Distribution and movements of West Indian humpback whales in winter

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The humpback whales which winter in the West Indies are principally found over banks which are at latitudes between 10° and 22° N, have substantial areas of flat bottom between 15 and 60 m deep, and lie less than 30 km from the North Atlantic 2000 m contour. The surface sea temperatures in these areas are between 24 and 28°C. The major concentrations of the humpbacks, which feed little in winter, are on Silver and Navidad banks. On Silver Bank the humpback and humpback song densities peak in the centre of the Bank. Mothers with calves are generally found in areas of calm water, and singers are found over areas with a flat bottom, where they meander slowly. Larger groups move considerably faster and in straighter lines. There is no evidence of whales possessing particular movement patterns, preferred ranges, or territories within the Bank. The concentration of humpbacks may be a significant feature for other humpbacks.

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Les rorquals communs qui passent l'hiver dans les Caraïbes ont des préférences d'habitat assez spécifiques: ils se retrouvent surtout aux latitudes situées entre 10° et 20° N, en des endroits où le fond est surtout plat entre 15 et 60 m de profondeur, à moins de 30 km de l'isobathe de 2000 m de l'Atlantique Nord. La température de surface de la mer est d'environ 24–28°C en ces régions. Les principales concentrations de rorquals, qui se nourrissent peu en hiver, se rencontrent sur les bancs Silver Bank et Navidad Bank. Sur le banc Silver Bank, c'est surtout au centre que la densité des rorquals et la fréquence des cris sont à leur maximum. Les mères avec des petits préfèrent les eaux calmes et les rorquals "chanteurs", les régions à fond plat où ils nagent lentement, en zigzaguant. Les groupes plus importants se déplacent beaucoup plus rapidement et selon un cours plus rectiligne. Les rorquals ne semblent pas avoir de patterns précis de déplacement, de régions favorites ou de territoires le long du banc. La concentration des rorquals a peut-être de l'importance pour les autres rorquals.

[Traduit par le journal]

Introduction

In all oceans humpback whales (*Megaptera novaeangliae*) make considerable migrations; during the summer months they are usually found in productive coastal waters at latitudes between 40° and 70°, whereas in the winter sightings are usually between 0° and 30° (Mackintosh 1965). In the northwest Atlantic the major concentrations in summer are off Newfoundland and Labrador and in the Gulf of Maine (Katona *et al.* 1980). Analysis of individual identification photographs has shown that many of these animals winter along the Antillean chain in the West Indies, with particularly striking concentrations being found on Silver and Navidad banks, north of the Dominican Republic (Katona *et al.* 1980; Winn *et al.* 1975). This migration is closely tied to the life cycle of the humpbacks; in summer they feed, while in winter conception and calving take place (Chittleborough 1965; Matthews 1937). The gestation period is about 1 year and, although some females show a postpartum oestrus, most wait 1 or more years between giving birth and becoming pregnant again (Chittleborough 1958).

It is in winter that the humpback songs are heard (Winn and Winn 1978). The humpback song is an intricate cyclical series of vocalizations (Payne and McVay 1971), which recent research suggests is made by male humpbacks to facilitate mating with females (Tyack 1981), although copulation has never been observed. The humpbacks also form groups of 4–11 animals in winter which generally consist of males competing for access to a central female (Tyack and Whitehead 1982).

In this paper we will describe the humpbacks' winter

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distribution and movements in the West Indies, on scales ranging from the whole geographic area to a few kilometres, and discuss the reasons underlying their distribution and movements.

Methods

During the winters of 1978 and 1980 the 44-m barquentine *Regina Maris* made circuits of Silver, Navidad, and Mouchoir banks at 2-week intervals following the route shown in Fig. 1. During 1978, at each of the nine stations marked in Fig. 1, "area watches" were carried out. These were counts of all humpback blows (exhalations) seen by one observer 15 m above sea level in a 90° arc about the ship during 30 min. There were 549 area watches. Also at each station humpback songs were monitored using hydrophones and graded from 0 (no songs) to 5 (strong chorus). When *Regina Maris* was sailing between stations on and near the banks, in both 1978 and 1980, censuses were taken of humpback whales, other cetacea, large fish, birds, and flying fish (family Exocoetidae). The methodology and population estimates derived from these censuses are described in detail by Whitehead (1982). During the censuses environmental variables such as wave height and wind speed were recorded at each 0.5 h and were used to compute a measure of sea surface roughness, namely wave height/wind speed (in units of metres for wave height and the Beaufort scale for wind speed).

During the winter of 1980 we made a study of the behaviour of the humpback whales on Silver Bank using the 10-m sloop *Elendil.* Most of the work was carried out within the primary study area which is shown in Fig. 1. During daylight, groups of humpbacks were followed for as long as possible and as discreetly as possible. As in similar watches off Newfoundland in the summer, observable behavioural activities were recorded, together with any whale faeces sighted. Navigation was by dead reckoning updated by regular sextant sights of the sun and(or) moon, so that our positions were usually accurate to within 1000 m. At each 0.5 h the following information was collected.

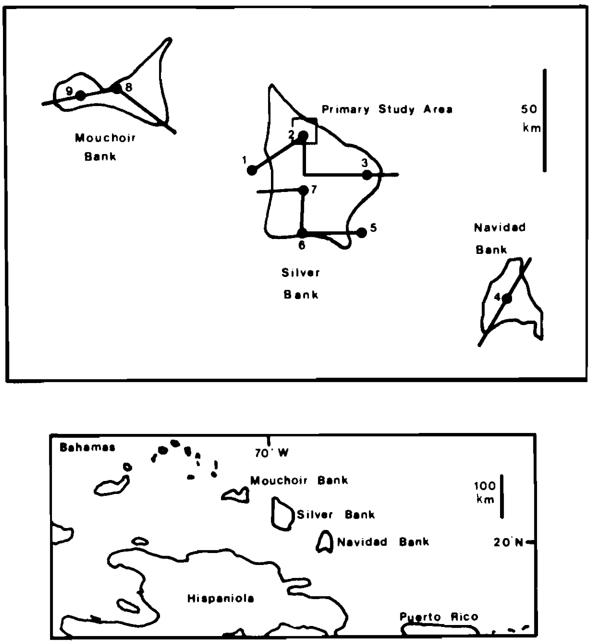

FIG. 1. The positions of Silver, Navidad, and Mouchoir banks are given below. *Regina Maris*' approximate census route is shown above, together with the stations used in 1978 and the primary study area.

Bottom profile

A recording depth sounder was run for 5 min and the greatest range of bottom depths obtained was used as an indicator of the bottom profile; e.g., if the range of depths was 15–23 m, the bottom profile indicator would be 8 m. Contours of the mean value of the bottom profile indicator are given in Fig. 8. These values indicate the height of the coral growth.

Song count

A count was made of the songs audible through the hydrophone which did not cause blocking at standard gain, but whose structure could be clearly distinguished. From listening to singers at known ranges we concluded that this was an approximate count of the singers at distances between 100 and 500 m from the boat. These standard 0.5-h listenings were also used to check whether the followed whales were singing.

Surface sightings

The observers on deck gave their best estimate of the number of whales within 500 m of the boat. During the watches and at other times, photographs were taken of humpback fluke patterns to identify individuals by the method of Katona *et al.* (1979). There were a total of 90 watches averaging 156 min per watch.

We wished to obtain indices of the spatial variation in the density of whales and songs from the 0.5-h counts and censuses. However, the whale densities varied considerably with time (Fig. 5), and counts were made in different areas at different dates. To compensate for these variations, maximum-likelihood methods were used (Silvey 1975, p. 70). The times were grouped into intervals (t) and the places were grouped into areas (a), and N_{at}, a count in an area during a time interval was modelled by:

$$N_{at} \sim \text{Poisson}\ (\lambda_a \cdot \mu_t)$$

where λ_a is an area parameter and μ_t a time interval parameter. This assumes that the expected number of whales in any area during any time interval is proportional to the product of independent area and interval parameters, the λ and μ values. The maximum-likelihood estimators of the λ and μ values and their estimated standard errors were found by iteratively solving the maximum-likelihood equations on a computer. The absolute values of the λ values were irrelevant and were multiplied by suitable scaling factors to produce whale and song density indices in the range 0–200. However if $\lambda_1 = 15$, and $\lambda_2 = 30$, this analysis shows that there were on average twice as many whales in area 2 as in area 1. The λ values are thus indices of spatial variation in whale or song density and are used as such later in this paper.

Results

Winter feeding

During the 235 h of individual watches on Silver Bank in 1980 only one faeces was observed. This contrasts

TABLE 1. Whale, calf, and song densities compared between banks and areas near but off the banks, from 1978 and 1980 surveys on *Regina Maris*. The bottom roughness is the interquartile range of charted depths on the bank. The index of surface roughness, wave height/wind speed, was calculated from the median of records during censuses aboard *Regina Maris* and is in metres/Beaufort scale

	Maximum whale density $\cdot$ km^{-2}	Maximum calf density $\cdot$ km^{-2}	Mean song density index	Mean bottom roughness, m	Wave height/ wind speed	Presence of coral reef
Silver	1.13	0.103	2.0	6.2	0.66	Yes
Navidad	1.25	0.011	2.1	6.8	0.81	No
Mouchoir	0.18	0.008	0.2	10.2	0.63	Yes
Off banks	0.16	0.002	1.1	—	0.80	No

with our work off Bay de Verde, Newfoundland, in summer where faeces were observed at a rate of one every 3.9 h of following humpback groups.

We never saw behaviour of the humpback whales on Silver Bank which we would automatically associate with feeding off Newfoundland (such as regular diving in one location or lunging with greatly distended throat grooves), and there were no aggregations with other species apparently concerned with feeding. The central peaks in the distribution of humpback whales on Silver and Navidad banks were in sharp contrast to the distributions of sightings of odontocete cetacea, birds, large fish, and flying fish, which were all most frequently found near the edges of the banks, where better mixing and productivity would be expected. No mysticetes, other than humpback whales, were sighted on or near the banks.

Therefore, in common with investigators in other areas (e.g., Chittleborough 1965; Matthews 1937), we believe that humpbacks feed little, if at all, during winter.

Distribution in the West Indies

The distribution of humpbacks in the West Indies has been documented by Winn *et al.* (1975) and Balcomb and Nichols (1978). From an examination of British Admiralty and United States Hydrographic Office charts, the areas where humpbacks are regularly sighted were found to possess the following characteristics: (1) latitudes between 10° and 22°N, lying nearly due south of the major summer concentrations; (2) surface water temperatures between 24 and 28°C; (3) substantial areas of flat bottom between 15 and 60 m deep; and (4) proximity to deep North Atlantic water. All areas lay within 30 km of the North Atlantic (as opposed to the Caribbean Sea or the Gulf of Mexico) 2000-m-depth contour, with the single exception of the Gulf of Paria off the Venezuelan coast.

Distribution on Silver, Navidad, and Mouchoir banks

Winn *et al.* (1975) estimated that 85% of the humpbacks in the West Indies were on Silver and Navidad banks. Mouchoir Bank has a similar location and size to Silver Bank, but very much lower whale densities (Table 1). Silver and Mouchoir have similar mean bottom depths, but the bottom on Mouchoir is less smooth (Table 1).

Although Silver and Navidad banks had similar peak humpback densities (Table 1), there were considerable differences between the different areas of Silver Bank and between the ways that the humpback density changed with time on the two banks.

The humpback densities on different parts of Silver Bank can be compared through the counts on area watches (Fig. 2) and the indices of whale density from the censuses aboard *Regina Maris* in 1978 and 1980 (Fig. 3). In both years densities were significantly higher towards the centre and north of Silver Bank and very low off the banks. Densities at station No. 4 on Navidad Bank were approximately the average of the Silver Bank stations.

The mean blow counts from the area watches are

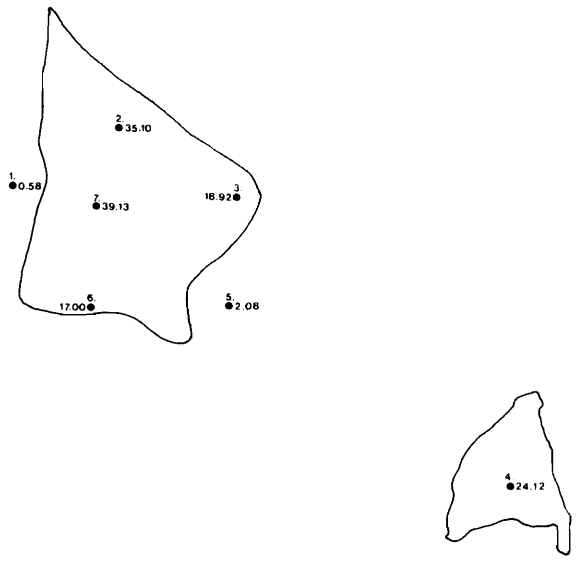

FIG. 2. Mean blows per hour per circuit, as indicators of whale density, for stations on and near Silver and Navidad banks. There is a significant difference between the rates at the different stations on Silver Bank (Kendall's $W = 0.51$, $P < 0.05$).

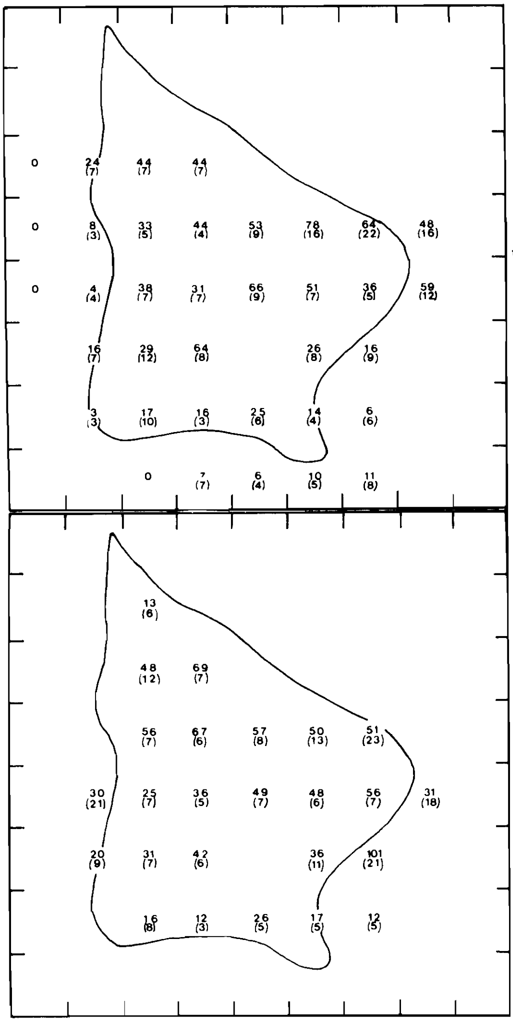

FIG. 3. Indices of spatial variation in whale density on Silver Bank from censuses on board *Regina Maris* (with estimated standard errors in parentheses) for 1978 and 1980.

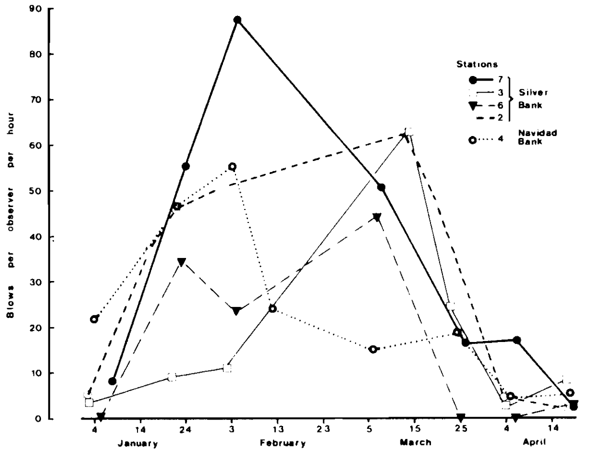

FIG. 4. Changes in whale density with date at different stations on Silver and Navidad banks, as indicated by blow counts on area watches.

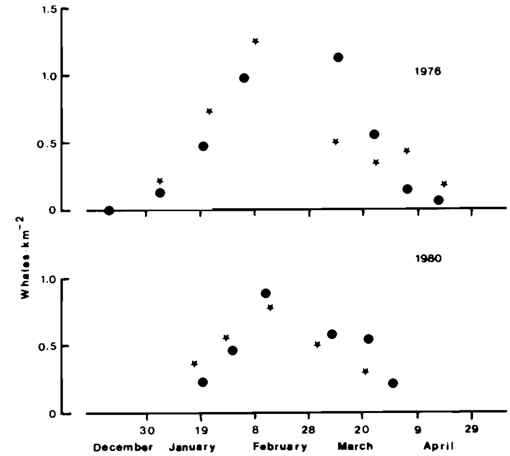

FIG. 5. Humpback densities on Silver (●) and Navidad (★) banks, as derived from the censuses on board *Regina Maris* (Whitehead 1982).

given for each station and circuit in Fig. 4. These show that the humpback densities were higher in February than March at the central stations on Silver and Navidad banks ($P < 0.10$, station No. 4; $P < 0.05$, station No. 7; two-tailed Mann–Whitney *U*-test), while at the peripheral stations densities were higher in March ($P < 0.05$, station No. 3; no significant difference, stations Nos. 2 and 6). Thus the central peak in density becomes less pronounced later in the season.

Similarly the estimates from the censuses aboard *Regina Maris*, shown in Fig. 5, indicate that the densities peaked earlier on Navidad Bank (although it is only clear in 1978) and were generally higher on Silver Bank in March.

Distribution of calves on Silver, Navidad, and Mouchoir banks

Calves were virtually absent from Navidad Bank, which has no coral reef and therefore no calm water (Table 1). Sightings of calves on Silver Bank during censuses aboard *Regina Maris* are shown in Fig. 6, which also gives contours of surface roughness. Calves were generally found in areas of calm water, usually amongst or in the lee of coral heads.

Distribution of singers on Silver, Navidad, and Mouchoir banks

Song, and therefore presumably singer, densities were high on both Silver and Navidad banks, but low on

Mouchoir (Table 1). The song densities were highest at stations Nos. 2 and 7 on Silver Bank, which have virtually flat bottoms (as shown by depth soundings from *Regina Maris*), and lowest at station No. 6, where there is considerable coral growth (Fig. 7). Within the primary study area a similar pattern showed (Fig. 8); although overall whale densities (as indicated by the surface sightings) were fairly even throughout those parts of the primary study area that were on the Bank, song densities were highest in the southwestern part of the primary study area, where the bottom is smoothest, and songs were virtually absent from areas of coral reef, indicated by the 9-m bottom profile contour.

Thus, from a comparison of Silver, Navidad, and Mouchoir banks, areas within Silver Bank and different parts of the primary study area on Silver Bank, there is evidence that singers usually sung over smooth bottoms.

Movements

The directions of movement of the groups of whales sighted during the surveys on board *Regina Maris* are given in Fig. 9. Groups moving counter to the ship's direction, principally clockwise around Silver Bank, will have been preferentially encountered, so that the whales appear to move generally anticlockwise. After

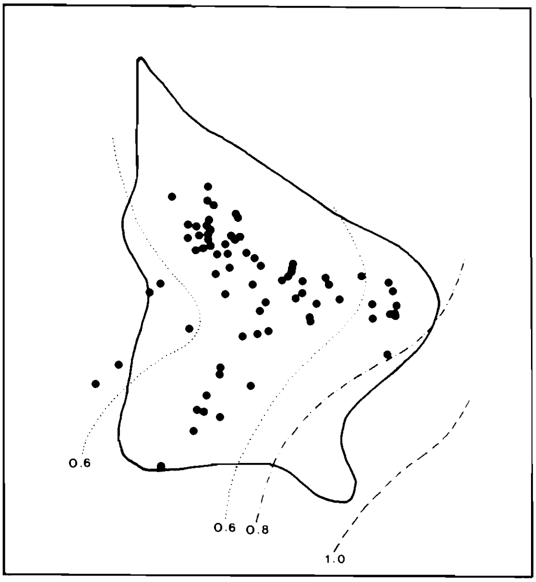

FIG. 6. Sightings of calves (●) on or near Silver Bank during censuses on board *Regina Maris*, with contours of wave height/wind speed.

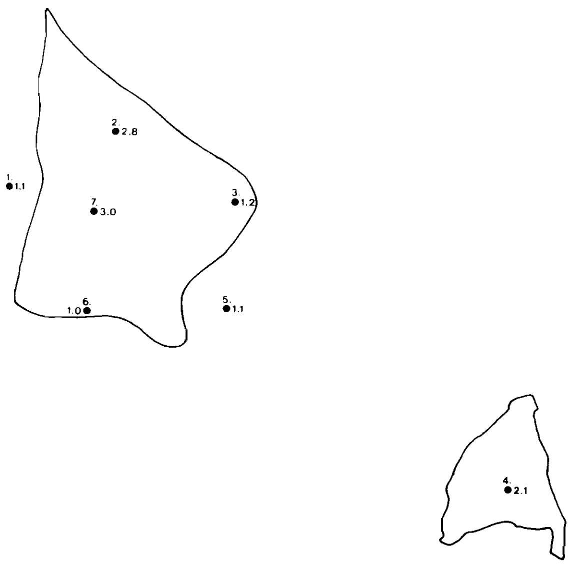

FIG. 7. Mean song indices at stations on and near Silver and Navidad banks, during surveys on board *Regina Maris* in 1978. There is a significant difference between the stations on Silver Bank (Kendall's $W = 0.74$, $P < 0.01$).

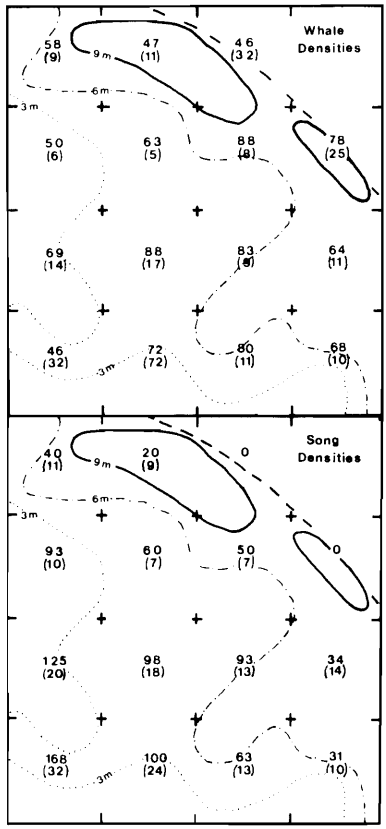

FIG. 8. Indices of spatial variation in general whale and song densities within the primary study area, with estimated standard errors in parentheses. Also shown are contours of bottom roughness (in metres) and the edge of the Bank (heavy dashed line). The edge of the coral reef is roughly shown by the 9-m coral-height contour.

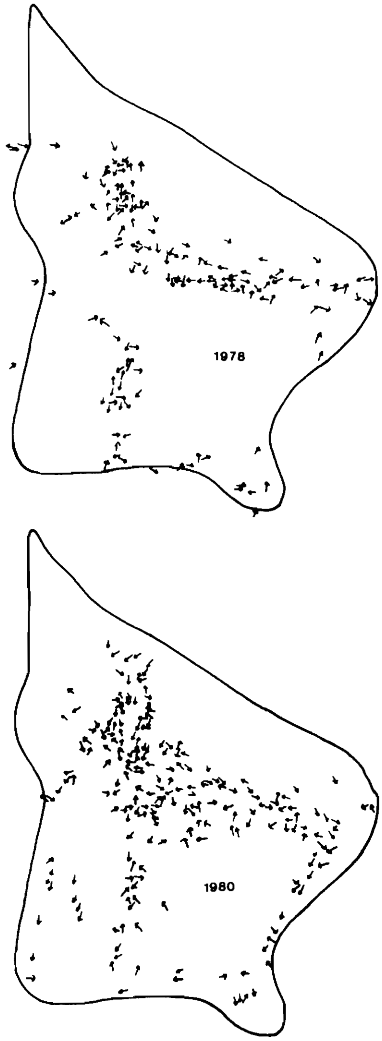

FIG. 9. Directions of movement of groups of humpbacks sighted during censuses aboard *Regina Maris* on Silver Bank.

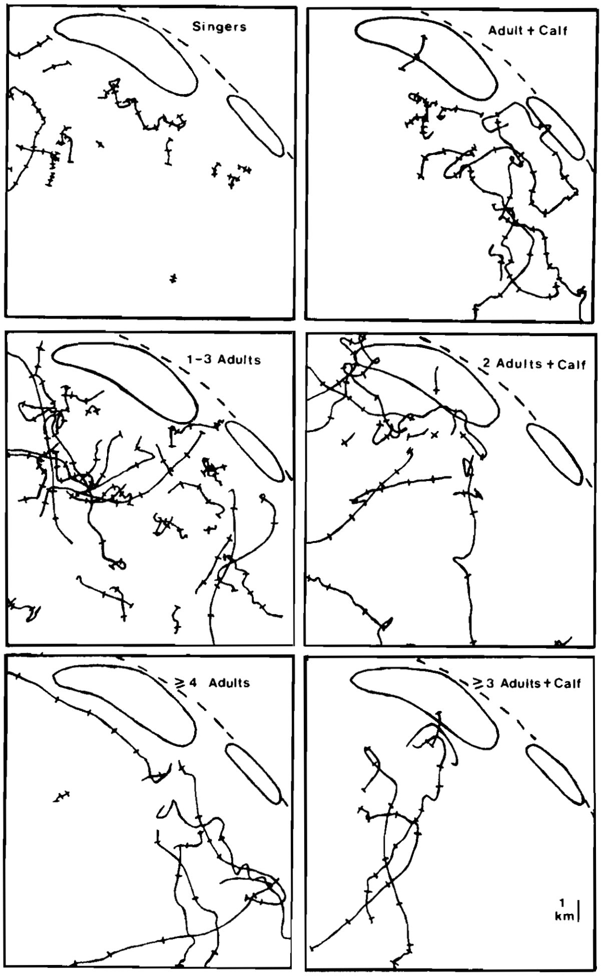

FIG. 10. Tracks taken by groups followed from *Elendil* within the primary study area. Tracks are hatched at each 0.5 h. The 9-m coral-height contour (solid line) and edge of bank (dashed line) are given.

compensating for this effect no tests (for preferred directions or circular patterns) rejected random movement.

The tracks taken by the watched groups when within the primary study area are shown in Fig. 10, while histograms of speeds are given in Fig. 11. Groups containing only a mother and calf mostly moved slowly in the lee of the coral reef and often parallel to it. With additional adults in the group, speeds were greater and ranges were more extensive. Groups with no calf moved much faster and had straighter tracks as the group size increased, with large groups sometimes moving great distances. In contrast singers meandered slowly.

Apart from the apparent preferences of mothers with calves for calm waters and singers for smooth floors, there is no indication of individuals staying in any particular geographic area or moving in set patterns, such as the supposed direction of seasonal migration; in the last watch of the season (No. 90 on 5 April 1980), when whales would have been expected to be moving north, we followed a group 50 km from the northern edge of Silver Bank southward until after they had crossed the southern edge.

Five of the 90 groups that we watched left Silver Bank: No. 1 on 16 January, No. 2 on 17 January, No. 77 on 19 March, No. 82 on 27 March, and No. 90 on 5 April. These were all at either the beginning or end of the season when whale densities were lower.

None of the 74 individual humpbacks photographed during the 1980 study on board *Elendil* (mostly within the primary study area) were found on more than 1 day, and thus we have no indications of preferred ranges on Silver Bank.

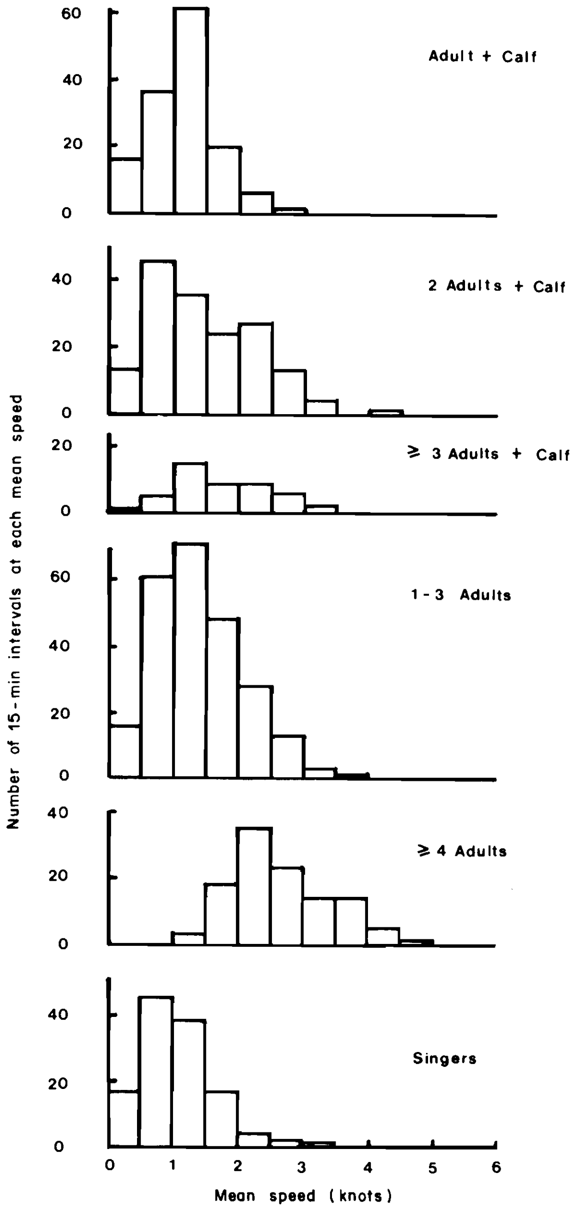

FIG. 11. Histograms of mean speed in each 15-min interval for the different classes of group followed on Silver Bank (1 knot = 1.852 km·h^{-1}).

Discussion

Food does not seem to be an important determinant of the winter distribution of the humpback whale. In the West Indies the humpbacks principally winter in waters of 24–28°C, on banks with smooth bottoms between 15 and 60 m deep.

The warm waters are probably functional for calving, as the calves are born with a thin blubber layer (Matthews 1937) and a relatively high surface area to volume ratio. The mothers with calves were most frequently found in the calm waters, amongst and to the leeward side of coral reefs. We saw no evidence that this was because of significant predation in rougher waters, and the mothers did not seem to make substantial use of the fish schools amongst the coral heads for feeding. Thus it seems that calm water itself was in some way advantageous for calves. However, on the few occasions that we followed mothers and calves into the rougher water to the windward side of the reef the calves seemed to cope, although they always returned to protected water before long. It is possible that they experienced a higher energy drain while swimming in rough water; it is also possible that very poor conditions would prove hazardous to the calf and that the mothers and calves wished to stay close to waters where they could find shelter in the event of storms. Right and grey whales (*Eubalaena glacialis* and *Eschrichtius robustus*) are also found to calve in protected waters (Payne 1976; Norris *et al.* 1977).

The singers also had preferences: they were almost never found amongst coral heads, rarely over deep water, and generally over a flat bottom between 20 and 40 m. Bathythermographs taken at the stations on Silver Bank showed the water to be isothermal, with constant temperature from the surface to the sea floor. In shallow isothermal water over a smooth bottom song propagation will be virtually two dimensional, while over deeper water the sound waves will tend to bend downwards and over a rough bottom and especially amongst coral heads there will be considerable scattering (Vigoureux and Hersey 1962). Although singers seemed to use those areas which gave the best propagation of their songs, the song densities in these areas were such that, during most of the season, the background was other songs. This means that although an individual received the theoretically best propagation of its song by singing over a shallow flat bottom, it would in fact have been detectable at greater distances at the peak of the season by singing over deep water rather than on Silver Bank. This suggests that the concentration of singers on Silver Bank was itself important, perhaps functioning in the manner of a lek, a possibility discussed later.

In addition to singing, the males apparently gained access to females through physical displacement of other males (Tyack and Whitehead 1982). An overall tendency for less singing and more displacement during March could be related to the less centrally peaked distribution of the whales on Silver Bank at this time, if the preference of the whales for the centre of the bank was concerned with singing.

The succession in the migration to colder waters by different segments of the population found by Dawbin (1966) is probably the reason for the differences in the whale density versus date curves for Silver and Navidad banks. The early departure to cold waters of the females without calves will have had proportionally more effect on Navidad, which had few females with calves, than on Silver, which had many.

There is no evidence that the humpbacks on Silver Bank possessed territories or even preferred ranges. The movements of the humpbacks seemed to be random in direction, with singers and groups containing calves generally moving slowly and staying in areas with smooth bottoms and calm water, respectively. The faster movement of larger groups was probably determined by factors within the group.

In addition to the physical and environmental factors determining the distribution of the whales, we believe that there is one other important characteristic of different areas to the humpbacks in the West Indies: the presence of other humpbacks. The humpbacks are not evenly distributed in the West Indies; they show overwhelming preferences for Silver and Navidad banks. The only times that groups that we followed crossed the edge of Silver Bank were at either the beginning or end of the season when whale densities were lower and the Bank was perhaps intrinsically less attractive.

Silver Bank has been compared with an avian or ungulate lek by J. Perkins (personal communication), as have the waters off Hawaii by Herman and Tavolga (1980). It has some of the features of leks as characterized by Emlen and Oring (1977); it is traditional and the males display (sing), concentrating their activities near the centre of the Bank. However, the males show no evidence of possessing territories or dominance hierarchies, and the Bank has considerable resource value to some females: calm and possibly undisturbed water for their calves. The males sing on those parts of this resource suitable for their songs, those areas with smooth floors and also nearby in places with little resource value to the females, such as Navidad Bank. Thus, although Silver and especially Navidad banks possess some of the features of leks, the mating system of the humpbacks is more reasonably compared with those of species in which the males congregate, display, and compete with one another in or near areas which have some resource value to the females, as do the amphibians of the genera *Bufo* and *Rana* (Wells 1977).

Finally the distribution of the humpbacks in winter may be partially determined by human interference or the lack of it; it is perhaps important that Silver and Navidad banks are considered dangers to navigation and are rarely visited by shipping. Herman *et al.* (1980) have found that off Hawaii humpbacks avoided the areas of greatest human interference.

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