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Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada

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We collected data on the distribution of fin whales (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*) in the Bay of Fundy, Canada from a whale-watching vessel during commercial tours between July and September 2002. A single observer recorded the positions, species, numbers and surface activity of whales encountered during boat tours. We controlled for biased search effort by calculating sightings rates for both species in cells measuring 2' latitude by 2' longitude throughout the study area. Sightings rates were calculated by dividing the number of sightings of fin and minke whales in each cell by the number of visits by the tour boat to that cell. We used generalized additive models and generalized linear models to examine the influence of benthic topography on whale distribution patterns. Models showed a non-linear relationship for minke whale sighting rates with increasing benthic slopes and a linear relationship for minke and fin whale sightings rates with increasing water depth. Sightings of minkes were concentrated in areas subject to tidal wakes near the northern tips of Grand Manan and Campobello Island. Fin whales were also found off the northern tip of Grand Manan but sighting rates for this species were highest in areas with less benthic sloping topography adjacent to the relatively deep Owen Basin. Foraging was recorded during 87% of all whale encounters and our results indicate that whale distribution in this area is likely to be influenced by depth, bottom topography and fine scale oceanographic features that facilitate foraging.

INTRODUCTION

Few detailed studies of baleen whales have been conducted in the inshore Bay of Fundy and most have focused on North Atlantic right whales (e.g. Baumgartner & Mate, 2003; Baumgartner et al., 2003a,b), with fewer directed towards other species such as fin whales and minke whales however (see Arnold & Gaskin, 1972; Woodley & Gaskin, 1996). Previous fine scale studies have examined the role of island wakes and tidal currents in the distribution and behaviour of cetaceans in the Bay of Fundy (Johnston et al 2005a,b). The opportunity to place an observer aboard a local whale-watching vessel provided us with a platform to collect data at a wider geographical scale. We used data collected from the tour-boat to examine factors affecting the distribution of fin and minke whales in the lower Bay of Fundy, focusing on the Quoddy region, the approaches to the Bay and offshore areas near the north end of Grand Manan Island.

The Bay of Fundy is characterized by large, semi-diurnal tides with amplitudes of up to 16 m at the head of the Bay (Garrett, 1972). Further south, in the lower Bay, tidal amplitudes are also large, often exceeding 8 m (Trites & Garrett 1983). The movement of strong tidal flow around islands and across variable bottom topography within the lower Bay of Fundy produces numerous fine scale tidal fronts and eddy systems that are known to attract large numbers of marine mammal and seabird predators (Smith et al., 1984). Indeed, the lower Bay is a summer feeding ground for several species of odontocete and mysticete cetaceans—fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*) are seasonally abundant (Gaskin, 1983) and harbour porpoises (*Phocoena phocoena*) are also common throughout the Bay in the summer (Gaskin, 1983; Palka et al., 1996). The lower Bay is also visited each summer by endangered North Atlantic right whales (*Eubalaena glacialis*) (Brown et al., 2001) that use the Bay as a foraging ground. The distribution of right whales has been associated with the local abundance of planktonic prey species such as *Calanus* copepods which become concentrated at fronts (Murison & Gaskin, 1989; Woodley & Gaskin, 1996) or at the interface of the bottom mixed layer in the Grand Manan Basin (Baumgartner et al., 2003a).

Marine mammals tend to be distributed non-uniformly within habitats at a range of spatial scales (Jaquet, 1996), and clumped distribution in cetaceans has been linked to heterogeneous habitat variables such as sea temperature (Gaskin, 1968; Brown & Winn, 1989; Baumgartner et al., 2001), benthic topography (Selzer & Payne, 1988; Baumgartner, 1997; Cañadas et al., 2002; Ingram & Rogan, 2002), ocean currents and frontal systems (Tynan, 1998; Mendes et al.,

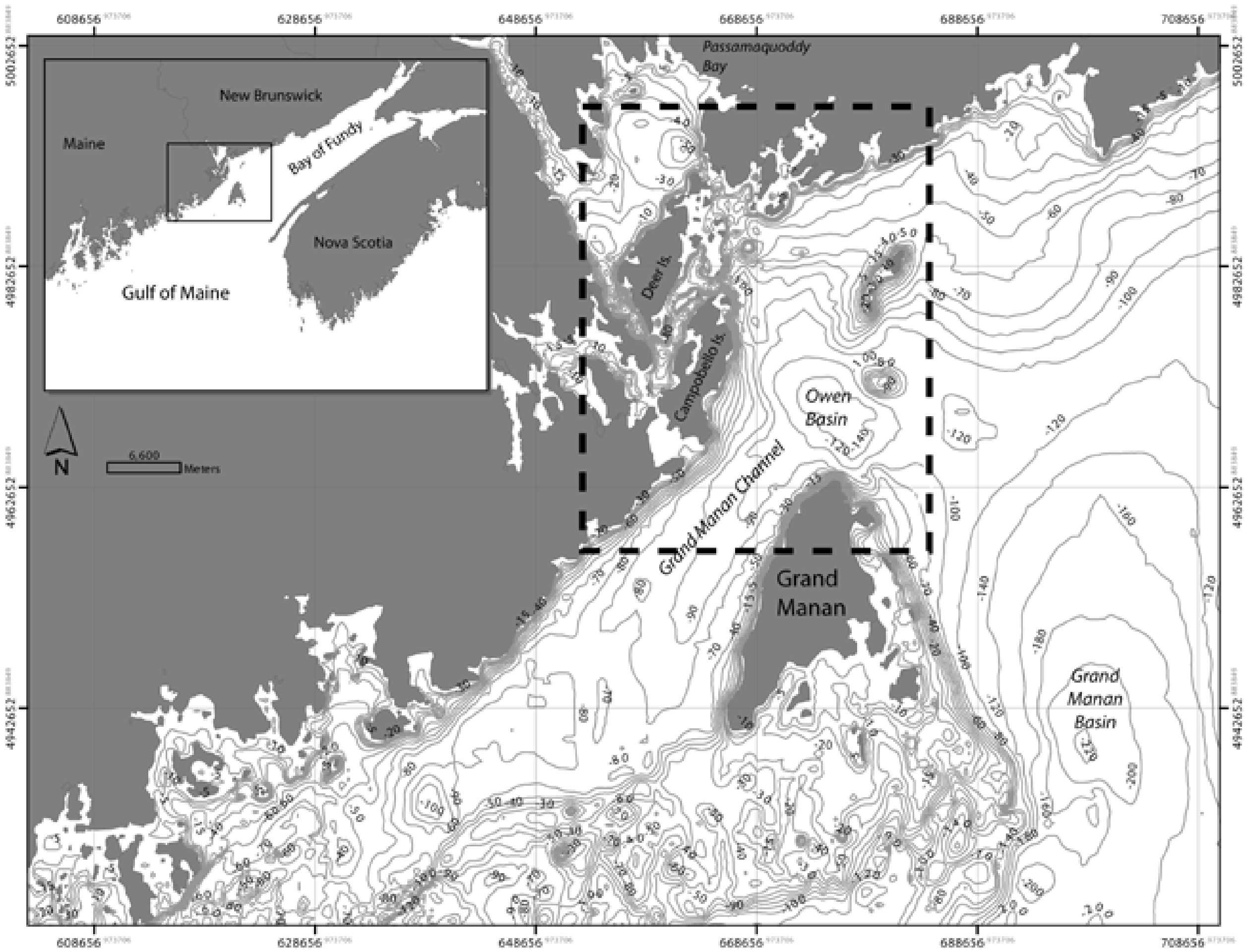

Figure 1. The lower Bay of Fundy showing the main study area between Passamaquoddy Bay and Grand Manan Island (shown with dashed box). Depth contours are given in metres.

2002; Johnston et al., 2005a,b), and, in association with these physical habitat variables, prey distribution patterns (Woodley & Gaskin, 1996; Jaquet & Gendron, 2002; Baumgartner et al., 2003a; Macleod et al., 2004).

Collecting data on the distribution of whales at sea presents numerous logistic and financial challenges to the researcher. Often these animals are found offshore in deep ocean waters requiring the use of a suitable seagoing vessel for data collection. The use of platforms of opportunity (POPs) offers the scientist the opportunity to visit and collect data on whales at sea with a marginal cost. These vessels are often ferries and research vessels regularly plying standard routes (Thiele & Gill 1999; Pinedo et al., 2002) and more recently with the increase in nature tourism, commercial whale-watching vessels (Williams, 2003). Whale-watching vessels offer the advantage of increased contact time with cetaceans as spending time near whales is their primary aim. Additionally, tours often target animals within near-reach of populated land and hence in areas where conservation management needs are particularly vital. However, the use of such vessels presents some fundamental problems to the researcher including non-standardized sampling effort, short duration of field time, and limits to sampling techniques imposed by the nature of the vessel and its primary function. Additionally, tour boats often adhere to codes of conduct that prevent close approaches to animals. Whilst some of these limitations may preclude the collection of some data (such as detailed sampling for plankton and the measurement of some physical parameters), POPs can provide a useful platform to collect a variety of ecological data including the relative abundance, distribution and activity of whales in certain areas.

MATERIALS AND METHODS

Study area and platform of opportunity

All data were collected from the 17 m catamaran whale-watching vessel 'Quoddy Link' during regular commercial whale-watching trips. Tours were conducted out of St Andrews, New Brunswick, Canada (45°4'N 67°4'W) in Beaufort sea states of 5 or less and trips lasted between two and four hours. The vessel concentrated on searching an area of the lower Bay of Fundy between the entrance to Passamaquoddy Bay in the north-west (45°3'N 66°55'W), the Wolves Islands in the east (44°58'N 66°43'W) and the northern tip of Grand Manan Island in the south (44°48'N 66°47'W) (Figure 1). Data presented here were collected on trips conducted during the months July to September 2002, the time of peak abundance of most species of cetaceans in the lower Bay (Gaskin, 1983).

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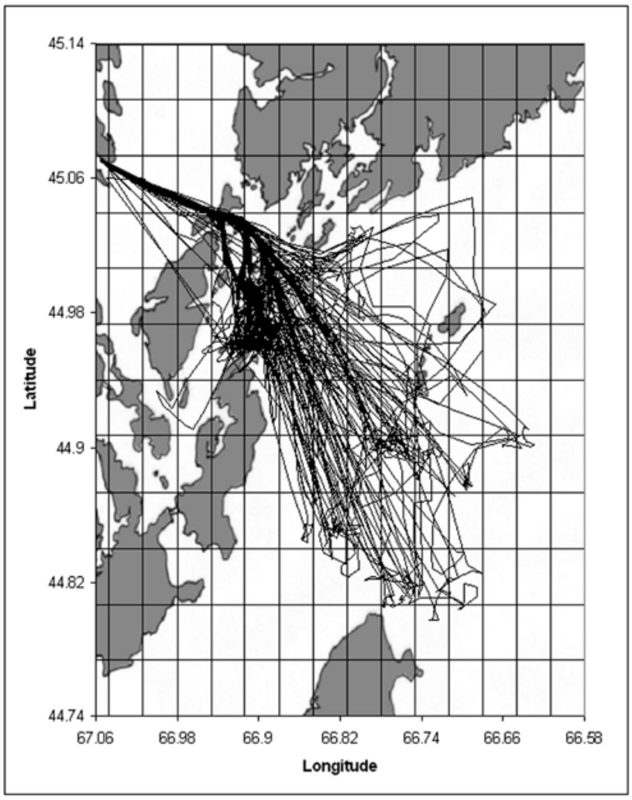

Figure 2. The GPS track of the whale-watching vessel recorded during the 100 data collection trips. The grid shows the cells used in the analyses.

Data collection

The observer (L.W.) and the vessel's skipper maintained a 360° lookout for whales throughout the trips from a height of approximately 4 m above sea level using the naked eye and binoculars (5× magnification). During all trips the vessel's track was recorded using a handheld global positioning system (GPS) unit (Garmin 40), which automatically recorded a position (±50 m) every five minutes. The presence or absence of shoaling fish was recorded at the start of each encounter using a Suzuki echo-sounder. Other environmental data, such as weather conditions, cloud cover and sea state were also recorded for each trip.

Animals were spotted from their characteristic blows and surfacing behaviour (Leatherwood & Reeves, 1983) and once sighted were approached in accordance with a local voluntary code of ethics (www.grandmanannb.com/ethics.htm). When one or more animals were sighted within approximately 300 m of the vessel (estimated by eye), the boat's position (±50 m) was recorded using the GPS receiver. All animals estimated to be within a 300 m radius of the vessel were considered as members of a group (although no association between individuals in a group was inferred) and a period of time spent collecting data relating to a group was defined as an encounter. The number and species of all animals present in each encounter were recorded and group sizes assigned to one of three categories: single or a pair of animals; groups of three or four; and groups of five or more whales. The surface activity of animals was also recorded during scan samples at the start of each encounter before any possible disturbance effects due to the boat's presence. Activities were classified

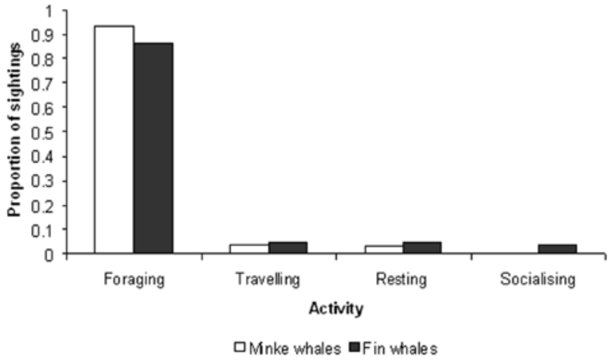

Figure 3. The frequency of activities recorded for observed whales at the start of each encounter.

according to a standardized ethogram (Mann, 2000), which classified behaviour into one of four categories: travelling, resting, foraging or socializing. Travelling was ascribed to animals moving at a constant speed in a single direction, and resting was assigned when little or no forward motion was observed with slow regular blows. Foraging included animals observed milling (moving in a convoluted direction within a small area) and in the act of lunging and surface swimming with mouth open. Socialising was ascribed to members of a group in close physical contact, interacting at the surface.

Data analysis

Spatial analysis

We divided the study area into a grid of rectangular cells each measuring 2' latitude by 2' longitude and assigned each cell a maximum charted depth using the relevant Admiralty charts (No. 4115 and No. 4340). We also calculated the maximum difference in charted depths for each cell as an indicator of benthic slope. To control for biases in sampling effort within the study area we calculated the sighting rates of each species in each of these cells rather than using actual encounter locations.

Track-line data from all whale-watching trips were used to measure the number of visits to each cell throughout the study period. The number of visits to individual cells was significantly correlated with the number of minutes spent searching in each cell ($P<0.01$) and was therefore considered to be a good representation of the search effort. Any cell searched on less than three occasions was excluded from subsequent analysis in order to reduce bias associated with poorly sampled areas. The number of sightings relating to each cell was counted and the sighting rate for each species was calculated for each cell as follows:

$$R_j = \left(\frac{s_j}{n_j} \right)$$

where R_j is the sighting rate for species R in cell j, s_j is the number of sightings of species R in cell j and n_j is the number of searches of cell j.

The sightings rates for fin and minke whales in each cell were compared to those expected from a hypothetical uniform distribution using χ^2 values to test the null hypothesis

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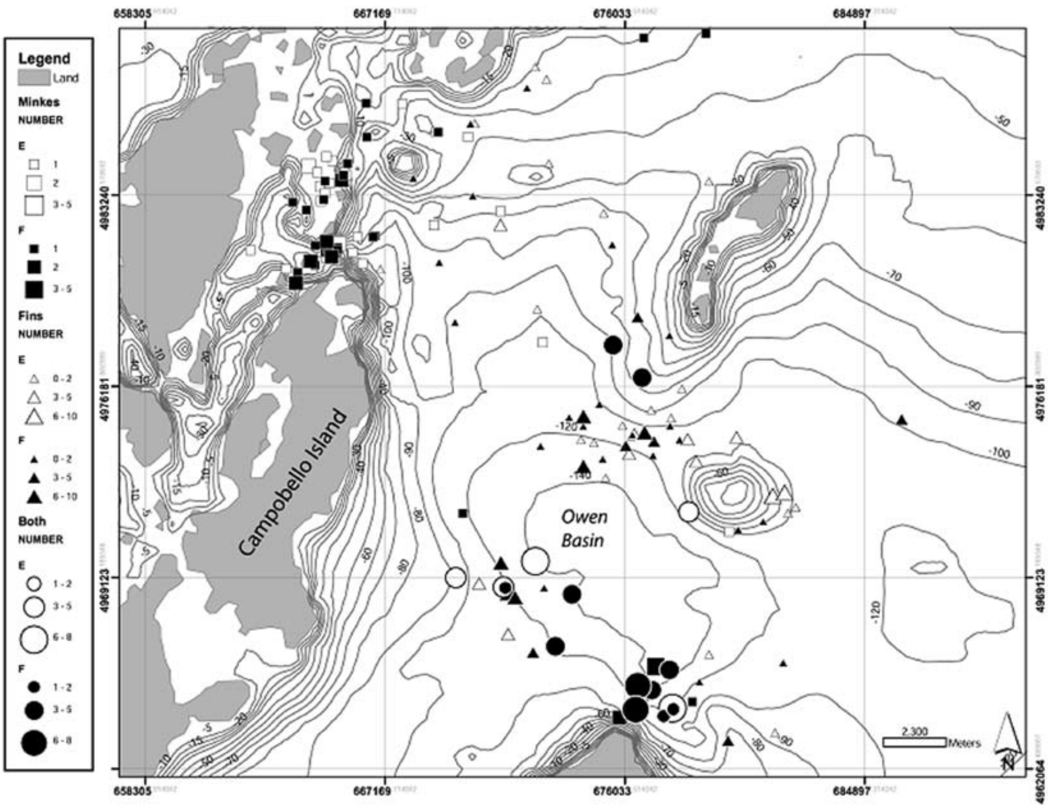

Figure 4. The distribution of fin whale and minke sightings in the lower Bay of Fundy with respect to depth contours. Minke schools are denoted by squares, fin whales by triangles and mixed species schools by circles. Shaded and white markers denote sightings made during flood tides, and ebb tides respectively.

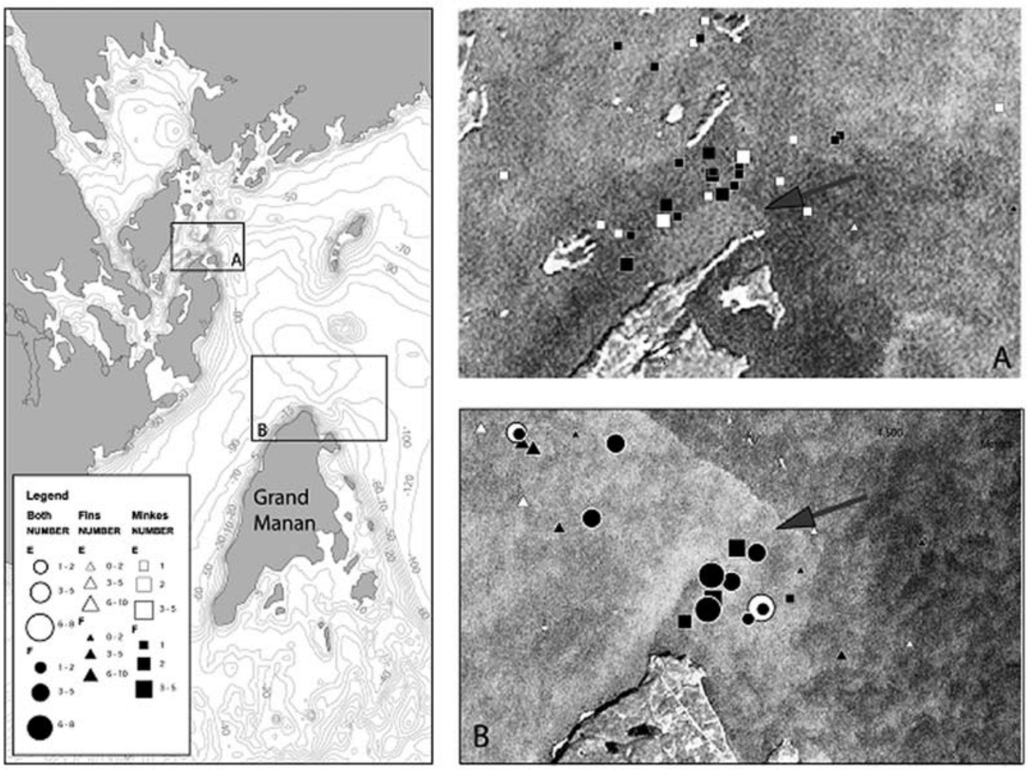

Figure 5. The locations of sightings of fin and minke whales with respect to satellite images of tidal wakes established during flood tides at (A) the northern tip of Campobello Island and (B) the northern tip of Grand Manan Island. Minke schools are denoted by squares, fin whales by triangles and mixed species schools by circles. Shaded and white markers denote sightings made during flood tides, and ebb tides respectively.

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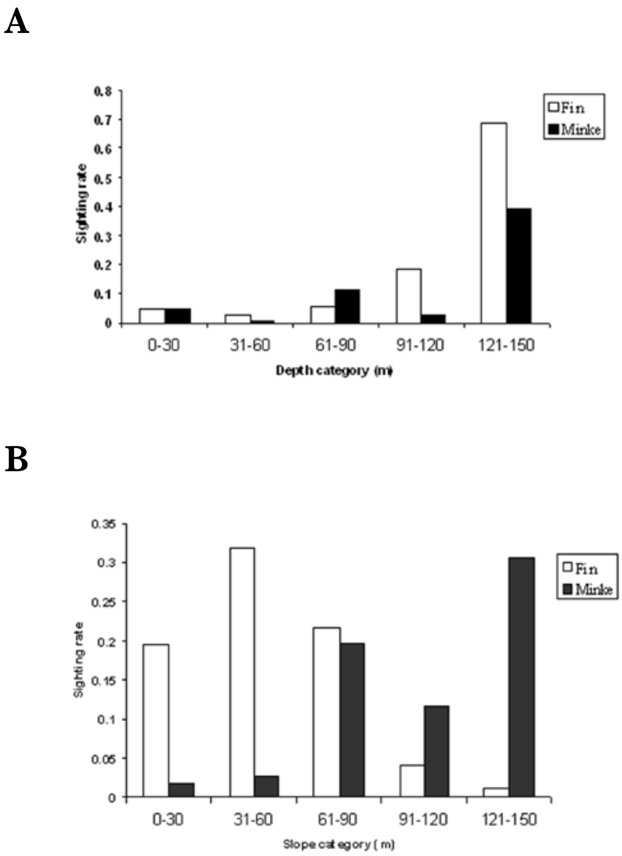

Figure 6. The sighting rates of fin and minke whales with respect to five categories of; (A) depth and (B) benthic slope (slope values were calculated as the maximum difference in charted depth in each 2'x 2' cell).

that animals were distributed uniformly throughout the study area. In addition, the sightings rates for both species in each cell were compared using a pair-wise correlation to test whether the two species were distributed similarly.

Data modelling

We used generalized linear models (GLMs) and generalized additive models (GAMs) to examine the role of environmental variables depth and slope on the sighting rates of minke and fin whales. Data were modelled using the freeware R (http://www.r-project.org). GLMs are useful for fitting linear relationships with non-Gaussian data distributions (McCullagh & Nelder, 1989). GAMs allow a data driven approach by fitting smoothed non-linear functions of explanatory variables without imposing parametric constraints (Hastie & Tibshirani, 1990). Smoother terms were derived using penalized regression splines using the MGCV library in R (Wood, 2006). GAMs were fitted to both minke and fin whale sightings rates using smoothers of depth and slope. Models with lower generalized cross-validation (GCV) scores (difference>0.005) were selected and the residuals were examined for patterns. GVC is the MGCV GAM equivalent to Akaike's Information Criterion (AIC) and scores both on fit and the number of parameters used in the model.

If the model reduced the smoothing spline to an estimated degree of freedom approximating to one and there was no apparent pattern in the residuals, then the smoother function was replaced by a linear term. Non-significant terms (P>0.05) and terms which did not reduce the GCV score by more than 0.005 were removed from the final model. We assumed a quasi-Poisson distribution and used a log-link function in all models.

Table 1. *Results of GLM models for fin whale sightings rates. Slope was found not to be significant so was removed from the final model. Asterisk indicates significance level.*

Linear term	Estimate	*t*- value	*P*-value	Overall deviance explained
Slope	ns	ns	ns	
Depth	0.020	2.12	<0.05*	13.7%

ns, not significant

State of tide

For each sighting the tide-state was classified according to two categories, flood or ebb. Slack water periods (the hour preceding and the hour after low or high water) were included with the preceding tide state since slack periods are likely to maintain prey aggregations or concentrations for some time before the change in tidal currents alters the configuration of fronts and eddies. In order to examine the effect of tide-state on the distribution of whales we used pairwise correlations to compare sighting rates in each cell during ebb and flood tides for each species.

RESULTS

Data were collected during 325 h on 100 trips conducted between 17 July and 18 September 2002 (Figure 2). Only 10 trips were conducted in seas of Beaufort 5 and 75% of trips were conducted on days with a sea state of Beaufort 2 or less, providing excellent sightings conditions. During these trips, data were collected during 151 encounters with a total of 344 whales, including 228 fin whales and 104 minke whales — some encounters comprised more than one species. Ninety-three per cent of minke whales were sighted alone or in pairs compared to fin whales, of which over a third of all encounters were of groups of three or more animals. The remaining 12 sightings were of humpback whales, which due to the paucity of sightings, were excluded from further analyses.

Surface activity of whales

Foraging was the most frequently observed activity for both species with all other activities combined recorded for only 14% and 7% of observations of fin and minke whales,

Table 2. *Results of GAM model for minke whale sightings rates including the variables depth and slope. Asterisks indicate significance level.*

Smoother term	edf	F value	*P*-value	Overall deviance explained
Slope	2.3	3.8	<0.01**	
Linear term	Estimate	t-value	*P*-value	42.0%
Depth	0.027	2.95	<0.01**	

edf, empirical distribution function.

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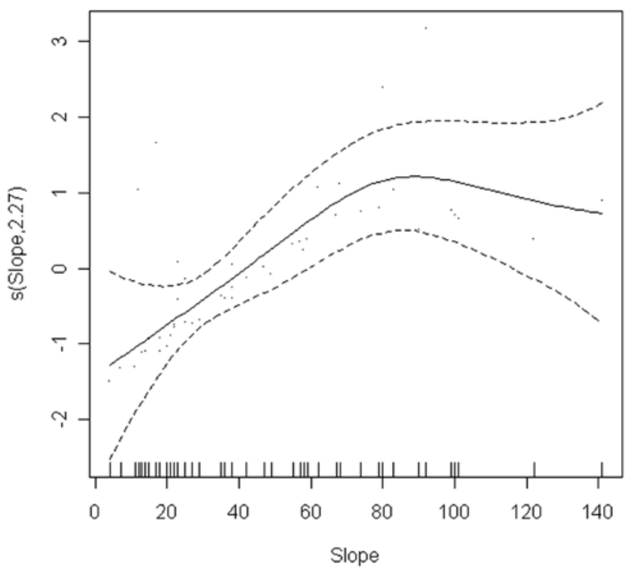

Figure 7. GAM smoothing curve of minke whale sightings rate and benthic slope. Benthic slope is expressed as the maximum difference in charted depth (metres) for each grid cell. Dotted lines represent 95% confidence intervals. Degrees of freedom are shown in parentheses on the y-axis label. The vertical lines above the x-axis show positions of the measured data points.

respectively (Figure 3). Additionally, schooling fish were detected during 78% of encounters for which foraging activity was recorded.

Influence of tide and topography on the distribution of whale sightings

The distributions of sightings of fin and minke whales were found to differ significantly from a hypothetical uniform distribution (χ^2 =232.27, df=42, P<0.001 and χ^2 =99.87, df=42, P<0.001 respectively). Furthermore, a pair-wise comparison of the sightings rate for both species in each cell showed that fin and minke whale sightings were not correlated (r=0.143, N=43, P>0.05) and instead were exploiting different areas of the lower Bay. Plots of sightings locations show differences in the distribution of minke whales and fin whales (Figure 4). Minke whale sightings were concentrated north of Campobello Island and near the northern tip of Grand Manan Island; areas associated with strong tidal wakes (Figure 5). Fin whales were most frequently sighted in the deeper waters adjacent to the Owen Basin between the Wolves Islands and Grand Manan Island (Figure 4) but fin whale sightings were also concentrated near the island wake of the northern tip of Grand Manan (Figure 5).

There was no difference between the distribution of sightings made during ebbing tides and flooding tides. In fact, distributions of sightings made during flood tides were strongly correlated with distributions of sightings during ebb tides for minke whales (r=0.495, N=47, P<0.01) and for fin whales (r=0.368, N=49, P<0.01).

Fin whales were most frequently encountered in deeper areas (Figure 6A) with less benthic slope and showed preferential use of cells with depth differences less than 60 m (Figure 6B). Models of fin whale sightings rate with depth and slope showed depth to be marginally significant as a positive linear term (P<0.05) indicating an increase in sightings rate with increasing depth, whereas, slope was not found to be a significant variable (Table 1). The final GLM for fin whales explained 13.7% of the deviance (Table1).

Minke whales were found to prefer deep areas (Figure 6A) with steeper benthic topography than shallow sloping areas and were encountered predominantly in cells with depth differences in excess of 60 m (Figure 6B). Results of GAMs with minke whale sightings rates, including the variables depth and slope, showed that slope had a significant positive non-linear effect (P<0.01) on the sightings rates of minke whales (Figure 7). Minke whale sightings increased with increasing benthic slope, peaking in cells with depth differences of approximately 90 m and decreased in cells with benthic slopes in excess of 90 m depth differences. Depth had a significant positive linear effect on sightings rates. The final GAM for minke data explained 42% of the deviance (Table 2) and was of the form:

$$m \sim s(slope) + depth$$

where m represents the minke whale sightings rate and s represents the smoother function.

DISCUSSION

Distribution and activity of fin and minke whales

Fin and minke whales were seen throughout the study area and both species showed non-uniform use of the lower Bay of Fundy. The distributions of these two species were not correlated statistically, indicating some degree of habitat partitioning within the Bay.

GAMs and GLMs indicated that both minke and fin whale sightings rates increased linearly with increasing depth, whereas benthic slope was only important to minke whales. Minke whales were found to increase non-linearly with increasing slope. In fact, the final GAM for minke whales explained 42% of the total deviance showing depth and slope to be important predictors of minke whale distribution. Fin whales were not found to be significantly influenced by slope and only weakly related to depth. The final model for fin whale sightings explained only 14% of the deviance, suggesting that other factors not included in these models were important for describing their distribution. For example, Gregr & Trites (2001) conducted GLMs using historic whaling data and found fin whale distributions to be closely related to salinity. GAM and GLM modelling is becoming a useful and standard tool for examining the relationship between cetaceans and their environment (Redfern et al., 2006) and has been applied to a variety of species including beaked whales (MacLeod & Zuur, 2005), dolphins (Cañadas et al., 2002; Hastie et al., 2005) and baleen whales (Macleod et al., 2004).

Foraging was by far the most frequently recorded activity for both species. During some encounters, fin and minke whales were observed foraging in mixed groups. These encounters all occurred in the deeper waters beyond the approaches to the Bay and occurred primarily near the northern tip of Grand Manan Island (Figure 3). Fin whales have been shown to feed primarily on euphausiids (usually *Meganyctiphanes norvegica*) in the Bay of Fundy (Brodie et al., 1978) although they have also been found to forage to a lesser extent on small schooling fish such as Atlantic herring,

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Clupea harengus harengus (Gaskin, 1983; Aguilar, 2002). In contrast, minke whales are often referred to as 'catholic' feeders and forage on a variety of fish and invertebrate crustaceans throughout their range (Perrin & Brownell, 2002). Indeed, recent stable isotope analyses of minke and fin whales sampled south in the Gulf of Maine indicate that minkes generally feed at a higher trophic level than fin whales (Todd et al. 2005). Considering the prey preferences of these species, the observed difference in habitat use may relate to the distributions and behaviours of their primary prey species. For example, as euphausiids generally exhibit vertical migrations to deeper waters during daylight hours (Tarling, 2003), foraging fin whales may also be restricted to deeper regions to exploit their preferred prey. In cases where fins and minkes were observed feeding together, minkes may be exploiting high densities (see Brodie et al., 1978) of various prey species whereas fin whales may be restricted to regions which exhibit highest densities of euphausiids. Regardless of which prey species are being exploited, the high frequency of observations of foraging behaviour of both species suggest the importance of this region for feeding.

Influence of fine scale oceanographic features on the distribution of whales

Fin whale sightings were also concentrated near the northern tip of Grand Manan Island (as reported previously—see Johnston et al. 2005a), as well as over the deep waters adjacent to the Owen Basin with depths similar to those reported by Woodley & Gaskin (1996). Although there is little benthic slope in this area, the region is immediately adjacent to the north side of the Owen Basin where the seabed rises from depths of 160 m to under 100 m just south of the Wolves Islands. The relatively deep Owen Basin may provide suitable habitat for vertically migrating euphausiids. Fin whales here may be foraging on dense patches of euphausiids aggregated in deep waters near the steeply sloping bathymetry of the north and south edges of the Basin.

Minke whale sightings were most frequent around the north of Campobello Island. This steeply sloping area is known to produce small scale tidal fronts and upwellings (Figure 5) which may make prey species such as herring, mackerel (*Scomber scombrus*) and larger zooplankton (e.g. *Meganyctiphanes* spp.) more available to foraging predators (Johnston et al., 2005a). The steep change in bathymetry in this region (Figure 4) leads to local upwellings and small fronts that tend to accumulate plankton and weak swimming nekton. The headland wake produced on the flood tide as water streams into Head Harbour (Figure 5a), is likely to also increase local upwelling and aggregate plankton and weak swimming nekton along its length and in the associated back-eddy behind (Wolanski & Hamner, 1988; Johnston et al., 2005b). These results are consistent with the hypothesis that the island mass effect (Doty & Oguri, 1956) contributes to the aggregations of prey found in this region (Smith et al. 1984; Watts & Gaskin, 1985). Additionally, minke whales were frequently encountered in the deeper waters at the northern tip of Grand Manan Island, where during flood tides a complex set of upwellings and fronts is produced that attract or aggregate prey (Johnston et al., 2005a). The rapid flow on flood tides creates an island wake downstream of the island (Figure 5b), functioning in a similar manner to the Head Harbour headland wake described above (see also Johnston et al., 2005a).

The suitability of whale watching vessels as platforms of opportunity

This study demonstrates that useful ecological data can be collected from platforms of opportunity such as whale-watching vessels despite associated constraints such as non-standard sampling protocols. Although we were limited to a non-regular non-uniform survey pattern, the use of data weighting techniques enabled us to derive corrected measures of relative distribution of two species over a period of months and relate these distributions to biophysical parameters such as bottom topography and fine scale oceanographic features which are known to structure some of the ecological relationships between marine mammals and their prey in this region. The use of such platforms would doubtless provide scientists in many locations around the world, particularly areas with limited research funding, opportunities to collect data on a wide range of marine fauna. With the increase in boat-based marine tourism such methods will yield valuable information to scientists and conservation managers alike without increasing vessel traffic or violating local whale-watching codes of conduct.

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