The significance of the Southeast Shoal of the Grand Bank to humpback whales and other cetacean species[1]

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During June and July of 1982 and 1983 studies were made of the humpback whales on the Southeast Shoal of the Grand Bank of Newfoundland from a 13-m ketch. The humpbacks were found to concentrate on the central part of the shoal where surface and deep water temperatures were warmest and depths were shallowest, over concentrations of prey producing strong depth sounder traces. These traces were almost certainly made by spawning capelin. The humpbacks and prey traces dispersed as the season progressed. Other large whale species were much less numerous than the humpbacks, of which about 900 were estimated to use the shoal in 1982 and 1983. The Southeast Shoal humpbacks are a reasonably discrete segment of the Newfoundland–Labrador feeding stock, which winter in the West Indies, with the Southeast Shoal animals showing a particular preference for the waters off Puerto Rico. In 1982, individual whales were found to be generally moving slowly northwest over the shoal. Apart from forming very large coordinated groupings early in the studies, when the prey was most concentrated, the feeding and grouping behaviour of the humpbacks was similar to that in the inshore waters off Newfoundland.

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Les rorquals mégaptères ont été observés d'un ketch de 13 m en juin et en juillet 1982 et 1983 le long du Southeast Shoal du Grand Banc de Terre-Neuve. Les rorquals étaient surtout rassemblés dans la partie centrale du haut-fond où la température de l'eau est le plus chaude en surface et en eau profonde, et où la profondeur est le moins grande; les rorquals se tenaient au-dessus de grandes concentrations de proies qui produisaient des sons bien marqués sur un sonar. Il s'agissait presque certainement de bancs de capelans en fraye. Les rorquals et les proies se sont dispersés progressivement au cours de la saison. Les autres grandes espèces de baleines étaient beaucoup moins nombreuses; les bancs de rorquals mégaptères contenaient environ 900 spécimens sur le haut-fond en 1982 et en 1983. Les rorquals mégaptères du Southeast Shoal constituent une portion relativement discontinue des stocks qui viennent se nourrir sur les côtes du Labrador et de Terre-Neuve, stocks qui passent l'hiver dans les Antilles; les rorquals du Southeast Shoal montrent une préférence particulière pour les eaux côtières portoricaines. En 1982, certains rorquals se déplaçaient lentement en direction nord-ouest au-dessus du haut-fond. À l'exception des grands rassemblements organisés du début de chaque année, au moment où les proies étaient particulièrement concentrées, les comportements alimentaires et sociaux des rorquals mégaptères se sont avérés semblables à ceux des rorquals des eaux côtières de Terre-Neuve.

[Traduit par le journal]

Introduction

Recent surveys have shown the humpback whale (*Megaptera novaeangliae*) to be the most common large whale in the waters around Newfoundland during summer (Lynch and Whitehead 1984). These animals are part of the northwest Atlantic stock which winters in the West Indies. In summer, the northwest Atlantic humpbacks are found in nearly discrete feeding substocks off Iceland, west Greenland, Newfoundland–Labrador, and in the Gulf of Maine (Katona *et al.* 1983).

Between 1977 and 1980 large numbers of humpbacks were found inshore along the Newfoundland coasts (Whitehead and Lien 1982). Here they became entrapped in inshore fishing gear, causing considerable economic loss to the fishermen and some mortality to the whales (Lien 1980). During this period research was carried out on the behaviour, ecology, populations, and migrations of the humpbacks inshore, as well as their interaction with the fishery (e.g., Lien 1980; Whitehead, Harcourt *et al.* 1982). Since 1981, humpback abundance inshore along the Newfoundland coasts in summer has returned to the moderate levels of the period 1973–1976.

Natural suspects in the search for a cause for this remarkable and destructive incursion were the stocks of capelin (*Mallotus villosus*), which Mitchell (1973) found to be the humpbacks' major food off Newfoundland. During the summer months mature capelin from four of the five stocks around Newfoundland come inshore to spawn on the beaches (Carscadden 1983). These mature capelin were found to be a principal target of the feeding humpbacks when inshore (Bredin 1983; Whitehead, Harcourt *et al.* 1982). The only capelin stock off Newfoundland which does not come inshore to spawn is that in NAFO (Northwest Atlantic Fisheries Organization) areas 3N and 3O; these animals spawn on the Southeast Shoal of the Grand Bank (Carscadden 1983).

Ship and aeroplane surveys of the offshore Newfoundland areas had shown there to be concentrations of humpbacks offshore, in particular on the Southeast Shoal, which is shown in Fig. 1 (Hay 1983; Parsons and Brownlie 1981). However, no detailed research had been performed on these animals.

The sudden influx of humpbacks inshore in 1977 and their

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TABLE 1. Summary of transects across the Southeast Shoal during the summers of 1982 and 1983, with total whale and dolphin counts, mean surface sea temperatures, and humpback whale latitude range

	Transect No.				
	1	2	3	4	5
Date	12–14 June 1982	17–18 June 1982	3–5 July 1982	11–16 July 1982	23–28 June 1983
Mean sea temperature (°C)	8.8	10.2	10.7	14.6	13.0
Humpbacks counted	19	12	12	6	7
Humpback range (latitude N)	44°12′–44°17′	44°09′–44°20′	44°21′–44°51′	43°57′–44°47′	44°14′–44°40′
Finbacks counted	0	1	0	1	0
Unidentified whales	1	0	7	0	1
White-beaked dolphins	23	24	0	0	5
Unidentified dolphins	2	8	0	0	0

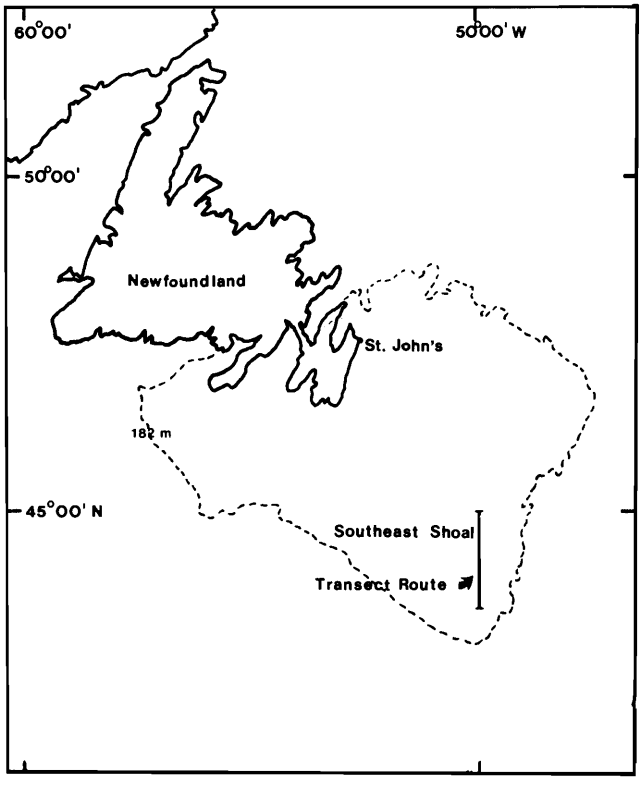

FIG. 1. The Southeast Shoal of the Grand Bank, showing the transect route.

equally abrupt departure in 1981 suggested the need for intensive studies of the whales offshore to clarify the relationships between the different concentrations in the Newfoundland region. Of particular significance were the humpbacks on the Southeast Shoal. It was important to estimate the population size, investigate to what extent the animals on the Southeast Shoal were those found inshore in previous years and (or) frequented other parts of the northwest Atlantic, and to examine their ecology.

The method of fluke photography, by which humpbacks are individually identified from photographs of the ventral surface of their flukes, provides a convenient way of investigating the populations, migrations, stock segregations, and some aspects of the behaviour of humpback whales (Katona and Whitehead 1981). In the catalogue compiled by Katona *et al.* (1980), over 1000 of the northwest Atlantic humpbacks are identified from fluke photographs, approximately half of which were found off Newfoundland between 1978 and 1980.

This paper reports on studies of the humpbacks on the Southeast Shoal of the Grand Bank in the summers of 1982 and 1983 during the period of capelin spawning.

Methods

The 13-m auxiliary ketch *Findrinny*, with a crew of four or five, was on the Southeast Shoal of the Grand Bank (Fig. 1) for the following three periods: 11 June to 27 June 1982, 2 July to 17 July 1982, and 22 June to 2 July 1983. Approximately 60% of the daylight hours were unavailable for research because of fog and gales.

Findrinny was equipped with a Tracor Transtar satellite navigator, Sitex-Koden Loran C, Decca 60 Radar, and Simrad Skipper 603 recording depth sounder. With these instruments positions could be fixed to within 1 nautical mile. Fluke photographs were taken with Canon AE1 and AT1 35-mm cameras equipped with 300-mm lenses and Ilford HP5 and Kodak Tri-X black and white film.

During the study a 90 nautical mile transect was made five times across the Southeast Shoal along longitude 50° W, from 43°30′ N to 45°00′ N (Fig. 1). The transect was carried out four times in 1982 and once in 1983. The transect route was sailed or motored in whichever direction was more convenient. The route was broken for darkness, fog (visibility less than 1800 m), or to study large concentrations of whales. The transect would be resumed at the break point when conditions permitted. The transect is included in the route taken by the aerial surveys of Parsons and Brownlie (1981).

While on transect one crew member would keep a watch for whales and dolphins, which were recorded when abeam, together with the time, distance abeam, and any observed activities. The recording depth sounder was left on at standard gain during the transect to record the distribution and abundance of capelin and other possible whale prey. At 10 nautical mile intervals we recorded environmental variables such as wave height, surface sea temperature, and wind speed.

While not on transect the major activity was taking fluke photographs. During this work the groupings in which the photographed humpbacks were found were recorded when feasible and the depth sounder was turned on to examine possible humpback prey. We also kept records of sightings of other species of Cetacea.

During the 1983 study, when conditions permitted, bathythermograph traces were obtained by lowering into the water a weighted thermistor that was connected to a digital temperature display on deck.

Results

Distribution of humpbacks

The information from the transects is summarized in Table 1 and Fig. 2. The humpbacks were generally found in the

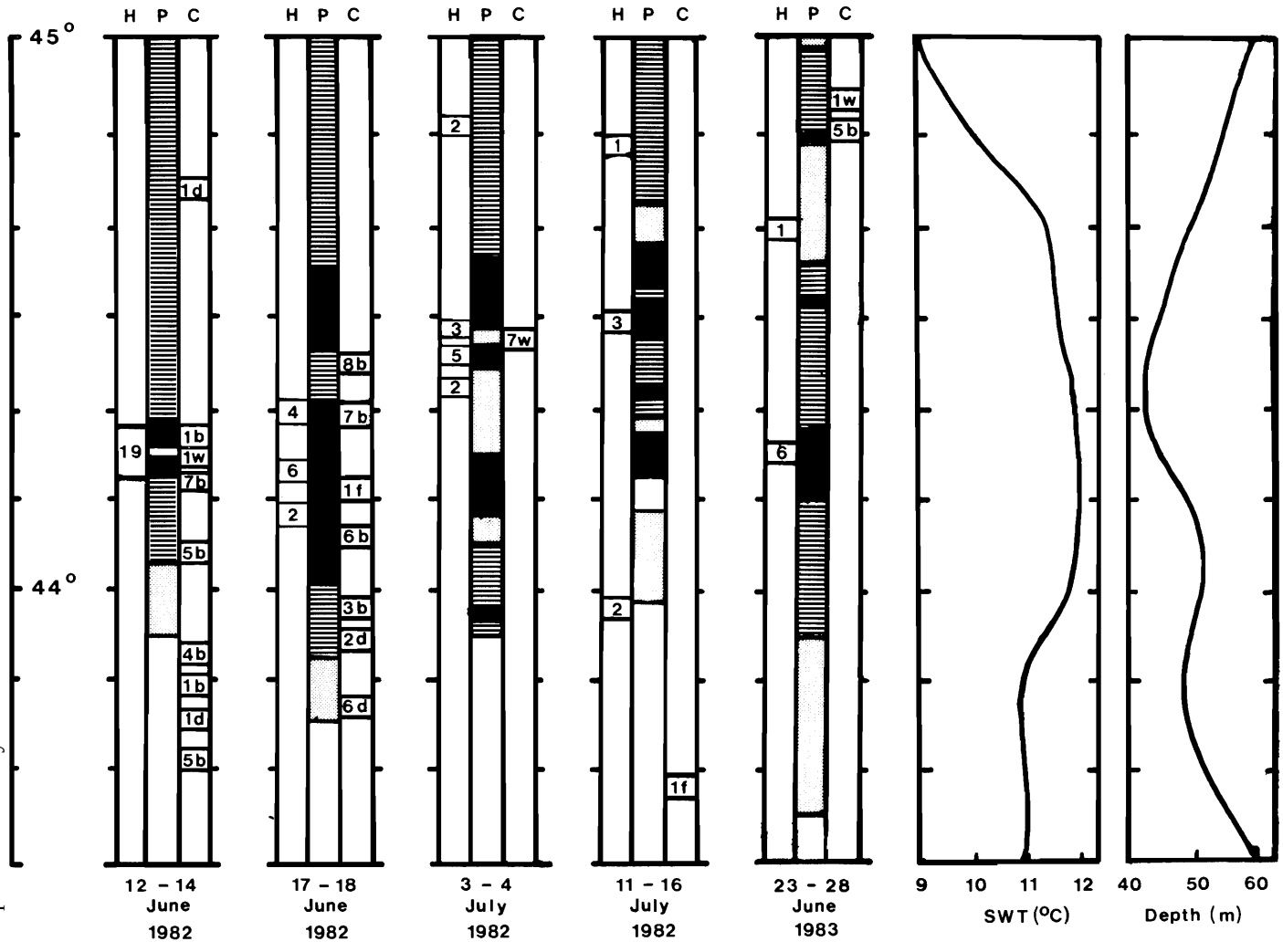

FIG. 2. Diagram showing information collected on transects of the Southeast Shoal of the Grand Bank along longitude 50° W. Latitude runs vertically from 43°30′ N (bottom) to 45°00′ (top). Each of the five transects is represented by three bars. The left-hand bar (H) gives the latitudes at which concentrations of humpback whales were sighted, together with the numbers sighted in each concentration. The right-hand bar (C) gives the latitudes at which other species of Cetacea were sighted and the numbers in each sighting (*f*, finback whales; *w*, unidentified whales; *b*, white-beaked dolphins; *d*, unidentified dolphins). The central bar (P) gives the grade of the depth sounder prey trace, indicated symbolically by different forms of shading as defined in Fig. 6. The darker shading indicates more extensive prey traces. At the right is the mean surface water temperature (SWT) in degrees Celsius over the four 1982 transects along the transect route, and the depth profile in metres along the transect route.

centre of the transect, on the shallowest part of the shoal, where the surface water was warmest. In this area there was also particularly warm water below the thermocline (which was usually at depths between 25 and 30 m) in 1983, as shown by the bathythermograph readings at 40 m below the surface. These readings were between 3.4 and 5.0°C. In contrast, on the deeper parts of the shoal (>56 m) 40-m bathythermograph readings were between 1.3 and 2.3°C, and in the nearby waters off the edge of the Grand Bank readings ranged between −1.2 and 0.7°C. During the early part of the 1982 study there was a particularly dense concentration of humpbacks near 44°15′ N. Later, as the surface water temperatures warmed, the humpbacks became more spread out, being found further north and in deeper water. The data collected during the 1983 study were consistent with a similar change in distribution having taken place, although mean water temperatures were generally warmer for the time of year.

Sightings of humpbacks while not on transect are given in Fig. 3. To show effort, the routes taken while not on transect in daylight are given in Fig. 4. The off-transect humpback sightings present a similar pattern to those found on transect: animals were principally found over the northern part of the Southeast Shoal. On 29 June 1983 several humpbacks were sighted along the edge of the Grand Bank (Fig. 4) in a region of very different oceanography (as indicated by very cold deep bathythermograph temperatures and different seabird and dolphin species) from the area of the main humpback concentration on the Southeast Shoal.

Distribution of other Cetacea

Five species of Cetacea other than humpback whales were seen on the Southeast Shoal: finback whales (*Balaenoptera physalus*), minke (*Balaenoptera acutorostrata*), white-beaked dolphins (*Lagenorhynchus albirostris*), saddleback dolphins (*Delphinus delphis*), and orcas (*Orcinus orca*). The sightings of these species, together with those of unidentified whales and dolphins, are given in Fig. 2 and Table 1 for the transect work and in Fig. 5 for the off-transect work.

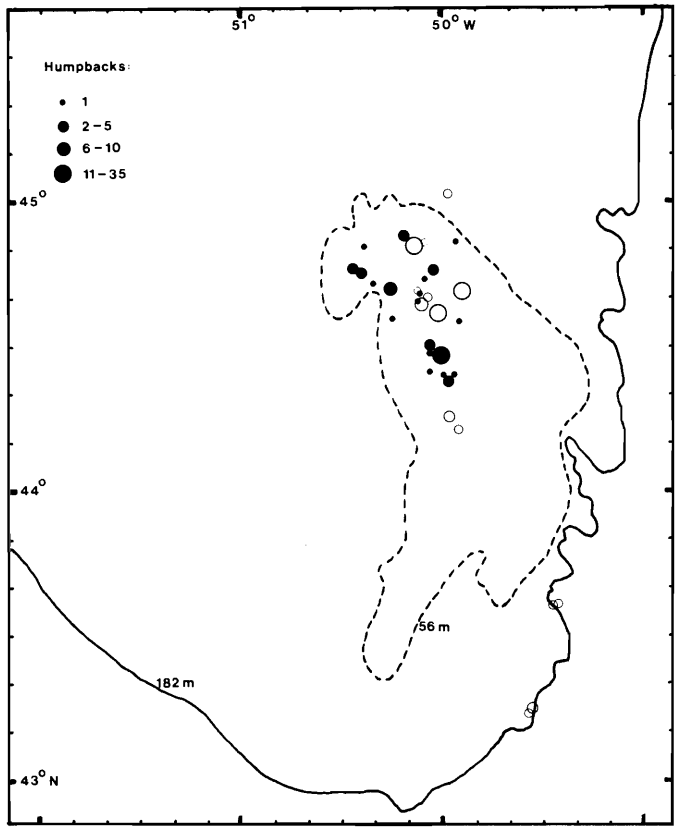

FIG. 3. Positions of sightings of concentrations of humpback whales on the Southeast Shoal while not on transect in 1982 (●) and 1983 (○).

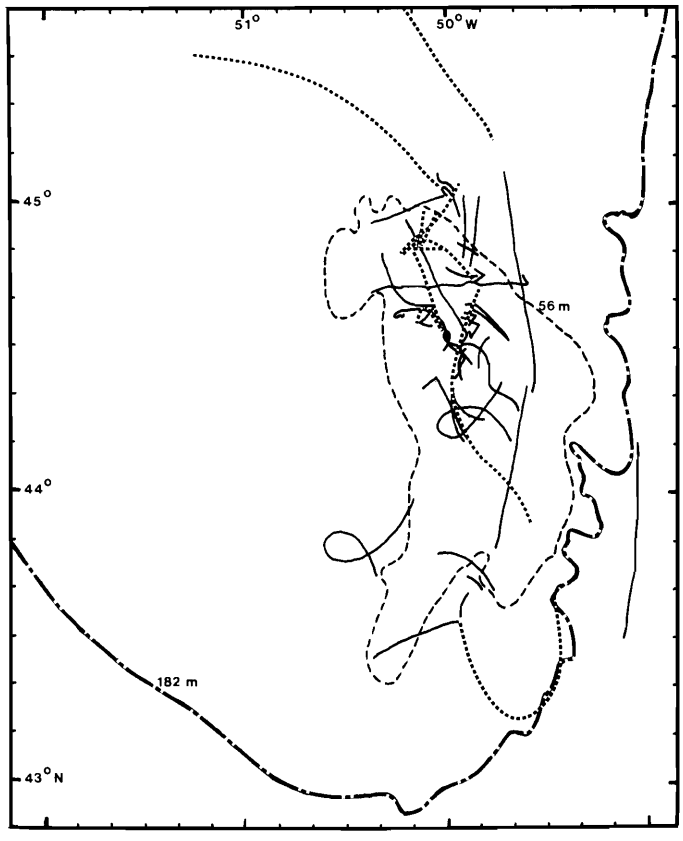

FIG. 4. Approximate routes of *Findrinny* while travelling, but not on transect, in daylight during 1982 (—) and 1983 (---). Some of the cetacean sightings shown in Figs. 3 and 5 do not coincide with these routes. This is because animals were sometimes sighted at night or while hove to.

Four of the finback sightings were in the centre of the shoal near the centre of humpback abundance. The other two were at the southern end of the transect. No finbacks were sighted during the 1983 study.

One minke whale was sighted on 29 June 1983 on the edge of the Grand Bank.

The white-beaked dolphins had a similar distribution to the finbacks; there were sightings with the humpbacks near the centre of the shoal and others at the southern end of the transect. As with the humpbacks, the density of white-beaked dolphins decreased considerably with date.

Saddleback dolphins were only seen near the southern edge of the Grand Bank on 29 June 1983.

Orcas were sighted once each year on 4 July 1982 and 25–26 June 1983. In each case they were attacking humpbacks towards the centre of the shoal. These attacks are described in detail by Whitehead and Glass (1985).

Prey

The depth sounder output from the transects was divided into five grades, depending on the intensity of the prey traces, as shown in Fig. 6.

The grades at different locations on the transects are shown symbolically in Fig. 2. Prey traces were particularly strong towards the centre of the shoal, where the water was shallower and warmer (Fig. 2). There was a marked lack of prey traces on the southern part of the shoal in both years. As with the humpbacks, the concentrations spread out later on in the study.

The only direct indication that these prey traces were made by capelin is that during the last transect in 1982, intense prey traces coincided with areas where dead or dying capelin were seen on the surface. By 15 July 1982 these dead capelin were very numerous, averaging up to an estimated one dead capelin per 100 m^2 in some areas.

Research on the Southeast Shoal by capelin biologists strongly suggests that the great majority of our prey traces were made by capelin. Surveys over the shoal were made between 1 and 4 July 1982 (44°20′ N to 45°10′ N) and 27 June and 2 July 1983 (44°00′ N to 45°10′ N). During these cruises 99.9% (1982) and 92.8% (1983) of midwater trawl samples made over acoustic targets were found to be capelin, largely from the dominant 1979 year class (Miller and Carscadden 1983; Miller 1984; J. E. Carscadden and D. S. Miller, personal communication).

The following table gives the rates of sighting humpbacks per nautical mile travelled for the different prey trace grades:

Prey trace grade (Fig. 6)	Nautical miles travelled	Humpbacks	Rate
O	102	4	0.039
A	83	6	0.072
B	193	3	0.015
C	55	17	0.309
D	17	26	1.530

There is a significant difference between these rates (χ^2 test, $P < 0.005$). It is clear that the humpbacks were much more

TABLE 2. Vertical extent of prey traces on depth sounder and bottom depth under feeding humpbacks

Date	Time range	Latitude (N)	Longitude (W)	Prey depth range (m)	Bottom depth (m)
1982					
13 June	1520–1613	44°16′	49°58′	16–46	46
23 June	1629–1740	44°13′	49°54′	18–46	46
4 July	1200–1205	44°28′	49°57′	38–45	45
6 July	1030–1032	44°28′	49°58′	38–50	50
6 July	1250–1330	44°27′	50°02′	10–30	50
6 July	1330–1600	44°28′	50°01′	10–50	50
6 July	1920–1950	44°30′	50°05′	10–50	50
7 July	0747–0914	44°33′	50°05′	37–54	48–54
7 July	1320–1500	44°36′	50°13′	40–56	56
7 July	1500–1925	44°36′	50°13′	32–56	56
10 July	1522–1700	44°41′	50°16′	36–54	54
15 July	1800–1820	44°50′	50°10′	50–56	56
1983					
24 June	1522–1745	44°51′	50°07′	30–55	55
25 June	2100–2200	44°49′	50°10′	5–55	55
30 June	1000–1430	44°14′	49°59′	26–52	52
30 June	1730–1810	44°41′	49°55′	16–45	53

concentrated over the areas producing the darkest traces. For the other cetacean species there were much less data and no such prominent trends were apparent.

The depths of prey under feeding humpbacks, as indicated by the recording depth sounder, are given in Table 2. Except during one case in each year, the schools were on the bottom and generally occupied the lower half of the water column (beneath 25 m).

Fluke photographs

During the 1982 study 149 individual humpbacks were identified from their fluke photographs. Of these, 24 were photographed on 2 days. In 1983, 111 individuals were identified, four on 2 days. In neither year were any animals photographed on 3 or more days. Seventeen animals were photographed in both years, giving a total of 243 identified animals from the Southeast Shoal.

Stock identity

The 243 fluke patterns from the Southeast Shoal were compared with 1010 catalogued by Katona *et al.* (1980) and 72 individuals photographed off west Greenland during 1981 (Whitehead, Chu *et al.* 1982). There were 29 matches between Southeast Shoal photographs and photographs from the following regions: 12 from Newfoundland and Labrador in previous years, 10 from Puerto Rico, and 7 from Silver and Navidad banks in the West Indies (see Table 3). There were no matches from Iceland, west Greenland, Bermuda, or the Gulf of Maine. Thus, the Southeast Shoal humpbacks seem to be part of the stock that winters in the West Indies and summers off Newfoundland–Labrador. However, as shown in Table 3, there were less matches between the Southeast Shoal and Newfoundland–Labrador feeding stocks than would be expected were there complete mixing.

This disjunction is shown in more detail in Table 4, where matches between photographs taken on the Southeast Shoal, off the Newfoundland coast, and off Labrador in 1983 are compared with those taken in different parts of the North Atlantic in previous years. This includes comparisons with photographs taken in 1982 and 1983, which are not yet available for

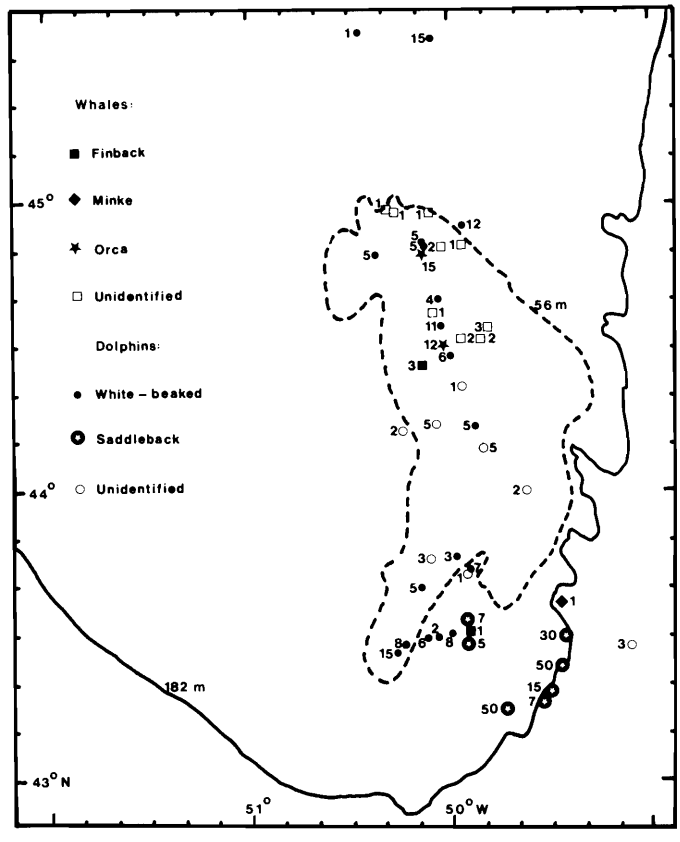

FIG. 5. Positions in which concentrations of cetaceans other than humpback whales were sighted on the Southeast Shoal while not on transect in 1982 and 1983. The numbers of animals sighted in each concentration is given beside each symbol.

the Southeast Shoal 1982 sample. Animals photographed on the Southeast Shoal in 1983 were significantly more likely to have been found there in previous years than off the Newfoundland coast or Labrador. The same tendency to return to a particular summering area is shown by animals from the New-

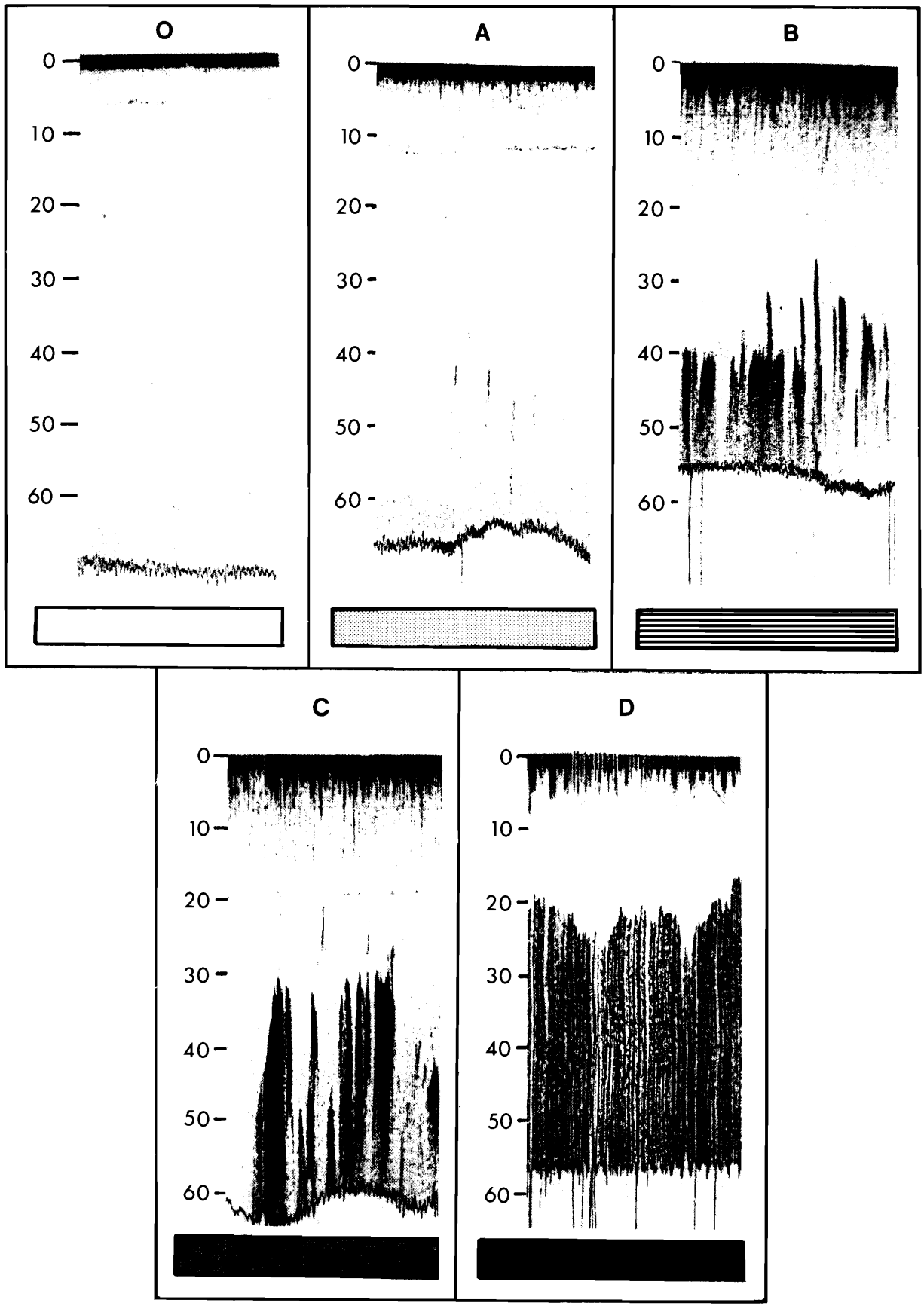

FIG. 6. Representative depth-sounder traces (depth in metres) of the five grades: O, A, B, C, and D. Beneath each grade is an example of the symbolic shading used in Fig. 2.

TABLE 3. Matches of humpback flukes from the Southeast Shoal with other areas of the northwest Atlantic. Also presented are the expected number of matches, given the sample of 243 identified individuals, if the Southeast Shoal humpbacks were part of the population frequenting other areas

Area	Approximate population estimate	No. of identified animals	No. of matches with Southeast Shoal	Expected no. of matches
Silver and Navidad banks	3000	61	7	5
Puerto Rico	?	44	10	—
Bermuda	?	32	0	—
Gulf of Maine	250	113	0	109
Newfoundland–Labrador	2100	758	12	88
West Greenland	150	72	0	72

NOTE: Expected numbers were calculated from the following equation: expected number of matches = number identified on Southeast Shoal × number identified in other area/population estimate in other area. The approximate population estimates are from Whitehead (1982) and Whitehead, Chu *et al.* (1982).

TABLE 4. Matches between photographs taken off the Newfoundland coast, off Labrador, and on the Southeast Shoal in 1983 with those taken previously in difference areas of the North Atlantic

	Newfoundland 1983	Labrador 1983	Southeast Shoal 1983
Photographs	56	66	111
Matches			
Newfoundland	20	16	4**
Labrador	0	5	0**
Southeast Shoal	0	0	17**
Gulf of St. Lawrence	0	2	0
Gulf of Maine	0	0	0
Bermuda	0	2	0
Silver and Navidad banks	6	5	5
Puerto Rico	0	0	7*
West Greenland	0	0	0
Iceland	0	0	0

NOTE: Significant differences between rates of matching from the three areas: *, $P < 0.05$; **, $P < 0.01$.

TABLE 5. Estimates of the population of humpback whales on the Southeast Shoal of the Grand Bank using mark–recapture methods on the fluke identifications, with estimated 95% confidence intervals

Period	Method	Population estimate	95% confidence interval
1982–1983	Petersen	932	572–1292
1982	Petersen	365	227–502
June 1982	Petersen	653	180–1126
July 1982	Petersen	228	−2–458
1982	Schnabel	474	310–637
June 1982	Schnabel	698	250–1145
July 1982	Schnabel	317	−94–728
15 June 1982	Seber–Jolly	900	0–2125
19–24 June 1982	Seber–Jolly	1541	0–4162

foundland coast and Labrador, although a considerable number of animals photographed off the Newfoundland coast between 1977 and 1980 were found off Labrador in 1982 and 1983. One animal was photographed both off the Newfoundland coast and off Labrador in 1983, and another was seen on the Southeast Shoal on 24 June and 591 nautical miles north, off Labrador, on 14 August 1983.

The Southeast Shoal animals had a significantly greater tendency to be found off Puerto Rico than those from the Newfoundland coast or Labrador, suggesting some correlation between summer feeding and winter breeding grounds. However, animals from all areas were found on Silver and Navidad banks at rates that did not significantly differ from one another.

Population size

The photographic identifications were used as input for the following three mark–recapture methods. (*i*) Petersen (equations from Seber 1973, p. 60): This method compares returns during two sampling periods. It assumes that sampling is random in the population during one of the sampling periods and that all animals in the population were available for sampling in this period. It is a robust method and easy to use. (*ii*) Schnabel (equations from Seber 1973, pp. 131 and 133): This method compares returns during several sampling periods. It assumes a closed population, with random sampling during each period. It produces accurate estimates, but is sensitive to departures from the assumptions. (*iii*) Jolly–Seber (equations from Seber 1973, pp. 202 and 204): This method compares returns over several sampling periods and produces estimates of the population size, immigration–birth numbers, and emigration–death rates for each sampling period. It assumes random sampling. It is robust, but produces imprecise estimates.

Estimates of the population on the Southeast Shoal, together with 95% confidence limits, which were calculated using these methods, are given in Table 5. Petersen estimates were made for the whole study by comparing returns between 1982 and 1983. Petersen and Schnabel estimates were made for the months of June 1982, July 1982, and the complete 1982 study. For these Petersen estimates the divisions between sampling periods were made on 17 June for June 1982, 7 July for July 1982, and 1 July for the whole 1982 study. Seber–Jolly estimates are given for 15 June 1982 and 19–24 June 1982, the only periods with worthwhile estimates. No satisfactory estimates could be obtained for the 1983 study, when there were only four whales photographed on more than 1 day.

To check the assumptions of the Schnabel estimate, the 1982 data were tested using the multinomial model (Seber 1973, p. 157). This assumes that all animals were equally likely to be photographed on any day. In Table 6 the 1982 study is divided into three periods, 13–15 June, 19–24 June, and 3–15 July, and the number of animals photographed in each pair of intervals is given. Also given are the expected number of animals if the assumptions of the Schnabel estimate held. Although

TABLE 6. Testing the 1982 fluke photograph data against the multinomial model

	Observed			Expected		
	13–15 June	19–24 June	3–15 July	13–15 June	19–24 June	3–15 July
13–15 June	69			71		
19–24 June	4	31		6	27	
3–15 July	12	2	31	7	3	34

NOTE: The 1982 study is divided into three periods: 13–15 June, 19–24 June, and 3–15 July. The diagonal entries give the number photographed in one period alone. The off-diagonal entries give the number photographed during each pair of periods. No animals were photographed in all three periods. On the right are given the expected entries in this table if the assumptions of the Schnabel census held. There is no significant difference between the expected and observed results ($P > 0.1$).

there is no significant difference between the observed and expected rates ($\chi^2 = 5.2$, $0.1 < P < 0.25$), there is an indication that the whales which were present early in the year left to return later.

This mark–recapture analysis suggests that a total population of about 900 humpbacks were using the Southeast Shoal, with roughly half appearing in 1982. In 1982, approximately twice as many were present in June as compared with July (in agreement with the transect data presented in Table 1). This compares with an estimated population of approximately 2000 using the Newfoundland–Labrador area, from mark–recapture analyses of fluke photograph returns (Whitehead 1982).

Movements

We compared the pairs of positions in which the 24 humpbacks photographed on more than 1 day in 1982 were found. Significantly more moved north rather than south (20 north, 4 south; $P < 0.005$; mean speed, 0.05 km/h) and west rather than east (17 west, 7 east; $P < 0.05$; mean speed, 0.04 km/h). Thus, on average, individual humpbacks were moving slowly northwest over the shoal during 1982.

Of the four humpbacks photographed on 2 days in 1983, two moved north while two made no change in latitude and three moved east with one making no change in longitude.

The information given in Table 6 confirms that many of the humpbacks were present on the shoal for periods of weeks.

Behaviour

The group sizes in which humpbacks were seen on transect are given in Table 7. These transect observations will tend to underestimate the group size as whales underwater are not seen and counted. Early in the 1982 study the humpbacks formed particularly large coordinating groups, occasionally of over 40 animals and on 24 June 1983 groups of up to 10 animals were seen. Otherwise, group sizes were similar to inshore studies along the Newfoundland coast, generally one to four animals (Whitehead 1983).

None of the 48 whales photographed on 2 days during a single season were found grouped with the same companions on both days. Nine pairs of identified whales were photographed on the same day in both 1982 and 1983. However, this number was very close to the expected number (7.4) if there was no tendency for pairs of whales to be photographed on the same day in both 1982 and 1983 (given the days on which they were photographed in 1983). Thus, as Whitehead, Harcourt *et al.* (1982) found inshore, there is no significant evidence in this study for long-term companionships between particular pairs of humpback whales, other than the mother–calf pair.

TABLE 7. Numbers of groups of different sizes of humpback whales observed on transects of the Southeast Shoal

	Group size				
Date	1	2	3	4	10
12–14 June 1982	6	0	1	0	1
17–18 June 1982	3	3	1	0	0
3–5 July 1982	2	3	0	1	0
11–16 July 1982	1	1	1	0	0
23–28 June 1983	2	1	1	0	0
Total	14	8	4	1	1

The feeding behaviour of the humpbacks, as we could see it, was also similar to that observed from humpbacks feeding at comparable depths inshore: approximately 2–3 min at the surface, followed by a "fluke up," with the whale remaining underwater 3–4 min (Bredin 1983; Whitehead 1981). However, apart from the changes in group size, there was less variation in humpback feeding behaviour during the longer 1982 study than was found inshore over similar time periods (Bredin 1983; Whitehead 1981). This is probably because of the remarkably uniform habitat of the Southeast Shoal.

Discussion

The number of humpback whales in the northwest Atlantic is thought to number between about 3000 and 6000 animals (Katona *et al.* 1983). Thus, although the confidence interval is wide, our estimate for the population visiting the Southeast Shoal (about 900) suggests that it is home to roughly 15–30% of the northwest Atlantic population. However, only about half of these animals were on the shoal at any time. The others may have been scattered on nearby parts of the Grand Banks; they do not seem to have frequented inshore Newfoundland or Labrador waters to any great extent.

Few of the humpbacks on the Southeast Shoal in 1982 and 1983 were amongst those who appeared in great numbers along the Newfoundland coast between 1978 and 1980 and became entrapped in inshore fishing gear. Instead, it seems that the animals involved in the conflict with fishermen have dispersed themselves along the Newfoundland coast and especially in the waters off Labrador. This agrees with a recent analysis by Whitehead and Carscadden (1985), who relate the influx of humpbacks inshore to the low abundance of immature capelin in the stock of NAFO areas 2J and 3K. These immature capelin inhabit the waters off Labrador. With low abundance of the 2J3K immatures, the humpbacks moved inshore to feed on the mature capelin spawning along the Newfoundland coast.

Despite the fact that we never saw a humpback eating a capelin, there is strong evidence that capelin were the reason behind the humpbacks' presence on the shoal, particularly the close relationship between humpback distributions and those of the depth sounder traces, which fisheries' surveys concurrent with our research found to almost entirely represent capelin. Additionally, Parsons and Brownlie (1981) found that humpback densities on the shoal were highest in June and July when the capelin in the 3NO stock are spawning.

The observed changes in the distribution and behaviour of the humpbacks through June and July on the Southeast Shoal are consistent with results from inshore. Prespawning schools

of capelin that are being preyed on by humpbacks are generally relatively large and compact, whereas after spawning the schools are usually small and dispersed (Bredin 1983). The group sizes of humpbacks feeding on a particular prey school are closely related to the size of the school, with large numbers of humpbacks feeding in a coordinated fashion on the larger schools, but often feeding singly or in pairs on the smaller (Bredin 1983; Whitehead 1983). Thus, the gradual dispersal and disintegraton of the large humpback groups through the season on the Southeast Shoal can be related to expected changes in their prey. The particularly large groups found early in the 1982 study may be due to exceptional concentrations of capelin on the shoal at this time. Like the Southeast Shoal animals, the humpbacks inshore moved slowly northwards along the coast as the summer progressed and the water temperature warmed (Whitehead, Harcourt *et al.* 1982). The much simpler topography of the Southeast Shoal allowed these trends to be identified more easily than inshore.

Our observations strongly suggest that the humpback whale is a major predator and almost certainly the most significant marine mammal predator on the spawning Southeast Shoal capelin.

The results of this study emphasize the importance of the Southeast Shoal and of the capelin which spawn on it in the Grand Bank ecosystem. This region, with its vital food resources, both for man and other higher predators, should be the subject of continued careful biological monitoring. This is especially true given its proximity to the developing Hibernia oil field.

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