RADIO TRACKING THE MOVEMENTS AND ACTIVITIES OF HARBOR PORPOISES, *PHOCOENA PHOCOENA* (L.), IN THE BAY OF FUNDY, CANADA

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ABSTRACT

Eight harbor porpoises were radio-tagged (172-173 MHz) and released in the western Bay of Fundy between August 1981 and August 1983. The duration of contact with radio-tagged animals ranged from 0.3 to 22.4 days. One harbor porpoise was tracked for 22.4 days and utilized a home range area of 210 km^2. In all observed cases, the movement of radio-tagged porpoises coincided with the direction of tidal flow in the major channels and passages of the region. Analysis of 39.2 hours of ventilation sequences revealed that radio-tagged porpoises were relatively inactive from midnight until 0600 and more active during other periods.

This report documents the results of a study on the movements and activities of radio-tagged harbor porpoises, *Phocoena phocoena*, in the Bay of Fundy, Canada. The primary objective of this research was to determine the home ranges of individual harbor porpoises during the summer months. The study also provided insights into the behavior and activities of radio-tagged animals.

Studies of cetacean home ranges often rely on resightings of tagged or naturally marked animals (Irvine et al. 1981; Bigg 1982; Dorsey 1983). These methods are of limited value if individual animals travel outside the area under observation and may result in underestimation of the utilized range. A more effective means of estimating home range area is to monitor the movements of radio-tagged individuals (McDonald et al. 1979). Several recent studies have successfully employed radio-tracking techniques in field studies of cetacean species (see review by Leatherwood and Evans 1979). Notable among these are investigations of *Delphinus delphis* by Evans (1971), of *Tursiops truncatus* by Irvine et al. (1981), and of *Lagenorhynchus obscurus* by Würsig (1982).

In a preliminary study of harbor porpoise movements (Gaskin et al. 1975), we demonstrated that radio-tracking techniques could be successfully applied to this species. Although this initial research was promising, we felt that the transmitters available at that time were too large to be carried by these small porpoises (see Watson and Gaskin 1983). The recent development of smaller transmitters and the continuing availability of live porpoises from herring weirs (Smith et al. 1983) have enabled us to undertake the present study.

METHODS

The study area encompases Passamaquoddy Bay, the channels and passages around Deer Island, and waters further offshore to Grand Manan Island (Fig. 1). During the summer, mean monthly water temperatures for the upper 25 m of the water column range from 6.4° in June to 11.0°C in September (Bailey et al. 1954). The oceanography of the region is dominated by large semidiurnal tides, which have a mean amplitude of 5.5 m at North Head, Grand Manan (Anonymous 1982). The large tides generate strong currents, with velocities reaching a maximum of 2.4 m/s in Letite Passage (Forrester 1960). Further information regarding the oceanography of the region may be found in Smith et al. (1984).

Harbor porpoises were seined from herring weirs (Smith et al. 1983), placed on a sheet of open cell foam, sexed, and measured. The porpoises were liberally sprinkled with seawater throughout the tagging procedure to prevent overheating. Two 0.64 cm diameter holes were bored through the dorsal fin with a laboratory cork borer, cleansed in alcohol prior to use. The holes were immediately cold-cauterized with a histological freezing spray.

Transmitters were attached to the dorsal fin with two 0.64 cm diameter stainless steel bolts, each covered with a thin sleeve of teflon (see Figure 2). A thin, neoprene-lined plastic plate was placed between the transmitter and dorsal fin and an identical plate was positioned on the opposite side of the

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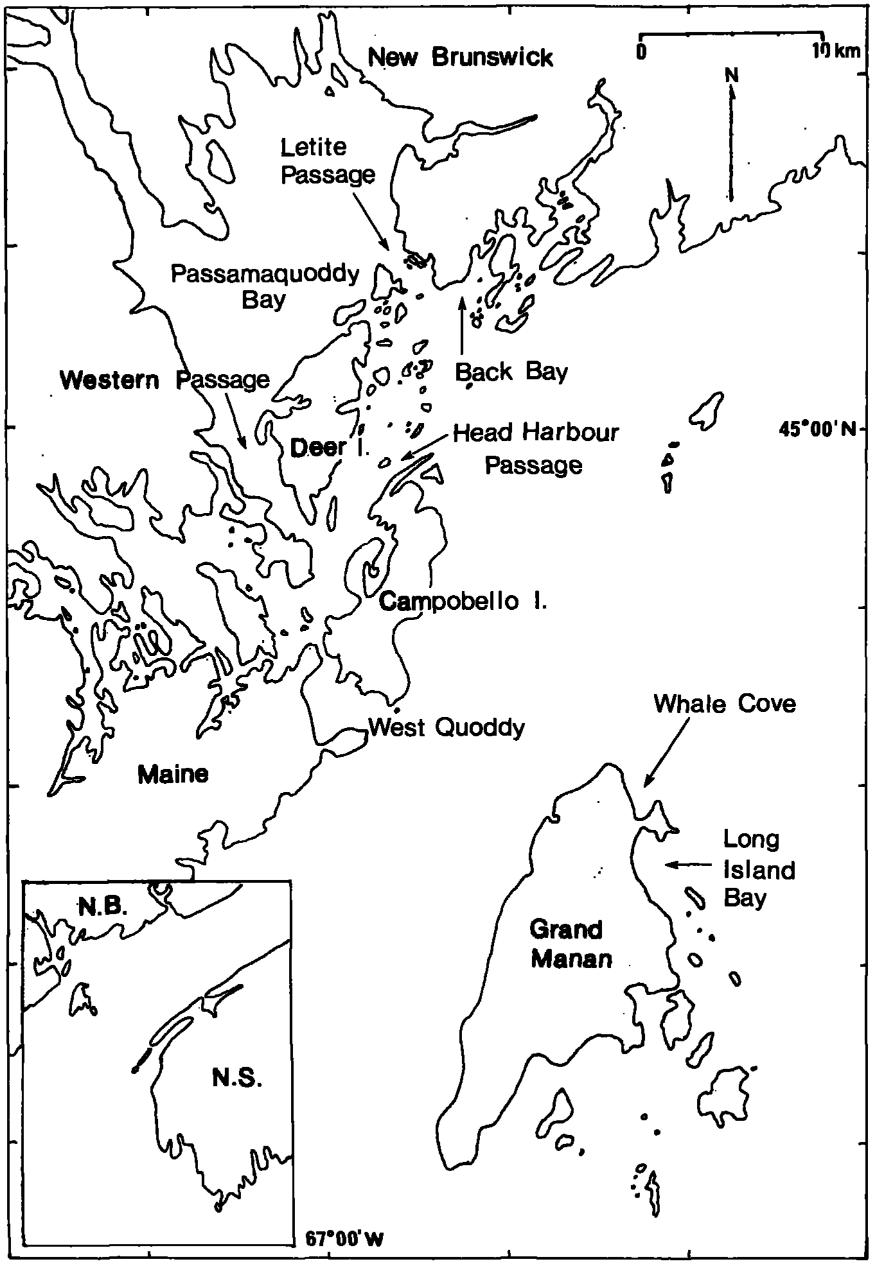


FIGURE 1.—The harbor porpoise study area with place names mentioned in text. The inset shows the study area in relation to the rest of the Bay of Fundy.

fin. The teflon-covered bolts, passed through the transmitter and plastic plates, were fastened with corrodable, low grade steel nuts.

The radio transmitters measured 3.2 × 3.8 × 6.0 cm and weighed about 170 g in air (Model 4-A, Telonics,[2] Mesa, AZ). The transmitting antennae consisted of 43 cm semiflexible whips, designed specifically for use with marine mammals.

Transmitted VHF signals (172-173 MHz) consisted

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

of 20-60 ms pulses at intervals of 0.4 s. Lithium batteries provided a maximum power output of 0.75 mW and an expected transmitting life of 1.6-6.0 mo. The maximum transmitting range across open water was about 15-20 km.

We used a Telonics TR-2 telemetry receiver with a two-element, hand-held directional antenna. The approximate direction of the transmitter was determined by rotating the antenna and noting the strongest signal. A digital data processor (Telonics TDP-2) provided a visual display of signal strength.

The position of a tagged porpoise was determined either by tracking the animal until visual contact was established, or by triangulation from shore. In the latter method, the receiving system was moved along the shore, and signal bearings at two or more locations were noted. The intersection point of these bearings was then used to approximate the position

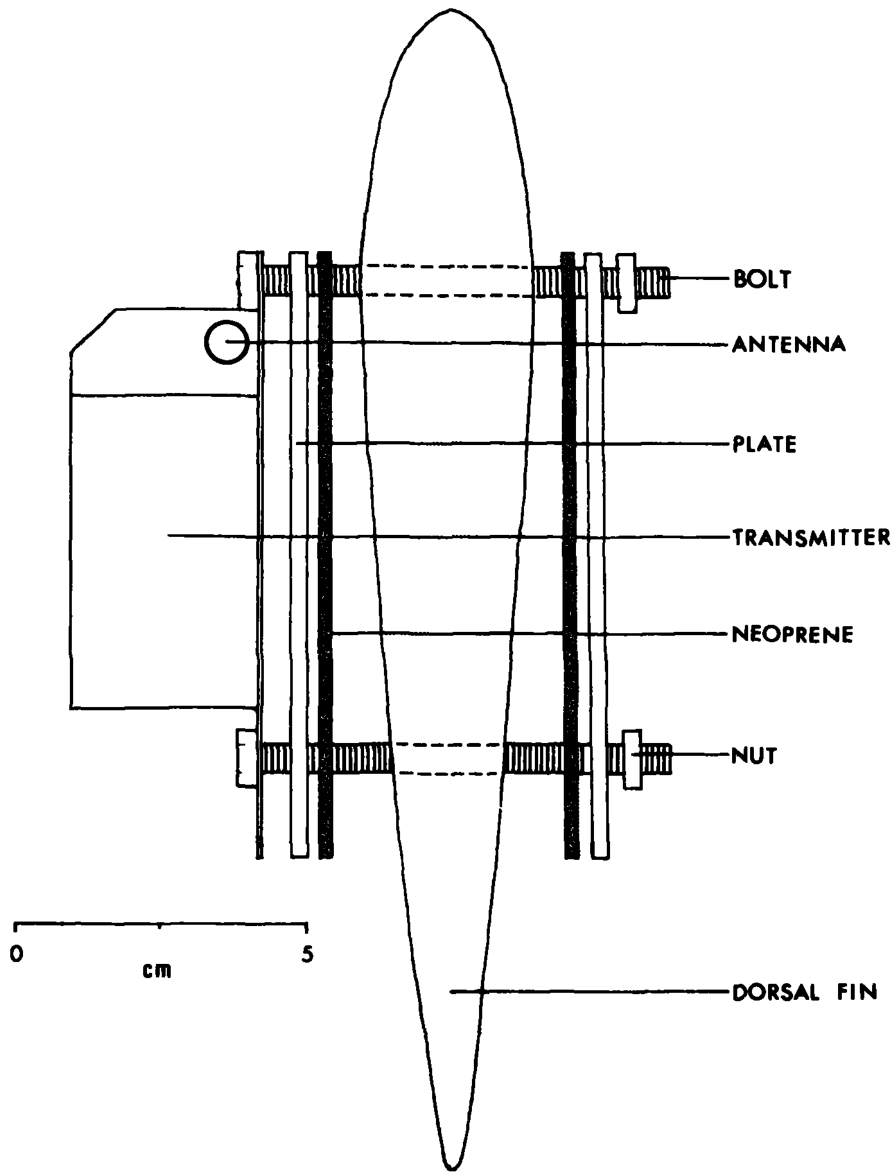


FIGURE 2.—The transmitter package used in radio-tracking studies of harbor porpoises in the Bay of Fundy. The bolts attaching the transmitter to the dorsal fin were covered by thin teflon sleeves.

of the porpoise. To ensure bearing accuracy, a series of readings were taken at each location, and the average used in triangulation (Springer 1979). Each sighting or radio location was assigned to a 1 km grid square of the Universal Transverse Mercator System. Derived radio locations were discarded if the triangulation could not place a porpoise within a 1 km square; the time elapsed between fixes and bearing error ($\pm 5°$) precluded more precise estimation. Positional data were collected at least once a day, but usually on a more frequent basis.

The radio signal was received only when the transmitting antenna was exposed, allowing the duration of both submergence and surface periods to be recorded. Such ventilation data were collected on an opportunistic basis throughout the tracking period of each porpoise.

A detailed analysis of the methods used in this study is presented in Read and Gaskin (1983).

RESULTS

Movements

Eight harbor porpoises were released carrying transmitters over the course of the study (Table 1). During the attachment procedure, porpoises were out of the water for a mean of 6.6 min (SD $\pm$ 1.4, n = 8), during which time most animals remained fairly still. Only two porpoises exhibited any trauma while being handled; RT-5 vomited briefly, and RT-7 (a 110 cm calf) repeatedly lashed its flukes. The latter porpoise appeared momentarily disoriented when returned to the water, but quickly resumed swimming and surfacing normally after being joined by a larger porpoise. The larger animal, presumably the calf's mother, had also been trapped in the weir, but escaped overnight and remained in the vicinity until the calf's release.

Duration of radio contact ranged from 0.30 (RT-5) to 22.4 d (RT-2), with a mean of 5.1 d (SD $\pm$ 7.1, n = 8). In some instances, loss of radio contact may have been due to the premature release of the transmitter package. The rear bolt attaching the transmitter to the dorsal fin of RT-3 was missing when the porpoise was photographed 5 h before signal loss occurred. The radio signals of RT-3 and RT-7 were being monitored when contact was lost, and in both cases termination of the signal was abrupt, a pattern compatible with the hypothesis of transmitter loss. In our limited observations of radio-tagged porpoises (see below), we did not see any evidence of displacement of the transmitter package (Irvine et al. 1982).

TABLE 1.—Data summary for harbor porpoises radio-tagged and released in the western Bay of Fundy.

Porpoise code	Length (cm)	Sex	Frequency (MHz)	Date of Release	Duration of contact (d)
RT-1	132	M	173.350	05 08 81	3.05
RT-2	119	M	173.550	20 08 81	22.4
RT-3	145	M	173.500	29 07 82	5.32
RT-4	131	F	173.100	31 08 82	3.16
RT-5	114	M	173.000	31 08 82	0.30
RT-6	116	M	173.700	01 09 82	2.72
RT-7	110	M	173.650	03 09 82	1.83
RT-8	114	M	172.600	09 08 83	2.25

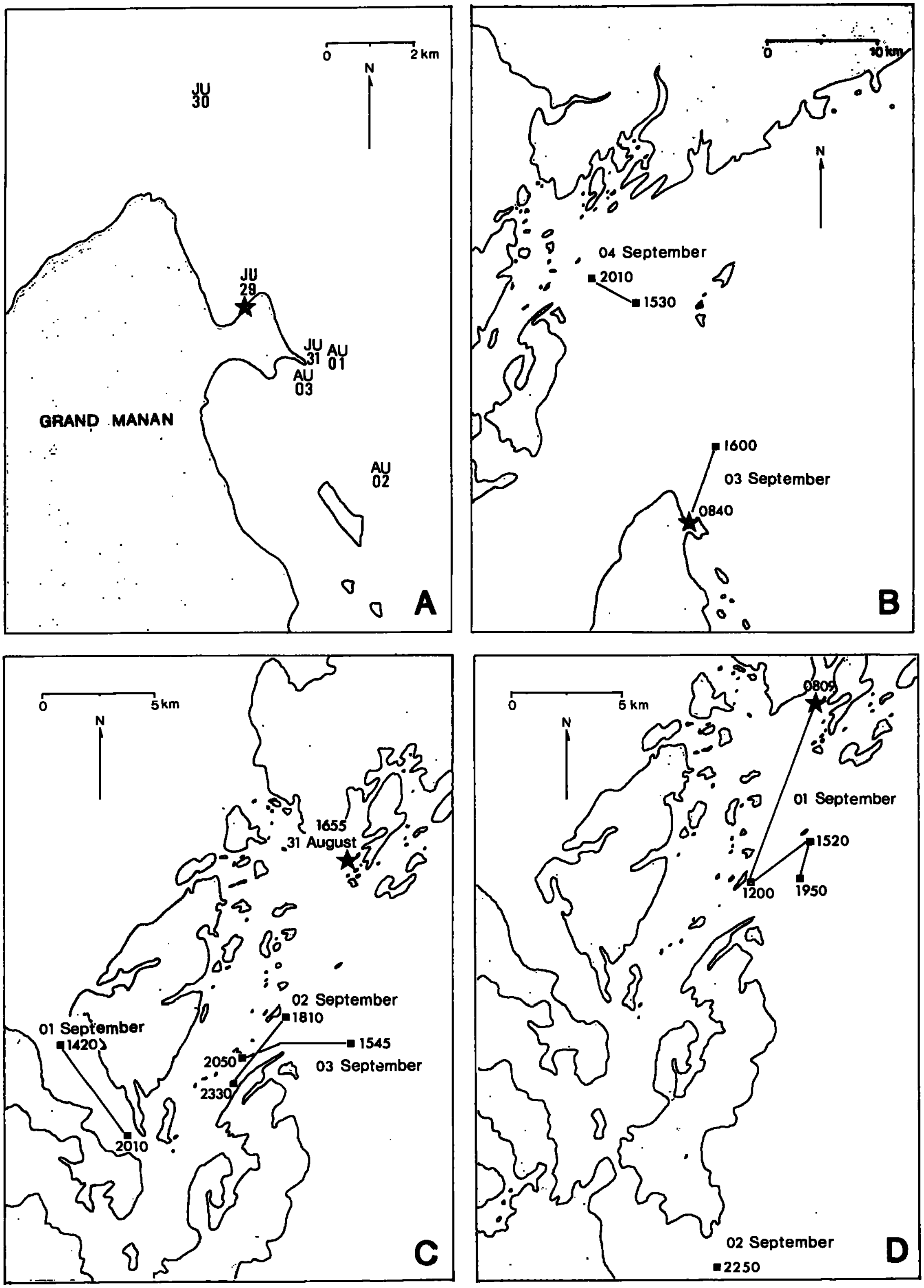
Over the course of the study, three porpoises were released from the same weir in Whale Cove, Grand Manan. Attempts to relocate RT-1, the first porpoise released in Whale Cove, were frustrated by fog and heavy seas which persisted for the entire 3-d tracking period. In addition, the shoreline configuration of northern Grand Manan prevented accurate triangulation. However, the strength and direction of the signal received from shore indicated that the porpoise remained in the vicinity of northern Grand Manan until signal loss occurred. The movements of the other two porpoises released in Whale Cove (RT-3 and RT-7) are illustrated in Figure 3A and B.

On 30 August 1982, four porpoises were reported trapped in a weir in Back Bay, mainland New Brunswick. A female (RT-4), accompanied by a 101 cm calf, and a young male (RT-5) were released on 31 August. The remaining porpoise, another young male (RT-6), was tagged and released the following day. RT-4 and RT-5 remained together for at least 7 h, after which contact was lost with RT-5. The movements of RT-4 and RT-6 are depicted in Figure 3C and D.

The longest tracking sequence recorded in this study was that of RT-2, released near St. Andrews, mainland New Brunswick. This porpoise spent the majority of its 22-d tracking period within Passamaquoddy Bay, although occasional excursions were made to the east of Deer Island (Fig. 4). The home range of RT-2, calculated using the convex polygon method, was about 210 km^2 (excluding land masses).

RT-8, the only porpoise to be radio-tagged in 1983, travelled from its release point in northern Passamaquoddy Bay to West Quoddy in about 48 h. Logistical constraints prevented more precise determination of the movements of this animal.

FIGURE 3.—Movements and positions of radio-tagged harbor porpoises in the Bay of Fundy. The release point of each porpoise is indicated by a star. A) Position of porpoise RT-3 at 1200 of each day of tracking period; B) Movements of porpoise RT-7; C) Movements of porpoise RT-4; D) Movements of porpoise RT-6.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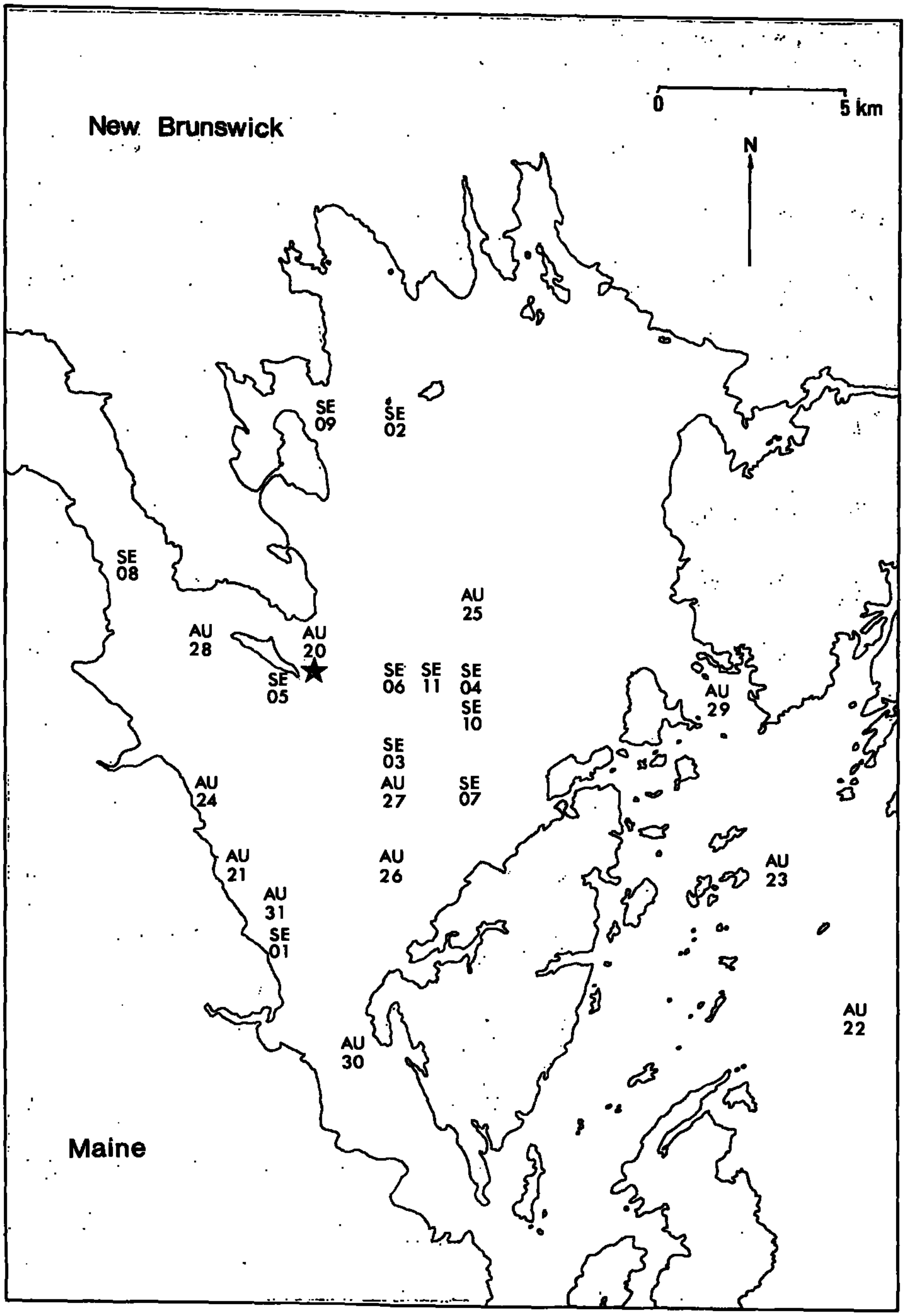

FIGURE 4.—Position of porpoise RT-2 at 1200 of each day of tracking period in the western Bay of Fundy.

The movements of three radio-tagged porpoises (RT-2, RT-4, RT-6) were tracked through the major passages around Deer Island on seven occasions. In all cases, the direction of movement coincided with the direction of tidal flow. The strong correlation between porpoise movements and current direction in these areas was demonstrated on 30 August 1981, when RT-2 moved up Western Passage with the flood tide, turned at slack high water and moved out with the ebb.

Two radio-tagged porpoises were resighted on several occasions. RT-2 was observed resting at the surface in the approaches to Head Harbour Passage on 22 August 1981. Although the porpoise was alone, several groups of resting animals were present in the vicinity. RT-3 was resighted on six occasions; during five of these sightings the radio-tagged animal was accompanied by a single large porpoise. These observations gave no indication that the transmitter packages affected the behavior of tagged porpoises.

Attempts to relocate radio-tagged animals demonstrated some of the inherent problems involved in censusing harbor porpoise populations. Even with the aid of directional receivers and brightly painted transmitters, it was difficult to sight a tagged porpoise or to follow its movements after it had been located. It proved particularly difficult to see radio-tagged porpoises while they lay motionless at the surface.

Patterns of Activity

In total, 39.2 h of ventilation sequences were recorded from four radio-tagged porpoises (RT-2, RT-3, RT-4, RT-7). These sequences comprised 4,680 individual dives, lasting from 2 to 195 s.

Two types of signals were received from radio-tagged animals. The most common signal was brief (1-3 s) and indicated that the porpoise had surfaced and submerged in a continuous motion. Such action patterns are commonly referred to as rolls (Amundin 1974; Smith et al. 1976). Other signals were more prolonged (4-100 s) and are referred to here as surface periods.

Prolonged signals received from radio-tagged harbor porpoises have previously been interpreted as near-surface swimming (Gaskin et al. 1975). However, visual observations of radio-tagged animals RT-2 and RT-3 indicated that such signals originated from porpoises resting motionless at the surface. The strength of the transmitted signal attenuated rapidly as the length of exposed antenna decreased, making it unlikely that signals could be received at any distance from porpoises swimming just below the surface (see also Frost et al.[3]).

Radio-tagged porpoises exhibited two readily discernible activity states (Fig. 5). Low activity (or relative inactivity) was characterized by frequent surface resting periods interspersed with rolls; resting periods accounted for over 55% of all signals in this activity state. Porpoises were considered active (high activity) when resting periods were absent or infrequently recorded. It is important to note that porpoises did not rest at the surface when wave height was >30 cm and winds speeds exceeded 13 km/h (see also Dudok van Heel 1962; Andersen and Dziedzic 1964).

[3]Frost, K. J., L. F. Lowry, and R. R. Nelson. 1983. Investigations of belukha whales in coastal waters of western and northern Alaska, 1982-1983; marking and tracking of whales in Bristol Bay. Final Report, Contract NA 81 RAC 00049, 104 p.

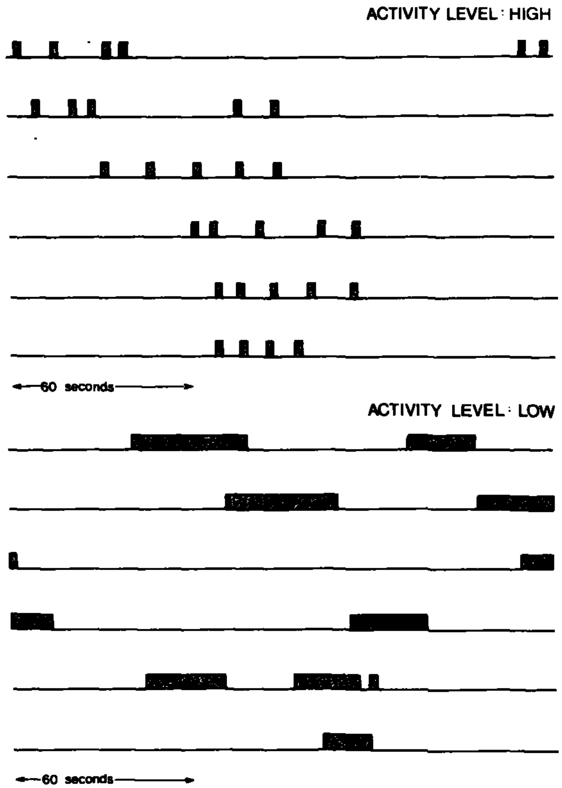

FIGURE 5.—Examples of signal patterns used to derive activity states of radio-tagged harbor porpoises (each example represents a continuous record). Activity level was considered high when signals were dominated by rolls (signal duration 1-3 s). Activity level was considered low when signals were dominated by surface resting intervals (signal duration >3 s). The signal pattern used to demonstrate the high activity level (top) is characteristic of Pattern B respiration (Watson and Gaskin 1983).

Radio-tagged porpoises exhibiting the high activity state expressed two ventilation patterns; these are described using the terminology of Watson and Gaskin (1983). Most data recorded in this activity state consisted of Pattern B, a series of long dives, each followed by a sequence of several rolls (see Figure 5). Less commonly observed was Pattern A, in which single rolls followed relatively short submergences (seldom exceeding 30 s in duration). Pattern A was exhibited for brief periods only (5-16 min) and comprised <4% of all signals recorded during high activity sequences.

Ventilation data recorded from RT-2 and RT-4 were dominated by low activity sequences. However, low activity sequences were not recorded from either RT-3 or RT-7. Although RT-3 was frequently observed resting at the surface, the loose transmitter package (see above) caused the antenna to reflect backwards, allowing signal reception only during rolls. Thus, it was not possible to accurately monitor the duration of resting periods for this porpoise. Data from RT-7 were acquired only during periods of high winds and heavy seas which precluded surface resting behavior.

Because surface resting was the criterion on which determinations of activity levels were based, it was impossible to ascertain the activity level of radio-tagged porpoises in periods of high winds and heavy seas. To construct an activity budget, therefore, it was necessary to exclude data recorded during periods when surface resting was not possible. A total of 10.5 h of ventilation sequences were recorded under such conditions. In addition, data acquired from RT-3 were excluded because of the bias imposed by the transmitting system. After these data had been deleted, 24.5 h of ventilation sequences recorded from RT-2 and RT-4 remained.

Both RT-2 and RT-4 were relatively inactive from midnight until 0600, spending over 90% of this period in the low activity state. Both porpoises spent a considerable portion of this time resting at the surface (Table 2). During this period of reduced activity, the porpoises were seldom located in nearshore areas, although they frequented such areas during other periods. The two porpoises were highly active for 35% (RT-2) and 36% (RT-4) of daylight and evening hours (0600 until midnight) (Table 2).

DISCUSSION

Movements and Ranges

Radio-tagged harbor porpoises demonstrated considerable mobility within the study area, often moving distances of 15-20 km in a 24-h period. These results are similar to those previously reported from radio-tagged harbor porpoises in the region (Gaskin et al. 1975). Other inshore odontocete species exhibit daily movements of a similar magnitude. For example, dusky dolphins, *Lagenorhynchus obscurus*, tracked by Würsig (1982), travelled a "mean minimum distance" of 19.2 km each day. However, pelagic species apparently travel over much greater distances. A pelagic spotted dolphin, *Stenella attenuata*, tracked by Leatherwood and Ljungblad (1979), travelled over 100 km in a 12-h period, while common dolphins, *Delphinus delphis*, may cover distances of 70-140 km each day (Evans 1971).

The mobility exhibited by the majority of radio-tagged porpoises suggest that the ranges of these animals were similar to that calculated for RT-2 (210 km^2). Only one other study has examined the areas of home ranges utilized by odontocete cetaceans. Wells et al. (1980) used resightings of naturally marked animals to estimate the size of bottlenose dolphin, *Tursiops truncatus*, ranges in the coastal waters of western Florida. The mean home ranges of these dolphins varied with age and sex, and ranged from 15 to 41 km^2. It is possible that the apparent difference in the size of home ranges of these two species reflects the exploitation of different prey species. In the Bay of Fundy, harbor porpoises feed predominantly on juvenile herring, *Clupea harengus* (Smith and Gaskin 1974), which exhibit a high degree of mobility (Jovellanos and Gaskin 1983). In contrast, Florida bottlenose dolphins are opportunistic predators on species such as mullet *Mugil cephalus*, which may be more sedentary in nature (Irvine et al. 1981).

Patterns of Activity

The patterns of activity observed in the present

TABLE 2.—Activity patterns of radio-tagged harbor porpoises RT-2 and RT-4 in the western Bay of Fundy. The low activity state was characterized by frequent surface resting periods, which were infrequent or absent in the high activity state. Only data recorded during calm conditions have been included.

Porpoise	Time	Observation time (min)	Activity: high (%)	Activity: low (%)	At surface (%)
RT-2	0000-0559	352.9	2.0	98.0	31.4
	0600-1159	274.8	14.9	85.1	18.8
	1200-1759	435.2	46.0	54.0	11.2
	1800-2359	165.2	41.0	59.0	12.2
Total		1,228.5	25.7	74.3	18.8
RT-4	0000-0559	116.0	7.0	93.0	18.5
	0600-1159	37.0	100.0	0.0	0.0
	1200-1759	0.0	—	—	—
	1800-2359	90.7	9.9	90.1	13.6
Total		243.7	22.2	77.8	13.9

study do not support previous contentions that the metabolic requirements of harbor porpoises (see Kanwisher and Sundnes 1965) are such that individuals must spend a large proportion of each day engaged in foraging behavior (Smith and Gaskin 1974; Watson and Gaskin 1983).

Herbers (1981) has hypothesized that behavioral inactivity is a product of predation efficiency. As predation efficiency increases, less time is spent searching for and capturing prey, and more time is available for other behavior, including inactivity. Therefore, if harbor porpoises are efficient predators, it seems reasonable to suggest that only a small portion of their day would be spent engaged in foraging behavior.

Many other mammalian predators are inactive for large portions of the day. For example, Serengeti lions, *Panthera leo*, are inactive for about 85% of each day (Schaller 1972). Similarly, spotted hyaenas, *Crocuta crocuta*, are inactive for 84% of the day (Kruuk 1972). Even the sea otter, *Enhydra lutris*, with a metabolic rate 2.4 times that predicted for a terrestrial mammal of equal size (Costa and Kooyman 1982), spends only 34% of each day foraging (Loughlin 1979).

The ventilation sequences recorded from RT-2 and RT-4 suggest that these harbor porpoises restricted the majority of their activity to daylight and evening hours (Table 2). If a circadian pattern of activity exists, it may be related to the schooling behavior of prey species. The structure of herring schools breaks down after dusk, as the visual cues used to maintain school structure become inoperative (Brawn 1960). Thus, the fish exhibit a dispersed distribution at night, presumably limiting prey capture by predators such as the harbor porpoises, which rely on dense schools to maintain maximum capture efficiency.

Other odontocete species exhibit various circadian patterns of activity. Observations of captive bottlenose dolphins indicate that, like the harbor porpoise, *Tursiops* is relatively inactive at night (McBride and Hebb 1948; McCormick 1969; Saayman et al. 1973). In contrast, Hawaiian spinner dolphins, *Stenella longirostris*, rest during the day and feed almost exclusively at night (Norris and Dohl 1980). The prey of spinner dolphins undertake extensive vertical migrations (Perrin et al. 1973) and may be more available to the dolphins at night.

We were interested in observing the nocturnal behavior of harbor porpoises (when they were presumably relatively inactive) under conditions of strong winds and heavy seas, when surface resting was not possible. Ventilation data recorded from RT-7 during a 5-h period (0000-0500, 5 September 1982) of heavy seas consisted almost exclusively of Pattern B sequences. Watson and Gaskin (1983) have suggested that this ventilation pattern is expressed primarily by foraging porpoises, but it seems unlikely that RT-7 (a calf) was foraging for 5 consecutive hours at night. An alternative explanation is that the porpoise was resting underwater and rising to the surface for a series of breaths (see similar observations by McBride and Hebb 1948; Layne 1958; McCormick 1969; Condy et al. 1978). It is possible, therefore, that harbor porpoises engaged in diverse behavioral activities may exhibit similar ventilation patterns.

During the period of reduced activity (from 0000 to 0600) radio-tagged porpoises were often located in open water some distance from shore. This may reflect a tendency for porpoises to rest in areas where the hazards of swift currents and shallow waters are minimized. Observations made in the inshore waters of the Deer Island region confirm that porpoises seldom rest at the surface in nearshore environments (Watson and Gaskin 1983).

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