Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada

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Studies of mature male sperm whales (*Physeter macrocephalus*) were carried out on the Scotian Shelf during the summers of 1986, 1988, 1989, and 1990. Sperm whales were found principally along the edge of the Shelf, although there were some encounters in water less than 100 m deep. Within the Gully, a prominent submarine canyon, sperm whales showed a consistent pattern of distribution between years, distinct from that of northern bottlenose whales (*Hyperoodon ampullatus*). Some male sperm whales were individually identified in the Gully after periods of 2–47 days, and in one case, after 2 years. The male sperm whales showed little evidence of social organization and rarely performed aerial behaviour. However, their diving behaviour was similar to that observed from female sperm whales in the tropics. On one occasion a group of presumed female and immature sperm whales entered the Gully, attracting the attention of resident mature males.

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Des Cachalots macrocéphales (*Physeter macrocephalus*) mâles à maturité ont été observés sur la plate-forme néo-écossaise au cours des étés de 1986, 1988, 1989 et 1990. Les cachalots se tenaient surtout en bordure de la plate-forme, bien que certains aient été rencontrés dans des eaux de moins de 100 m de profondeur. Dans un canyon sous-marin important (appelé « the Gully »), les cachalots avaient la même répartition d'année en année, répartition qui différait de celle des Baleines à bec communes (*Hyperoodon ampullatus*). Certains cachalots mâles ont été reconnus individuellement dans le canyon après des périodes de 2–47 jours et un individu a été reconnu après 2 ans. Les cachalots mâles ne semblaient pas avoir d'organisation sociale et manifestaient rarement des comportements aériens. Cependant, leur comportement de plongée ressemblait à celui de femelles dans les tropiques. En une occasion, un groupe composé semble-t-il de cachalots femelles et immatures est entré dans le canyon et a attiré l'attention des mâles adultes résidants.

[Traduit par la rédaction]

Introduction

Male and female sperm whales (*Physeter macrocephalus*) have very different sizes, morphologies, life histories, and behaviour. Whereas female sperm whales and their immature offspring are almost invariably found in highly social groupings in the tropics and subtropics, the much larger sexually mature males are generally encountered at high latitudes, singly or in small groupings (Best 1979; Caldwell et al. 1966; Rice 1989). Scientists have long been interested in the evolution and adaptive significance of these differences between the sexes (e.g., Best 1979). However, to properly examine this topic, unbiased and comparable data are needed on the various characteristics of the two sexes. Although much useful information has come from the extensive hunt for sperm whales, it is biased in a number of ways because of the logistics, economics, and other characteristics of the whaling industry, and contains very few behavioural data (Best 1979).

During the past decade, long-term studies of undisturbed sperm whales have been started in a few tropical and subtropical locations (e.g., Gordon 1987; Whitehead 1990). These have been principally concerned with the social organization and behaviour of female sperm whales and their offspring. If we are to have a clear picture of the natural behaviour of the entire sperm whale population, we need results from similar studies of males at higher latitudes.

In this paper we present findings from research on mature male sperm whales carried out on the Scotian Shelf, a region that supported a fishery for sperm whales in the 1960s and 1970s (Mitchell 1975). Where relevant, we compare our results with those from recent studies of females and their offspring in tropical areas.

Methods

Studies were carried out on the Scotian Shelf during 1986 (17–26 June), 1988 (8–21 July, 25 July – 6 August), 1989 (16–30 July, 1–14 August), and 1990 (14–28 June, 2–18 July, 25 July – 11 August) from the 10-m auxiliary sloop *Elendil* with crews of 4–6. (During 1989 and 1990 research on sperm whales was subsidiary to studies of northern bottlenose whales, *Hyperoodon ampullatus*.) Except in 1986, much of the research was carried out in the region of "the Gully," a prominent submarine canyon on the edge of the Scotian Shelf (Fig. 1). Positions were principally taken from a Tracor Transtar Satellite Navigator (SATNAV) in 1986 and a Seaport Loran-C in other years.

Routes sailed included passages to and from port or shelter off Sable Island, traverses of regions where we hoped to find sperm or northern bottlenose whales, periods drifting hove-to at night or in the fog, and (especially in 1990) systematic surveys using a radial pattern in the region of the Gully. During much of the time at sea we monitored Benthos AQ17 or Atlantic Research LC32 hydrophones for approximately 1 min every 30 or 60 min, listening for the distinctive click trains of sperm whales (Backus and Schevill 1966). Individual sperm whales produce click trains approximately 60% of the time (e.g., Mullins et al. 1988; Whitehead and Weilgart 1990), which can be heard at about 7 km with our equipment.

We use the proportion of the monitorings during which sperm whales were heard as an index of sperm whale abundance in different areas (Figs. 1, 2). Monitorings made while tracking sperm whales and those made less than 2 h from the end of a tracking period or less than 30 min after the previous counted monitoring were excluded. There remained 1220 monitorings, during 337 of which sperm whales were heard.

On occasion, and as circumstances permitted, individual sperm whales (and in one case a group of sperm whales) were tracked visually and by use of a specially built Dev-Tec directional hydrophone. Details of the tracking procedure are given by Mullins et al.

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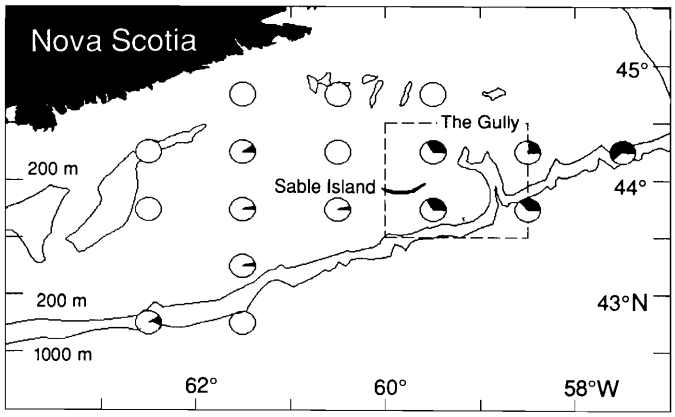

FIG. 1. Distribution of sperm whales on the eastern Scotian Shelf, as indicated by the proportion of acoustic monitorings in each 30′ latitude × 1° longitude rectangle (shown by the proportion of the circle filled). The broken line encloses the region of the Gully (see Fig. 2).

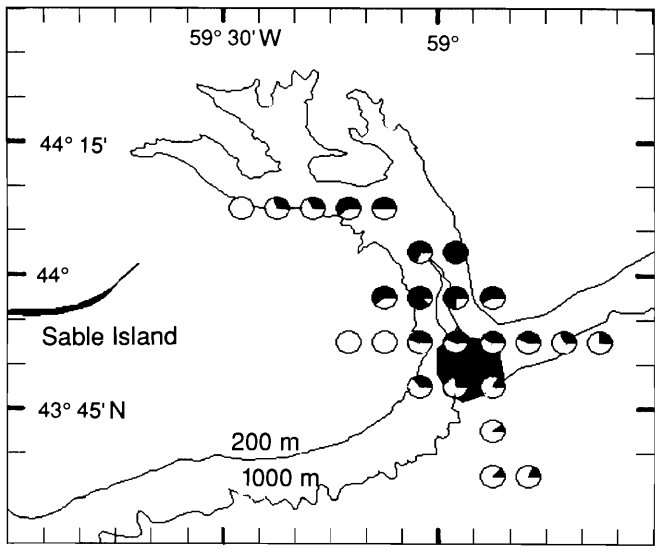

FIG. 2. Distribution of sperm whales in the Gully region, as indicated by the proportion of acoustic monitorings in each 5′ latitude × 5′ longitude rectangle (shown by the proportion of the circle filled). The area where northern bottlenose whales were almost exclusively seen is shaded (Faucher and Whitehead 1991).

(1988). Sperm whales were tracked for a total of 72 h, during which time they travelled a total of 386 km.

Individual sperm whales were identified using photographs of their flukes (Arnbom 1987), which they raise at the start of a deep dive, called a "fluke-up." Only photographs of high quality (Arnbom's Q = 4 or 5) were used for subsequent analysis. Photographs were taken while tracking whales and during incidental encounters, both as part of our studies, during fieldwork carried out by the New England Aquarium on the western Scotian Shelf in 1988, and by Brier Island Ocean Studies off Brier Island, Nova Scotia, in 1991 (Table 1). Three photographs of stranded dead whales from Nova Scotia and Prince Edward Island were also examined (Table 1).

Sperm whales were measured by means of photographs taken from a height of 9.2 m above the water surface with a Canon AE1 35-mm camera and 50-mm lens. Lengths of the animals were estimated from body segments measured on these images, using the methods of Gordon (1990) and Waters and Whitehead (1990*a*). Only estimates from high-quality images, with clear end points of the body segment, a distinct horizon, and less than 30° between the whale and the horizon, were considered.

A Simrad Skipper 603 vertically mounted depth sounder was used to track the sperm whales underwater. As in Papastavrou et al. (1989), dive traces were divided into 1-min intervals, and rates of descent and ascent were calculated from the change in depth during these intervals. Depths at which the rate of ascent or descent was 0 m/min (i.e., horizontal traces) or the trace reached the ocean floor were recorded as "dive depths."

During the studies in 1986 and 1988, blows and other visible surface activities were noted when whales were being followed at the surface. Data from 1988 during surfacing sequences in which attempts were made to fire biopsy darts into the whale (Whitehead et al. 1990) were excluded from this analysis. Blow rates were calculated from the number of blows recorded in the period during which a whale was closely observed at the surface. Rates of observation of other activities are standardized as the number seen per observed fluke-up, to assist in comparing studies from different areas in which numbers of whales present, viewing conditions, and observational techniques differed (Waters and Whitehead 1990*b*).

All observational data, except those from 23 June 1990, refer to male sperm whales. Data from 23 June 1990, when a group of presumed females was found and tracked, are not used in statistical summaries of behaviour, speeds, dives, and associations.

Results

Distribution

In Fig. 1 the distribution of sperm whales on the Scotian Shelf is indicated by the proportion of acoustic monitorings during which sperm whales were heard in 30′ latitudes × 1° longitude rectangles (only rectangles with at least 10 monitorings are included). Sperm whales were heard occasionally over many parts of the Scotian Shelf, but they were particularly abundant in the region of the Gully, where they were heard during approximately 30% of all monitorings. Note that the high apparent abundance in the most easterly rectangle (44−44°30′N, 57−58°W) should be viewed with some caution: it is based on only 10 monitorings in Shortland Canyon, during 6 of which sperm whales were heard on 2 days in 1990. Note too that sperm whales are also found on the western part of the Scotian Shelf, outside the range of our surveys (Table 1) (Mitchell 1975).

The distribution in the Gully region is given in more detail (5′ latitude × 5′ longitude rectangles) in Fig. 2 (only rectangles with at least 5 monitorings are included). The centre of the sperm whale distribution is about 10 km north of the core region used by northern bottlenose whales at the entrance of the Gully (Fig. 2). Densities rise from about 15% of monitorings containing sperm whale clicks in the deep water south of the Gully to about 75% in the central part (44°N, 59°W), and then fall again in the northwestern part of the Gully. These indicators of density seem reasonably consistent among neighbouring rectangles, giving some measure of confidence concerning the indicated distribution.

Some aspects of the distribution of sperm whales in the Gully region are consistent between years. In Table 2 we present the indices of abundance for each 5′ latitude range from 43°40′N to 44°05′N, combining longitudes 58°45′W − 59°05′W, for 1988, 1989, and 1990 separately. There is a significant consistency in the ranking of the indices of abundance for the different regions in the different years (Kendall's W = 0.889, P = 0.020). In all years abundance generally rose with increased distance northward into the Gully.

As can be seen in Figs. 1 and 2, sperm whales were found in locations with a variety of water depths. Because we can hear sperm whales at several kilometres' distance, and inten-

TABLE 1. Individual identifications of adult male sperm whales (and 13 females on 23 June 1990), from high-quality photographs of flukes, in the general area of the Scotian Shelf, 1986–1991

Period	Location	Approx. position		No. of individual whales[a]	Notes
		Lat. N	Long. W		
1986					
21–23 June	Central Scotian Shelf	43°00′	62°30′	1	
1988					
11 July – 4 Aug.	Gully	44°00′	59°00′	14	—[b]
22 Aug. – 1 Sept.	West Scotian Shelf	43°00′	65°30′	3	New England Aquarium
13 Dec.	Prince Edward Island	47°00′	64°00′	1	Dead (P. Daoust)
1989					
23–27 July	Gully	44°00′	59°00′	3	
1990					
23 June – 9 Aug.	Gully	44°00′	59°00′	7+13 ♀?	—[b]
6 Oct.	Sable Island	44°00′	60°00′	1	Dead (Z. Lucas)
1991					
24 Apr.	Cape Breton Island	45°00′	61°00′	1	Dead (Nova Scotia Stranding Network)
18 Sept.	Brier Island	44°00′	66°30′	1	Brier Island Ocean Studies

[a]Total: 28 ♂ alive, 13 ♀? alive, and 3 ♂ dead.
[b]One individual in common between 1988 and 1990 studies in the Gully.

TABLE 2. Indices of sperm whale abundance (proportion of monitorings during which sperm whales were heard) in 5′ latitudinal ranges in the Gully (58°45′W – 59°05′W) in 1988, 1989, and 1990

Latitude range (N)	1988	1989	1990
43°40′ – 43°45′	0.00	0.07	0.25
43°45′ – 43°50′	0.02	0.17	0.39
43°50′ – 43°55′	0.41	0.25	0.49
43°55′ – 44°00′	0.75	0.38	0.97
44°00′ – 44°05′	0.56	1.00	0.93

sity is not always a good indicator of range, we cannot give reliable water depths in which acoustically contacted sperm whales were swimming in areas, like the Gully, where there are considerable bottom gradients. However, we did see and follow sperm whales, and also encounter them acoustically, in areas with a flat ocean floor. Sperm whales were located in waters from 63 to 2000 m deep, but were virtually never heard on the shallow (ca. 40 m deep) part of Sable Island Bank just west of the Gully. Sperm whales were located four times (twice in 1986 and twice in 1989) in depths of about 100 m or less. The plots in Figs. 1–3 suggest that on the eastern Scotian Shelf, they generally inhabit water depths of 200–1500 m.

Movements and residency

The movements of sperm whales tracked in the area of the Gully are shown in Fig. 3. Tracks made outside this region were presented by Mullins et al. (1988, Fig. 2). In the Gully some tracked whales meandered with no obvious direction, whereas others moved on a reasonably consistent heading along the deep axis of the Gully.

Rates of movement (over the bottom) of whales during tracking were estimated from SATNAV or Loran positions at least 30 min apart (92 intervals). The overall mean speed was 2.5 kn (4.6 km/h), with a standard deviation of 1.4 kn (2.6 km/h). Most speeds fell between 0.5 and 4.5 kn (0.9–8.3 km/h). As currents in the region are generally slight (<0.5 kn (0.9 km/h)), these are reasonably representative of the horizontal speed of the sperm whales through the water. However, they will be underestimates on occasions when whales changed direction frequently within 30-min periods.

In 1988, two individuals were identified on 2 different days and another two on 3 different days. For each of these individuals, on each day that they were sighted we calculated the midpoint between the positions of the first and last identifications. Within this data set, there was no significant evidence of individually preferred ranges within the sperm whale habitat in the central part of the Gully (MANOVA using latitudes and longitudes, Wilks' $\Lambda = 0.443$, $P = 0.670$).

Of the 23 male sperm whales identified in the Gully between 1988 and 1990, 8 were photographed on more than 1 day. In 1988, one individual was observed in the Gully on 13 July, 16 July, and 1 August, and another on 14 July, 16 July, and 4 August. Three of the males identified with the group of females on 23 June 1990 were also each identified on 1 other day: 19 July 1988, 8 August 1990, and 9 August 1990, respectively.

Structure and size of the population

Apart from those observed on 23 June 1990, all sperm whales observed appeared, from their size, relatively prominent spermaceti organs, and lack of a dorsal fin callus (which is primarily found in mature females and never in mature males (Kasuya and Ohsumi 1966)), to be sexually mature males. The three identified dead animals (Table 1) were all males. Three individuals were photographically measured at 12.8, 14.3, and 15.2 m. The maximum length for female sperm whales is about 12.0 m, and this is also the approximate length of males at sexual maturity (Berzin 1971; Rice 1989).

Social organization

There was little apparent social organization among the male sperm whales observed on the Scotian Shelf. Of seven pairs of whales identified within 30 min of one another, only one pair was observed this close together on 2 days: whales 1 and

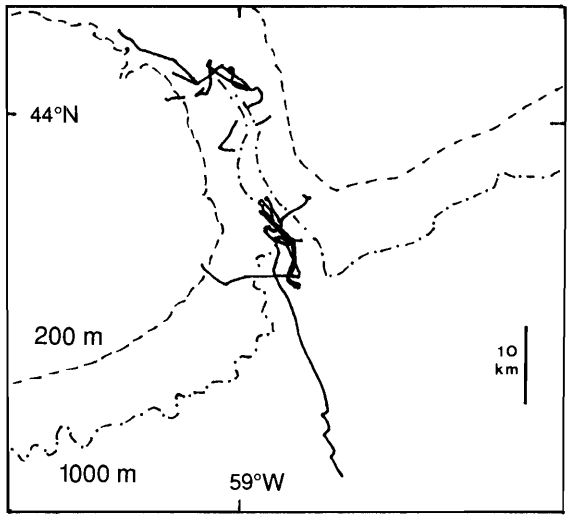

FIG. 3. Tracks taken by followed sperm whales in the region of the Gully. The (generally southward) track taken by the group of female and immature sperm whales on 23 June 1990 is shown in bold.

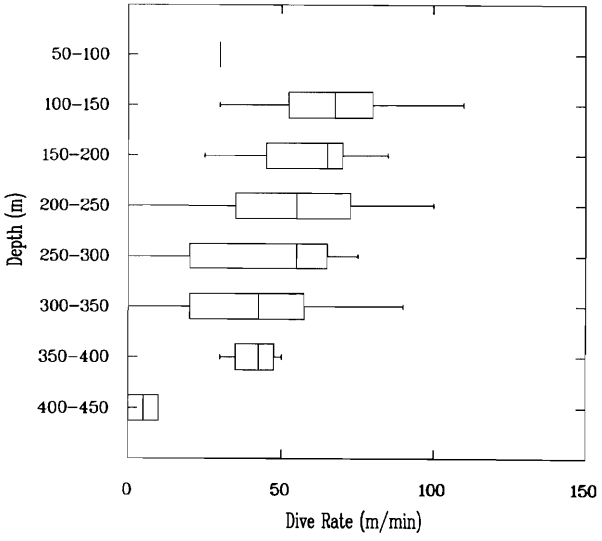

FIG. 4. Box plots of dive rates of Nova Scotian sperm whales at different median depths, showing the median (central vertical line), interquartile range (box), and total range of the values.

2 were identified from fluke photographs 22 min apart on 14 July 1990 and 3 min apart on 16 July 1990.

Of the 78 occasions on which sperm whale fluke-ups were photographed, on 74 we observed only one whale, not coordinating its movement with, or within 100 m of, another whale. In the remaining four cases, pairs were observed together at the surface. The mean size of observed clusters (number of whales within 100 m and coordinating movements) is then 1.1 animals (82/78). Invervals between the fluke-ups of the members of the pairs were 3 min 9 s, 2 min 0 s, 1 min 25 s, and 5 min 15 s.

Diving behaviour

Whales were generally tracked on the recording depth sounder just after a fluke-up signalling the start of a dive. Thus, there were many more records of descending whales than ascending ones. Most traces were less than 5 min in length, with the whales becoming difficult to follow with the vertically mounted depth sounder when they reached about 350 m, presumably mainly because at this depth they started making substantial horizontal movements.

The distribution of the 89 descent rates calculated from the 1-min segments of the dive traces are plotted against median depth in Fig. 4. The whales generally dove at 40–80 m/min (1.3–2.6 kn (2.4–2.8 km/h)) when less than 250 m deep, with descent rates decreasing with depth, so that by the time they had reached 400 m most dives had levelled out. The maximum calculated descent rate was 110 m/min (3.6 kn (6.6 km/h)). During the five 1-min ascending segments the rates were 55, 55, 25, 5, and 45 m/min.

Ten dive depths were recorded (Table 3), ranging from 215

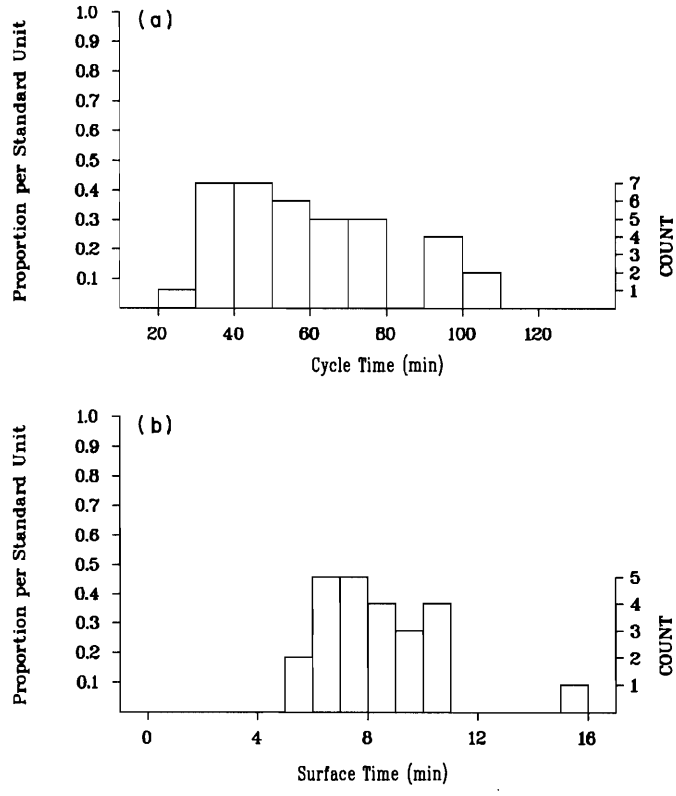

FIG. 5. Distributions of cycle times (interval between consecutive fluke-ups (*a*) and surface times (interval at the surface between dives) (*b*) for Nova Scotian sperm whales.

TABLE 3. Dive depths, with water depths, of sperm whales, recorded using a recording depth sounder

Dive depth (m)	Water depth (m)
305	305
405	405
375	375
415	500
275	275
355	355
275	470
245	470
270	550
215	400

TABLE 4. Comparison between the behaviour of sperm whales on the Scotian Shelf (only mature males are considered) and off the Galápagos Islands and Sri Lanka (mainly groups of females and their young)

	Males	Groups of females	
	Scotian Shelf	Galápagos Islands	Sri Lanka
Mean cluster size (no. of animals)	1.1	3.4[a]	3.1[b]
Mean speed over bottom (kn)	2.5 (SD = 1.4)	2.1 (SD = 1.1)[a]	—
Initial descent rate (usual range; m/min)	40–80	40–100[c]	45–195[b]
Dive depth (usual range; m)	215–415	250–450[c]	300–600[b]
Cycle time (usual range; min)	30–80	40–65[c]	30–60[b]
Median surface time (min:s)	7:57	9:30[d]	7:30[b]
Mean blow interval(s)	20.9	—	12.7[b]
No. of breaches per fluke-up	0.027	0.177[e]	—
No. of lobtails per fluke-up	0.000	0.220[e]	—
No. of spyhops per fluke-up	0.068	0.100[e]	—
No. of sideflukes per fluke-up	0.068	0.167[e]	—

[a]Mean of values for 1985 and 1987 from Whitehead (1989).
[b]From Gordon (1987), recalculated for consistency of measures and units when necessary.
[c]Descent rates when at depth of less than 250 m (Papastavrou et al. 1989).
[d]Mean of values for 1985 and 1987 from Papastavrou et al. (1989).
[e]From Whitehead and Weilgart (1991).

to 415 m, and half of them reached the ocean floor. This method of examining diving behaviour may be biased against recording particularly deep dives because of the limited power of the depth sounder and the short durations of the traces.

The durations of dive cycles (dive time plus subsequent surface time), as indicated by the times between consecutive photographed fluke-ups of the same individual (<120 min), are shown in Fig. 5*a*. The data suggest that dive cycles generally lasted between 30 and 80 min. The 6 observations between 90 and 110 min may represent two cycles in which the middle fluke-up (if one occurred) was not photographed.

The distribution of observed durations at the surface between first appearance and fluke-up, for those occasions on which we saw the whale emerge after a deep dive, is shown in Fig. 5*b*. During the normal dive cycle about 6–11 min seems to have been spent at the surface. However, on occasion, whales spent considerably longer at the surface. Individual sperm whales were observed to remain at or near the surface, moving very slowly, for periods of 36 min 30 s, 87 min 45 s, and 100 min, with none of these periods being terminated by a fluke-up.

Surface behaviour

Blow rates during surfacing periods followed by a fluke-up averaged 3.3 blows/min (SD = 0.7 blows/min, n = 39). During surface periods that were not concluded with an observed fluke-up, blow rates averaged 1.5 blows/min (SD = 0.62 blows/min, n = 3). There is a significant difference between these rates ($t = 4.271, p < 0.001$). The overall mean interval between blows was 20.9 s, and the mean blow rate 3.2 blows/min.

Apart from blows and fluke-ups, other surface activities were rarely observed. While observing individual sperm whales at the surface we recorded 2 breaches (leaps from the water, showing at least half the body), 5 spyhops (slow raisings of part of the head above the surface), and 5 sideflukes (a portion of the flukes visible above the surface but oriented vertically). No lobtails (thrashes of the flukes onto the water surface) were seen. The rates at which these activities were observed are given per observed fluke-up in Table 4.

Incursion of presumed females on 23 June 1990

From 07:50 until 13:00 on 23 June 1990, we observed a group of about 15 small sperm whales, including two individuals less than 7 m in length and thus less than 3 years old (Rice 1989). These whales were accompanied by 4 or 5 large male sperm whales who periodically joined and left the main group. During this incursion 2 males were measured at 12.8 and 13.7 m, and 5 other whales at 8.5, 8.9, 9.2, 10.7, and 10.8 m. One whale was photographed with a definite callus on its dorsal fin, indicating that it was a female. During our studies on the Scotian Shelf, this was the only occasion when a small whale or a whale with a callus was seen, or more than 2 whales could be observed coordinating movements.

The group of whales was tracked moving south along the axis of the Gully (Fig. 3) at speeds of 1.1–2.3 kn (2.0–4.3 km/h) until they left our principal study area. During the encounter 13 probable females and 4 males were identified from fluke photographs (Table 1). None of the presumed females, but 3 of the 4 males, were also identified in the Gully on other days (see above).

The sea surface temperature at 09:00 during the encounter was 9.2°C.

Discussion

Distribution

The sperm whale distribution that we observed on the eastern Scotian Shelf (Figs. 1 and 2) has much in common with the distribution of the positions in which whalers caught sperm whales on the western Scotian Shelf between 1970 and 1972 (Mitchell 1975). High densities of sperm whales were most frequently found along the edge of the Shelf, especially in the Gully and Shortland canyon, and more rarely in shallower regions on the Shelf. Although generally described as deep-water animals, sperm whales have occasionally been reported in shallow water in other areas (Caldwell et al. 1966). The regular occurrence of sperm whales in waters less than 200 m deep, as on the Scotian Shelf (this study; Mitchell 1975), seems to be unusual. The sperm whales on the Scotian Shelf appear to feed regularly on or near the bottom (Table 3).

Other reports seem to suggest feeding at or near the bottom (e.g., Berzin 1971; Clarke 1976; Gordon 1987; Martin and Clarke 1986), although in some areas they clearly feed in the mid-water (e.g., Papastavrou et al. 1989).

In the Gully, patterns of sperm and bottlenose whale distribution are consistent and distinctive (Fig. 2, Table 2). Bottlenose whales occur, year-round, almost exclusively in a small area at the entrance of the Gully (Faucher and Whitehead 1991). The distribution of sperm whales is less concentrated and has only been observed in the summer months, but it shows a consistent peak a few kilometres north of the habitat of the bottlenose whales (Fig. 2, Table 2). Unfortunately, little useful information is available on the oceanographic structure of the Gully with which these patterns might be correlated. The observed distributions might result partially from competitive exclusion, since beaked whales, such as the northern bottlenose, have similar diets to sperm whales (Rice 1989).

Residence patterns and migrations

Some individual males were observed in the Gully after periods of 2–47 days, and one after 2 years. Similar results were obtained off northern Norway by Lindhard and Strager (1989), who identified 50 male sperm whales in three summer seasons. Of these, 21 were identified on more than 1 day, and 4 were identified in all 3 years, always within a 18 × 9 km rectangle. However, it is also known that male sperm whales can make long-distance migrations (Rice 1989). A sperm whale marked on the Scotian Shelf was recaptured over 7 years later off Spain (Mitchell 1975).

Structure of the population

Apart from the incursion of females into the Gully on 23 June 1990, our observations of sperm whales on the eastern Scotian Shelf are consistent with data obtained during the Nova Scotian fishery on the western part of the Scotian Shelf. The fishery caught exclusively males, principally 12.0–17.0 m in length (Mitchell 1975). The lengths of the three dead males whose identifications were examined (Table 1) were also within this range. The approximate latitudinal range of female sperm whales is often given as 40°S–40°N, although in some areas, such as the North Pacific, female sperm whales are regularly found at higher latitudes (Berzin 1971; Rice 1989). The Gully, and the Scotian Shelf region in general, are probably marginal habitat for female sperm whales.

Social organization

During our studies, apart from the observations on 23 June 1990, we never saw more than two males together, and only rarely were pairs observed. The mean cluster size was 1.1 as opposed to 3.1–3.4 obtained from studies of groups of female sperm whales (Table 4). The males appeared to behave independently, although they were sometimes observed within 1000 m of one another. This lack of social cohesion was in strong contrast to the coordinated behaviour observed during the one observation of a group of females. Most other reports testify to a comparative lack of social organization among mature male sperm whales, although they are quite often reported as being found in groups of 2–6 (Best 1979; Caldwell et al. 1966; Gaskin 1964), and all three dead whales reported in Table 1 stranded with at least one other sperm whale.

The presence of the group of females on 23 June 1990 seems to have attracted many of the males in the region. The only time we saw more than two males clustered together was when they were attending the group of females. Most, and probably all, of these males were temporary attendants, as they were observed joining and leaving the group of females at the time, and the majority were photographed apart from the group of females on other days.

Behaviour

In Table 4 we compare, as far as is possible, the observed behaviour of the Scotian Shelf sperm whales with results of studies of female sperm whales and their offspring off the Galápagos Islands and Sri Lanka. We have not carried out statistical tests for significant differences in behavioural measures, as there are substantial discrepancies in the circumstances of the different studies as well as potential problems of independence of data points.

Movements on the Scotian Shelf are a little faster than those recorded from the groups of females off the Galápagos Islands (Table 4), but still generally less than those recorded for "unalarmed' sperm whales by whalers (Berzin 1971; Caldwell et al. 1966; Gaskin 1964). Our speeds between fixes will be less than swimming speeds if whales do not swim in a straight line, although this does not seem to have had a major effect off the Galápagos Islands (Whitehead 1989). The activities of the whalers may have caused the whales to swim rather faster than normal, even when they did not appear to be alarmed.

Dive rates, dive depths, cycle times, and surface times for the Scotian Shelf males are similar to those calculated using similar methods for the Galápagos and Sri Lankan females and immatures (Table 4). Observations made from whaling vessels or during whaling operations, often with side-scanning sonar, have generally suggested much more variable dive rates, shallower dives, shorter dive times, and shorter surface times (Lockyer 1977; Mano 1986). These differences are probably largely due to the reaction of the whales to the whaling vessel as well as to technical aspects of the use of side-scanning sonar (Gordon 1987; Papastavrou et al. 1989).

Because of the very different circumstances of the different studies, comparisons between the observable behaviour of males and females must be made very cautiously. The Scotian Shelf males had a lower blow rate than the females and immatures off Sri Lanka. Blow intervals given for sperm whales in the literature are generally closer to those from Sri Lanka (ca. 12 s) than those on the Scotian Shelf (ca. 21 s), although there is considerable variation (Caldwell et al. 1966; Berzin 1971; Gaskin 1964). It is clear that breaches and lobtails are seen much more rarely from mature males than females and immatures (Table 4) (Waters and Whitehead 1990*b*). These activities generally appear to have a social function (Waters and Whitehead 1990*b*), so this observation conforms with the general low level of sociality observed among male sperm whales.

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