals semble reliée à la variabilité de l'abondance des proies et peut-être aussi à des préférences régionales.

[Traduit par la rédaction]

TABLE 1. Number of cruises made, number of individuals photographed, mean occurrence (in days) of individuals, and maximum and mean occupancy (in days) of individuals for each year of the study period

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
No. of cruises	164	238	515	625	730	773	835	1042	977	1145
No. of individuals	51	59	95	137	116	184	232	240	244	289
Mean occurrence	3.4	7.4	9.1	11.3	15.4	11.3	15.2	3.5	3.4	9.8
Occupancy										
Maximum	157	195	180	243	209	240	293	324	227	285
Mean	62.0	88.4	88.2	110.3	100.9	111.9	92.6	73.9	63.1	84.4
SD	58.1	65.8	60.6	64.9	57.1	60.6	54.9	58.7	55.5	60.6

NOTE: The mean occupancy for all years was 88.1 days.

### Introduction

The introduction in the mid-1970s of a technique for identifying individual humpback whales, *Megaptera novaeangliae*, led to considerable advances in understanding of the biology and behavior of this species (Katona et al. 1980; Hammond et al. 1990). Investigations based upon photographic mark-recapture of identified individuals have shown that the western North Atlantic population is made up of several relatively discrete high-latitude feeding stocks which summer in the Gulf of Maine, the Gulf of St. Lawrence, Newfoundland, Labrador, West Greenland, and Iceland (Katona and Beard 1990).

In the southern Gulf of Maine a population of humpbacks has been under continuous long-term study since 1979. Humpbacks occur there during spring, summer, and autumn, where their primary prey since the mid-1970s has been the American sand lance, *Ammodytes americanus* (Overholtz and Nicolas 1979; Payne et al. 1986). On this feeding ground, commercial whale watching has provided a high level of survey effort on a daily basis for 6 months of each year; as a result, this population is the most intensively studied group of mysticetes in the world, the resighting histories of individual whales being generally longer and more detailed than those gathered from other regions. These histories have provided sometimes extensive information on reproductive rates (Clapham and Mayo 1987, 1990), age at attainment of sexual maturity (Clapham 1992), and social organization (Weinrich 1991; Weinrich and Kuhlberg 1991; Clapham 1993).

Previous work on individual humpbacks first recorded as calves has strongly suggested that members of this population exhibit maternally directed foraging area philopatry (Clapham and Mayo 1987, 1990). Here, we summarize data on seasonal occurrence and annual return of all identified individuals observed by us in the southern Gulf of Maine during the period 1979–1988.

### Methods

This study was conducted between 1979 and 1988 in the waters of the southern Gulf of Maine. The study area is illustrated and described in detail in Clapham and Mayo (1987) and includes the waters of Massachusetts Bay and the Great South Channel (30 mi (1 mi = 1.609 km) southeast of Cape Cod, Massachusetts). The majority of observations were made from 30-m commercial whale-watching vessels in Massachusetts Bay. Beginning in 1984, additional directed cruises to this area and to the Great South Channel were made on a 14-m auxiliary ketch and an 11-m diesel-powered motor vessel. A total of 7052 cruises was made during the study period; 97% of these were 4-h trips aboard whale-watching vessels operating daily from Provincetown, Massachusetts, between mid-April and the end of October each year. The exception was 1979, when no cruises

were run during the period from mid-June to mid-September. Trips to the Great South Channel were begun on a sporadic basis in 1984; a total of 79 such trips of varying lengths was made during this study.

Individual humpback whales were recognized from photographs of variations in the ventral fluke pattern (Katona et al. 1980) and of the shape, size, and scarring of the dorsal fin. Photographs were taken on ISO 400 black and white print film using a 35-mm camera equipped with a 200-, 300-, or 400-mm telephoto lens, power winder, and recording databack. Many individuals were readily identifiable in the field, but all sightings were photographically confirmed.

### Definitions

The following terms are used in this report: *occupancy*: the period, in days, between the first and last sightings of an individual whale in a given year. Occupancies were calculated only for whales seen on at least 2 days in a year. We do not assume that the whale was necessarily present in the study area for the entire period between sightings; *occurrence*: the number of separate days on which an individual humpback whale was observed in the study area in a given year.

### Results

#### Within-season occurrence and occupancy

Table 1 summarizes data on effort and on occurrence and occupancy of individual whales during the period 1979–1988. The number of individuals identified each year ranged from 59 to 289 and totalled 518. Observed occupancy of individuals ranged from 1 day to 324 days; the mean occupancy for all whales observed in a year varied from 62.0 days (1979) to 111.9 days (1984), with an overall mean for all years of 88.1 days. There was a high rate of resighting of individuals within a season: the mean occurrence of individuals ranged from 3.4 days in 1979 and 1987 to 15.4 days in 1983. Overall, 77.3% of individuals were resighted on more than 1 day during a year, with some individuals observed on up to 83 days. Interyear variations in observed patterns of occurrence are illustrated in Fig. 1.

A total of 50 surveys made in Massachusetts Bay during January and February from 1984 to 1988 produced sightings of only 13 individual humpbacks. Of these, four were known juveniles (less than 5 years old) and one was an adult female whose 1-year-old calf was known to have died 2 days earlier. The other eight whales were of unknown age-class, although visual estimates of size suggested that the majority were young animals. Six of the 13 whales were female, 1 was male, and 6 were of unknown sex.

#### Annual return

A high rate of return of individuals between years was observed in this study. On average, 73.2% of whales identified in one year were resighted the following year (minimum

TABLE 2. Return rates of humpback whales to the study area

Year	N	1980	1981	1982	1983	1984	1985	1986	1987	1988
1979	51	66.7	82.4	90.2	70.6	82.4	70.6	62.7	51.0	58.8
1980	59		84.7	89.8	71.2	86.4	76.3	64.4	50.8	64.4
1981	95			87.4	66.3	78.9	74.7	68.4	53.7	58.9
1982	137				59.1	71.5	70.8	62.8	46.7	54.7
1983	116					86.2	82.8	67.2	58.6	57.8
1984	184						76.1	66.3	56.0	62.0
1985	232							70.3	58.6	61.2
1986	240								64.6	65.4
1987	244									63.9
1988	289									—

NOTE: Each cell shows the percentage of individuals from the base year that were resighted in the subsequent year. N is the number of individuals observed in the base year. For example, of the 51 whales observed in 1979, 66.7% were resighted in 1980, 82.4% in 1981, 90.2% in 1982, etc. See Table 3 for the means of interyear resighting rates.

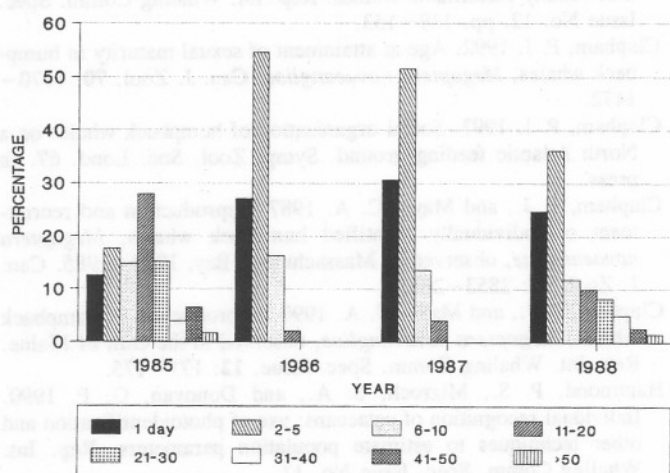


FIG. 1. Occurrence (number of days seen) of individual humpback whales during the 4 years from 1985 to 1988. Results are grouped by interval, the y-axis value representing the percentage of individuals observed that year.

59.1%, maximum 87.4%; Table 2), and the majority were still being resighted up to 9 years later (Table 3), although a gradual decline was observed overall. The lowest rate of return between any 2 years was 46.7% (1982–1987), and the highest 90.2% (1979–1982). Of the 518 individuals identified during the study period, 190 were observed in only 1 year, 88 in 2 years, 68 in 3 years, 42 in 4 years, 32 in 5 years, 26 in 6 years, 21 in 7 years, 29 in 8 years, 7 in 9 years, and 15 in all 10 years. In all, 270 individuals were seen every year from first sighting to the end of the study period.

### Discussion

During the period of this study, the individual humpback whales using the southern Gulf of Maine were characterized by high rates of within-season occurrence (up to 83 days), occupancy (up to 324 days), and annual return (up to 90.2%). These rates are considerably higher than those reported by Baker et al. (1985) and Perry et al. (1990) for another high-latitude population of this species in southeastern Alaska. Furthermore, the annual return rate is greater than the 56% reported for the whole Gulf of Maine by Katona and Beard (1990). This is almost certainly a reflection of the intensive effort made possible by daily surveys aboard commercial

TABLE 3. Mean values for the resighting rates given in Table 2

Resighting period	n	Mean	SD
Consecutive years (e.g., 1979–1980)	9	73.2	10.698
Base year + 2 years (e.g., 1979–1981)	8	72.9	10.848
Base year + 3 years (e.g., 1979–1982)	7	70.8	11.245
Base year + 4 years (e.g., 1979–1983)	6	69.2	10.327
Base year + 5 years (e.g., 1979–1984)	5	66.3	14.318
Base year + 6 years (e.g., 1979–1985)	4	60.9	8.095
Base year + 7 years (e.g., 1979–1986)	3	57.5	6.080
Base year + 8 years (e.g., 1979–1987)	2	57.5	9.475
Base year + 9 years (1979–1988)	1	58.8	—

NOTE: There were, for example, three periods (n) of base year + 7 years (1979–1986, 1980–1987, and 1981–1988) for which the mean resighting rate was 57.5%.

whale-watching vessels in Massachusetts Bay; given an equivalent level of effort on other feeding grounds, one might expect to record similar rates of occurrence and return elsewhere, and it is likely that even these data underrepresent the true rates for this population. Overall, the results reported here, together with data on recruitment gathered by Clapham and Mayo (1987, 1990), provide the strongest evidence to date for the existence in this species of foraging area philopatry, the tendency for individuals to return consistently to the feeding ground to which they were brought as calves by their mothers. While studies conducted elsewhere have suggested that this is also the case for humpbacks on other high-latitude feeding grounds in the western North Atlantic (Katona and Beard 1990), further analysis of the distribution of mitochondrial DNA haplotypes in the population (Baker et al. 1990) is required to determine whether such maternally directed fidelity remains constant over many generations. The gradual decline in the percentage of whales returning to the study area over years may in part reflect a mortality rate (see Buckland 1990), a tendency for individuals to expand their range with age and experience, and (or) the inclusion within longer intervals of a crash in the local population of the primary prey species (see below).

The considerable variation observed in the occurrence of individuals is probably the result of two factors. Firstly, fluctuations in the abundance of prey, both within a season and from year to year, produce sometimes marked variations in the occurrence of whales in a particular area. This has been demonstrated for humpback whales in the southern Gulf of Maine by Payne et al. (1990), who noted a positive correlation

between the abundance of *Ammodytes* and sighting rates of humpbacks. The variation in these rates is mirrored by similar fluctuations in the observed rates of within-season occurrence of individuals for the same years during the present study (Fig. 1). In particular, very low rates (means of 3.5 and 3.4 days) were observed during 1986 and 1987, a period when the *Ammodytes* population crashed in Massachusetts Bay, and sighting rates of humpbacks were extremely low (Payne et al. 1990). Indeed, the rates of occurrence given above over-represent the situation in the Massachusetts Bay area during these 2 years, since they include resightings made during cruises to the Great South Channel, where *Ammodytes* were abundant and where sometimes large concentrations of humpbacks were present.

Secondly, variations in occurrence may also be due to regional preferences on the part of individual whales. Some whales were consistently seen every year and were resighted many times during a season, while others were observed rarely. Exchange of sighting data with other institutions indicates that the humpbacks observed in our study area often roam widely during spring, summer, and autumn. Matches confirmed by the *North Atlantic Humpback Whale Catalogue* reveal that many individuals observed off the Massachusetts coast are frequently resighted on Georges Bank and off southwestern Nova Scotia, and 14 have been photographed up to 600 miles away in the Gulf of St. Lawrence or on the Grand Bank of Newfoundland (J. Allen, personal communication). Furthermore, the individuals that were resighted in distant areas (such as Newfoundland) were characterized by few sightings in the southern Gulf of Maine during this study, a fact which suggests that their primary foraging range lies elsewhere and that they represent transients in our area. Further study is required to determine whether apparent regional preferences remain stable over periods of many years and whether they are maternally influenced.

Our level of effort at the extremes of the season (early spring and late autumn) was insufficient to allow us to reliably assess gross migratory movement in and out of the area. Straley (1990) reported that sometimes significant numbers of humpbacks (of all age-classes and both sexes) were present in midwinter in southeastern Alaska. In Massachusetts Bay, however, the few sightings made of humpbacks during our sporadic winter surveys suggest that the great majority of individuals undertake the migration from the Gulf of Maine to the West Indies each year. The occurrence of a number of known and probable juveniles among animals observed by us in January and February suggests that reproductively immature whales are more likely than others to overwinter in high latitudes, but existing data are insufficient for this question to be addressed.

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