Behaviour and Vocalizations of Two Single Sperm Whales, *Physeter macrocephalus*, Off Nova Scotia

Julia Mullins,[1] Hal Whitehead, and Linda S. Weilgart

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

Mullins, J., H. Whitehead, and L. S. Weilgart. 1988. Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Can J. Fish. Aquat. Sci. 45: 1736–1743.

During June 1986, two male sperm whales, *Physeter macrocephalus*, on the Scotian Shelf were tracked by listening for their clicks with a directional hydrophone for periods of 12.5 and 7 h, respectively. Each whale travelled along the edge of the shelf at about 2 kn (3.6 km/h), and one whale, on two occasions at least, dived to the ocean floor. After about 30 min underwater, the whales spent approximately 9 min at the surface breathing. When the whales were visible at the surface, they were silent, except on one occasion when "slow clicking" (mean interclick interval of 4.6 s) was heard from Whale 2. While underwater, most of the sound production consisted of "usual clicks" (mean interclick interval 0.96 and 0.69 s for the two whales) interrupted by frequent short silences (mean durations 21.06 and 27.82 s) and occasional "creaks" (with interclick intervals less than 0.2 s) and "slow clicks." No "codas" (stereotyped patterns of clicks) were heard from these two single whales. These results are consistent with the hypotheses that "usual clicks" and "creaks" are used for echolocation and "codas" for communication.

En juin 1986, deux cachalots macrocéphales (*Physeter macrocephalus*) mâles de la plate-forme Scotian ont été suivis au mo9yen d'un hydrophone directionnel pendant des périodes respectives de 12,5 et 7 h. Chaque cachalot s'est déplacé le long du bord de la plate-forme à une vitesse de 2 km (3,6 km/h) environ, et à deux reprises, au moins, un des cachalots a plongé au fond de l'océan. Après avoir passé environ 30 min sous l'eau, les cachalots sont remontés à la surface pendant près de 9 min pour respirer. Lorsqu'ils étaient visibles à la surface de l'eau, ils étaient silencieux, sauf à une occasion où l'on a entendu un « clic lent » (intervalle moyen entre les clics de 4,6 s) émis par le cachalot numéro 2. Lorsqu'ils étaient sous l'eau, presque tous les sons produits étaient des « clics ordinaires » (intervalle moyen entre les clics de 0,96 et 0,69 s pour les deux cachalots) interrompus par des silences courts fréquents (durée moyenne de 21,06 et 27,82 s), et des « gémissements » occasionnels (avec des intervalles entre les clics de moins de 0,2 s) et des « clics lents ». Aucun code (représentations stéréotypées de clis) provenant de ces deux cachalots n'a été entendu. Ces résultats sont conformes aux hypothèses selon lesquelles les « clics ordinaires » et les « gémissements » servent à l'écholocation et les codes à la communication.

Received December 14, 1987
Accepted May 19, 1988
(J9520)

Reçu le 14 décembre 1987
Accepté le 19 mai 1988

Until recently, most available information on the behaviour of sperm whales, *Physeter macrocephalus*, was based on observations made "at one moment in time (normally after death)" (Best 1979). However, during the past 5 yr, techniques have been developed for the study of the behaviour of living sperm whales for extended periods of time (Whitehead and Gordon 1986). These techniques are based on tracking sperm whales from sailing vessels passively using a directional hydrophone, identifying individuals using photographs of natural markings, and following them underwater with a recording depth sounder. This research has almost entirely concerned groups of sperm whales, and especially groups of females with their calves, which generally inhabit tropical waters. Important results have been obtained on the social organization of sperm whales in two principal study areas, off Sri Lanka and the Galapagos Islands (Gordon 1987; Whitehead and Arnbom 1987), but during these studies, there were no opportunities to track individual sperm whales for considerable periods. Male sperm whales, as they grow, are found at generally higher latitudes and in smaller groups (Best 1979), so better opportunities for finding and tracking single sperm whales are likely to exist away from the tropics.

Studies of single animals over extended periods of time are vital for an understanding of feeding patterns, diving behaviour, respiration, energetics, and diurnal patterns as well as the population variation of these variables. Like many other cetaceans, sperm whales are vocal, although, unusually, their vocalizations seem restricted to clicks (Backus and Schevill 1966). However, they can use clicks in a number of ways: regularly spaced clicks at various repetition rates, high repetition rate "creaks," and stereotyped patterns of clicks called "codas" (Backus and Schevill 1966; Watkins and Schevill 1977; Watkins 1980). Studies of individual animals over extended periods of time in which acoustic output is related to the dive cycle and other observable behaviour will help determine the functions of the different forms of vocalization. With good correlations between vocalizations and behaviour, we can also interpolate the behaviour of whales when we can hear but not see them, such as at night.

As sperm whaling is halted, there is increasing interest in assessment methods which do not depend on catches. Acoustic and visual censuses of sperm whales are two techniques whose development is receiving special attention (Whitehead and Gordon 1986). In order to obtain absolute estimates of abundance from such censuses, it is necessary to know the statistical properties of the time each individual spends at the surface (for

[1]Current address: R.R. 4, Stirling, Ont. K0K 3E0.

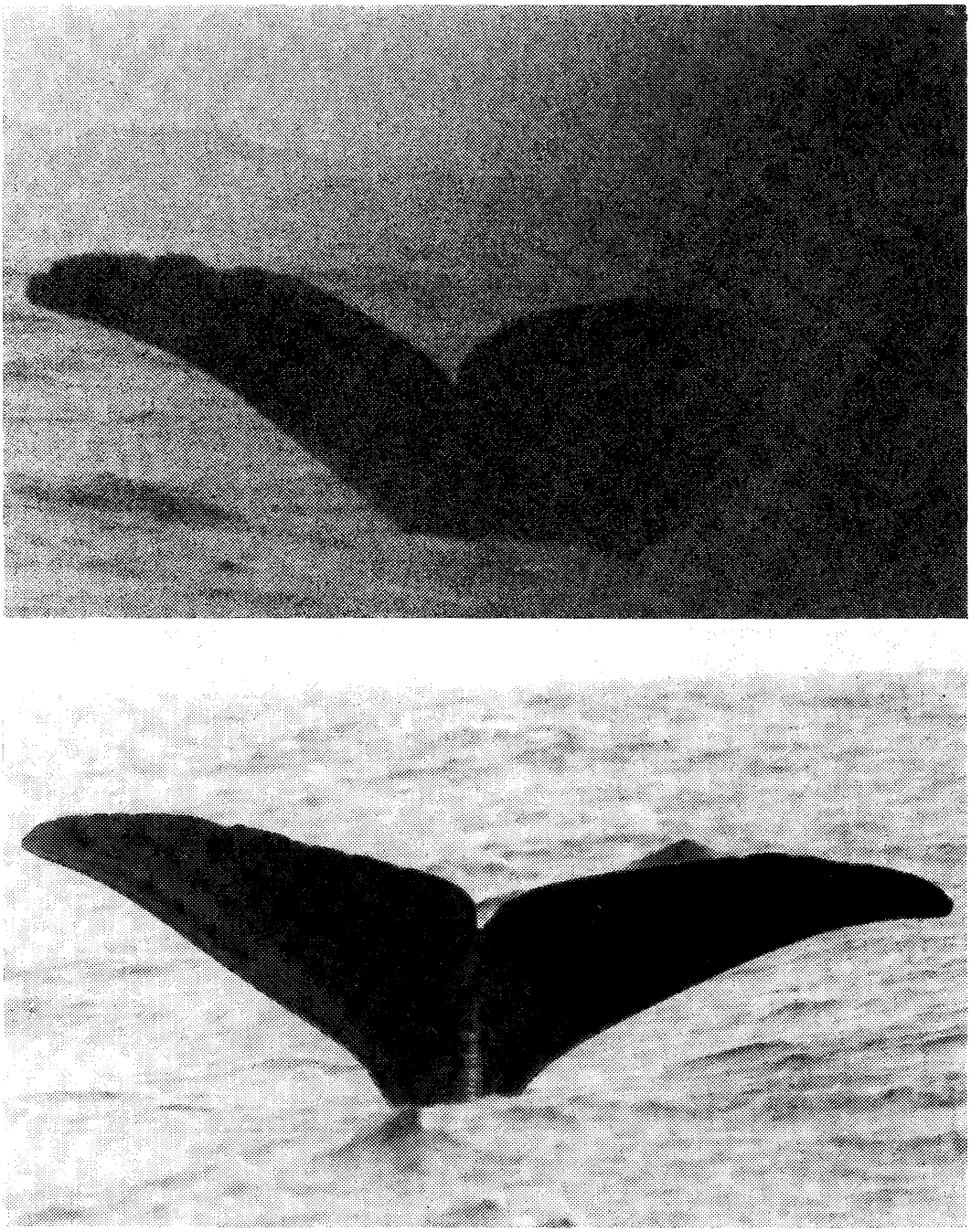

FIG. 1. Fluke photographs from Whale 1 (above) and Whale 2 (below).

visual censuses) or vocalizing (for acoustic censuses). Ideally these data should come from extended continuous studies of individual whales.

This paper reports on a study of sperm whales off Nova Scotia during the summer of 1986. Two sperm whales were tracked acoustically for periods of several hours during which their sounds were recorded continuously. The movements, diving behaviour, and acoustic output of these two whales are described and compared with results of other studies. The long continuous recordings also allow direct comparison between the acoustic output of the whale and the stage of its dive cycle.

Methods

The 10-m sloop *Elendil* with a crew of five was used to track sperm whales in an area along the continental slope off Nova Scotia (42°50′ to 43°40′N and 60°00′ to 62°50′W) from 17 to 25 June 1986.

Sperm whales were located by cruising the areas from where they have been reported (Mitchell 1975) and listening for their clicks with a Benthos AQ17 omni-directional hydrophone for 5 min every 30–60 min.

Once found, sperm whales were tracked for as long as possible by means of a Dev-Tec directional hydrophone. This hydrophone was monitored approximately every 30 min when following sperm whales to obtain bearings to, and approximate acoustic intensities of, the clicks. The course and speed of the boat, which was under sail, were adjusted to follow the track of the whales. While following whales, a continuous recording

(except for changing tapes) was made with a Benthos AQ17 hydrophone, an Ithaco 453 preamplifier (using low-frequency "roll-off" filters to minimize wave noise), and a Nagra IV SJ tape recorder (tape speeds of 1.5 and 3.75 cm/s). The recordings were continued until the whale(s) were lost or until sounds from other ships interfered with the recording.

During daylight, if the whale being tracked was visible at the surface, the number of blows, time first seen at the surface, and time of the fluke-up (flukes are shown when the whale dives) were recorded. Photographs were taken of the tail flukes with a Canon AE1 Program camera and 300-mm lens. Fluke photographs are used to identify individual animals (Arnbom 1987). A Simrad Skipper 603 recording depth sounder was used to obtain a trace of the diving whale whenever possible. Navigation was by Tracor Transtar satellite navigator. This provided positional fixes accurate to 0.2 nautical miles (0.4 km) approximately every 2 h.

The results presented in this paper are for two single whales for which the data collection was particularly clear and unambiguous: Whale 1 was recorded from 17:35 on 21 June to 07:30 on 22 June and Whale 2 from 14:20 to 21:30 on 23 June (all times Atlantic summer time, $Z + 3$). For Whale 1 the recordings of whale sounds from 05:50 to 07:30 on 22 June were obscured by noise from fishing vessels and these time periods were not included in the statistical compilation of the acoustic analysis (see Table 2; Fig. 5). There were no visual or acoustic indications of other sperm whales nearby during these periods. In other cases we were following more than one whale, or the track was of less than 2 h duration. Strong winds during the research facilitated tracking under sail but made surface observation and photography difficult. Fluke photographs (Fig. 1) showed that Whale 1 and Whale 2 were different animals. Both whales were assumed to be immature males from estimates of their length (approximately 11–13 m) and relatively large foreheads. Twenty-three percent of the sperm whales, all males, caught in the area between 1967 and 1972 were in this size range, despite selection for larger animals (Mitchell 1975).

During analysis, the acoustic recordings were broken down into the following categories: "usual clicks", "creaks", "slow clicks", short silences, and long silences. Usual clicks are series of clicks with an interval of less than 3 s between clicks but which are heard as separate distinct clicks (Weilgart and Whitehead 1988). Creaks are very rapid clicks that sound similar to a rusty door hinge. The individual clicks in a creak cannot be distinguished from one another by the human ear when the tape is played at the recorded speed (interclick interval less than 0.2 s). Slow clicks were arbitrarily designated as series of clicks having an interval of greater than 3 s between clicks (cf. Weilgart and Whitehead 1988). Short silences are less than 5 min but longer than 20 s between series of clicks. Long silences are greater than 5 min between series of clicks. "Trains" of usual clicks were separated by creaks, short silences, long silences, or slow clicks. Trains of slow clicks were separated by creaks, short silences, long silences, or usual clicks. Interclick intervals for usual clicks were measured by listening to approximately 3.5 min of randomly chosen usual clicking per tape and timing the intervals between the clicks. Interclick intervals for slow clicks were measured from all adjacent pairs of slow clicks within each train. More detailed acoustic analysis, using an oscilloscope and sound spectrograph, was hindered by loud ambient noise mainly from waves and the motion of the hydrophone through the water.

In order to estimate the average speeds of the sperm whales along the ocean floor, distances between adjacent satellite fixes were compared with the time intervals between fixes. Intervals of less than 30 min were discarded because in these cases the fixes were too close together in time to give an accurate speed.

Results

Movements of Sperm Whales

The movements of the research vessel while tracking and recording the whales provide a general description of the movements of Whales 1 and 2, since the research vessel was usually within about 2 km of the tracked whales as estimated by the strength of the acoustic contact. The whales travelled in fairly straight lines along the edge of the Scotian Shelf (Fig. 2) at about 2 kn (3.6 km/h) over the bottom (Table 1). Their tracks roughly followed bottom contours (75 m for Whale 1 and 200 m for Whale 2).

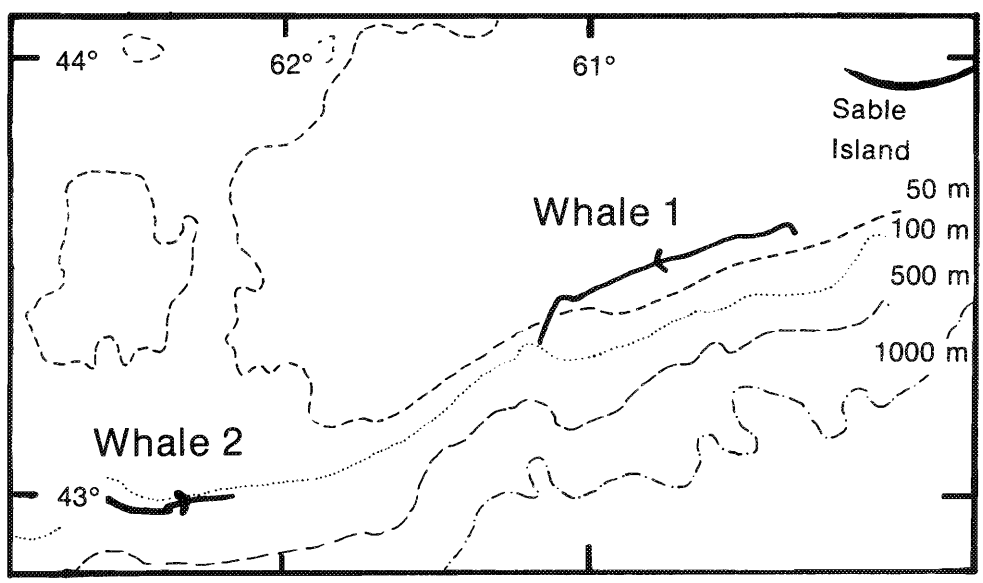

FIG. 2. Movements of the research vessel while tracking Whales 1 and 2 on the Scotian Shelf.

TABLE 1. General behaviour of Whale 1 and Whale 2.

General behaviour	Whale 1 Mean	Whale 1 SD	Whale 1 *n*	Whale 2 Mean	Whale 2 SD	Whale 2 *n*
Speed (km/h)	5.3	1.81	7	3.4	1.66	7
Diving descent rate (km/h)	—	—	—	5.3	—	2
Breathing rate (exhalations/min)	3.2	0.40	3	2.9	0.18	3
Observed time at surface (min)	7.7	0.33	3	9.8	1.16	3

Dive Cycle

Whale 1 and Whale 2 were each observed at the surface on three occasions (Fig. 3). These periods lasted from 6.5 to 10.5 min, with a mean of 8.7 min. All surface periods ended with a fluke-up. The recorded durations at the surface may have been underestimated, possibly by up to 2 min, because the occasion when the whale was first observed at the surface was not necessarily when it first surfaced. The breathing rates of both whales were approximately 3 exhalations/min while they were being observed at the surface (Table 1).

Two clear dive traces of Whale 2 were collected (Fig. 4). In each case, the depth sounder was turned on approximately 1 min after the fluke-up was observed. On both occasions the whale dived straight down to the bottom, at 305 and 400 m, respectively, descending at a speed of about 3 kn (5.3 km/h) (Table 1).

Intervals between observed periods at the surface were 41.7 and 31.5 min for Whale 1 and 47.5 and 52.9 min for Whale 2.

Vocalizations and the Dive Cycle

Generally, no sounds were heard from whales while they were observed at the surface (Fig. 3). Clicking stopped 0–2 min before the whale was first seen. These periods of silence were

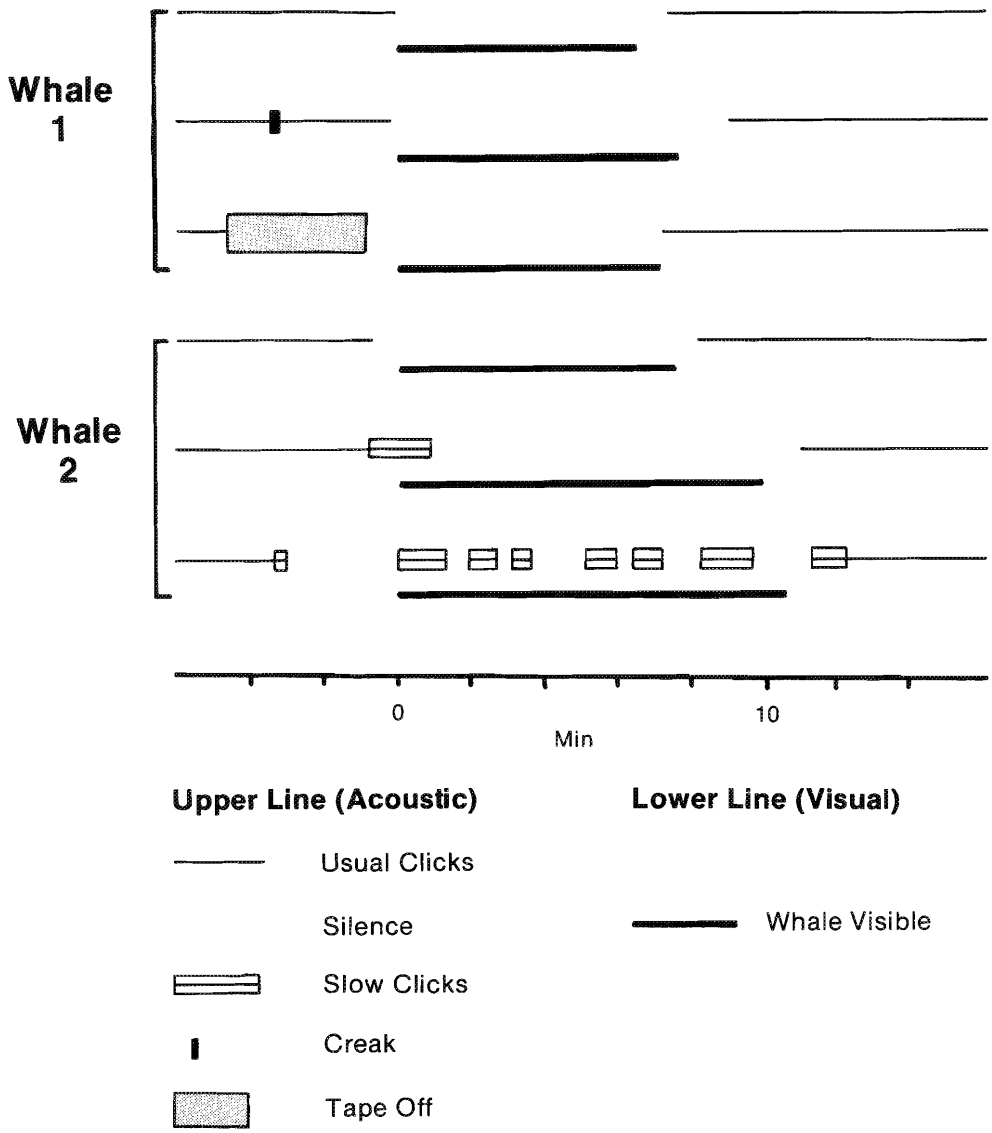

FIG. 3. Comparison between acoustic recordings and periods observed at the surface for Whales 1 and 2. In each case the upper line represents the acoustic recording and the lower the visual record of the whale at the surface. The scale on the *x*-axis is in minutes from the time at which the whale was first seen.

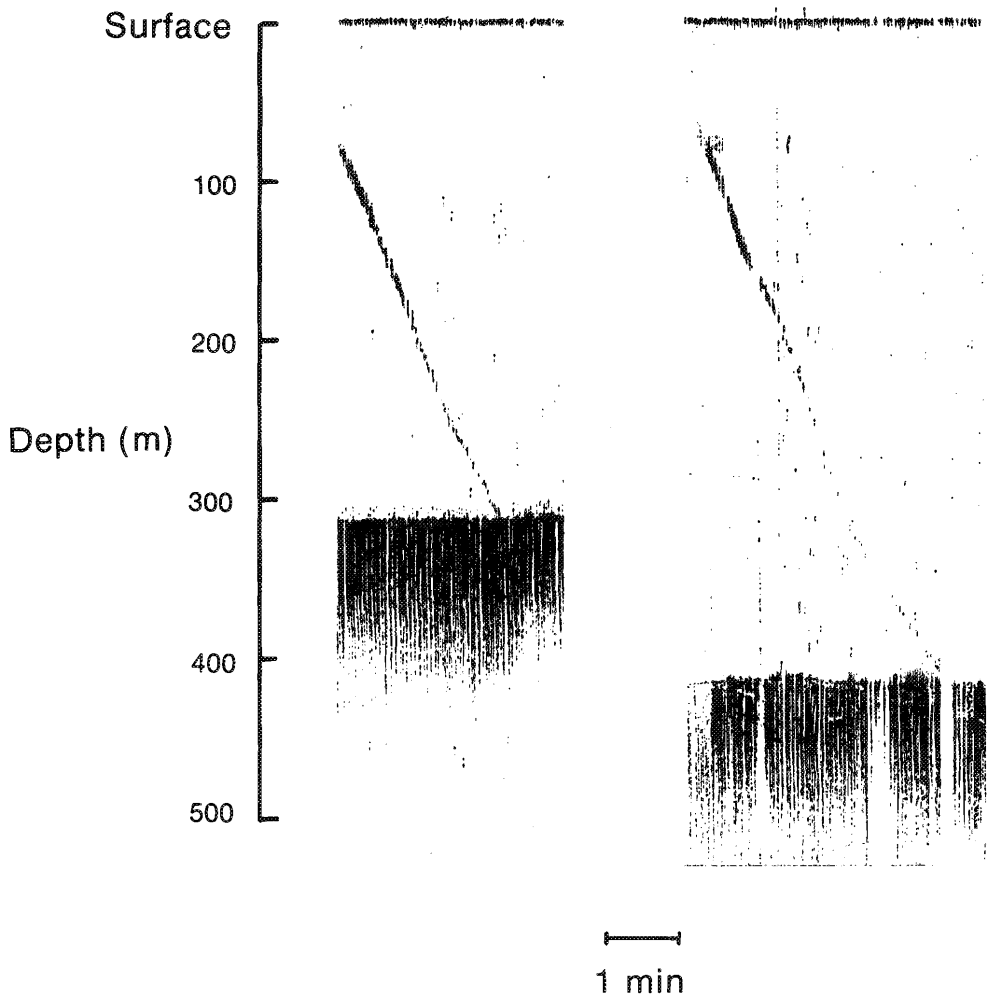

FIG. 4. Two depth sounder traces from Whale 2 (diagonal lines). The flecks on the trace are from clicks emitted by the whale.

usually preceded and followed by usual clicking. Usual clicks and creaks were never heard from a whale visible at the surface. However, on one occasion, Whale 2 produced slow clicks while it was visible at the surface and on another it made slow clicks just as it came to the surface (Fig. 3).

The median durations of the long silences and/or long slow clicking periods (of greater than 5 min), 9.0 min (Table 2), for both whales, are very similar to the mean observed times at the surface, 7.7 and 9.8 min (Table 1). Also, the intervals between observed periods at the surface (means of 36.6 min for Whale 1 and 50.2 min for Whale 2) are similar to the intervals between long silences and/or long slow clicking, medians of 27.0 min for Whale 1 and 46.5 min for Whale 2 (Table 2).

Acoustic Behaviour

The general acoustic behaviour of the two whales consisted of 30–50 min of usual clicking, alternating with 6–30 min of long silence or slow clicking (Fig. 5). The periods principally consisting of usual clicking were interrupted by short slow clicking periods, creaks, and short silences. No patterns of clicks similar to those called codas (Watkins and Schevill 1977) were heard from these single whales.

Approximately two thirds of each hour of acoustic recording consisted of usual clicking (Table 2). Usual clicking trains produced by Whale 1 were generally longer, and had a longer interclick interval, than those produced by Whale 2 (Table 2).

Both whales produced creaks. The duration of creaking trains was shorter for Whale 1 than Whale 2, but the few creaks produced by Whale 2 were highly variable in duration (Table 2). Whale 1 creaked almost twice as often as Whale 2 per hour of acoustic recording (Table 2).

Most periods of silence for Whale 1 were 15–30 s in duration whereas most silences were 7.5–15 s for Whale 2. The silences of Whale 1 were clumped into two groups, from less than 7.5 s to 2 min and from 4 to 32 min, whereas the silences of Whale 2 were distributed from less than 7.5 s to 16 min. On two occasions the whale being tracked and recorded (Whale 1) was silent for approximately 30 min (Fig. 5). It is unknown whether the whale was at the surface breathing or whether it was silent during a dive. The durations of short silences of both whales were highly variable (Table 2). Whale 2 had three times as many short silences per hour of acoustic recording as Whale 1 (Table 2).

Slow clicking was heard only from Whale 2. Slow clicking trains varied in duration (Fig. 5) and the intervals between slow clicks in a train were usually 3–8 s.

Discussion

The sperm whales tracked in this study were found and followed in locations close to the sperm whale catches off Nova Scotia between 1967 and 1972, often in water less than 200 m

TABLE 2. Summary of the acoustic behaviour of Whale 1 and Whale 2.

Acoustic behaviour	Whale 1 Mean	Whale 1 SD	Whale 1 *n*	Whale 2 Mean	Whale 2 SD	Whale 2 *n*
Usual clicks						
Train duration (min)	2.94	2.43	105	2.36	1.07	162
Interclick interval (s)	0.96	0.14	18	0.69	0.18	20
Hours usual clicking per hours acoustic recording	6.0/11.8 = 0.51			5.2/6.5 = 0.80		
Short silences						
Duration (s)	21.06	16.60	146	27.82	37.28	213
No. short silences per hour of acoustic recording	146/11.8 = 12.37			213/6.5 = 32.68		
Creaks						
Duration (s)	26.76	15.69	17	61.0	71.04	5
No. creaks per hour of acoustic recording	17/11.8 = 1.44			5/6.5 = 0.77		
Slow clicks						
Train duration (s)				32.01	23.40	41
Interclick interval (s)				4.57	1.82	40
No. slow clicking trains per hour acoustic recording	0.00			41/6.5 = 6.30		
Periods of silence or slow clicking of >5 min						
Duration (min)	9.0	7.05	17	9.0	4.77	7
Intervals between (min)	27.0	10.78	16	46.5	6.54	6

deep (Mitchell 1975). Sperm whales are generally considered deepwater animals (e.g. Caldwell et al. 1966; Berzin 1971; Gaskin 1982). However, there have been other reports in the literature of sperm whales in shallow waters. Caldwell et al. (1966) summarized accounts of sperm whales captured in depths between 73 and 162 m, as well as much deeper.

It is likely that Whales 1 and 2 swam along the edge of the Scotian Shelf in order to utilize food resources which congregate in this area. Sperm whales caught off Nova Scotia had stomach contents consisting principally of monkfish, *Lophius americanus* (V. Kozicki, Arctic Biological Station, Ste-Anne-de-Bellevue, Que. H9X 3R4, pers. comm.). The edge of the Scotian Shelf is an area where upwelling occurs (Fournier et al. 1977), and therefore, food supplies are likely to be plentiful. Gaskin (1971) noted that sperm whales may concentrate on the edges of cyclonic zones of upwelling.

The sperm whales that we tracked acoustically swam at 2 kn (3.6 km/h), similar to the 2–3 kn reported by Berzin (1971) for undisturbed animals and the 2.1 kn (SD 1.1 kn) for groups of female sperm whales with their young tracked acoustically off the Galapagos Islands (H. Whitehead, Biology Department, Dalhousie University, Halifax, N.S. B3H 4J1, unpubl. data).

The two whales followed off Nova Scotia spent almost two thirds of the time underwater. Their dive cycle consisted of about 9 min at the surface followed by a dive of about 30 min. Off the Galapagos Islands, female sperm whales were found to spend about 10 min at the surface followed by a dive of approximately 45 min (H. Whitehead, unpubl. data), although, as with the sperm whales off Nova Scotia, there was considerable variation. Other reported dive durations vary from greater than 2 h (Watkins et al. 1985) to 50 min (Clarke 1980) to less than 10 min (Lockyer 1977). In this latter case the whales were being chased by a whaling vessel and therefore probably not exhibiting normal behaviour. While at the surface the whales exhaled approximately 3 times/min which is in agreement with Gaskin (1964) who found that undisturbed sperm whales exhaled 2–3 times/min. Berzin (1971) reported a slightly higher rate of 4–6 exhalations/min. The dive rates indicated on the two recording depth sounder traces for Whale 2 of 3 kn (5.4 km/h) are almost identical to rates obtained in the same manner from diving sperm whales off Sri Lanka and the Galapagos Islands (Papastavrou 1987). The results of Lockyer (1977), who measured dive rates of sperm whales using sonar, are much more variable than those found here or presented by Papastavrou (1987). This discrepancy might be explained by difficulties in accurately estimating depths when the transducer is not vertically mounted (as was the case in Lockyer's work) and the fact that her whales were being chased by a whaling vessel. The Sri Lankan and Galapagos whales generally dove to about 410 m below the surface, although the water depth was usually greater than 2000 m (Papastavrou 1987) whereas the whales tracked off Nova Scotia seemed to dive to the shallower bottom.

Thus, some aspects of sperm whale behaviour (such as swimming speed, diving descent rate, period at the surface, and breathing rate) seem reasonably invariant of geographical area and water depth. The differences between Whale 1 and Whale 2 in dive times and some acoustic behaviour might be attributed to the different water depths in which they were swimming, different prey types, or to temporal or individual variations in behaviour. Further data, of the type presented here, would help distinguish between these possibilities.

During the dive phase of the activity cycle the whales produced clicks almost continuously. The intervals between usual clicks of sperm whales off the Scotian Shelf (means of 0.96 and 0.69 s for Whales 1 and 2) were generally in the range of those measured from whales off the Galapagos Islands (0.2–

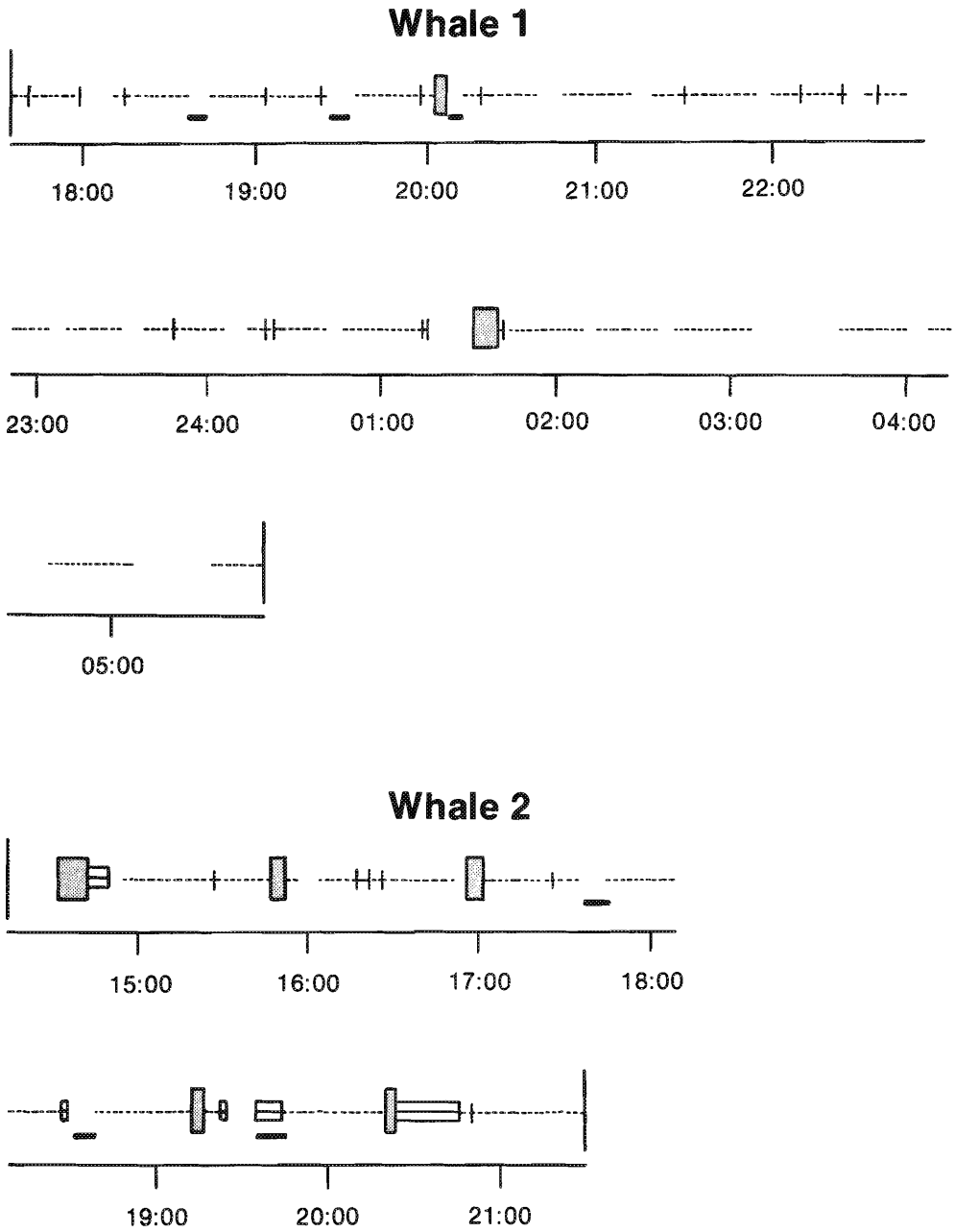

FIG. 5. Acoustic behaviour of Whales 1 and 2. In each case the upper line represents the acoustic recording and the lower the visual record of the whale at the surface. Notation is as in Fig. 3. The line representing usual clicking is broken to represent short silences. Because of the small scale of this diagram and high rate of short silences, especially for Whale 2, the correspondence between breaks in the usual clicking line and short silences is not always one-to-one. For similar reasons, some short slow clicking trains are joined.

1.0 s; Weilgart and Whitehead 1988) and the repetition rates of 0.025–1.250 clicks/s given by Backus and Schevill (1966). Backus and Schevill (1966) and Norris and Harvey (1972) hypothesized that these usual clicks are "search mode" echolocation: the whale is scanning the ocean, not examining anything in particular, but looking for things. Although Watkins (1980) found little evidence for sperm whale echolocation, Gordon (1987) has recently presented correlations between the acoustic output and fine-scale movements of sperm whales which strongly suggest that at least some vocalizations, and especially creaks, are used to echolocate.

Creaks were emitted very infrequently. Creaks are probably produced when the whale is examining an object at extremely close range. The object might be prey, the ocean floor, or other marine organisms. Norris and Harvey (1972) noted that very high repetition rates of clicks occurred when a phonating whale swam over and hit their hydrophone. They reported rates of 60–80 clicks/s lasting a minute or more.

Slow clicks, unlike other vocalizations, were produced at the surface as well as underwater. Like usual clicks and creaks, slow clicks may function in echolocation. The interclick interval of slow clicks is much longer than that of either usual clicks or creaks, suggesting that the object of interest is at a greater distance. However, it appears unlikely that slow clicks produced while breathing at the surface were used for either nav-

igation or feeding. Weilgart and Whitehead (1988) found that slow clicks seem to be characteristic of maturing or mature male sperm whales and hypothesized that this vocalization may function in informing other whales of a male's maturity and/or competitive ability on the breeding grounds. As far as we could tell, there were no other sperm whales, and almost certainly no females, near Whale 2 when he produced slow clicks. If slow clicking is important in male mating success, practicing slow clicking before reaching the breeding grounds might be functional. Alternatively, slow clicks could have multiple functions.

Although no codas were recorded while tracking Whales 1 and 2 which were always single, codas were heard at other times during our study on the Scotian Shelf when more than one sperm whale was present. These observations support Watkins and Schevill's (1977) conclusion that codas are used for communication between sperm whales.

Our observations are not necessarily representative of the complete behaviour cycle of sperm whales: we only consider single whales, and our locating and tracking techniques may bias observations towards some subsections of the population or certain behavioural patterns. Nevertheless, the potential for further insight into sperm whale behaviour from passive observation of their behaviour and vocalizations is considerable.

Acknowledgements

We thank crew members Veronika Brzeski, Paul Foster, Mary McLaren, and Dave Leeson, some of whom had the opportunity to take part in the research for longer periods than others. We are indebted to Paul Foster who most generously provided the invaluable tape recorder. We are grateful to WWF-Netherlands for loaning equipment, especially the recording depth sounder. V. Kozicki gave us important information on the diet of sperm whales off Nova Scotia. We thank Carole Carlson, Susan Waters, and an anonymous reviewer for helpful comments on the manuscript. The study was funded by a NSERC operating grant to Hal Whitehead and a NSERC summer scholarship to Julia Mullins.

References

ARNBOM, T. 1987. Individual identification of sperm whales. Rep. Int. Whaling Comm. 37: 201–204.

BACKUS, R. H., AND W. E. SCHEVILL. 1966. *Physeter* clicks, p. 510–528. *In* K. S. Norris [ed.] Whales, dolphins, and porpoises. University of California Press, Berkeley, CA.

BERZIN, A.A. 1971. The sperm whale. Pac. Sci. Res. Inst. Fish. Oceanogr. 394 p. (Transl. from Russian by Israel Program for Scientific Trans., No. 600707, Jerusalem, 1972)

BEST, P. B. 1979. Social organization of sperm whales, *Physeter macrocephalus*, p. 227–289. *In* H. E. Winn and B. L. Olla [ed.] Behavior of marine animals. Vol. 3. Plenum Press, New York, NY.

CALDWELL, D. K., M. CALDWELL, AND D. W. RICE. 1966. Behavior of the sperm whale, p. 755–789. *In* K. S. Norris [ed.] Whales, dolphins, and porpoises. University of California Press, Berkeley, CA.

CLARKE, M. R. 1980. Cephalopods in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Disc. Rep. 37: 1–324.

FOURNIER, R. O., J. MARRA, R. BOHRER, AND M. VAN DET. 1977. Plankton dynamics and nutrient enrichment of the Scotian Shelf. J. Fish. Res. Board Can. 34: 1004–1018.

GASKIN, D. E. 1964. Recent observations in New Zealand waters on some aspects of behaviour of the sperm whale (*Physeter macrocephalus*). Tuatara 12: 106–114.

1971. Distribution and movements of sperm whales *Physeter catodon* L. in the Cook Strait region of New Zealand. Norw. J. Zool. 19: 241–259.

1982. The ecology of whales and dolphins. Heinemann, London, Great Britain. 459 p.

GORDON, J. C. D. 1987. The behaviour and ecology of sperm whales off Sri Lanka. Ph.D. thesis, University of Cambridge, Cambridge, Great Britain.

LOCKYER, C. 1977. Observations on the diving behavior of the sperm whale, *Physeter catodon*, p. 591–609. *In* M. Angel [ed.] A voyage of discovery. Pergamon Press, Oxford, Great Britain.

MITCHELL, E. 1975. Preliminary report on Nova Scotia fishery for sperm whales (*Physeter catodon*). Rep. Int. Whaling Comm. 25: 226–235.

NORRIS, K. S., AND G. W. HARVEY. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon*), p. 397–417. *In* S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville [ed.] Animal orientation and navigation. NASA Spec. Publ. 262.

PAPASTAVROU, V. 1987. Feeding ecology of sperm whales *Physeter macrocephalus* in the Galapagos Islands. M.Sc. thesis, University of Bristol, Bristol, Great Britain.

WATKINS, W. A. 1980. Acoustics and behavior of sperm whales, p. 283–289. *In* R.-G. Busnel and J. F. Fish [ed.] Animal sonar systems. Plenum Press, New York, NY.

WATKINS, W. A., K. E. MOORE, AND P. TYACK. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. Cetology 49: 1–15.

WATKINS, W. A., AND W. E. SCHEVILL. 1977. Sperm whale codas. J. Acoust. Soc. Am. 62: 1485–1490.

WEILGART, L. S., AND H. WHITEHEAD. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Can. J. Zool. 66. (In press)

WHITEHEAD, H., AND T. ARNBOM. 1987. Social organization of sperm whales off the Galapagos Islands, February–April 1985. Can. J. Zool. 65: 913–919.

WHITEHEAD, H., AND J. GORDON. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Rep. Int. Whaling Comm. (Special Issue 8): 149–166.