The migration of humpback whales along the northeast coast of Newfoundland

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Humpback whales migrate along the northeast coast of Newfoundland in summer. Individuals were identified which moved from St. Vincent's on the south coast to Bonavista Bay on the northeast coast, and from there to southern Labrador. The mean migration rate northward along the northeast coast in summer was estimated to be 1.2° latitude per month, although animals moved through a study area at the end of the Bay de Verde Peninsula at about twice this rate. The animals arriving at Bay de Verde in early July, when humpback densities were higher, were on average larger than those arriving either earlier or later. Over periods of more than 1 day there was no evidence for consistent companionships (other than mothers with their 1st-year calves), and only one animal appeared to have a preferred range within the Bay de Verde study area, although some whales preferentially returned to certain stretches of the coastline in different years.

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Les rorquals mégaptères migrent le long de la côte nord-est de l'Ile de Terre-Neuve durant l'été. Des individus identifiés sont partis de St-Vincent sur la côte sud et se sont déplacés jusqu'à Bonavista Bay sur la côte nord-est, puis, de là, jusqu'au sud du Labrador. La vitesse moyenne de migration vers le nord le long de la côte en été est de 1,2° de latitude par mois, quoique la vitesse de certains animaux ait été estimée à deux fois cette valeur à l'extrémité de la péninsule de la Baie de Verde. Les rorquals qui arrivent à Baie de Verde au début de juillet, moment où les densités sont maximales, sont en moyenne plus gros que ceux qui arrivent plus tôt ou plus tard. Des observations de plus d'une journée ne permettent pas de croire à l'existence d'un compagnonnage durable entre individus (à l'exception des mères avec leurs petits de l'année) et un seul animal a semblé avoir une préférence de "territoire" dans la Baie de Verde; certains rorquals retournent cependant de préférence à certains endroits de la côte durant plusieurs années.

[Traduit par le journal]

Introduction

The humpback whale *Megaptera novaeangliae* makes long seasonal migrations from winter breeding grounds, usually at latitudes between 10° and 30° N and S, to summer feeding areas, mostly between 45° and 65° N and S (Mackintosh 1965). Humpbacks are generally coastal animals, and reasonably distinct stocks are associated with each side of each ocean (Mackintosh 1965).

The major winter concentrations of the humpbacks in the western North Atlantic are on Silver and Navidad banks, which lie north of the Dominican Republic, although some are dispersed along all the Antillean chain (Winn *et al.* 1975). In summer humpbacks are found in the Gulf of Maine, off eastern Newfoundland, southern Labrador, and southwestern Greenland.

The ability to distinguish individual humpbacks from photographs of the ventral side of their flukes has made it possible to examine humpback migrations and stock segregations without a current whaling industry (Katona *et al.* 1979). There are many year-to-year and place-to-place fluke photograph matches within the Gulf of Maine and Newfoundland–Labrador regions, but to date no individual has been photographed in both (Katona *et al.* 1980). Animals from these two main summering areas have been photographed on Silver Bank in winter and off Bermuda in spring (Katona *et al.* 1980).

Mitchell (1973) showed capelin (*Mallotus villosus*) to be the major food for the humpbacks off Newfoundland. In an earlier paper (Whitehead *et al.* 1980), we related the distribution and northward migration speed of the

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humpbacks off the Bay de Verde Peninsula, Newfoundland, during the summer of 1978 to the density of depth sounder traces in the 80–120 m range believed to have been made by postspawning capelin schools. Additional studies of the humpbacks off Bay de Verde were carried out in 1979 and 1980, and surveys were made along the northeast coast of Newfoundland in 1978 and 1979. This paper describes the migration of the humpback whales along the coast, using data (principally fluke photographs) collected during these and other studies.

Capture–recapture analysis of these photographic data suggested a total population of between 1535 and 2720 humpback whales summering off the northeast coast of Newfoundland and southern Labrador (Whitehead 1981).

Methods

Small-scale studies were carried out off the Bay de Verde Peninsula between 1 June and 10 August 1978, 5 June and 31 July 1979, and 14 June and 3 August 1980. Most of the research was performed from a 10-m yawl with a crew of three or four. During standard transects (as described by Whitehead *et al.* 1980) counts of humpback whales were made and a recording depth sounder was used to monitor prey distributions. Additional time at sea was spent following groups of whales for as long and discreetly as possible. The differences in latitude and time of day between the endpoints of these watches provided the raw material for analysing the migration rates past Bay de Verde.

Surveys were made from St. John's, Newfoundland, to Batteau, Labrador, to Wesleyville, Newfoundland, between 12 August and 13 September 1978, and from St. John's to Batteau, to Old Perlican, Newfoundland, between 7 August and 4 September 1979. During these surveys and the Bay de Verde studies, fluke photographs were taken whenever possible. Katona *et al.* (1980) have catalogued those photographs submitted to them before May 1980. We have augmented these with our Bay de Verde 1980 sample and some taken in Trinity Bay, Newfoundland, during August 1980 by M. Moore and R. Silver. Only good quality photographs of flukes were considered in the analysis. The sample sizes from the different areas are given in Table 1. Of these 700 animals, 506 were photographed by us, although P. Beamish and associates at Ceta-Rescue/Research Inc., J. Lien and associates at the Memorial University of Newfoundland, and the Ocean Research and Education Society also made substantial contributions.

Information recorded with each fluke photograph included the date, time, place, length of the whale estimated by eye (in 1979 and 1980), group size, other known photographs of the same whale, and photographs of whales in the same group. The estimated lengths may have had a consistent bias; however, estimated lengths of the same whales on different days (identified later from fluke photographs) had standard errors of 0.30 m in 1979 and 0.16 m in 1980, significantly ($P < 0.01$) less than the variations between different whales (standard errors of 1.0 m in 1979, 1.1 m in 1980). Thus any biases in our length estimates were consistent. For each Bay de Verde study, correlations were calculated between all pairs of the following variables: date of first photographing at Bay de Verde, date of last photographing at Bay de Verde, duration of stay (as indicated by the time between the first and last photographs), estimated length of whales, whiteness of fluke pattern, scratches on flukes, marks of the teeth of orcas, *Orcinus orca* (Katona *et al.* 1980), and various characteristics of the dorsal fin (curliness, markings, etc.). Only those pairs of variables which showed significant, nontrivial (date of arrival naturally correlated with date of departure), and consistent correlations across the 3 years are mentioned in the Results section of this paper.

TABLE 1. Number of different individual northwest Atlantic humpbacks photographed during 1975–1980 (*i*) during the Bay de Verde study, (*ii*) off the Newfoundland coast including the Bay de Verde study, and (*iii*) off the Labrador coast

Year	Bay de Verde	Newfoundland including Bay de Verde	Labrador
1975		7	
1976		10	
1977		13	1
1978	145	184	31
1979	150	329	62
1980	54	63	

Results

Extent of migration

The positions at which individual humpbacks were photographed along the Newfoundland and Labrador coasts during the same year are shown linked together in Fig. 1. The lines drawn do not indicate the actual routes taken; these remain unknown. It should be stressed that photographic effort was not evenly distributed either with respect to the coastline or areas of whale abundance. However, Fig. 1 shows that there were within-year movements from St. Vincent's on the southeast corner of Newfoundland to Bonavista Bay on the northeast coast, and from there to southern Labrador.

Rate of migration

The northward migration rate in degrees north per month and the minimum migratory speed, using the shortest distance through the ocean between the positions at which each individual was photographed, were calculated for each individual migration given in Fig. 1. Histograms of the northward migration rate and minimum migratory speed are shown in Fig. 2. Because of the arrangement of the surveys, proceeding generally northward down the coast, long southward movements were unlikely to be detected. The mean northward rate from this analysis, 1.2° latitude per month, is rather less than that calculated from the individual watches at Bay de Verde, 2.4° latitude per month. In 1978 the rate of northward migration through the Bay de Verde study

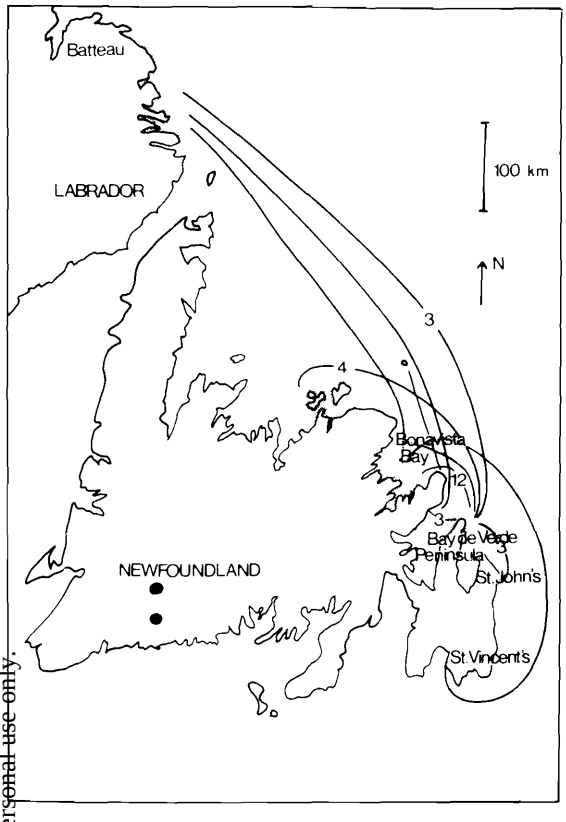

FIG. 1. Within-year migrations of humpback whales along the northeast coast of Newfoundland as indicated by fluke photograph matches. Shaded areas are treated as one for clarity. Where more than one animal made a specific migration, the numbers are given. (The lines drawn do not indicate the actual routes taken.)

area was negatively correlated with food abundance (Whitehead *et al.* 1980). The data from the 1979 and 1980 Bay de Verde studies, when studied in the same manner, also showed this trend, although in neither case was it statistically significant at the 0.05 level.

The mean northward migration rates through the Bay de Verde study area meant that most individuals only resided there for a few days during each year, and, as shown by the histogram of residence times in Fig. 3, many were photographed on just 1 day. In all there were 39 individuals who resided longer than 10 days, and 6 whose first and last photographs at Bay de Verde were separated by more than 1 month. However, from an examination of the dates on which these animals were photographed (e.g. Whitehead *et al.* 1980, Fig. 3), it seems that some may have left the Bay de Verde area to return later in the study.

Arrival dates of different classes of animal

There was significant variation in the mean estimated lengths of humpbacks arriving at Bay de Verde at different dates in 1979, and a similar, but not significant,

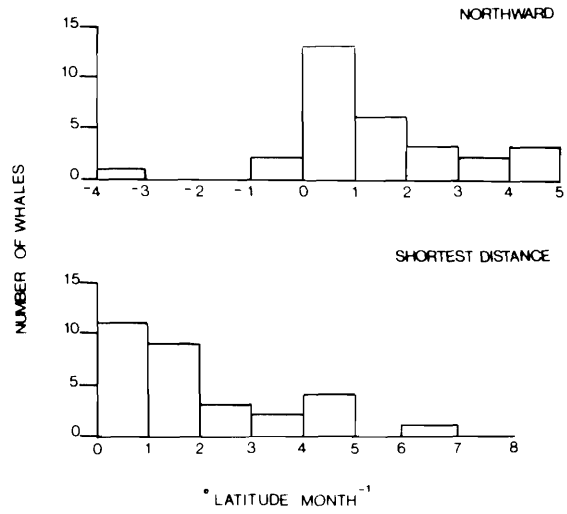

FIG. 2. Migration speeds of humpback whales along the Newfoundland coast from whales photographed twice in 1 year. In the upper histogram the latitudes of the endpoints were subtracted to obtain the northward rate; in the lower diagram the shortest reasonable route was used to give a minimum migratory speed (1° latitude/month = 0.154 km/h).

trend was found in 1980. As shown in Fig. 4B, the whales arriving in the middle of the studies were on average longer than those arriving at either the beginning or the end (the outliers at the end of the season came from very small samples: four in 1980, two in 1979). Except in 1980, there were generally more whales in the study area during the middle of the study period, as indicated in Fig. 4A by the transect counts. Mothers with calves did not seem to come through the Bay de Verde study area at a different time from the humpbacks in general (Fig. 4C). The only morphological trend to show significant and consistent variation with date of arrival at Bay de Verde was the presence of orca tooth marks on the flukes: humpbacks arriving later at Bay de Verde tended to have more tooth marks (Fig. 4D).

Individual variations in date of arrival

Thirty-two individuals were photographed during more than 1 year at Bay de Verde, and the dates on which they were first photographed are compared in Fig. 5. Significantly ($P < 0.05$) more whales arrived earlier and at cooler water temperatures during the 2nd of the 2 years in which they were photographed. Thus, individuals tended to arrive at Bay de Verde earlier and earlier each year, although this was not obviously the case for the population as a whole (Fig. 4A).

Consistent companionships

In each year the repeat pairwise groupings were examined; these were the numbers of pairs of days on both of which two particular individuals were

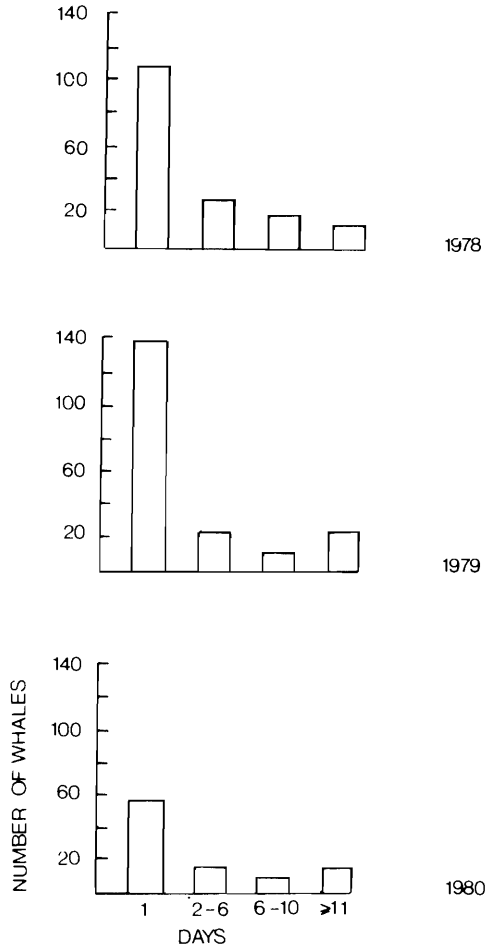

FIG. 3. Residence times at Bay de Verde as indicated by the number of days from first to last photographing of individual humpbacks.

photographed grouped together, and are given in Table 2. Also shown are the maximum number of repeat pairwise groupings for each year, given the days on which individuals were photographed. In none of the 3 years were the actual number of repeat groupings significantly different from the expected number if individuals grouped independently of the groupings that occurred on previous days. The distribution of the expected number of repeat groupings was found by randomly permuting the groupings on each day, keeping the number of pairwise groupings of each individual constant, and counting the resultant number of repeat groupings for each permutation. There was no tendency for whales to group with whales of a similar or different length. There were also no repeat groupings over more than 1 year at Bay de Verde.

Preferred ranges

In our analysis of the 1978 Bay de Verde data we found that one individual humpback possessed a

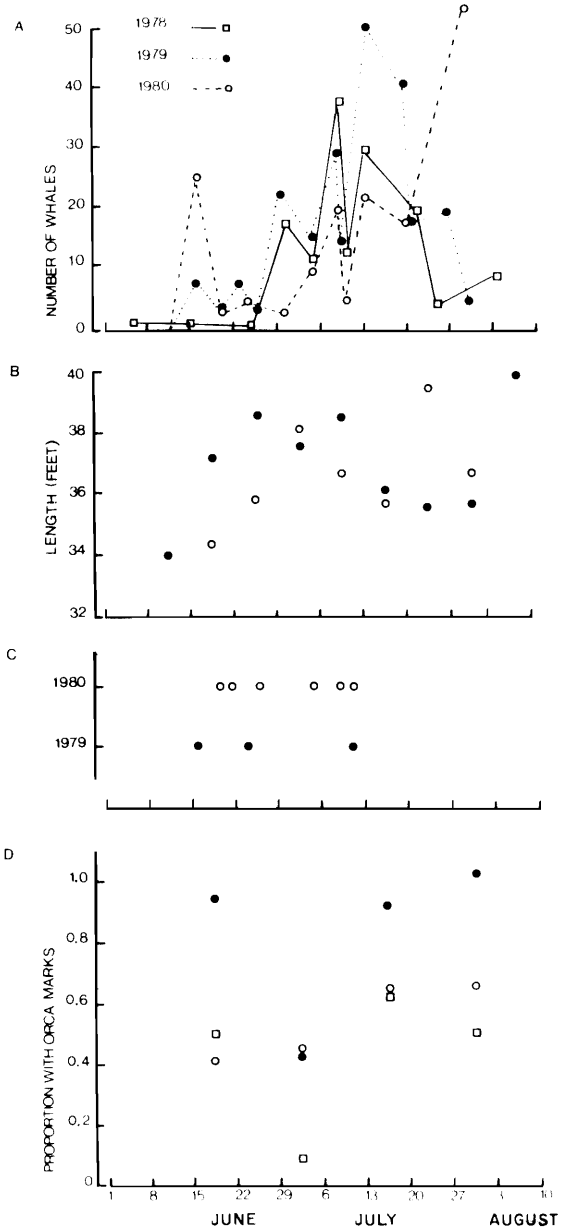

FIG. 4. (A) Counts of humpbacks on transects at Bay de Verde on different dates. (B) Mean estimated lengths of whales first photographed in each observation week of 1979 and 1980. Sample sizes for the 9 weeks in 1979 (●) and 1980 (○), respectively, were the following: 8–15 June, 2 and 0; 15–22 June, 5 and 7; 22–29 June, 12 and 7; 29 June – 6 July, 22 and 7; 6–13 July, 12 and 7; 13–20 July, 37 and 9; 20–27 July, 16 and 4; 27 July – 2 August, 4 and 4; 3–10 August, 2 and 0. (C) Dates of individual watches of groups containing calves at Bay de Verde. (D) Proportion of animals with orca tooth marks on their flukes first photographed in each 2-week period at Bay de Verde. Sample sizes for 1978 (□), 1979 (●), and 1980 (○), respectively, were the following: 8–22 June, 7, 11, and 12; 22 June – 6 July, 27, 53, and 12; 6–20 July, 85, 91, and 27; and 20 July – 3 August, 32, 40, and 12.

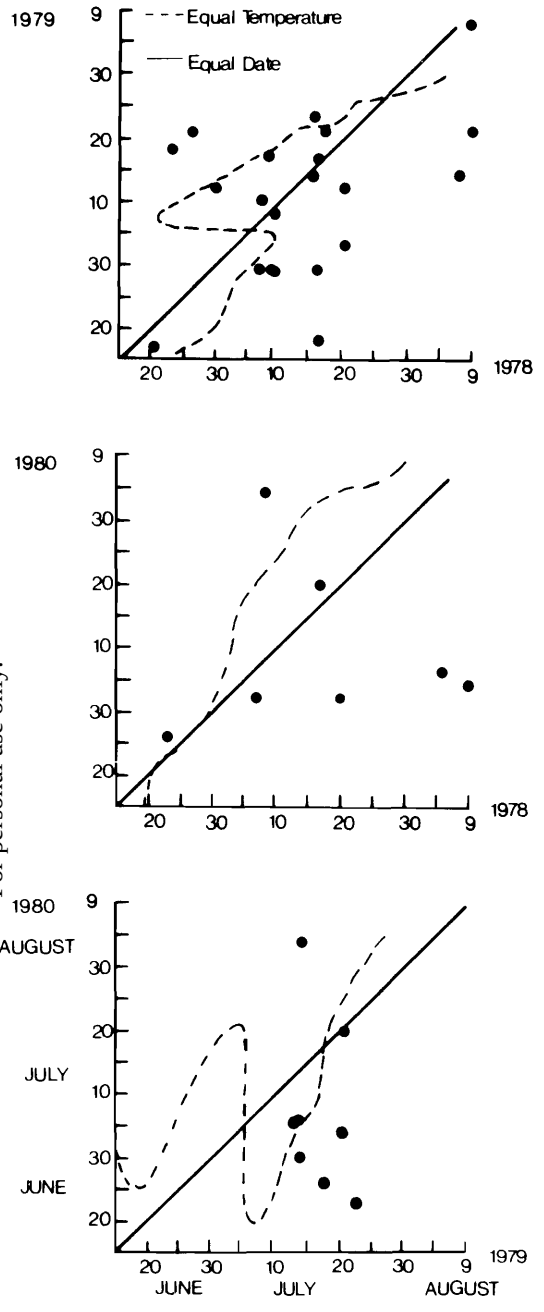

FIG. 5. Dates of first photographing of individual humpbacks at Bay de Verde for those humpbacks photographed in more than 1 year. The solid line indicates equal dates and the broken line indicates equal surface sea temperatures.

preferred range, where it was more likely to be found than individuals chosen from the population at random, but there was no evidence that the same was true of any other animal (Whitehead *et al.* 1980). Repeating this analysis for the 1979 and 1980 studies gave no indication of any further preferred ranges.

Although within each year some individuals moved from Bay de Verde to Labrador, a comparison of returns between areas and years showed this mixing to be incomplete: whales photographed at Bay de Verde in one year were significantly more likely to be seen there the next than those found elsewhere along the coast ($P < 0.05$). Comparing Newfoundland and Labrador returns showed a similar, but not so significant ($P < 0.10$), lack of random mixing. Thus, individuals tended to return preferentially to sections of the coast where they had been photographed in previous years.

TABLE 2. The number of times in each Bay de Verde study that two whales were photographed in the same group on 2 different days

		Repeat pairwise groupings	
Year	Actual no.	Max. possible no.	Expected no.
1978	5	206	5
1979	2	56	—
1980	2	20	1

NOTE: The third column gives for each study the maximum possible number of these repeat pairwise groupings, given the days on which individuals were photographed. The last column gives the expected number of these repeat pairwise groupings, if groupings were random, given the number of individuals grouped with each individual on each day, calculated by Monte-Carlo methods (Sokal and Rohlf 1969, p. 636). This calculation was not performed on the 1979 data as it was obviously not significant.

Discussion

Results given in this paper are principally concerned with the migrations of the humpback whales within their feeding grounds rather than the much longer migration between breeding and feeding areas. Nevertheless, in Table 3 some migration rates for the western North Atlantic are compared with Dawbin's (1966) findings from New Zealand. It seems that the western North Atlantic animals moved more slowly from Silver Bank to the Newfoundland coast than the New Zealand animals when making their springtime journey to warmer waters. The western North Atlantic animals may have spent some time on the Grand Banks before arriving at the Newfoundland coast in the vicinity of St. Vincent's with the spawning capelin. The migration rate along the coast was slower still: the whales were principally feeding and gradually moved northwards, perhaps with the spawning capelin; capelin spawning generally happens at later dates further north along the coast (Jangaard 1974). The higher mean rate of progression through the Bay de Verde study area is probably due to its geographical prominence at the end of a peninsula, so that it lies on a coastal migratory route as well as possessing food resources.

The different mean dates of arrival at Bay de Verde of the different sized animals, and those with or without orca tooth marks, could be related to Dawbin's (1966) findings off New Zealand: in the migration from tropical

TABLE 3. A comparison of migration rates between those humpbacks which migrate past the New Zealand coast and the North Atlantic population

Population	Between	Rate	
		° latitude/month	km/h
New Zealand	Tonga to Foveaux Strait (New Zealand)	10.9	1.7
Northwest Atlantic	Silver Bank to St. Vincent's (South Newfoundland)	6.2	0.9
Northwest Atlantic	Past Bay de Verde	2.4	0.4
Northwest Atlantic	Along Newfoundland Coast	1.2	0.2

NOTE: The peak sighting times at Tonga and the Foveaux Strait are compared for the first entry (Dawbin 1966) and those on Silver Bank and at St. Vincent's, Newfoundland, for the second (Lien 1980; Whitehead 1981). The derivations of the migration rates past Bay de Verde and along the northeast coast of Newfoundland are given in the text.

waters the pregnant and resting females travelled first, followed by the immatures, males, and finally the lactating females. Older females might have a higher probability of possessing orca marks, the results of defending their young; but if Dawbin's (1966) progression was strictly followed we would have expected the calves to be predominantly sighted at the end of the season, and the immatures and males, who are generally smaller, to produce a dip in the mean length during the middle of the season. The rise in mean length during the middle of the season can be explained if the older and larger animals were better able to follow and utilize their prey and so would arrive relatively more frequently in the middle of the season, when prey was more abundant. Reasons for individuals arriving earlier each year are obscure.

More extensive surveys of the western North Atlantic (e.g., Gwinn *et al.* 1977) have shown the coastal area covered by the returns in Fig. 1, from St. Vincent's to Batteau, Labrador, to be reasonably isolated from other humpback concentrations; humpbacks are rarely sighted on the Labrador coast north of the Hamilton Inlet or off the Atlantic coast of Nova Scotia. This eastern Newfoundland – southern Labrador area also constitutes the major extent of capelin spawning along the North American coast, outside the Gulf of St. Lawrence. Thus the Newfoundland–Labrador substock of humpbacks appears to occupy the range of its major prey. In the Gulf of Maine the humpbacks seem to utilize sand lance (*Ammodytes americanus*) and herring (*Clupea harengus*) (Watkins and Schevill 1979; Hain *et al.* 1980). The segregation into feeding areas of whales which breed together may facilitate prey specialization, and increase feeding efficiency. The short residence times, and lack of preferred areas will also be functional for capelin feeders, as the spawning concentrations of this fish are rarely predictable or long-lived. In contrast, in the Gulf of Maine, when feeding on the much less mobile sand lance, humpbacks have longer residence times and a greater tendency for preferred areas (Mayo 1981). With the exception of mothers and their 1st-year calves, the humpbacks appeared to pursue their search for food independently, forming short-lived groupings.

Acknowledgements

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