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Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy

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ABSTRACT: We describe an integrative approach to studying the fine-scale distribution of harbour porpoises *Phocoena phocoena* in the Bay of Fundy, using satellite telemetry, line transect surveys and remote sensing techniques. Analysis of satellite telemetry data from 6 porpoises (5 male, 1 female) revealed that over the course of a month individuals ranged across large areas (7738 to 11 289 km²) but concentrated their movements in small focal regions (August mean = 294 km², September mean = 252 km²), often proximate to islands, headlands, or restricted channels. Line transect surveys (n = 25 flood tide, n = 20 ebb tide) in the focal region of 2 tagged animals revealed that relative porpoise density (animals km⁻²) was significantly greater during flood (9.59) than ebb tide phases (1.79). Hydro-acoustic prey surveys revealed aggregations of prey along localized fronts in this region. Remote sensing images indicated the presence of an island wake in the focal region during flood tides, providing an ecological context for our observations of high densities of porpoises. Remote sensing revealed the existence of a headland wake in the focal region of another porpoise near Campobello Island. These results support the hypothesis that regions of enhanced relative vorticity, like island and headland wakes, aggregate prey and represent important foraging habitat for harbour porpoises in the Bay of Fundy.

KEY WORDS: Harbour porpoise · Foraging · Fine-scale oceanography · Island wake · Satellite telemetry · Line transects · Remote sensing

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INTRODUCTION

Many large marine predators use vast areas of the ocean, but typically concentrate their activities in smaller, localized regions for periods of time. For example, many species of pelagic seabirds, such as albatrosses, range across entire ocean basins, but forage in small areas for extended periods (Hyrenbach & Dotson 2001, Hyrenbach et al. 2002). Some marine mammals undertake long annual migrations, but return seasonally to forage in localized areas (Stewart & Delong 1995, Read & Westgate 1997, Mate et al.

1999, Baumgartner et al. 2003). Such distribution patterns are usually interpreted as the result of foraging decisions made at meso- (10s to 100s of km) and fine-scales (1 to 10 km), based on the assumption that such highly mobile animals will remain near a prey patch until it becomes energetically profitable to move on to the next patch (MacArthur & Pianka 1966, Charnov 1976, Stephens & Krebs 1986).

In marine systems, heterogeneity of productivity is the result of complex interactions of wind, currents, and land masses. At fine-scales (1 to 10 km), oceanographic features such as upwellings, fronts, and eddies

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can increase primary productivity (St. John & Pond 1992, St. John et al. 1992) and physically aggregate plankton and weak nekton (Wolanski & Hamner 1988, Mann & Lazier 1996). This, in turn, attracts larger numbers of small consumers—often schooling fish—and results in localized patches of food for marine predators that feed at low and medium trophic levels. It is now recognized that such fine-scale oceanographic features can be of great importance to pelagic predators (Wolanski & Hamner 1988), providing mechanisms which enhance concentrations of prey that can be exploited by whales, seabirds and large pelagic fishes (e.g. Brodie et al. 1978).

Harbour porpoises *Phocoena phocoena* are small odontocete cetaceans that inhabit the temperate waters of the northern hemisphere in a nearly circum-polar distribution (Gaskin 1984). Throughout this range, their distribution is restricted to waters of the continental shelf (Read 1999). In the Bay of Fundy, harbour porpoises feed primarily on juvenile Atlantic herring *Clupea harengus harengus* (Smith & Gaskin 1974, Recchia & Read 1989, Gannon et al. 1998), although weaning calves consume euphausiids *Meganyctiphanes norvegica* (Smith & Read 1992). In both the summer and fall, Atlantic herring comprise the largest portion of the diet. In the fall, however, porpoises expand their diet to a wider range of prey as they move south into the Gulf of Maine (Gannon et al. 1998), including silver hake *Merluccius bilinearis*, hake *Urophycis* spp. and pearlsides *Maurolicus weitzmani*. Because of their small size, harbour porpoises are unable to carry large energy stores (Koopman 1998), so their patterns of movement are likely to be strongly related to the distribution of their prey.

Previous studies in the Bay of Fundy and Gulf of Maine indicate that porpoise movements occur on at least 2 spatial and temporal scales. Individuals inhabit relatively restricted areas for days to weeks (fine-scales) and then make rapid movements over periods of hours to days across larger scales (meso-scales) to other restricted areas (Read & Westgate 1997). Telemetry studies of harbour porpoises in European waters reveal similar patterns (Teilmann 2000). It remains unclear, however, what environmental factors drive their distribution at both large and small scales (Watts & Gaskin 1985, Cox 2003). In the early 1980s, D. Gaskin hypothesized that tidally driven oceanographic features in the Bay of Fundy might concentrate zooplankton and small fishes, making these prey more available to harbour porpoises and other marine predators (Jovallanos & Gaskin 1983, Smith et al. 1984). Gaskin's work described the habitat of harbour porpoises in the Bay of Fundy, but it did not explain how environmental characteristics influenced the distribution of porpoises at fine-scales (Watts & Gaskin 1985).

The purpose of the present study was to address Gaskin's original hypothesis in greater detail by examining the distribution and movements of harbour porpoises in the Bay of Fundy during the summer months (a period of high porpoise abundance) in relation to fine-scale oceanography. Specifically, we hypothesized that harbour porpoises in the Bay of Fundy exploit predictable fine-scale oceanographic features that aggregate prey to facilitate foraging. To do this, we chose an integrative approach, first using satellite telemetry data to examine the movements and distribution of harbour porpoises and to identify focal regions of porpoise distribution. We then employed line transects, hydro-acoustic surveys of prey and remote sensing techniques to explore why porpoises utilized these core regions of habitat.

MATERIALS AND METHODS

Satellite telemetry. Study area and timeframe: We obtained positional data from satellite-linked transmitters attached to 6 harbour porpoises released from herring weirs around Grand Manan Island, New Brunswick, Canada (44°45' N, 66°45' W; Fig. 1). These 6 represent a subset of harbour porpoises tagged and released as part of a larger study during the summers (July to September) of 1995 to 2000, as described in Read & Westgate (1997), Westgate & Read (1998) and Neimanis et al. (2004). Briefly, the dorsal fin of each porpoise was fitted with a satellite-linked transmitter, also referred to as a platform terminal transmitter (PTT). The mass of these tags represents a small proportion of a porpoises mass (<1%) and we assumed that any effects of the capture process, or of carrying the tag, were short in duration (Read & Westgate 1997). Individual tags varied in the time they transmitted data, with the shortest providing locations for 78 d and the longest for 174 d. The tags were programmed to transmit on various duty cycles: 2 tags transmitted for 6 h followed by 16 h of quiescence (PTT 16291 & PTT16300); the remaining 4 tags initially transmitted for 8 h followed by 16 h of quiescence. After 10 d the latter 4 tags reverted to 6 h of transmission followed by 16 h of quiescence.

Data treatment and spatial analysis: To maximize our sample of observations for each animal, and to maintain consistency among data sets, we only examined porpoises tagged during the early summer (before 10 August). Positional data were filtered to remove erroneous positions using a 2-stage speed filter (McConnell et al. 1992, Austin et al. 2003) and further subsampled by eliminating points which were obtained within less than 1.5 h of each other, to maintain a relatively consistent sampling rate. Table 1 provides infor-

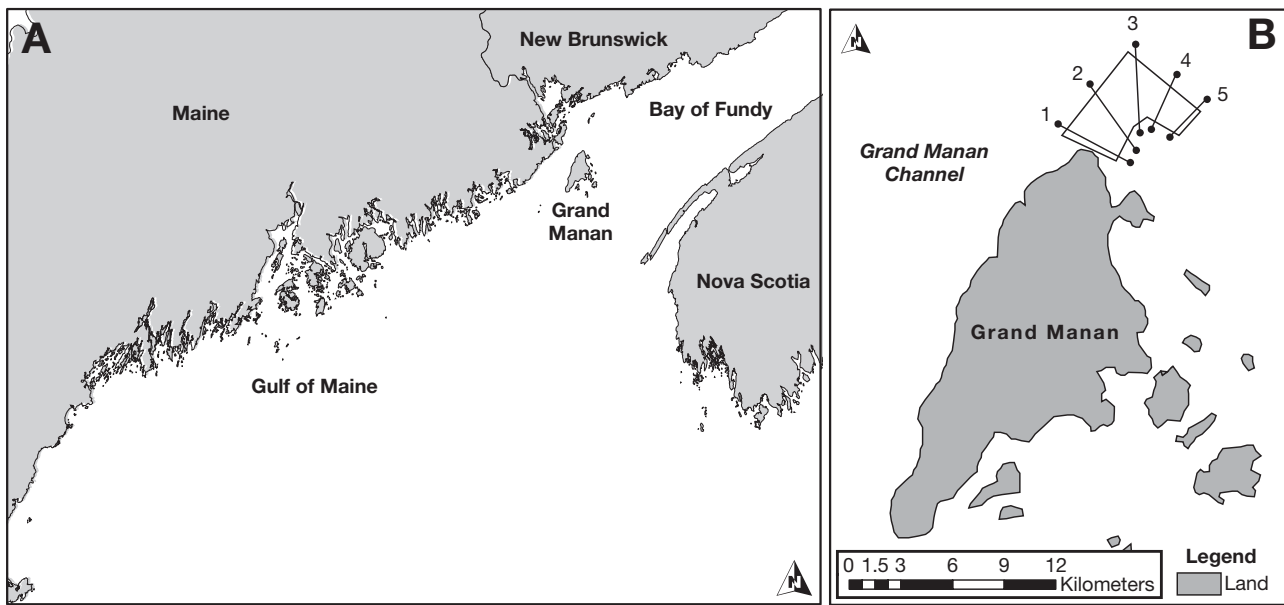


Fig. 1. Study area, detailing (A) the Gulf of Maine and Bay of Fundy and the location of Grand Manan Island and (B) the location of line transects and hydro-acoustic prey surveys (labelled 1 through 5)

mation on each tagged porpoise and details on transmission period for each tag. Summaries of the number of positions and the minimum timing between subsequent telemetry positions for each animal used in our analysis are also provided in Table 1.

We imported the telemetry data into ArcGIS 8.1 (ESRI) and mapped these observations with the Zone 19 (N) Universal Transverse Mercator (UTM) projection, using the WGS 1984 datum. We produced monthly Kernel density utilization grids for each porpoise using 1 to 3 telemetry positions per tide phase (flood or ebb and excluding those on land) to illustrate the fine-scale regions used by the porpoises. We calculated utilization grids with the Kernel Density function in the Spatial Analyst extension in ArcGIS 8.1 with a search radius of 10 000 km² and an output cell size of

1 km². We relaxed the frequently asserted requirement for independence of telemetry observations to maximize sample size and increase the precision and accuracy of utilization distributions for our fine-scale analysis (De Solla et al. 1999).

We categorized kernel density grids into 5 separate regions: cells where porpoise density was 0, and cells corresponding to the 25th, 50th, 75th and 95th percentiles of the density of position estimates. To draw comparisons among telemetered animals, we calculated the area of focal regions (95% density—to identify the core region that porpoises used) and range regions (to the 0% contour—to illustrate the extent to which each animal moved during the month) by enumerating all focal and range grid cells not covered by land. To illustrate fine-scale movements of porpoises,

Table 1. *Phocoena phocoena*. Life history and telemetry data details for harbour porpoises employed in kernel density utilization grid analysis. The average time between samples did not include the duty cycle of the tag

ID	Nickname	Tag date	Last day	Duration (d)	Sex	Length (cm)	Weight (kg)	Percent rejected by filter	August		September	
									No. of positions	Time between samples	No. of positions	Time between samples
PTT7235	David	2 Aug 1999	17 Jan 2000	168	M	150	53	18.0	90	2.0	72	2.0
PTT 7244	Mitchell	9 Aug 1999	18 Jan 2000	162	M	150	56	12.6	64	2.3	65	1.7
PTT 16291	Otis	9 Aug 1997	9 Dec 1997	122	M	146.5	48	30.0	45	2.1	67	2.0
PTT 7250	Sacagawea	8 Aug 1998	25 Oct 1998	78	F	164	53	23.1	37	2.1	47	1.8
PTT 16300	Shackleton	6 Aug 1998	24 Nov 1998	110	M	138	43	20.4	64	1.8	72	1.8
PTT 8531	Stanley	29 Jul 1999	19 Jan 2000	174	M	132	38.6	14.0	55	1.8	63	1.7
	Mean			136		147	48.6	19.7	59.2	2.0	64.3	1.8
	SD			38		11	6.7	6.4	18.5	0.2	9.2	0.1

we imported the telemetry data into ArcView 3.2 (ESRI) and connected lines between subsequent (chronological) positions with the Animal Movement Extension (Hooge & Eichenlaub 1997). Movement polylines were then mapped in ArcGIS 8.1 and projected as above.

Line transect surveys. Study area and timeframe:

We conducted a series of fine-scale line transect surveys in one of the focal regions identified by the preceding telemetry analysis to assess porpoise density in August 2000. This area, located off the north tip of Grand Manan Island (Fig. 1), attracts large numbers of marine predators, presumably to forage in the tidal fronts and eddies that form during the flood tide. We conducted preliminary theodolite surveys in July 2000 to define the region to be sampled by line transect surveys. From these observations we defined a 24 km² region that encompassed the visible surface effects of a localized oceanographic feature that formed on flood tides, by recording the spatial location of obvious surface turbulence with a Geodimeter Total Station Model 600 digital theodolite (Spectra Precision Software) using methods described in Johnston (2002) and Ronconi & St. Clair (2002). Briefly, the extent of the feature was delineated by recording its outer edge and marking all inflection points along this boundary. Vertical angles, horizontal angles and station height were used to calculate the distance to points sighted offshore. To account for tidal fluctuations, the station height for a given day and time was calculated using tidal amplitude as determined with WXTide32 (Version 3.0) and corrected for Northern Head, Grand Manan Island. We converted each point to northings and eastings relative to the theodolite station and, subsequently, to geographic coordinates. Finally, we mapped a polygon encompassing the perimeter of the feature (Fig. 1) using ArcGIS 8.1.

Line transects, sampling and density estimation: We established a series of 5 line transects of unequal length (Thomas et al. 2002a), each of which crossed the gradient of the major arc of the oceanographic feature defined by the theodolite survey (Fig. 1). We conducted surveys along these transects in August 2000 on clear days with a Beaufort Sea State of 2 or less. Each transect was sampled daily for a single tide phase (ebb or flood), starting at 1 h following slack tide and finishing at approximately 5 h past slack tide. The order in which transects were conducted and the starting point for each transect was randomized for each survey day. The distance sampling method typically requires that transects are randomly placed within the area of interest to generate density estimates (Thomas et al. 2002a), but we wanted to ensure that our transects did not run parallel to the axis of the oceanographic feature during flood tides, which exhibited a

predictable arc within the study area (Fig. 1). Transects that paralleled the feature could lead to biased sampling of the region if porpoises were attracted to it (Buckland et al. 1993). Therefore, we report only relative porpoise density for the study region.

We conducted line transect surveys in our research vessel 'Ahqik', a 6 m Fundy runabout with methods similar to those used for other fine-scale surveys of small cetaceans using small vessels (Dawson et al. 2004). All surveys were conducted by the same 2 observers—1 at starboard and 1 to port—with eye level approximately 2 m above water. Each observer scanned a 90° arc on their side of the vessel and recorded observations of the radial distance and bearing to groups of porpoises encountered on the survey. The observers also made estimates of the size of each group. Observers were randomly assigned an initial position, and alternated between port and starboard for each subsequent survey on that day. The boat driver recorded sightings of animals along the track line. The observers and driver were all experienced at sighting porpoises, and we conducted a series of training surveys with objects at known distances to ensure estimated radial distances to groups of porpoises were both accurate and consistent.

We generated density estimates from these surveys using Distance 4.0 software and the conventional distance sampling analysis engine (Thomas et al. 2002b) with the following parameter estimation specifications. Encounter rate, expected cluster size and density were estimated by tide phase (stratum) and the detection probability generated for all data combined. Our analysis considered exact distances to groups of observed porpoises, and the transect strip width estimation was based on the largest observed distance to a group of porpoises. The model used a half-normal key detection function with automatic selection of adjustment terms. The appropriate detection function was chosen automatically based on minimum Akaike Information Criterion (AIC). We did not attempt to correct our analysis for animals that may have been missed on the trackline.

Hydro-acoustic prey surveys and mid-water trawls:

We conducted a series of hydro-acoustic prey surveys in the fine-scale study area on 15 and 16 August 2000 using a Simrad SM2000 200 kHz multibeam sonar (produces 128 beams in 180° semi circle with each ping) and a Simrad 50 kHz single beam sounder in a towable body deployed from a 12 m commercial fishing vessel. This equipment is used in herring stock assessments in the Bay of Fundy and is described in detail in Melvin et al. (2003). We completed 4 surveys of all 5 transects defined above during the flood tide phase, as well as a single transect along the length of

the oceanographic feature during the flood tide. We subsequently conducted several mid-water trawls along the length of the oceanographic feature in August 2002 using a modified Isaacs–Kidd mid-water trawl towed at 1.5 m s^{-1} .

Remote sensing. RADARSAT synthetic aperture radar: Oceanographic features may be visualized by synthetic aperture radar (SAR) sensors from patterns of surface roughness caused by interactions of wind and currents (Martinez et al. 1992) at shear or convergence zones. This type of remote sensing is frequently used in marine science and conservation, including oil spill detection (e.g. Lu 2003) and the visualization of fine-scale oceanographic features (e.g. Farmer et al. 1995).

We obtained an SAR image encompassing the fine-scale study area at approximately mid-flood (2.25 h before a high tide of 5.36 m above mean low water). This image was obtained through the Data for Research Use Program of the Canadian Space Agency and covered the area within the following coordinates in decimal degrees: upper left corner – latitude = 45.049735° , longitude = -67.174257° ; upper right corner – latitude = 45.032944° , longitude = -66.322946° ; lower left corner – latitude = 44.503460° , longitude = -67.191396° ; and lower right corner – latitude = 44.486984° , longitude = -66.348056° . The image was collected with fine beam mode, in the F1 near position, producing a nominal swath of $50 \times 50 \text{ km}$ with a resolution of less than 8 m. We obtained the image from RSI as a Map Image product (corrected to North Up orientation and geo-referenced for use in image-analysis and GIS applications) in the RADARSAT CEOS format, analyzed it with ERDAS Imagine 8.6 Version (Leica Geosystems GIS & Mapping) and then exporting the image as an ARC grid image for incorporation into the GIS.

LANDSAT 7 CanImage: Physical and biological oceanographic features are also detectable by remote sensing satellites, which detect energy reflected (or the lack of it) from the Earth's surface at various wavelengths (Wolanski et al. 1984, Ekstrand 1992, Lubin et al. 2001). We obtained an archived CanImage orthoimage from the Canadian Centre for Topographic Information (Department of Natural Resources, Government of Canada) archive to search for oceanographic features in our fine-scale study area. CanImages are raster images derived from LANDSAT 7 orthoimages that have been resampled and based on the National Topographic System (NTS) at the $1:50\,000$ scale. CanImage comprise 7 spectral bands: a panchromatic band with a pixel size of 15 m and 6 multispectral bands with a pixel size of 30 m. They are produced in accordance with North American Datum 1983 (NAD83) using the UTM projection (Anonymous 2002). We used catalog image NTS 021B10 with 3 spectrum bands—infrared ($0.750\text{--}0.900 \mu\text{m}$), red ($0.630\text{--}0.690 \mu\text{m}$) and green

($0.525\text{--}0.605 \mu\text{m}$)—often used to enhance the appearance of hydrographic features. The original image was obtained by the satellite on the 29 September 2000 at 15:04:10 h GMT, during a flood tide phase, approximately 1.35 h before a high tide of 6.26 m above mean low water. This image covered these coordinates in decimal degrees: upper left corner – latitude = 44.75° , longitude = -67.00° ; upper right corner – latitude = 44.75° , longitude = -66.50° ; lower left corner – latitude = 44.50° , longitude = -67.00° ; and lower right corner – latitude = 44.50° , longitude = -66.50° . We also analyzed this image with ERDAS Imagine 8.6 and subsequently exported it as an ARC grid image for incorporation into the GIS.

RESULTS

Satellite telemetry

The kernel density utilization grids (representing porpoise density probabilities in percentiles) are presented in Figs. 2 to 7. The areas within which porpoises traveled within a month varied considerably, but each porpoise exhibited a core-use area, surrounded by a larger region that was occasionally visited. The monthly core and range areas for each porpoise are presented in Table 2. Most porpoises restricted their movements to the western Bay of Fundy, close to Campbellello and Grand Manan Islands. The core areas for each porpoise did not overlap, except for those of PTT16300 and PTT7235, whose August and September core areas both encompassed the northern end of Grand Manan (Figs. 2 & 6). There was no consistent shift in ranges between months. Animals PTT7235, PTT7250 and PTT16300 ranged over larger areas in September (Figs. 2, 5 & 6, Table 2), but PTT16291 and PTT8531 exhibited a smaller range in September than August (Figs. 4 & 7, Table 2).

Table 2. *Phocoena phocoena*. Core and range areas (km^2) for telemetered harbour porpoises in the Bay of Fundy/Gulf of Maine generated by kernel density analysis for August and September. PTT: platform terminal transmitter

PTT	Porpoise	August		September	
		Core	Range	Core	Range
7235	PTT7235	269.0	8428.0	246.0	22103.0
7244	PTT7244	269.0	8421.0	226.0	8726.0
16291	PTT16291	415.0	10577.0	384.0	9694.0
7250	PTT7250	254.0	4728.0	229.0	11435.0
16300	PTT16300	234.0	5283.0	307.0	12923.0
8531	PTT8531	323.0	8990.0	122.0	2850.0
	Mean	294.0	7737.8	252.3	11288.5
	SD	66.2	2265.3	87.9	6324.0

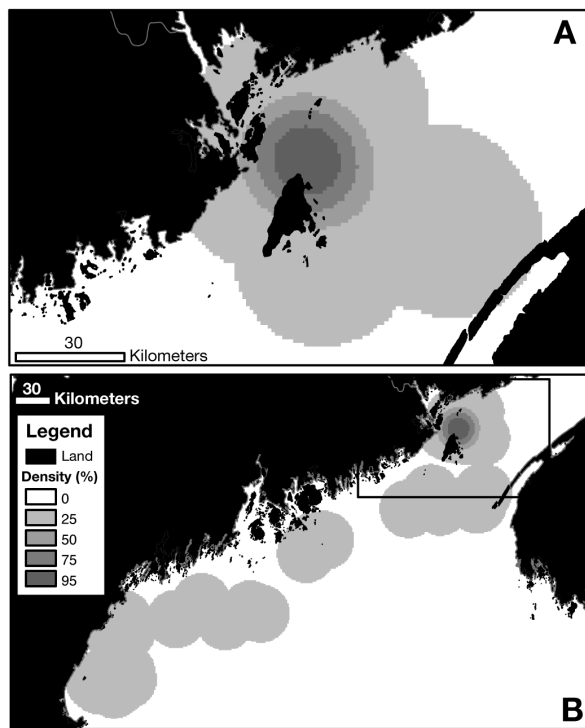


Fig. 2. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT7235. Densities are presented in percentiles



Fig. 4. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT16291. Densities are presented in percentiles

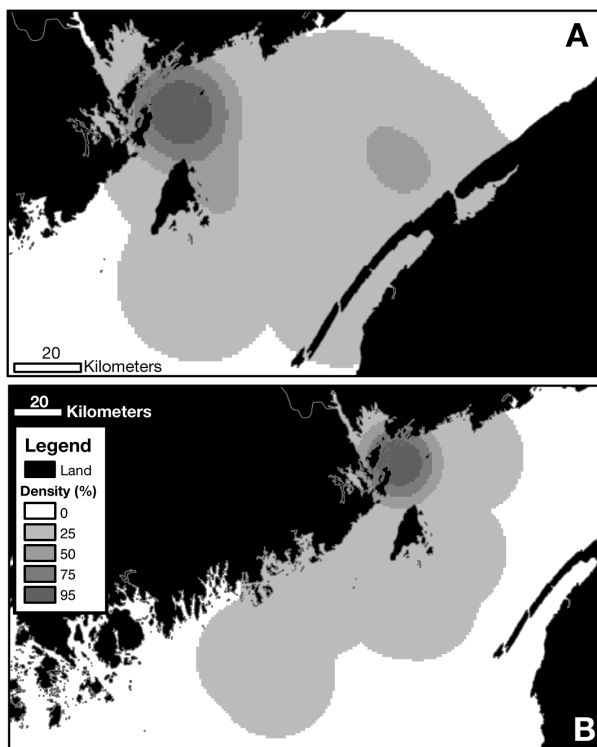


Fig. 3. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT7244. Densities are presented in percentiles

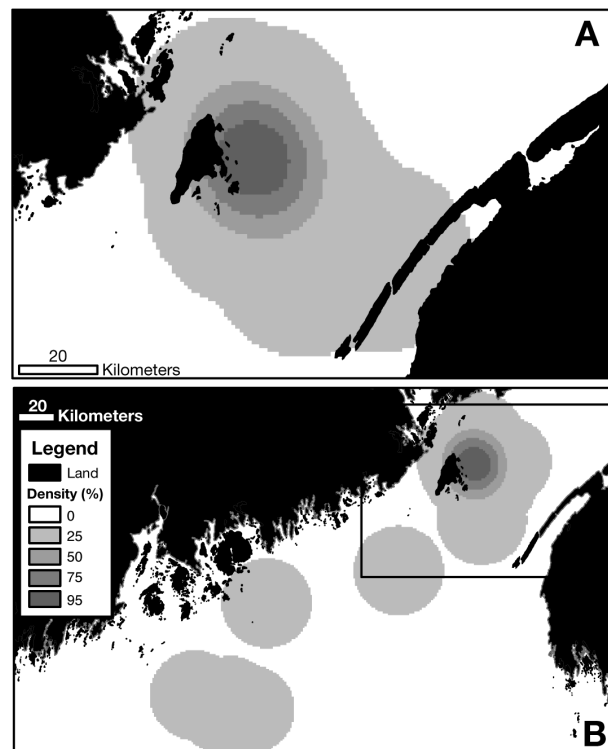


Fig. 5. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT7250. Densities are presented in percentiles

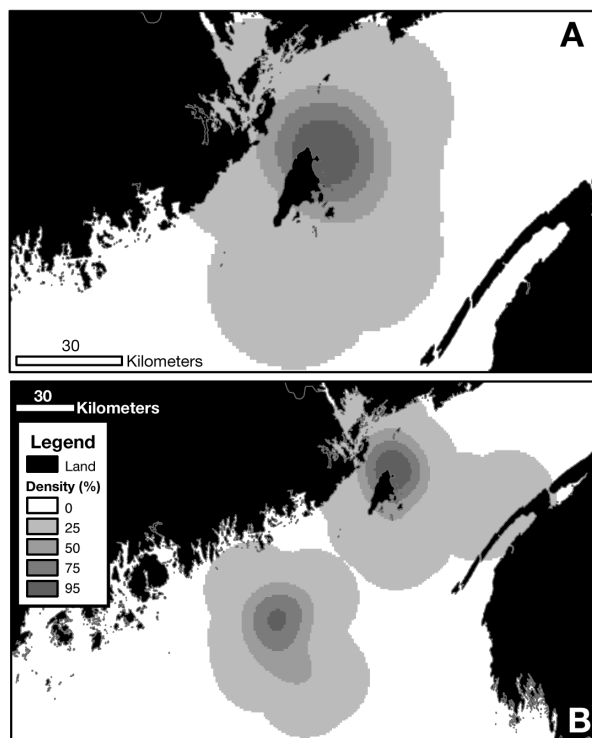


Fig. 6. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT16300. Densities are presented in percentiles

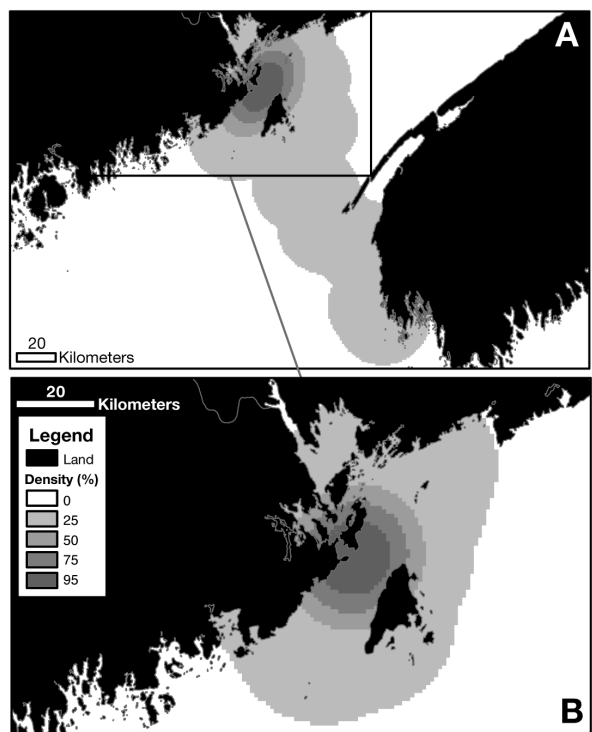


Fig. 7. *Phocoena phocoena*. (A) August and (B) September kernel density utilization grids for harbour porpoise PTT8531. Densities are presented in percentiles

Line transects and distance sampling

We conducted a total of 45 line transect surveys (25 surveys during flood tide phases and 20 during ebb tides) in 9 days during August 2000. This resulted in a total of 185.3 km of survey effort, 102.9 km during flood tide phases and 82.3 km during ebb phases. The detection probabilities and the detection function model illustrated a wide 'shoulder', where the detection probability remained high (>0.80) out to 200 m from the trackline—a property that provides for more reliable density estimation (Thomas et al. 2002a). The numerical results of distance sampling analysis are presented in Table 3. There was a dramatic increase in the encounter rate, density of porpoises and porpoise groups, and relative abundance during the flood tide phase. The number of porpoises within the study area was 5.3 times higher during flood tides compared to ebb tides.

Hydro-acoustic prey surveys

The hydro-acoustic survey design provided limited information on the distribution of acoustic targets in the oceanographic feature due to the short interval of recordings actually taken within it. Typically the visible extent of the oceanographic feature only occurred during a very short segment (50 to 100 m) of the transect. Values for the observed mean area backscatter for the 5 porpoise density transects and the along-feature transect are presented in Table 4. Backscatter values for transects 1 to 5 were relatively consistent, but the transect we conducted along the feature revealed a much higher backscatter level (the minimum 18 dB difference is nearly 100 times the across-transect backscatter intensities). The high current velocities in the oceanographic feature greatly hampered our ability to conduct mid-water trawls. However, we were able to confirm that herring and euphausiids (primarily *Meganyctiphanes norvegica*) were present in the feature.

SAR remote sensing

The SAR image of the study area during flood tide revealed the presence of a large anti-cyclonic eddy and a frontal system that extended northeast of the tip of the island (Fig. 8B). Following mid-flood, this feature was approximately 3430 m long and extended from the island at an azimuth of approximately 26° . The eddy was approximately 2044 m wide. These data are consistent with the results of our preliminary theodolite survey for line transects described above. The SAR

Table 3. *Phocoena phocoena*. Sighting probability, strip width, encounter rates, group density and size, density and relative abundance of harbour porpoises sighted during line transects (n = 25 for flood, n = 20 for ebb) off the northern tip of Grand Manan Island in the Bay of Fundy

	Mean	SE	CV (%)	95 % CI	
Flood					
$f(0)$	3.43×10^{-3}	1.92×10^{-4}	5.59	3.07×10^{-3}	3.83×10^{-3}
Sighting probability	0.32913	1.84×10^{-2}	5.59	0.29487	0.36737
Effective strip width (m)	291.72	16.304	5.59	261.35	325.61
Encounter rate	2.35×10^{-3}	3.62×10^{-4}	15.4	1.71×10^{-3}	3.22×10^{-3}
Group density (m ⁻²)	4.03×10^{-6}	6.60×10^{-7}	16.38	2.89×10^{-6}	5.61×10^{-6}
Expected group size	2.3811	0.12634	5.31	2.1449	2.6432
Density (km ⁻²)	9.59	1.65	17.22	6.79	13.56
Relative abundance	230	39.602	17.22	162	324
Ebb					
$f(0)$	3.43×10^{-3}	1.92×10^{-4}	5.59	3.07×10^{-3}	3.83×10^{-3}
Sighting probability	0.32913	1.84×10^{-2}	5.59	0.29487	0.36737
Effective strip width (m)	291.72	16.304	5.59	261.35	325.61
Encounter rate	6.43×10^{-4}	1.52×10^{-4}	23.6	3.95×10^{-4}	1.05×10^{-3}
Group density (m ⁻²)	1.10×10^{-6}	2.67×10^{-7}	24.25	6.71×10^{-7}	1.81×10^{-6}
Expected group size	1.6226	0.22087	13.61	1.2363	2.1296
Density (km ⁻²)	1.79	0.50	27.81	1.03	3.11
Relative abundance	43	11.957	27.81	25	75

image also revealed the presence of a fine-scale headland wake originating from the northern tip of Campobello Island (Fig. 9B). This feature is much smaller than the island wake, extending 721 m from the point at an azimuth of 348°.

LANDSAT CanImage remote sensing

The flood tide LANDSAT image also revealed the presence of both oceanographic features. The island wake originating off the northern tip of Grand Manan (Fig. 8C) extended northeast from the island at an azimuth of approximately 32° and was 3600 m long. The headland wake originated on the northeast tip of Campobello Island (Fig. 9C) and was approximately 1000 m long and separated from the tip of the island at an azimuth of 323° before curving southwards to parallel the axis of Head Harbour Passage.

Table 4. Mean transect length and depth-averaged mean surface-area backscatter for hydro-acoustic prey surveys conducted off the northern tip of Grand Manan Island in the Bay of Fundy

Transect	n	Distance (km)	Mean backscatter m ⁻² (dB)	SD
1	4	3.34	-48.24	15.86
2	4	4.10	-54.11	15.08
3	4	4.38	-55.68	10.50
4	4	3.76	-50.31	4.82
5	4	3.24	-59.52	24.40
Along	1	7.02	-30.65	

DISCUSSION

The results of our analysis indicate that harbour porpoises have restricted focal regions within their summer monthly ranges and support our hypothesis that these focal areas coincide with fine-scale oceanographic features driven by tidal circulation. Furthermore, our results support Gaskin's original hypothesis that these features serve to aggregate prey and make it more available to upper trophic level predators, such as harbour porpoises. This enhanced prey availability likely results from the physical effects of fine-scale oceanographic features, such as island and headland wakes in tidal flow, which aggregate plankton and weak nekton. The details of each section of the study, and 2 integrative examples, are discussed below.

Satellite telemetry

Harbour porpoises use restricted focal areas in the Bay of Fundy during the late summer. The size of each monthly focal area was quite small—ranging from 122 to 415 km². This finding is particularly striking given the mobility of these animals (Read & Westgate 1997), which suggested that the monthly habitat available to a porpoise encompasses the entire Bay of Fundy and Gulf of Maine.

Kernel density functions (Worton 1989, Seaman & Powell 1996) represent the best method for estimating utility distributions for animals (Powell 2000). Most studies employ kernel density estimates of habitat utilization to describe areas within which an animal is most likely to be found while engaging in its daily routine of foraging, resting and social behaviour—referred to as its home range (Burt 1943). In the present analysis, however, we use kernel density estimation to identify focal regions within the distribution of each animal. A similar approach was employed by Kenney & Winn (1985) to identify 'high use' cetacean habitat in the northeastern United States using aerial survey and platform of opportunity data. The calculation of kernel density estimates does not require serial independence of observations (De Solla et al. 1999), but several studies have addressed spatial autocorrelation by restrictive sampling regimes or through post hoc sub-sampling or averaging of data (e.g. Heide-Jorgensen et al. 2002). Other researchers have noted that such corrections can result in biased utilization

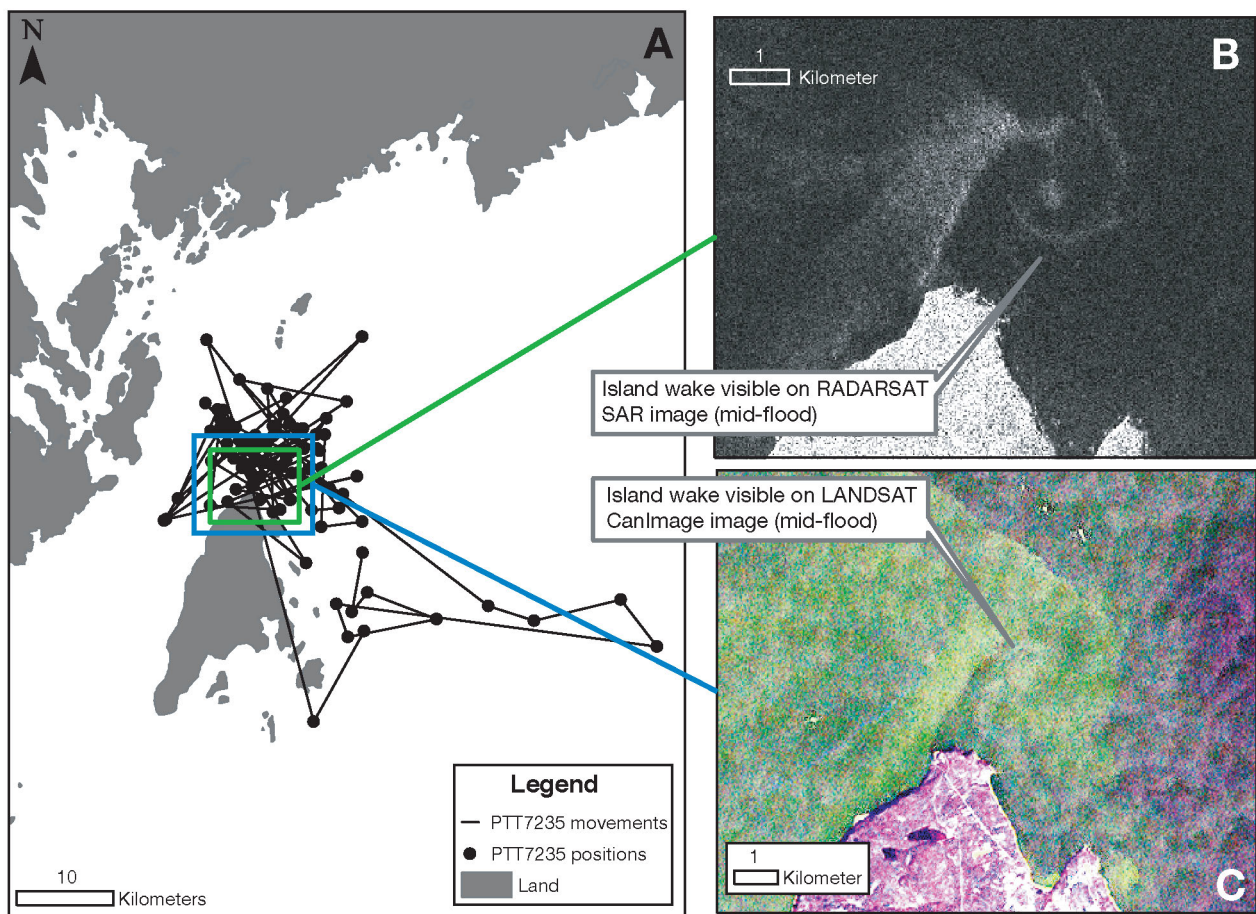


Fig. 8. *Phocoena phocoena*. (A) Spatial relationships between the August movements of harbour porpoise PTT7235 and the Long Eddy island wake forming off the northern tip of Grand Manan on flood tides as visualized by (B) RADARSAT synthetic aperture radar and (C) LANDSAT remote sensing imagery

grids (e.g. Reynolds & Laundre 1990) and tend to reduce the biological relevance of the analysis (Lair 1987, De Solla et al. 1999). Our approach reduced the chance of producing biased estimates and ensured that time intervals between positions was short enough to capture the fine-scale movements of each animal (Cameron & Spencer 1985).

Many studies have revealed that patterns in the distribution of cetaceans correlate well with physical features within the available habitat (e.g. Selzer & Payne 1988, Hooker et al. 2002), and it is now becoming clear that such hotspots are likely related to foraging behavior (Hastie et al. 2004). This is likely to be true for harbour porpoises in the Bay of Fundy. Harbour porpoises must remain close to food resources and consume prey frequently to meet the energetic demands of maintenance, growth, and reproduction (Koopman 1998). This is especially true for mature female porpoises—considered to be income breeders (Read 2001)—that must meet the costs of pregnancy and lactation through increased energy intake rather than relying

on energy stores (Sibly & Calow 1986). Unfortunately, we had only 1 female in our sample and cannot, therefore, draw comparisons between males and females. The focal areas of most porpoises (5 out of 6), were coastal in nature, and the focal regions of 4 animals (PTT7235, PTT7244, PTT8531 and PTT16300) were proximate to headlands, restricted channels or the tips of islands. Only 1 animal, PTT16291, focused its movements away from land, at the northern edge of the Grand Manan basin.

Each of these focal regions represents a unique location in terms of depth, bottom slope, and distance from shore, illustrating why previous attempts to build predictive models of porpoise habitat using these types of physical features (e.g. Watts & Gaskin 1985, Cox 2003) have been largely unsuccessful. Indeed, physical features such as depth, slope and distance from shore may be poor proxies for describing cetacean habitat, as they are at least one step removed from the actual elements the model seeks to describe. At fine-scales, cetacean habitat could be better described by modeling the

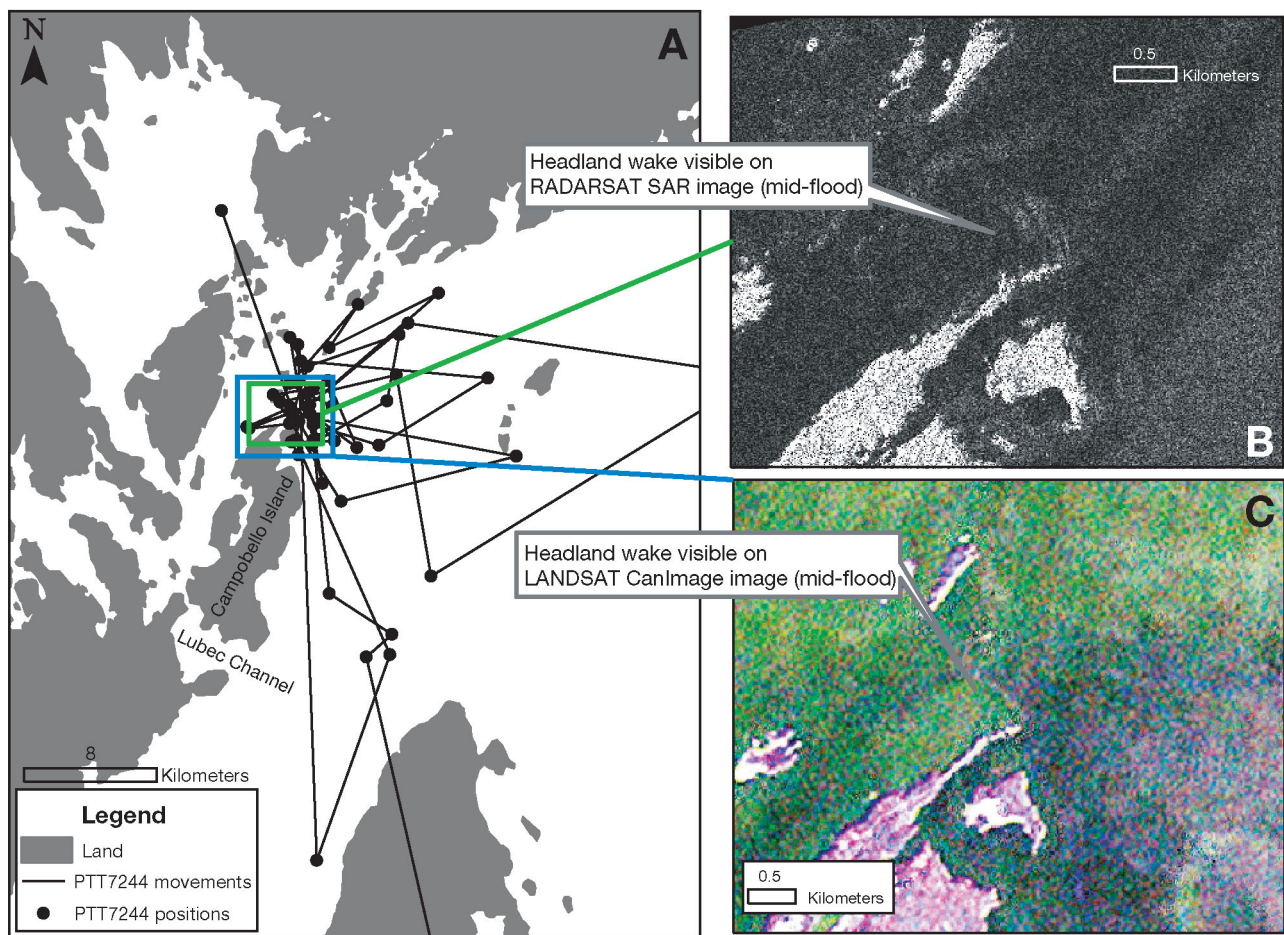


Fig. 9. *Phocoena phocoena*. (A) Spatial relationships between the September movements of harbour porpoise PTT7244 and the Head Harbour headland wake forming off the northern tip of Campobello Island on flood tides as visualized by (B) RADARSAT synthetic aperture radar and (C) LANDSAT remote sensing imagery

interactions between these physical features and time-variant phenomena such as winds, currents, tides, day length and time of day. For example, the region off the northern tip of Grand Manan exhibits a relatively gentle slope, yet the areas at both ends of Campobello Island exhibit rapid changes in depth with proximity to shore. These locations are likely to exhibit different current regimes, but all 3 areas exhibit enhanced relative vorticity (see Mann & Lazier 1996) due to the interactions between fast tidal currents and shoreline configuration (Signell 1989, Signell & Geyer 1991). Both PTT8531 and PTT7244 exhibited focal regions coinciding with the restricted passages into the inshore waters of the Quoddy Region proximate to Campobello Island. Animal PTT8531 focused on the entrance to the Lubec Channel, an area of high tidal velocity on both ebb and flood tides, and PTT7244's focal region was adjacent to the northeastern tip of Campobello Island. This latter area was intensively studied by David Gaskin's research group in the early 1980s and is known to

attract large numbers of marine predators to forage within eddies and upwellings produced on flood tides (Gaskin 1983, Smith et al. 1984).

Two porpoises (PTT7235 and PTT16300) exhibited overlapping focal areas at the northern tip of Grand Manan Island. Previous studies have revealed that porpoise abundance can be high in this region, especially during flood tides (Read 1983). As well, an early treatise on the hunting of harbour porpoises in the Bay of Fundy noted that members of the Passamaquoddy tradition knew that this region was frequented by porpoises that fed on abundant schools of herring and mackerel (Ward 1880). This feature is commonly referred to by local people as the Long Eddy.

Line transects and prey surveys

Our line transects revealed that relative porpoise density was highest in our fine-scale study area during

flood tides. It is difficult to compare the results of our uncorrected surveys with density estimates generated by other line transect surveys for harbour porpoises, due to differences in observation platforms, corrections for animals missed on the trackline and changes in the behaviour of animals in response to survey vessels (Palka & Hammond 2001). Porpoise densities in the Long Eddy during flood tides were more than an order of magnitude higher than estimates of corrected porpoise densities (adjusted for animals missed on the trackline) found by Hammond et al. (2002) in the North Sea and adjacent waters. The density estimate during ebb tide phases in the present study (1.79 porpoises km^{-2}) was similar to uncorrected estimates found by Palka (1995) for high-density regions of the Gulf of Maine (1.46 to 3.97 porpoises km^{-2}). This is not surprising, perhaps, considering that some of Palka's (1995) high-density stratum surveys overlapped with our study area. However, our flood estimates of density are up to 3 times higher than Palka's (1995), suggesting that consideration of tide phase may be important when conducting surveys for porpoises in tidally active regions.

We found it very difficult to assess the availability of prey within the Long Eddy due to the high current velocities and the dynamic nature of the system. However, our hydro-acoustic survey results suggest that prey is concentrated along the length of the feature and that these prey concentrations contain Atlantic herring and euphausiids, the prey of juvenile and adult porpoises. Hydro-acoustic methods have been employed successfully in other marine mammal foraging studies, for example, to assess changes in the quality, depth and location of the meso-pelagic scattering layer near the Hawaii islands in relation to foraging spinner dolphins (Benoit-Bird & Au 2003). Further research is required to develop robust acoustic and traditional sampling procedures for highly dynamic oceanographic features like the Long Eddy.

Our line transect results complement the analyses of satellite telemetry data and illustrate that harbour porpoises congregate in this region during flood tides. A wide variety of marine predators exploit fine-scale fronts, upwellings and eddies while foraging. For example, foraging basking sharks use small-scale oceanic fronts (Sims & Quayle 1998); indeed, it is becoming apparent that some important aspects of the social behaviour of these animals may depend on the predictable occurrence of these fronts (Sims et al. 2000). Seabirds exploit coastal fronts in the North Pacific (Decker & Hunt 1996, Hunt et al. 1996), feeding primarily on small fishes which aggregate there to consume zooplankton. Similar patterns have been found for prions *Pachyptila* sp. that use fine-scale oceanographic features within the Antarctic Polar Front (van

Franeker et al. 2002); there are numerous other examples of seabirds foraging in regions of enhanced relative vorticity (reviewed in Hunt & Schneider 1987). Sea turtles also associate with oceanic fronts (Polovina et al. 2000), and the observations of several species of large pelagic fishes correlate with larger-scale oceanographic phenomena (Barkley 1972, Polovina et al. 2001).

A growing number of examples link marine mammal foraging behavior to oceanographic phenomena, although most observations have been made at larger spatial scales than those examined in the present study. For example, Griffin (1999) found that sperm whales were associated with the edges of warm core Gulf Stream rings as they encountered the continental shelf of the eastern US, presumably feeding on squid which occur in the faster-moving water at the edges of the ring. Similar relationships have been found for sperm whales in the Gulf of Mexico (e.g. Biggs et al. 2000). Pinnipeds are also known to exploit fine-scale oceanographic features for foraging. For example, Zamon (2001) found that harbour seals *Phoca vitulina richardsii* foraged in tidal currents within restricted channels in the San Juan Islands, WA, preying upon aggregations of schooling fish. Similarly, Mendes et al. (2002) found that bottlenose dolphins *Tursiops truncatus* associated with the surface features of a tidal intrusion in the inner Moray Firth, presumably to exploit accumulations of prey in a front which formed between brackish river outflow and saline oceanic tide waters.

Remote sensing and integrative examples

Both the LANDSAT and RADARSAT images confirm the presence of a front and eddy system—an island wake—forming off the northern tip of Grand Manan Island on flood tides. This is the first demonstration of the formation of an island wake forming behind Grand Manan Island in tidal flow, and there are no detailed examinations of the local physical or biological oceanography to draw on for comparison. However, as noted above, Ward (1880) reported that aboriginal people in the area knew about and understood the complex pattern of fronts and eddies caused by the obstruction of Grand Manan to tidal currents. These images provide context for the high density of porpoises in our fine-scale study area on flood tides and help explain the locations of the focal regions of PTT7235 and PTT16300. They also provide details on the physical mechanisms that regulate the system (see below).

Both images also indicate that a similar feature occurs within the core range of PTT7244, near the northern tip of Campobello Island. Here a headland

wake forms on flood tides, as rapid tidal flow inshore is obstructed by the northern tip of the island. Previous studies of the oceanographic regime in this localized area described little coherence in the complex pattern of upwellings and fronts found there and suggested that they originated from a combination of rapid tidal flow over sharp reductions in depth (Smith et al. 1984) and, possibly, island mass effects. Our observations confirm the latter portion of this hypothesis, revealing a headland wake in the vicinity of the greatest temperature anomalies and plankton and fish accumulations in that region (Smith et al. 1984). We did not conduct line transects in this area to confirm whether porpoises congregate in this feature, but previous surveys in or near this feature reported more than twice the number of porpoise sightings in this region compared with other inshore areas (Watts & Gaskin 1985). In addition, Berggren (1995) surveyed this area in 1990 and 1991 and found similar results: porpoise densities were consistently high in this area.

The production of eddies and fronts downstream from obstructions to flow is a common phenomena, existing at spatial scales ranging from rocks in freshwater streams (Crowder & Diplas 2000) to entire islands in geostrophic flow in oceanic systems (Caldeira et al. 2002). These phenomena—referred to as island stirring effects (Aristegui et al. 1997), island mass effects (Doty & Oguri 1956) or island wakes (e.g. Coutis & Middleton 2002)—have significant effects on biological systems (Coutis & Middleton 2002). Island and headland wakes are known to increase nutrient levels (St. John & Pond 1992), stimulate primary production (St. John et al. 1992, St. John & Pond 1992), aggregate plankton (Alldredge & Hamner 1980) and the larvae of fish, crustaceans and molluscs and their predators (Wolanski & Hamner 1988, Rankin et al. 1994). Prey aggregations within headland and island wakes are believed to result from complex secondary flows which concentrate plankton and weak nekton near the surface at convergences and at the edges of eddies (Wolanski & Hamner 1988, Mann & Lazier 1996).

Figs. 8 & 9 are integrative examples of porpoise movements in relation to fine-scale oceanographic features detected by remote sensing. In both cases, the focal region in the porpoises range corresponded with the location of a topographically controlled oceanographic feature that can aggregate plankton and weak nekton (Wolanski & Hamner 1988). Both PTT7235 and PTT7244 appear to have focused on relatively small areas proximate to an island wake and a headland wake respectively. These systems would provide predictable concentrations of prey throughout the summer months.

We sub-sampled our telemetry data to provide a standard sampling rate and comparable kernel density estimates between porpoises, but examining the over-

all telemetry records from individual animals can elucidate, in greater detail, the importance of these features. For example, PTT7235 spent 45 d in the Bay of Fundy (2 Aug to 20 Sept); we received a minimum of 1 position within 5 km of the center of the Long Eddy on 32 (71%) of these days and at least 1 position within 10 km of Long Eddy on 42 (93%) of these days.

Foraging theory predicts that predators should spend more time in areas of abundant accessible prey, thereby maximizing the energetic profitability of their efforts (MacArthur & Pianka 1966, Stephens & Krebs 1986). This type of behavior can be detected by looking for changes in speeds and turning rates in the movements of animals, where they are expected to slow down and turn more frequently in regions of greater prey abundance—often referred to as an area-restricted search pattern (Tinbergen et al. 1967, Krebs et al. 1978, Stephens & Krebs 1986, Kareiva & Odell 1987, Fauchald & Tveraa 2003). We cannot accurately measure the rate of travel for our porpoises, and our standardized sampling rate limits our ability to quantify turn rates and radii in their fine-scale movements. However, chronological reconstructions of the paths of both PTT7235 and PTT7244 clearly illustrate that both animals made occasional forays away from their core areas, followed by movements back into the core region. This suggests that these porpoises likely encountered greater prey densities in their focal regions and that they restricted their movement patterns to maximize energetic profitability.

CONCLUSIONS

Our observations suggest the porpoises target specific regions of enhanced relative vorticity, such as island and headland wakes, as foraging sites during the summer months in the Bay of Fundy. Not all porpoises choose the same focal regions, indicating that some level of specialization in foraging habitat use may exist. However, 3 out of the 6 tagged porpoises chose regions that exhibit predictable, tidally induced fine-scale oceanographic features clearly detectable with remote sensing techniques. Further research is required to assess whether individual harbour porpoises specialize within specific habitats, as occurs in other marine mammals (Estes et al. 2003). These oceanographic features likely enhance foraging efficiency for porpoises by aggregating prey in a predictable manner in localized areas. Integration of data from satellite telemetry, line transect surveys and remote sensing of oceanographic features would be a useful way of developing objective criteria for designating critical habitat for harbour porpoises in the Bay of Fundy and elsewhere.

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