

A. J. Read · A. J. Westgate

## Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry

Received: 4 February 1997 / Accepted: 25 August 1997

**Abstract** The movements of nine harbour porpoises, *Phocoena phocoena* (L.), in the Bay of Fundy and Gulf of Maine were tracked using satellite telemetry. Transmitters were attached to the porpoises in August 1994 and 1995 after they were captured near Grand Manan Island at the mouth of the Bay of Fundy. Tracking periods ranged from 2 to 212 d (mean  $50 \pm 65$  d). Porpoises exhibited a high degree of individual variation in movement patterns; five moved out of the Bay of Fundy into the Gulf of Maine. The porpoise with the longest tracking period moved extensively throughout the Gulf of Maine. These data suggest that seasonal movement patterns of individual harbour porpoises are discrete and are not temporally coordinated migrations. Porpoises that moved out of the Bay of Fundy into the Gulf of Maine did so following the 92 m isobath, which may represent an important movement corridor. The movement of porpoises from the Bay of Fundy into the Gulf of Maine supports the hypothesis that harbour porpoises from these two regions comprise a single population at risk of entanglement in both Canadian and US fisheries.

### Introduction

Harbour porpoises (*Phocoena phocoena*) are distributed throughout coastal waters of the temperate northern hemisphere. The general distribution of the species is known from sighting data, strandings, and incidental catches in commercial fisheries (IWC 1996). Little is known, however, about the daily movements of indi-

vidual porpoises or of the seasonal movements of porpoise populations.

An understanding of the scale, pattern and variability of movements is of both fundamental and applied interest to biologists studying the ecology of this species. Information on distribution and movement patterns is required to understand the relationships between porpoises, their prey, and abiotic factors such as temperature. Such information is also necessary for the conservation of this species. Throughout their range, harbour porpoises are vulnerable to entanglement and mortality in gillnets (Jefferson and Curry 1994). Mortality in these gillnets may threaten the viability of affected populations (IWC 1996). For example, recent estimates of harbour porpoise mortality in gillnet fisheries in the Bay of Fundy and Gulf of Maine range from 2.7 to 4.3% of the total population size (Bravington and Bisack 1996; Trippel et al. 1996). These removals are unlikely to be sustainable (Woodley and Read 1991), which has prompted conservation action, such as time-area restrictions on commercial fisheries, in both Canada and the United States (Palka et al. 1996). For conservation strategies intended to reduce porpoise mortality in commercial fisheries to be effective, information is required on the movement patterns of porpoises and the distribution of fishing effort.

Knowledge of the movements of harbour porpoises has been limited because they are difficult to study at sea due to their small size, subtle individual markings (Koopman and Gaskin 1994) and the limited time they spend at the surface (Westgate et al. 1995). To overcome these logistical difficulties, VHF radio transmitters have been placed on harbour porpoises in the Bay of Fundy, allowing researchers to follow the movements of individuals for periods up to 22 d (Gaskin et al. 1975; Read and Gaskin 1985; Westgate et al. 1995). Despite the potential of this technique, these telemetry studies were hampered by short periods of contact with tagged porpoises due to the difficulty of tracking at sea. This radio telemetry approach is not feasible for long-term studies

---

Communicated by J.P. Grassle, New Brunswick

A.J. Read (✉) · A.J. Westgate  
Nicholas School of the Environment,  
Duke University Marine Laboratory,  
135 Duke Marine Lab Road, Beaufort,  
North Carolina 28516, USA

of the movements of marine mammals because of the logistical difficulty tracking individuals at sea for months at a time.

The use of satellite-linked telemetry (Fancy et al. 1988) has revolutionized the study of marine mammals. It is now possible to obtain long-term data on the movements and behaviour of tagged individuals via computer uplink to the laboratory. Satellite-linked transmitters have been successfully deployed on several species of cetaceans (Mate 1989; Martin and Smith 1992; Mate et al. 1992, 1994, 1995; Martin et al. 1993, 1994; Davis et al. 1996; Watkins et al. 1996), but their use on smaller species, such as harbour porpoises, has been restricted because the transmitters were too large. Recent advances in tag miniaturization have made satellite-linked telemetry appropriate for use with harbour porpoises for the first time.

In this paper we describe the long-term movements of nine harbour porpoises in the Bay of Fundy and Gulf of Maine using data obtained from satellite-linked telemetry. Our objectives were twofold: to improve our understanding of the scale over which porpoises travel on a seasonal basis; and to better understand their seasonal movements in relation to large-scale patterns of gillnet fishing effort in these areas.

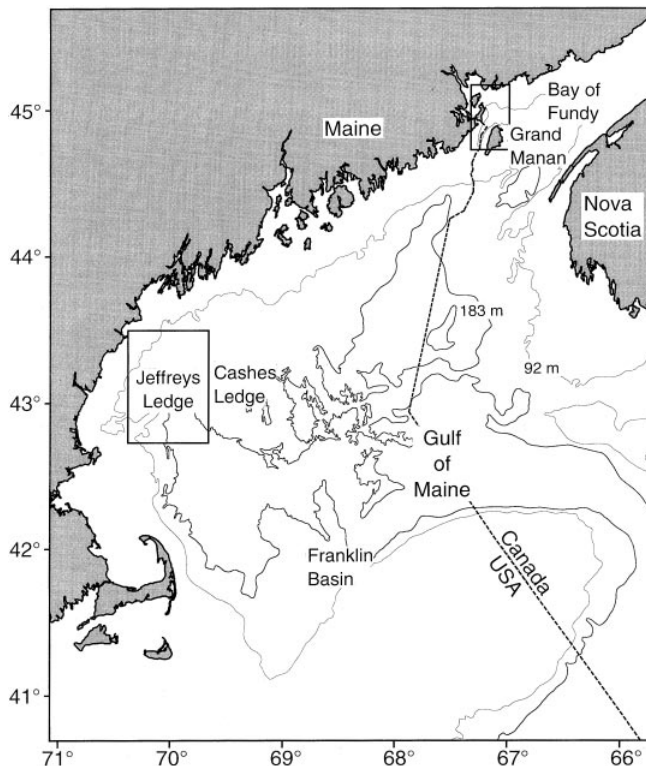
**Materials and methods**

**Porpoise capture**

Satellite-linked transmitters were placed on nine harbour porpoises, *Phocoena phocoena* (L.), released from herring weirs around Grand Manan Island, New Brunswick, Canada (44°45'N; 66°45'W), in August 1994 and 1995 (Table 1; Fig. 1). Porpoises were removed from weirs with a seine net, placed on a closed-cell foam pad and sponged with sea water. Body mass was measured with a spring balance or estimated from regressions using length and girth as predictive variables (Read and Tolley 1997) (Table 1). The blood chemistry and hematology of seven porpoises indicated that they were healthy, based on values of Koopman et al. (1995). The two adult females exhibited elevated levels of progesterone and were likely in the first trimester of pregnancy; one of these females (No. 1) was also lactating and accompanied by a calf.

**Transmitters**

Satellite-linked transmitters, or platform transmitter terminals (PTTs), were attached to the dorsal fin of each porpoise. Prior to



**Fig. 1** Map of study area including the lower portion of the Bay of Fundy and the Gulf of Maine. Boxes indicate the principal areas of harbour porpoise bycatch in bottom-set gillnets determined from Canadian (Trippel et al. 1996) and US (Bravington and Bisack 1996) fisheries observer programs

attachment, the dorsal fin was cleaned with a topical antiseptic and the tagging site was injected with 1 cc of lidocaine HCL 2%, epinephrine 1:100 000 at the location of each attachment pin. There were two PTT configurations (Telonics, Mesa, Arizona, USA): front-mount (*n* = 5) and side-mount (*n* = 4). The front-mount design used a stacked-board ST-10 PTT. This transmitter was encased in a steel cylinder and attached to a thin, neoprene-lined, polyethylene saddle which provided a firm base to secure the cylinder to the dorsal fin. The plastic saddle wrapped around the front of the dorsal fin and extended caudally approximately 3.5 cm; the transmitter was mounted on the leading edge of the saddle. The saddle was attached to the dorsal fin using three 8.0 mm diameter high density polyethylene or Delrin pins secured with steel lock nuts. The PTT was 15 cm long with a 17-cm whip antenna. The entire cylindrical PTT package, including saddle, weighed approximately 300 g in air. The side-mount configuration consisted of

**Table 1** *Phocoena phocoena*. Data on harbour porpoises equipped with satellite transmitters in 1994 and 1995 in the Bay of Fundy, Canada

	Ident. no.	Sex	Standard length (cm)	Body mass (kg)	Period of contact	Configuration	Tracking period (d)
1994	1	F	141	53 <sup>a</sup>	11 Aug–12 Aug	Front/VHF	2
	2	M	145	53 <sup>a</sup>	17 Aug–22 Aug	Front/VHF	6
	3	M	140	46	24 Aug–4 Sep	Front/VHF	21
1995	4	M	142	48	13 Aug–3 Sep	Front	21
	5	M	147	51	13 Aug–2 Sep	Front	19
	6	F	147	56	16 Aug–18 Sep	Side	33
	7	M	141	48	21 Aug–20 Mar (96)	Side/VHF	212
	8	M	151	54 <sup>a</sup>	21 Aug–26 Oct	Side	66
	9	M	140	47	21 Aug–27 Oct	Side	67

<sup>a</sup> Body mass estimated by predictive equations using length and girth (Read and Tolley 1997)

a flat-board ST-10 mounted in a low profile, rectangular, lexan box. These tags were attached directly to the side of the dorsal fin using three 6.5 mm Delrin pins. The backing plate on the transmitter housing provided attachment points for the pins. The pins passed through the backing plate and dorsal fin and were secured on the opposite side of the fin with steel lock nuts backed with small (30 × 1.5 mm) Delrin washers. Both backing plate and washers were lined with open cell foam. This tag had a 17-cm whip antenna, measured 11 × 5 × 2 cm, and weighed approximately 150 g in air.

To minimize the size of the PTT packages, we only used one environmental sensor, a surface time counter, which provided a cumulative record of the time the tag was above the water surface. The value of the surface time counter was transmitted twice during each signal, allowing us to detect transmission errors. Each tag also incorporated a salt-water switch, which prevented transmission when a porpoise was submerged. To further conserve battery life, we used a duty cycle of 8 h d<sup>-1</sup>. The PTTs were powered by two 2/3 A lithium cells which, under these operating conditions, were predicted to provide several months of battery life.

We also attached standard Model 2 VHF transmitters (ATS, Ipsanti, Minnesota, USA) on four porpoises fitted with PTTs. These tags transmitted at frequencies in the 148 MHz range at 110 pulses min<sup>-1</sup>, without a salt-water switch or duty cycle. VHF transmitters had life expectancies of > 50 d. Each tag was attached to a livestock ear tag (Jumbo roto-tag, Dalton Supplies, Nettlebed, England) which we applied to the trailing edge of the dorsal fin. VHF tags had 33-cm-long whip antennae, measured 1.1 × 2.5 × 5.5 cm and weighed 15 g. VHF transmitters had an effective range of ~5 km at sea level, with greater ranges for receivers on cliff tops or in airplanes.

#### Data analysis

Location and sensor data from each porpoise were obtained from Service ARGOS, Inc. (Landover, Maryland, USA) in ASCII format on magnetic media. In addition to the location and surface time data, Service ARGOS provided information on the quality of the estimated location. Location quality depends on the number of transmissions received from a PTT during a satellite overpass, the time elapsed between these receptions, movement of the PTT, and the stability of the transmitter oscillator. Each location was classified into one of four categories: Class 3 (at least six uplinks received in a single satellite pass, position accuracy better than 150 m), Class 2 (five uplinks received in a single satellite pass, position accuracy within 350 m), Class 1 (four uplinks received in a single satellite pass, position accuracy within 1 km), Class 0 (less than four uplinks received in a single satellite pass, position accuracy greater than 1 km). In addition, location estimates in Classes A (three uplinks received) and B (two messages received) were provided. The location estimates of these latter two classes were of unknown quality. All estimated locations were filtered using a speed plausibility check; consecutive positions resulting in an average travel speed of greater than 7.5 km h<sup>-1</sup> were excluded. This

filter value was selected based on published travel speeds (Gaskin et al. 1975; Westgate et al. 1995) and field observations of wild harbour porpoises. We tested each tag on shore prior to deployment, and obtained position estimates from known locations allowing us to ground-truth the accuracy of the location classes as provided by ARGOS.

Analysis of movement data was performed using Arcview Geographic Information System (GIS) (ESRI 1994). We included only the best position obtained per day from each porpoise to avoid bias associated with multiple daily positions. Mean daily distance travelled was calculated by summing the distance (km) between the best position received each day for all days of the deployment and then dividing this value by the number of days of the deployment. Mean rate of travel was calculated by dividing the distance (km) between sequential best daily positions by the time (h) that had elapsed between those positions. Mean distance from shore (km) was calculated by averaging the distance from the best daily position to the nearest mainland shoreline (including Grand Manan Island). The proportion of time spent in various water depths was estimated by assigning best daily positions to one of three bathymetric brackets: 0–92 m, 92–183 m, and > 183 m. Depth was estimated using bathymetry contours on digitized National Ocean Service (USA) and Canadian Hydrographic Service marine charts. The proportion of time spent at the surface was estimated using telemetered data from the surface time counter.

## Results

Data were obtained from tagged harbour porpoises (*Phocoena phocoena*) for periods ranging from 2 to 212 d. A total of 1334 locations were received on 447 tracking days. The mean number of positions per day for all location classes ranged from 1.9 ± 0.8 to 3.9 ± 0.9. Reliable location classes (0, 1, 2, 3) accounted for 53.8% of all position estimates (Table 2).

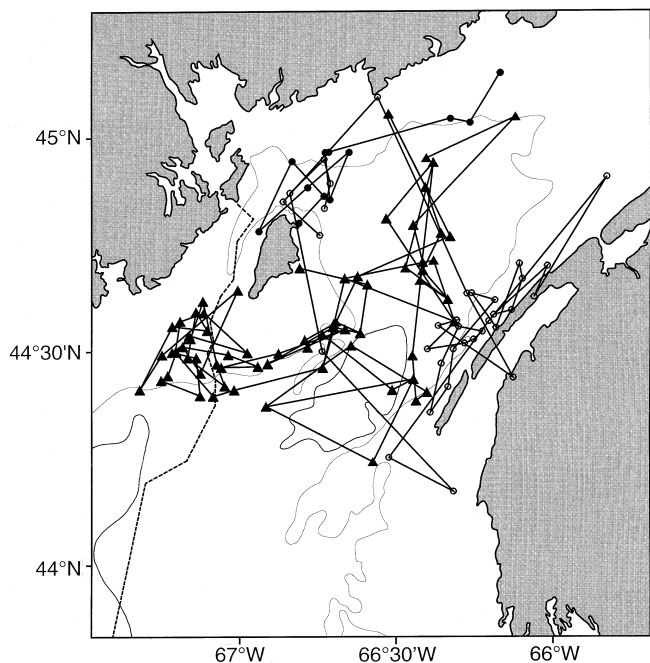
We used conventional radiotracking techniques to locate two of the four VHF tagged porpoises after release. The other two porpoises carrying VHF transmitters moved quickly out of range after release, making it impossible to relocate them. Porpoise No. 1 was relocated on the day following release and again 4 d later, after we had lost satellite contact with the PTT. From visual observation and photographs taken on this day, we noted that the polyethylene attachment pins had sheared and the entire PTT package had been lost. This observation led us to employ more robust Delrin attachment pins for the remaining deployments. We continued to monitor VHF radio signals from No. 1 until

**Table 2** *Phocoena phocoena*. Data on movements and surface behaviour calculated from tracking harbour porpoises equipped with satellite transmitters

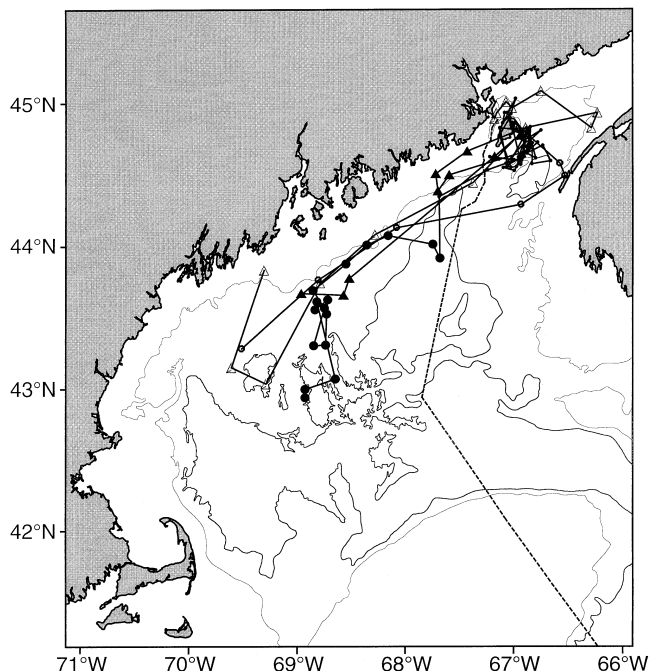
Ident. no.	Mean no. uplinks d <sup>-1</sup>	Mean daily distance travelled (km)	Mean rate of travel (km h <sup>-1</sup> )	Mean distance from shore (km)	Proportion of time spent at surface
1 <sup>a</sup>	NA	NA	NA	NA	NA
2	3.5	58.5	2.3 ± 1.3	27.3 ± 20.3	NA <sup>a</sup>
3	3.8	13.9	0.6 ± 0.4	11.5 ± 4.7	NA <sup>b</sup>
4	1.9 ± 0.8	34.1	1.6 ± 1.2	23.4 ± 20.9	0.05 ± 0.01
5	2.1 ± 0.7	22.6	1.1 ± 1.1	16.0 ± 15.4	0.07 ± 0.04
6	3.6 ± 0.7	18.1	0.8 ± 0.7	6.6 ± 5.1	0.04 ± 0.01
7	2.6 ± 1.2	28.1	1.2 ± 1.0	81.4 ± 44.8	0.03 ± 0.01
8	3.7 ± 1.0	15.0	0.6 ± 0.4	18.5 ± 6.4	0.05 ± 0.01
9	3.9 ± 0.9	17.6	0.7 ± 0.5	26.0 ± 26.1	0.04 ± 0.01

<sup>a</sup> Due to the short duration summary statistics were not calculated

<sup>b</sup> Due to an attachment failure that affected the salt-water switch, surface data were not calculated



**Fig. 2** *Phocoena phocoena*. Tracks of three harbour porpoises in the lower Bay of Fundy obtained from satellite telemetry. Only best daily positions are shown. Due to the brief tracking period of No. 1, movements of this porpoise are not shown (● No. 3; ○ No. 6; ▲ No. 8)

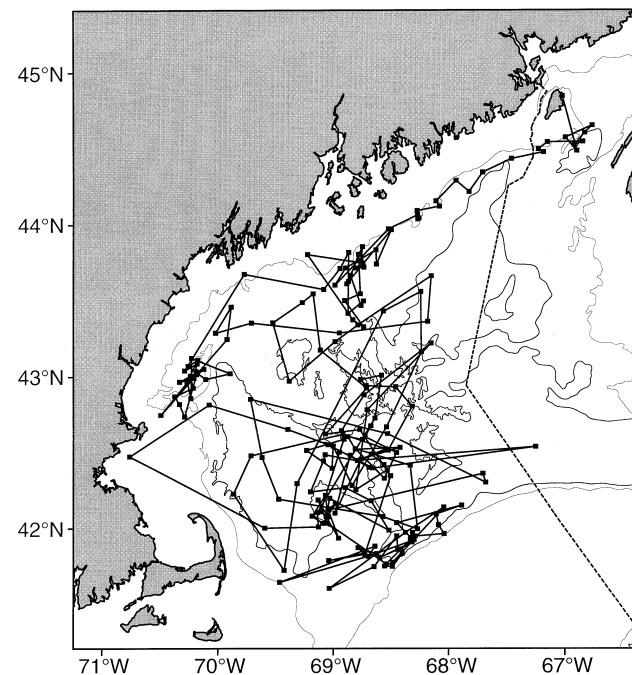


**Fig. 3** *Phocoena phocoena*. Tracks of four porpoises in the Bay of Fundy and Gulf of Maine obtained from satellite telemetry. Only best daily positions are shown (○ No. 2; △ No. 4; ▲ No. 5; ● No. 9)

31 August, visually relocating her and her calf on four other occasions. We also located No. 3, 7 d after release in a large group of feeding porpoises east of Grand Manan Island. In all of these sightings, tagged porpoises were swimming normally, usually in the company of other porpoises.

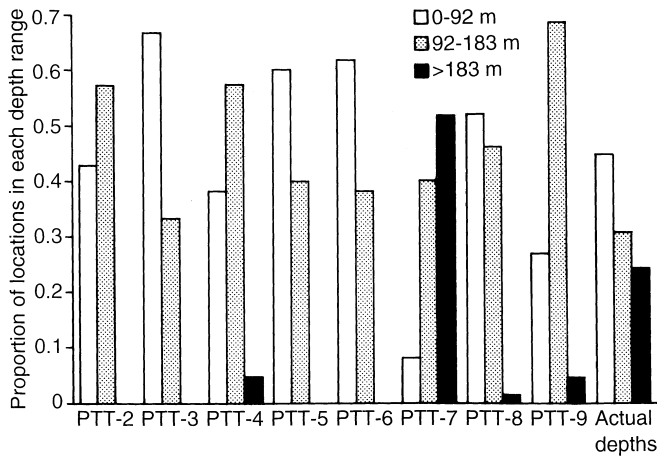
Tagged harbour porpoises displayed considerable variability in their movement patterns. Four (Nos. 1, 3, 6 and 8) remained in the Bay of Fundy throughout their tracking periods (2 to 66 d) (Fig. 2). These porpoises did not remain in the deep, central portions of the Bay for extended periods, although several traversed the deep water (>200 m) between Grand Manan and Nova Scotia. One porpoise (No. 8) spent several weeks to the southwest of Grand Manan. Tagged porpoises rarely moved further northeast into the Bay of Fundy than the northern tip of Grand Manan Island. All of the individuals that remained in the Bay of Fundy spent at least some time in the primary areas of Canadian gillnet fishing effort, located to the northeast and southwest of Grand Manan Island (Fig. 1).

Five tagged porpoises (Nos. 2, 4, 5, 7, 9) left the Bay of Fundy and did not return during their tracking periods (6 to 212 d) (Figs. 3, 4). None of these porpoises left the Gulf of Maine. When porpoises left the Bay of Fundy they moved southwest along the 92 m isobath. One of these porpoises, No. 7, had the longest tracking period (212 d) and moved extensively throughout the Gulf of Maine (Fig. 4). After release, this porpoise moved from the Bay of Fundy to Cashes Ledge in the



**Fig. 4** *Phocoena phocoena*. A 212-d track of a single harbour porpoise (No. 7) obtained from satellite telemetry. Only best daily positions are shown

Gulf of Maine, covering 300 km in 21 d. Porpoise No. 7 stayed in this area for approximately 1 month before travelling south to Jeffreys Ledge, where it remained during the height of the US autumn gillnet fishery. In mid-November, No. 7 moved directly east to the



**Fig. 5** *Phocoena phocoena*. Histogram showing the proportion of time spent in various water depths by porpoises as determined by satellite telemetry. Depths were calculated by assigning the best daily positions to one of three bathymetric brackets: 0–92 m, 92–183 m, or >183 m. Actual depths of the entire study area are shown in the column at far right

Franklin Basin and remained there through December. Between January and mid-March this porpoise travelled throughout the central Gulf of Maine.

Individual variability in porpoise movements was exemplified by the tracks of three adult male porpoises released from the same weir on 21 August 1995. One of these porpoises (No. 8) spent the entire 66-d tracking period in the Bay of Fundy (Fig. 2). The second porpoise (No. 9) remained southeast of Grand Manan Island in the Bay of Fundy for 25 d before moving southwest to Cashes Ledge in the Gulf of Maine (Fig. 3). The last porpoise (No. 7) immediately left the Bay of Fundy and spent the entire tracking period in the Gulf of Maine (Fig. 4).

Estimates of daily distance travelled were similar for all porpoises (13.9 to 28.1 km) with the exception of No. 2 with a mean daily distance of 58.5 km. Mean rates of travel ranged from 0.6 to 2.3 km h<sup>-1</sup>, but the rates of travel in longer tracking periods (>30 d) were similar (Table 2). Mean distances from shore ranged from 6.6 to 81.4 km with an overall mean of 50.2 ± 46.2 km. Porpoises spent between 3 ± 1 and 7 ± 4% of their tracking periods at the surface (Table 2). Tagged porpoises were most frequently (55% of locations) in water depths of 92 to 183 m and least frequently (12%) in depths >183 m (Fig. 5).

## Discussion

### Ecological significance

The movements of harbour porpoises (*Phocoena phocoena*) monitored by satellite telemetry can be interpreted at several scales. Individual porpoises often spent periods from days to weeks in fairly restricted areas.

Many of these areas, particularly in the waters to the southeast of Grand Manan Island (Fig. 3), the western shore of the Digby Peninsula (Fig. 2) and Jeffreys Ledge (Fig. 3), are known, from sighting surveys and aggregations of incidental catches in commercial fisheries, to be important habitat for this species (Gaskin 1984; Palka 1995; Palka et al. 1996). Other areas, like the waters to the southwest of Grand Manan Island (Fig. 2) and the Franklin Basin (Fig. 4) were not previously considered important porpoise habitat. Harbour porpoises are small endotherms (ca. 50 kg) which inhabit temperate waters (<10 °C) and are suspected to have a limited energy storage capacity (Koopman 1994). Given these energetic constraints, it may be advantageous for porpoises to maintain close proximity to aggregations of prey. Many areas that harbour porpoises frequented are known to support seasonal concentrations of Atlantic herring (*Clupea harengus*) (Stephenson et al. 1993), the primary prey of harbour porpoises in the Bay of Fundy and Gulf of Maine (Recchia and Read 1989). The periods of restricted movements recorded with satellite telemetry were consistent with previous findings from VHF telemetry studies of porpoises in the Bay of Fundy (Gaskin et al. 1975; Read and Gaskin 1985; Westgate et al. 1995).

Porpoises also made fairly rapid point-to-point excursions that lasted from several hours to several days. This directed travel was seen most frequently by porpoises exiting the Bay of Fundy along the 92 m isobath (Figs. 3, 4). This area may represent an important movement corridor connecting the Bay of Fundy and lower Gulf of Maine. The impetus for such short-term movements is unclear. Porpoises may undertake such movements in response to changes in local prey availability, the presence of predators, or to social factors. These rapid long-distance movements were not captured in previous VHF telemetry studies (Gaskin et al. 1975; Read and Gaskin 1985; Westgate et al. 1995) because of the limited range of the transmitters, the relatively small areas that could be effectively surveyed and the fact that porpoises were not tracked at sea for extended periods.

When the movements of tagged individuals are examined at their largest scale, it is clear that the home range of harbour porpoises occupies most of the Gulf of Maine and is much larger (ca. 50 000 km<sup>2</sup>) than the 210 km<sup>2</sup> previously estimated (Read and Gaskin 1985). Tagged porpoises moved throughout the Bay of Fundy and Gulf of Maine, covering hundreds of kilometers in a relatively short time. The mobility of these small porpoises was surprising and has forced us to reassess our concept of the scale at which they use their habitat on a seasonal and annual basis. In particular, the movements of Porpoise No. 7 illustrate the extensive use of the Gulf of Maine by these marine mammals. Prior to this study, our knowledge of the habitat use of harbour porpoises in the autumn and winter was limited to observations of incidental catches in gillnets. We can now better appreciate the dynamic nature of habitat utilization during this period.

The movements of porpoises from the Bay of Fundy into the Gulf of Maine, but not around the southwestern tip of Nova Scotia, supports Gaskin's (1984) hypothesis that harbour porpoises in the Bay of Fundy and Gulf of Maine comprise a single population. This finding corroborates other evidence from mtDNA studies (Wang et al. 1996), life history parameters (Read and Hohn 1995), and organochlorine profiles (Westgate et al. 1997). The current management strategy, based on the assumption of a single population in this region, is appropriate. These data also show that the seasonal movements of individual porpoises are discrete. The seasonal decline in harbour porpoise density in the Bay of Fundy during autumn (Gaskin 1984) is not the result of a coordinated migration, but a gradual net movement of porpoises into a wider geographic region. Records from strandings and incidental catches in commercial fisheries indicate that the winter distribution of harbour porpoises extends as far south as North Carolina (Gaskin 1984; Read et al. 1996). The movements of Porpoise No. 7, however, show that some individuals do not leave the Gulf of Maine during winter.

The values for the mean daily distance and mean rate of travel represent minimum estimates for harbour porpoises. The scale at which we measured these parameters, based on best sequential positions per day, misses much of the fine-scale movement exhibited by free-ranging porpoises (Westgate et al. 1995). The congruence between the mean daily distance and mean rate of travel among the discrete movements recorded from Porpoises Nos. 7, 8 and 9 (Figs. 2, 3, 4) reflects the coarseness of this scale. These values may therefore be more indicative of average porpoise movements within restricted areas (as discussed above) rather than between such areas. This is illustrated by the record from Porpoise No. 2, which had a much greater daily travel distance (58.5 km), a consequence of its relatively straight movement during the short tracking period.

Knowledge of the proportion of time a harbour porpoise spends at the surface is important for the design and analysis of abundance surveys. Data from the present study reflect the actual proportion of time (3 to 7%) that the salt-water switch, and hence the dorsal fin, was above the water surface. These values are very close to the true time that a harbour porpoise would be visible to observers aboard a survey vessel, and much less than estimates of the time porpoises spend in the upper 2 m of the water column (33 to 60%) (Westgate et al. 1995).

#### Conservation significance

The movements of harbour porpoises from areas of gillnet fishing effort in the Bay of Fundy to similar fishing grounds in the Gulf of Maine indicate that individuals in this population are at risk of entanglement during several periods of the year. For example, Porpoise No. 7 travelled from the most concentrated area of Canadian gillnet fishing effort in August to an area of

intense US gillnet activity later in the fall. These movements emphasize the trans-boundary nature of the Bay of Fundy/Gulf of Maine population.

These data allow us to evaluate, albeit in preliminary fashion, the efficacy of time-area fishery closures as a management strategy for reducing the level of incidental mortality. Our data indicate that porpoises exhibit a high degree of individual variability in their movements, suggesting that effective closures will have to be extensive in time and space. The fishing industry has proposed the use of trigger mechanisms, so that fishery closures would be tied to the appearance of harbour porpoises in particular areas, thus minimizing disruptions to fishing activity. Our results suggest that the movement patterns of individual harbour porpoises are extremely variable and are not currently predictable on a scale that would serve as a useful trigger mechanism.

The bathymetric analysis showing that in the Bay of Fundy and Gulf of Maine, harbour porpoises are found most frequently in areas where depths range between 92 and 183 m are consistent with observations of high rates of incidental catches in this depth range (Bisack and Northridge 1993). It is unclear why porpoises use these waters to a greater extent than other areas, but it may be related to the distribution of their prey. This is an area of study that may offer considerable insight into the nature of entanglement and factors that contribute to its risk. We hope to obtain detailed information on harbour porpoise foraging behaviour in relation to prey distribution and bottom topography in the future.

The high degree of individual variability in the movements of these porpoises has important consequences for the practice of applying telemetry data to both basic ecology and conservation problems. It is clear that large data sets are required to capture the full extent of variation among individuals of different ages and sexes. Our results are limited by the relatively small number of porpoises we studied and the brief tracking periods of some porpoises. A larger data set might reveal other areas of the Bay of Fundy and Gulf of Maine that constitute important habitat for these porpoises. Two such regions identified in the present study are the area southwest of Grand Manan used by Porpoise No. 8 and the Franklin Basin used by No. 7 during the late fall and winter.

Finally, we note that this technology offers great promise for the study of the ecology, behaviour, and conservation of small cetaceans. Our observations represent the first satellite telemetry data obtained from harbour porpoises and the longest period of satellite contact yet obtained from a cetacean (212 d). Despite the limited time that porpoises spend at the surface, it was possible to obtain reliable location estimates from most porpoises on most days. It was not possible to make any objective assessment of the effects of PTT packages on tagged porpoises. Over the course of the longest deployment (212 d, No. 7) we noted a significant increase ( $p < 0.01$ ) in the average daily distance travelled and a significant decrease ( $p < 0.01$ ) in the pro-

portion of time spent at the surface. Neither of these findings are consistent with trends one might expect from a sick individual, suggesting that any effects were within the tolerance limits of harbour porpoises. Utilization of two tags (VHF and PTT) enabled us to relocate porpoises after release and to modify and improve the tag design after identifying a problem. The side-mounted design holds more promise as a long-term attachment configuration. We believe that the short longevity of the front-mount design resulted from increased drag, as measured from mock tags in wind tunnel testing (Brad Hansen, National Marine Mammal Laboratory, Seattle, Washington, personal communication).

These data provide new insights into the movement patterns of harbour porpoises. Porpoises do not confine their movements to the Bay of Fundy during the summer but also utilize extensive parts of the Gulf of Maine. Generally, porpoises made relatively fast linear movements between apparently productive habitats where they then remained for extended periods. There was a high degree of individual variability in porpoise movements and there was no evidence that porpoises engaged in a coordinated migration out of the Bay of Fundy/Gulf of Maine during the autumn. The movements of porpoises from Canadian to US gillnet fishing areas shows that they are at risk of entanglement for a significant portion of the year. These movements underscore the trans-boundary nature of this population and emphasize the need for co-ordination between management agencies in Canada and the USA in resolving conflicts between porpoises and gillnet fisheries.

**Acknowledgements** This paper is dedicated to the memory of Frank G. Carey, a pioneer in the study of free-ranging pelagic animals. This research was supported by the US National Marine Fisheries Service, Northeast Fisheries Science Center (NEFSC), the US Office of Naval Research, the Endangered Species Recovery Fund of World Wildlife Fund Canada, and the Canadian Wildlife Service. D. Gaskin (University of Guelph) contributed funds, field equipment and logistical support. D. Potter (NEFSC) made this work a reality through his consistent support and encouragement. T. Cox (Duke University) deserves special recognition for her patient and thorough analysis of these data. We also thank: K. Anderson and H. Koopman (Duke University); K. Murray and D. Palka (NEFSC); D. Gannon, T. Howald, T. Spradlin and W. Watkins (Woods Hole Oceanographic Institution); M. Scott (Inter-American Tropical Tuna Commission); W. McLellan and A. Pabst (University of North Carolina, Wilmington); the Grand Manan Whale and Seabird Research Station; and especially the weir fishermen of Grand Manan, without whose dedicated assistance this work would not have been possible. Insightful comments from A. Martin and one anonymous reviewer improved the manuscript greatly. This work was carried out under Permit 1995-168 (Department of Fisheries and Oceans, Canada) and University of Guelph Animal Utilization Protocol 94-R082.

## References

- Bisack K, Northridge SP (1993) Factors affecting harbor porpoise catch rates in the Gulf of Maine sink gillnet fishery. In: Abstracts of the 10th Biennial Conference on the Biology of Marine Mammals. Society for Marine Mammalogy, Galveston, Texas, p 28
- Bravington MV, Bisack KD (1996) Estimates of harbour porpoise bycatch in the Gulf of Maine sink gillnet fishery, 1990–1993. Rep int Whaling Commn 46: 567–574
- Davis RW, Worthy GAJ, Wursig B, Lynn SL, Townsend FI (1996) Diving behavior and at sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. Mar Mammal Sci 12: 569–581
- ESRI (1994) Using Arcview GIS. Environmental Systems Research Institute, Redlands, California
- Fancy SG, Pank LF, Douglas DC, Curby CH, Garner GW, Amstrup SC, Regelin WL (1988) Satellite telemetry: a new tool for wildlife research and management. US Fish Wildl Serv biol Rep 172: 1–54
- Gaskin DE (1984) The harbour porpoise *Phocoena phocoena* (L.): regional populations, status, and information on direct and indirect catches. Rep int Whaling Commn 34: 569–586
- Gaskin DE, Smith GJD, Watson AP (1975) Preliminary study of the movements of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy using radiotelemetry. Can J Zool 53: 1466–1471
- IWC (International Whaling Commission) (1996) Report of the subcommittee on small cetaceans. Rep int Whaling Commn 46: 160–179
- Jefferson TA, Curry B (1994) A global review of porpoise (Cetacea: Phocoridae) mortality in gillnets. Biol Conserv 67: 167–183
- Koopman HN (1994) Topographical distribution and fatty acid composition of blubber in the harbour porpoise (*Phocoena phocoena*). MSc thesis, University of Guelph, Guelph, Ontario
- Koopman HN, Gaskin DE (1994) Individual and geographical variation in pigmentation patterns of the harbour porpoise, *Phocoena phocoena* (L.). Can J Zool 72: 135–143
- Koopman HN, Westgate AJ, Read AJ, Gaskin DE (1995) Blood chemistry of wild harbor porpoises *Phocoena phocoena* (L.). Mar Mammal Sci 11: 123–135
- Mate BR (1989) Watching habits and habitats from earth satellites. Oceanus 32: 14–18
- Mate BR, Nieukirk S, Mesecar R, Martin T (1992) Application of remote sensing methods for tracking large cetaceans: North Atlantic right whales (*Eubalaena glacialis*). Final Report for US Department of the Interior, Minerals Management Service, Washington DC
- Mate BR, Rossbach KA, Nieukirk SL, Wells RS, Irvine AB, Scott MD, Read AJ (1995) Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Mar Mammal Sci 11: 452–463
- Mate BR, Stafford KM, Nawojchik R, Dunn JL (1994) Movements and dive behavior of a satellite-monitored Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. Mar Mammal Sci 10: 116–121
- Martin AR, Kingsley MCS, Ramsay MA (1994) Diving behaviour of narwhals (*Monodon monoceros*) on their summer grounds. Can J Zool 72: 118–125
- Martin AR, Smith TG (1992) Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. Can J Fish aquat Sciences 49: 462–466
- Martin AR, Smith TG, Cox OP (1993) Studying the behaviour and movements of high Arctic belugas with satellite telemetry. Symp zool Soc Lond 66: 195–210
- Palka DL (1995) Abundance estimate of the Gulf of Maine harbor porpoise. Rep int Whaling Commn 16 (Spec Issue): 27–50
- Palka DL, Read AJ, Westgate AJ, Johnston DW (1996) Summary of current knowledge of harbour porpoises in US and Canadian Atlantic waters. Rep int Whaling Commn 46: 559–565
- Read AJ, Gaskin DE (1985) Radio tracking the movements and activities of harbour porpoises, *Phocoena phocoena* (L.), in the Bay of Fundy, Canada. Fish Bull US 83: 543–552
- Read AJ, Hohn AA (1995) Life in the fast lane: the life history of harbour porpoises from the Gulf of Maine. Mar Mammal Sci 11: 423–440
- Read AJ, Nicolas JR, Craddock JE (1996) Winter capture of a harbor porpoise in a pelagic drift net off North Carolina. Fish Bull US 94: 381–383

- Read AJ, Tolley KA (1997) Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Can J Zool* 75: 122–130
- Recchia CA, Read AJ (1989) Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Can J Zool* 67: 2140–2146
- Stephenson RL, Lane DE, Aldous DG, Nowak R (1993) Management of the 4WX Atlantic herring (*Clupea harengus*) fishery: an evaluation of recent events. *Can J Fish aquat Sciences* 50: 2742–2757
- Trippel EA, Wang JY, Strong MB, Carter LS, Conway JD (1996) Incidental mortality of harbour porpoise (*Phocoena phocoena*) by the gill-net fishery in the lower Bay of Fundy. *Can J Fish aquat Sciences* 53: 1294–1300
- Wang JY, Gaskin DE, White BN (1996) Mitochondrial DNA analysis of harbour porpoise, *Phocoena phocoena*, subpopulations in North American waters. *Can J Fish aquat Sciences* 53: 1632–1645
- Watkins WA, Sigurjonsson J, Wartzok D, Maiefski RR, Howey PW, Daher M (1996) Fin whale tracked by satellite off Iceland. *Mar Mamm Sci* 12: 564–569
- Westgate AJ, Muir DCG, Gaskin DE, Kingsley MCS (1997) Concentrations and accumulation patterns of organochlorine contaminants in the blubber of harbour porpoises, *Phocoena phocoena*, from the coast of Newfoundland, the Gulf of St. Lawrence and the Bay of Fundy/Gulf of Maine. *Envir Pollut* 95: 105–119
- Westgate AJ, Read AJ, Berggren P, Koopman HN, Gaskin DE (1995) Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Can J Fish aquat Sciences* 52: 1064–1073
- Woodley TH, Read AJ (1991) Potential rates of increase of a harbour porpoise (*Phocoena phocoena*) population subjected to incidental mortality in commercial fisheries. *Can J Fish aquat Sciences* 48: 2429–2435