



Challenges in marine mammal habitat modelling: evidence of multiple foraging habitats from the identification of feeding events in blue whales

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ABSTRACT: Effective conservation of animal species depends on accurate identification of their critical habitat. Marine mammals, however, often transit through heterogeneous habitats and perform various activities within short periods of time. The predictive power of habitat modelling techniques can thus suffer from variability in behaviour and the use of multiple habitat types. We used data loggers and ecological-niche factor analysis (ENFA) modelling techniques to determine blue whale *Balaenoptera musculus* associations with underwater topography on a feeding ground in the St. Lawrence River estuary, Canada. We compared a naïve model that had no knowledge of behaviour with a model that used the locations of feeding events inferred from specific velocity signatures. Blue whales travelled over several habitat types with different characteristics, which confounded modelling efforts when pooled together. The model based on the feeding set had considerably higher predictive power but could not highlight all suitable habitats at the same time. Using cluster analysis, we identified 4 habitat types used for feeding, each corresponding to distinct underwater topographies. Feeding depth and behaviour varied across these habitats, which were used preferentially at different times of the tidal cycle and appeared linked to known prey aggregation mechanisms. Our results suggest that failure to identify feeding activity or to take into account the existence of multiple foraging habitats at a fine scale could result in spurious modelling results.

KEY WORDS: Habitat modelling · Feeding behaviour · Habitat suitability · ENFA · Blue whale · St. Lawrence River · Marine mammals

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INTRODUCTION

In habitat modelling, locations where organisms are present are often compared to available but unused areas to assess relationships between species and their environment (Johnson 1980). Mobile species, however, rarely use an area for only one purpose, nor do they always fulfil biological needs in only one habitat (Firle et al. 1998). The longer individual animals are observed, the higher the likelihood that several behaviours will be captured in a data set (Morales & Ellner 2002). Therefore, knowledge of the

behaviour of an animal is essential to quantify the function and value of a habitat (Beyer et al. 2010).

Linking habitat to specific functions has been challenging in marine species because of the difficulty of documenting underwater behaviour. Recent advances in biologging now allow feeding behaviour to be inferred in several ways, e.g. stomach temperature (Lesage et al. 1999, Kuhn & Costa 2006) and head or jaw movements (Suzuki et al. 2009, Naito et al. 2010). Large cetaceans, however, cannot be captured and thus cannot be equipped with tags that require such precise positioning. Feeding can be observed di-

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rectly via a submersible video camera attached to animals, but this technology is greatly limited by turbidity and darkness (Marshall 1998). An alternative method has been to use speed or acceleration data to investigate feeding behaviour in large whales (Goldbogen et al. 2006, Simon et al. 2009). Blue whales *Balaenoptera musculus*, for instance, perform feeding lunges characterised by rapid speed changes (Goldbogen et al. 2011), which can be used to pinpoint the exact moment of each feeding attempt (Doniol-Valcroze et al. 2011).

Although little is known of their winter distribution and migration routes (Reeves et al. 2004), North Atlantic blue whales are found during summer on a range of high-latitude feeding grounds from eastern Canada to Greenland (Sears & Calambokidis 2002). Whaling records (Mitchell 1974) and field studies (Sears et al. 1990, Kingsley & Reeves 1998) indicate that portions of the Gulf of St. Lawrence are important seasonal feeding sites for blue whales from late May to December. They are found as far upstream as the St. Lawrence Estuary (SLE), where the largest concentrations have been recorded in August and September (Edds & Macfarlane 1987, Comtois et al. 2010). Recurrent resightings of individuals in the SLE suggest some form of site fidelity and attest to the importance of the area for part of the population (Ramp et al. 2006).

Photo-identification studies suggest that blue whales from eastern Canadian waters and West Greenland all belong to the same eastern North Atlantic stock (Gambell 1979, Sears & Larsen 2002). This stock is among the most threatened populations of baleen whales worldwide (Clapham et al. 1999) and was designated 'endangered' by the Committee on the Status of Endangered Wildlife in Canada in 2002. Coastal areas such as the SLE are often the most at risk from human development (McIntyre 1999). Indeed, SLE blue whales face several sources of habitat degradation, including pollution by persistent contaminants (Ross et al. 1996, Metcalfe et al. 2004), pressure from whale-watching activities (Edds & Macfarlane 1987, Michaud & Giard 1998), and anthropogenic underwater noise, which can result in masking of social sounds (Nowacek et al. 2007). Blue whales in the SLE have been shown to modify their vocal behaviour in response to noise from seismic surveys (Di Iorio & Clark 2010).

Assessing and monitoring habitat quality on this feeding ground is therefore of utmost importance for conservation purposes. Habitat modelling for large rorquals, however, is challenging and usually yields low predictive power (Ingram et al. 2007, Doniol-

Valcroze 2008), with absence being typically easier to predict than presence (Gregg & Trites 2001, Panigada et al. 2008). Failing to take into account the behavioural context of space use may explain these modelling difficulties (Beyer et al. 2010). Different habitats may be required to fulfil biological needs and may be used at different times (Cooper & Millsbaugh 1999). For instance, fin and minke whale distribution in a tidally driven island wake ecosystem changed with tidal phase (Johnston et al. 2005). Moreover, feeding behaviour can depend on when and where foraging is taking place (e.g. Goldsworthy et al. 2010). Indeed, humpback whales have been shown to change feeding strategies over the diurnal cycle (Friedlaender et al. 2009).

Going beyond the limitations of traditional habitat modelling thus requires a better understanding of blue whale behaviour. Here, we used data-loggers to gain insights into habitat-use patterns and feeding behaviour of blue whales in the SLE. We applied an automated method for detecting lunge-feeding events to discriminate between feeding and non-feeding dives. Our objectives were to: (1) inform management efforts by identifying areas used specifically for feeding; (2) model the bathymetric characteristics of feeding areas and develop maps of habitat suitability; and (3) gain insights into the variability of feeding behaviour and habitat selection in relation to tides, and how this variability can impact predictive habitat modelling.

MATERIALS AND METHODS

Deployment of data-loggers

From 2002 to 2009, blue whales *Balaenoptera musculus* in the St. Lawrence River estuary were equipped with velocity-time-depth recorders (VTDRs Mk8 and Mk10, Wildlife Computers) and radio-transmitters during the time of greatest abundance in the region (August to September; Edds & Macfarlane 1987). Tags were deployed from a 5 m rigid-hulled inflatable boat using a 6.4 m pole or 150 lb (~68 kg) compound crossbow and were attached to whales with suction-cups. VTDR recorded time, water temperature, instantaneous swim speed, and depth every 1 s, with a pressure transducer resolution of 0.25 m for the first 15 m. A digital acoustic recording tag (D-tag; Johnson & Tyack 2003) was also deployed. The D-tag lacked a velocity meter but recorded the animal's pitch, roll and heading, as well as ambient noise (including flow noise) every second. Whales were radio-tracked from a distance of 500 to 1000 m

to minimise disturbance from the research vessel. Whale locations after each sequence of respirations were recorded using a GPS. Tracking lasted until the tag was released due to the corrosion of a magnesium cap and entry of air or water under the suction cup, or until nightfall. Whales were photo-identified using standard techniques (Sears et al. 1990), which allowed us to verify that our sample was composed of different individuals.

Diving and feeding behaviour

Data were corrected for electronic drift (zero-offset) using the software Instrument Helper (Wildlife Computers). Sensor drift depended mostly on temperature differences and was exacerbated when such differences were sudden. For this reason, zero-offset corrections differed with whale behaviour (shallow vs. deep dives) and had to be adapted to different phases of the dive records. These corrections were validated by comparing depth and swimming velocity patterns of a large number of dive sequences with observations of feeding and breathing recorded from the research vessel. Estimates of swim speeds for the D-tag were obtained from flow noise, following the procedure outlined in Goldbogen et al. (2008), and detailed in Doniol-Valcroze et al. (2011).

Depth and swim speed data were analysed using a custom-made program in Visual Basic to calculate various dive characteristics, as well as the number of feeding events per dive. Lunges were identified automatically, independently of depth values, by detecting the characteristic speed signatures associated with this behaviour (i.e. rapid acceleration followed by abrupt deceleration). Details and validation procedures are given in Doniol-Valcroze et al. (2011). Briefly, we first flagged swim speeds >95th percentile of velocity values recorded for each individual. When these extreme velocities were followed by a period during which mean speed over the next 10 s was less than half the mean speed during the acceleration period, it was considered indicative of a feeding event. The start of each deceleration was considered indicative of the exact moment of the opening of the mouth (Goldbogen et al. 2006), and was used to extract the time and depth of each feeding attempt.

Movements and location of feeding dives

Movement patterns were determined for each tagged individual from recorded surface observations

using Bézier curves, which yield more realistic trajectories than linear interpolations (Tremblay et al. 2006). Time records of lunging activity were then used to interpolate the geographical location of feeding events along these trajectories. To minimise error, no interpolation was performed during intervals when animals could not be located for >1 h, i.e. approximately 4 to 5 breathing sequences. Although some tags remained attached during the night, we quickly lost the ability to accurately track whales after sunset. Therefore, we restricted our analysis to daytime data, i.e. movements and feeding behaviour measured between sunrise and sunset. From the positions of feeding dives (i.e. dives with at least 1 feeding event), we identified the main feeding sites using fixed-kernel density contours (Seaman & Powell 1996).

Study area and habitat characteristics

The upstream boundary of the study area was defined based on previous knowledge that large whales rarely occur farther upstream than the mouth of the Saguenay River (Edds & Macfarlane 1987). For lack of better information, we defined the downstream limit of the study area based on the farthest north-east location of tagged individuals, plus an arbitrary buffer of 5 km. Since it was obvious from ranging patterns of the tagged whales that they could easily have crossed the estuary during the time they were tracked, we considered the entire width of the St. Lawrence River as available habitat.

The dominant topographic feature of the area is the Laurentian Channel that extends from the Scotian Shelf, outside the Gulf of St. Lawrence, to Tadoussac in the SLE. The 200 to 300 m deep channel is characterised by steep slopes on both sides, and comes within 100 m of the north shore in some places, while leaving wide, shallow plateaux in other places. At the western end of the Laurentian Channel, as well as along the slopes, tidal mixing and interaction with bathymetry are responsible for rich krill aggregations (Simard et al. 1986). For this reason, we used bathymetric features (depth, slope) as habitat descriptors. These physiographic variables were also the most successful at predicting rorqual whale occurrence at medium and fine scales in other studies (Ingram et al. 2007, Panigada et al. 2008).

We used a digital bathymetric chart to calculate mean depth and slope in each 100 × 100 m cell in the study area (Fig. 1). We then extracted depth and slope for the location of each feeding dive. The variable 'Depth' was bimodal, and 'Slope' was uni-

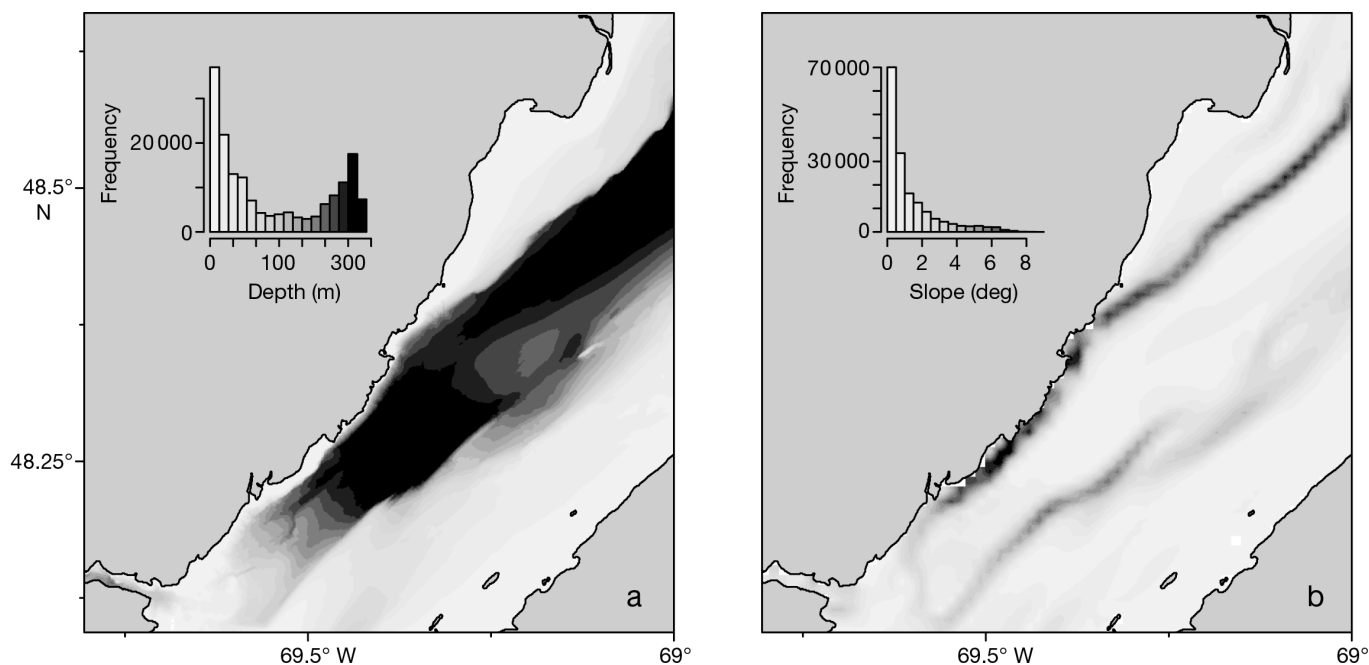


Fig. 1. Bathymetry of the study area (St. Lawrence River estuary, Canada). Each cell is 100 × 100 m: (a) depth and (b) slope. Inserts: frequency (no. of cells with respective depth/slope values) histograms of bathymetric characteristics (shading as in main figure)

modal but skewed (Fig. 1, inserts). Various transformations were applied, but none improved normality substantially.

Habitat modelling

Although presence–absence models are likely to provide the best understanding of species distribution within a surveyed area, presence-only models have been shown to perform almost as well (MacLeod et al. 2008). Since we lack accurate absence data, we used the ecological-niche factor analysis (ENFA; Hirzel et al. 2002) to determine associations between blue whales and habitat characteristics. The ENFA provides a measure of the realised ecological niche within the available habitat by measuring departure of selected habitats from the average available habitat. It is a factorial analysis that extracts 1 axis of marginality and several axes of specialisation. Here, we used the biplots proposed by Basille et al. (2008) to project both the pixels of the map and the environmental variables in the subspace extracted by the ENFA as a way to visualise and interpret the ecological niche of the whales.

We used 2 data sets for this analysis. A naïve data set, with no information on feeding activity, was obtained directly from the tracking data. A feeding set

was composed of the interpolated locations of feeding dives. Since high-resolution movement data are highly autocorrelated, we resampled both data sets. We resampled the naïve set by selecting a position every 2 km on each individual trajectory, and the feeding set, by randomly selecting 20% of the feeding events, which resulted in sample sets of similar sizes.

We performed an ENFA on the naïve data set, as well as on the feeding data set. We then created predictive maps of habitat suitability (HS) for each of these analyses (ranging from 0 to 1, with 1 corresponding to the most suitable habitat). We assessed their predictive power with the ‘continuous Boyce index’, which is appropriate when reliable absence data are unavailable (Hirzel et al. 2006). We calculated the number of points predicted by the model to fall in a certain range of HS, as well as the frequency expected from a random distribution based on the area covered by that same range of HS in the study area as a whole (Boyce et al. 2002). We then plotted the predicted-to-expected ratio against HS. A good model is expected to show a monotonically increasing curve. The continuous Boyce index B measures this increase using the Spearman rank correlation coefficient between the predicted-to-expected ratio and HS. Positive values indicate model predictions that are consistent with the distribution in the data set, values close to zero indicate that the model does

not perform better than a random model, whereas negative values indicate inconsistent predictions.

Habitat types and feeding behaviour in relation to tidal phase

Exploratory analysis revealed multimodality in the characteristics of used habitat, which might indicate the use of multiple habitat types. Using *k*-means cluster analysis, we classified feeding dives into different habitat types based on slope and depth (both variables were standardised). We used the Calinski criterion to determine the appropriate number of clusters (Calinski & Harabasz 1974). We then examined whether the habitat types defined by the cluster analysis were used at different times of the tidal cycle and if they differed in terms of feeding behaviour. Specifically, we tested for differences between the groups using Kruskal-Wallis (KW) tests for 3 factors: time since the last low tide, depth of feeding activity (average depth of feeding events in each dive) and number of feeding lunges per dive.

All analyses were performed using the R programming language (R Development Core Team 2008). The ENFA was performed using the *adehabitat* package for R (Calenge 2006).

RESULTS

We deployed instruments on 11 blue whales *Balaenoptera musculus* from 2002 to 2009 (Table 1). Tags remained on whales for 2 to 25 h, and individuals were tracked from the surface for 2 to 11 consec-

utive hours. Analysis of archived data yielded 5611 dives over 139 h of data, of which 73 h included surface observations.

Movements and feeding activity

Tagged blue whales concentrated their movements in the northern portion of the study area (Fig. 2a). None of the tagged individuals crossed the channel towards the southern shore. When combining all tagged whales, the area used was >15 km wide and >60 km in length.

All 11 whales engaged in feeding during the time they were tagged. In total, we identified 1049 feeding events during 542 feeding dives, over the 73 h of tracking from the surface (Table 1). Kernel density contours showed that blue whales concentrated their feeding activity in 3 main, distinct areas along the shore, with some additional feeding dives taking place mid-channel, i.e. 10 to 12 km offshore (Fig. 2b). Two of the sites close to the shore were used by 2 individuals, while the northernmost site was used by 5 different whales tagged in different years. Mid-channel feeding occurred in 3 deployments, with each whale using a different location.

Habitat modelling

Once resampled, the naïve data set contained 121 locations (Fig. 3a). Application of the ENFA to the naïve set provided an overall marginality of $M = 0.78$ and an eigenvalue of specialisation of $S = 0.48$ for the only axis of specialisation kept. Depth and slope were almost equal components of the marginality and specialisation axes (Fig. 3b). However, examination of the biplot showed that cells corresponding to used habitat spread over a vast range of environmental characteristics, creating a 'horseshoe' shape in the ENFA subspace. Consequently, the centroid of the whale's niche fell in the middle of this shape (white dot in Fig. 3b), where there were in fact very few locations, artificially suggesting a selection towards areas of average depth and slope. These characteristics did not correspond to those of areas actually used by whales, providing a misleading view of habitat selection patterns.

Table 1. *Balaenoptera musculus*. Summary of diving and feeding behaviour for 11 St. Lawrence blue whales equipped with velocity-time-depth recorders and tracked during daytime. Duration: no. of hours that tagged individuals were tracked from the surface

Date	Duration (h)	No. of dives	No. of dives with feeding	Max. feeding depth (m)	No. of lunges
5 Aug 2002	2.15	65	8	117	48
14 Aug 2003	6.18	214	43	50	133
18 Aug 2004	10.50	431	115	12	153
26 Aug 2004	5.83	171	20	101	100
2 Sep 2004	4.60	201	29	38	61
8 Sep 2004	5.45	151	12	112	46
13 Sep 2005	6.33	98	18	106	38
16 Sep 2005	8.83	484	152	128	277
10 Aug 2006	10.82	432	56	93	217
17 Aug 2006	6.38	245	20	101	60
25 Aug 2009	6.02	427	69	95	125

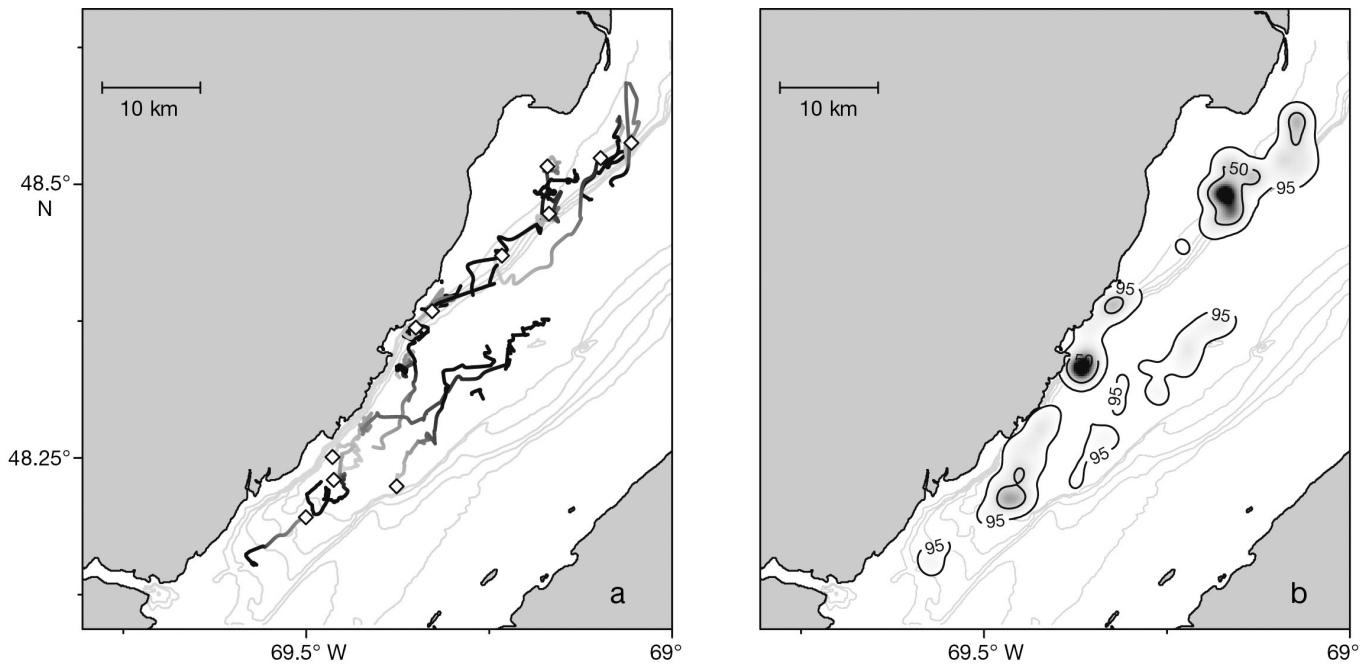


Fig. 2. *Balaenoptera musculus*. (a) Movements of individual blue whales equipped with velocity-time-depth recorders (lines) and locations of tag deployments (\diamond). Light- to dark gray-scale gradient on lines represents time elapsed since deployment. (b) Intensity of feeding activity for all individuals combined. Darker shades of grey represent higher intensity. Black lines: 50% and 95% fixed-kernel density contours

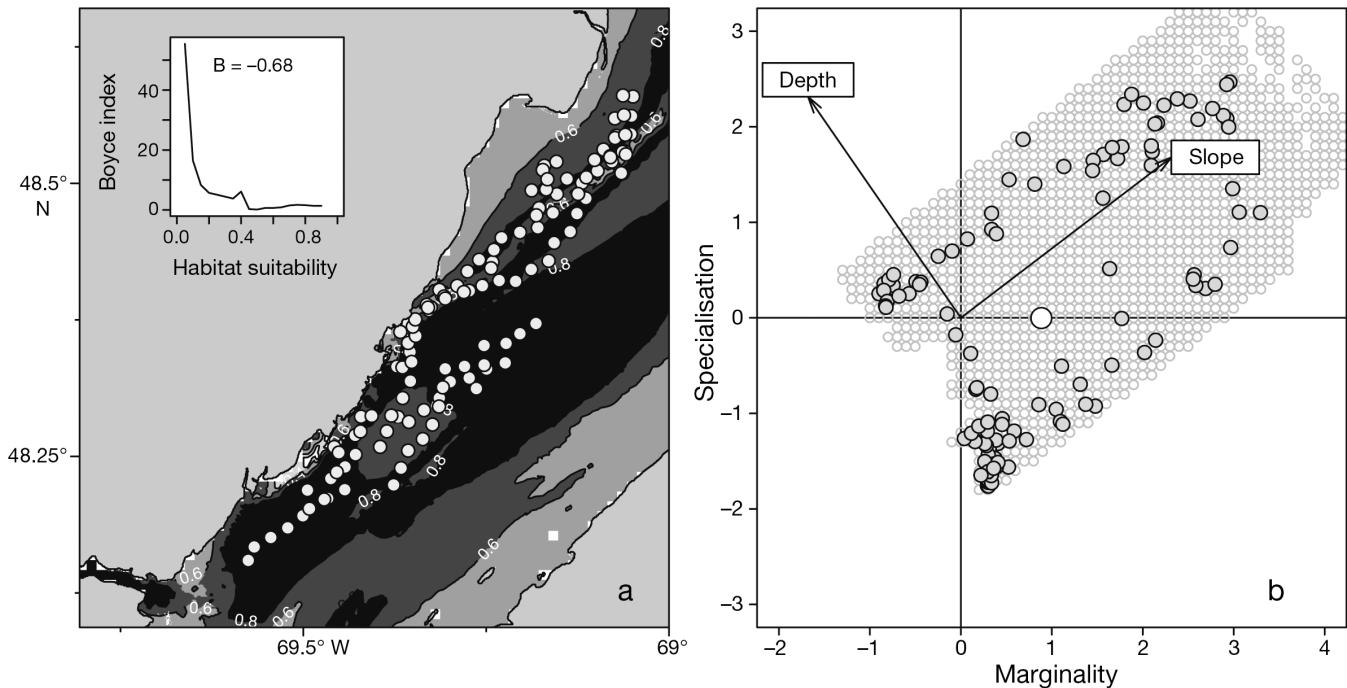


Fig. 3. *Balaenoptera musculus*. (a) Map of predicted habitat suitability, based on ecological-niche factor analysis (ENFA) of the naïve data set. Circles indicate locations of tracked blue whales, resampled every 2 km. Darker shades of grey indicate higher habitat suitability (HS; values 0.6 and 0.8 indicate HS contours). Insert: plot of the continuous Boyce index. (b) Biplot of environmental characteristics in the subspace defined by the ENFA, in the plane formed by the marginality axis (x-axis) and the first specialisation axis (y-axis). Background open circles represent cells of available habitat. Closed circles represent cells used by blue whales. The white dot on the x-axis corresponds to the centroid of the used habitat. The arrows are the projections of the environmental variables

The results from the ENFA performed on the naïve data set were used to compute a habitat suitability map (Fig. 3a). Because of the centroid's position, cells of moderate slope and average depth were identified as areas of high suitability, resulting in large swaths of the study area being considered highly suitable ($HS > 0.8$) and almost the entirety of the map being considered suitable ($HS > 0.6$). Consequently, the plot of the continuous Boyce index showed a decreasing curve (Fig. 3a, insert) and $B = -0.68$, indicating an incorrect model predicting a higher presence in poor-quality areas than in highly suitable ones (Boyce et al. 2002).

The ENFA performed on the 108 dives of the feeding set (Fig. 4a) was characterised by $M = 0.85$ and $S = 1.40$, indicating that blue whales were more restrictive on the range of conditions they selected for feeding purposes. Bottom slope was almost the only contributor to the marginality axis (Fig. 4b), and thus the main factor that distinguished used from available habitat. Used habitat still exhibited a large spread of physiographic characteristics, but the centroid of the niche fell closer to the characteristics of cells used for feeding than it did for the naïve set. Consequently, the HS map based on the feeding set yielded a better fit to the observed data (Fig. 4a). The plot of the con-

tinuous Boyce index showed an increasing curve, although not monotonic (Fig. 4a, insert), and $B = 0.67$, indicating that the model better predicted areas of high habitat quality (for feeding purposes). Predicted areas of high HS (> 0.8) included steep slopes and shallow plateaux on both sides of the SLE, while deeper areas of flat or intermediate topography were not considered of high quality ($HS < 0.4$).

Feeding behaviour in different habitat types

Plotting the habitat characteristics of the locations of feeding dives clearly indicated multimodality (Fig. 5a). The Calinsky criterion reached a maximum at 4 groups (Fig. 5a, insert), suggesting separating feeding dives into 4 clusters representing distinct habitat types that differed in terms of slope and depth. Type I habitat (72 feeding dives by 9 individuals) was characterised by large depths and steep slopes. Type II habitat (119 feeding dives by 6 individuals) corresponded to intermediate depths and steep slopes. Type III habitat (198 feeding dives by 5 individuals) was characterised by relatively shallow depths and a gradient of flat to intermediate slopes. Finally, Type IV habitat (152 feeding dives by 7 individuals) was

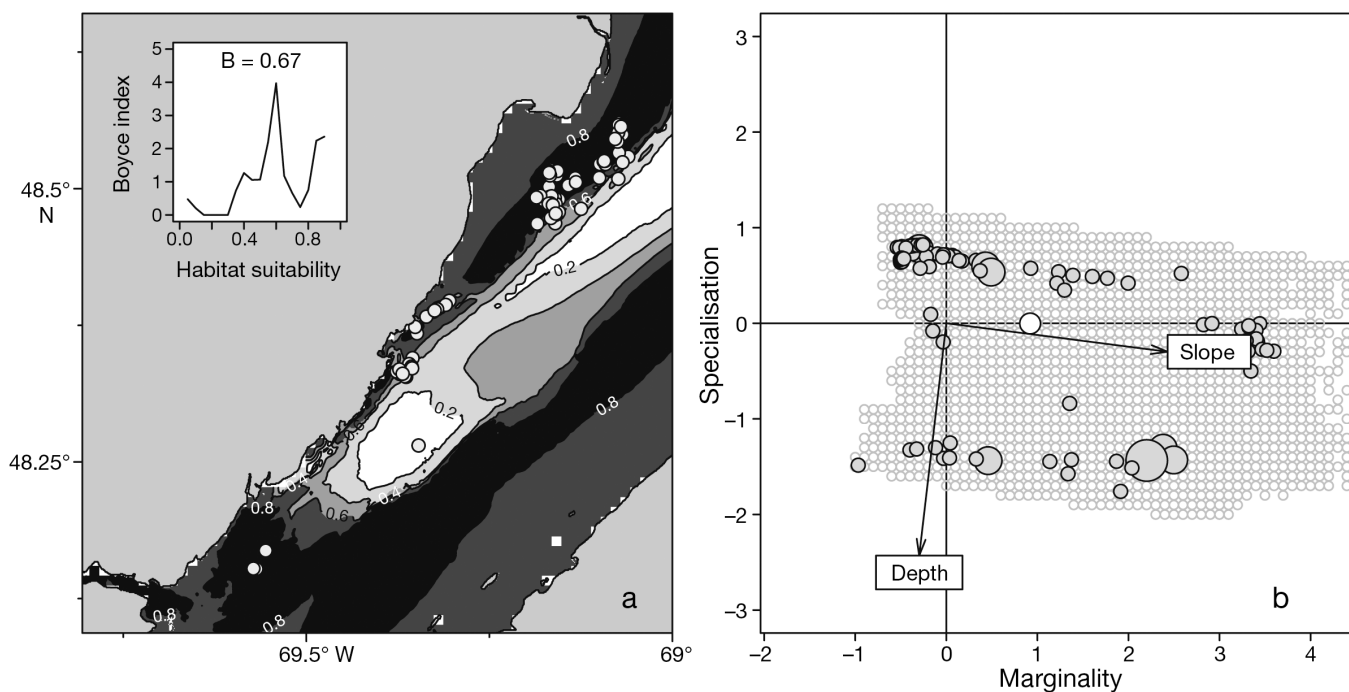


Fig. 4. *Balaenoptera musculus*. (a) Map of predicted habitat suitability, based on ecological-niche factor analysis (ENFA) of the feeding data set. Circles indicate feeding dives. Darker shades of grey indicate higher habitat quality. Insert: Plot of the continuous Boyce index (B). (b) Biplot of environmental characteristics in the subspace defined by the ENFA. Closed circles represent cells used by blue whales, with their size proportional to the intensity of use (no. of locations). For explanation of other symbols, see Fig. 3

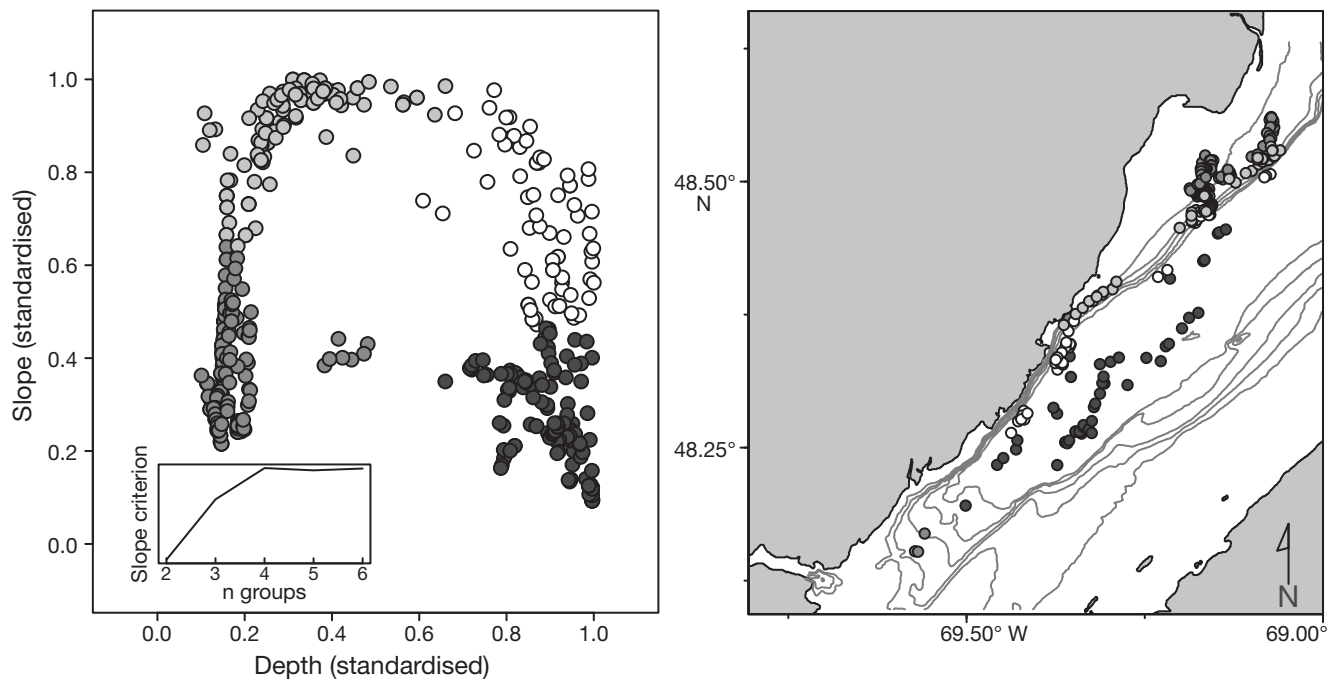


Fig. 5. *Balaenoptera musculus*. (a) Bathymetric characteristics of feeding habitat. Each circle corresponds to a feeding dive. Feeding dives were classified into 4 groups by *k*-means cluster analysis. (b) Location of feeding dives corresponding to each habitat type. For (a) and (b) — white: Type I habitat (lower slopes); light grey: Type II habitat (upper slopes); medium grey: Type III habitat (plateaux); dark grey: Type IV habitat (offshore)

representative of large depths and flat slopes. When identifying these types on the map (Fig. 5b), it became apparent that Types I and II corresponded to the lower and upper portions, respectively, of the steep slopes along the sides of the Laurentian Channel, Type III to the shallow plateaux close to the north shore and Type IV included offshore locations beyond the slopes. Overall, 7 individuals used 2 habitat types during the time they were tracked, 3 individuals used 3 habitats and 1 individual used all 4 types.

These 4 habitats differed in terms of when they were used for feeding in relation to the tide (KW test, $p < 0.01$). This is particularly obvious when plotting the time since the last low tide for each habitat using violin plots (Fig. 6a), which allow us to check for multiple modes in the distributions (Hintze & Nelson 1998). Feeding occurred on lower slopes predominantly during flood tide, and to a lesser extent at the end of ebb tide, with a decrease immediately after high tide. Upper slopes were used mostly during the 2 h preceding high tide, while the plateaux were used slightly later in the cycle, i.e. immediately after high tide and during part of ebb tide. Distribution of feeding dives in the offshore habitat type was more diffuse, with the bulk of observations at flood and high tides, and little activity during ebb tide.

Feeding behaviour also differed across habitats in terms of feeding depth and number of lunges per dive (KW tests, $p < 0.01$). Feeding in all habitats except the plateaux was bimodal, with a strong peak near the surface and a weaker peak between 50 and 100 m. However, the lower slopes and the offshore types were characterised by the most frequent occurrence of feeding at depths > 50 m (Fig. 6b) and the highest median feeding depths. Feeding deeper than 50 m occurred more infrequently on upper slopes and not at all on plateaux, which showed a low median depth and a short range of feeding depths. The number of lunges per dive followed a similar pattern across habitat types (Fig. 6c), with lower slopes and offshore sites being the only habitats with a median value of 2 lunges per dive and a non-negligible proportion of dives with 4 lunges or more.

DISCUSSION

We tracked the daytime movements and feeding behaviour of 11 blue whales *Balaenoptera musculus* in the St. Lawrence River estuary. Although each individual was only followed for a few hours, all of them were observed feeding. Obviously, critical

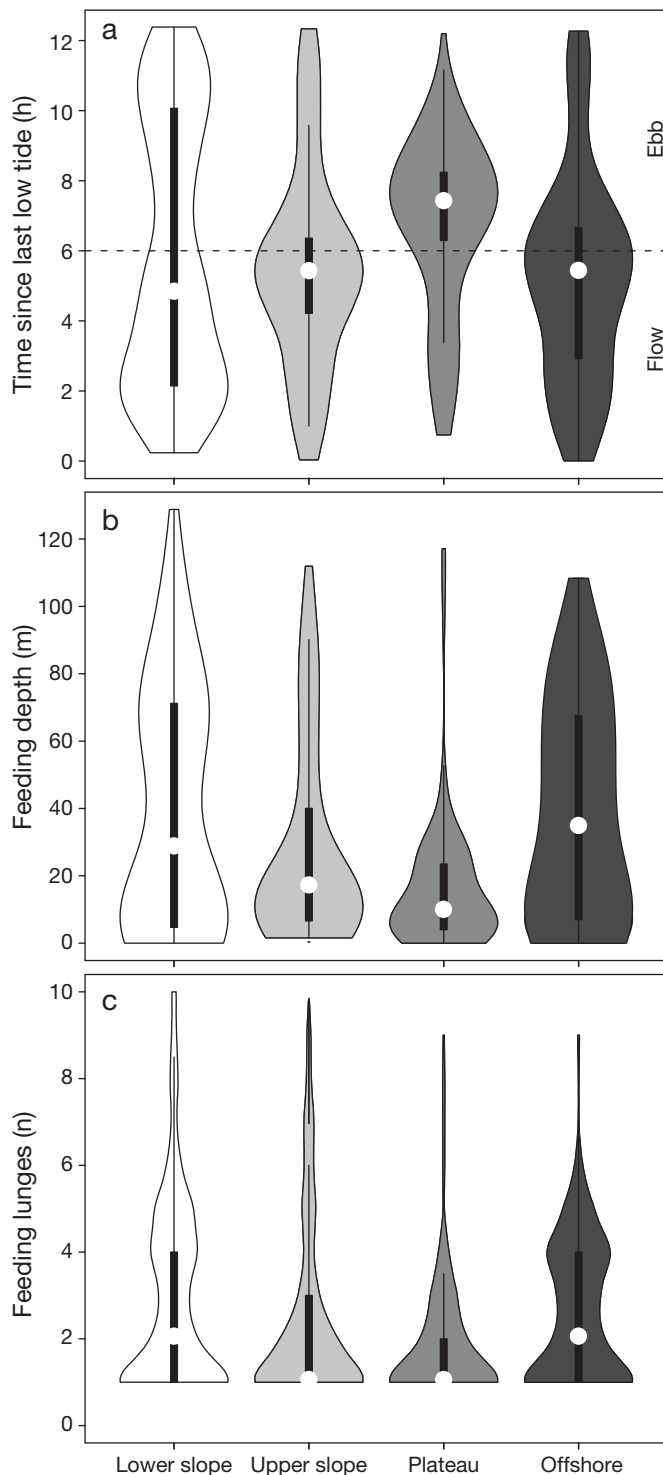


Fig. 6. *Balaenoptera musculus*. Characteristics of feeding dives across habitat types: (a) tidal phase, (b) feeding depth and (c) number of feeding lunges per dive. Violin plots illustrate the distribution of each variable, as well as the median (white dot), the quartiles (black box) and the range of points lying within 1.5 times the interquartile range of the box (solid lines), as in regular boxplots. Shading represents habitat type: for details see Fig. 5. Dashed line in Panel (a) indicates high tide

habitat cannot be fully described or modelled from a small number of individuals tracked over relatively short periods. However, even data sets of modest sample size have been useful to inform conservation efforts and increase our understanding of animal ecology (e.g. Aebischer et al. 1993, Calenge et al. 2005). Here we show that tagging of 11 blue whales yielded novel insights into patterns of habitat selection, which are of value both for management purposes and to understand the difficulties met when trying to conduct habitat modelling studies.

Habitat use

Feeding is a discrete event within the broader behavioural state of foraging. There are several techniques that can be applied to tracking data to determine if animals are travelling, resting, or performing restricted search behaviour that would yield a more inclusive picture of foraging activities (Weimerskirch et al. 1997, Bailleul et al. 2008, Breed et al. 2009). When resources are scarce or mobile, however, time spent by animals in a particular area may reflect unsuccessful search, or behaviours other than feeding that would be difficult to identify based on movements alone (Garshelis 2000). When this is the case, characteristics of habitat used more intensively may not be representative of habitat quality (Van Horne 1983). Identification of feeding lunges from dive data allowed us to focus on habitats where feeding actually took place, and thus to avoid this problem.

Blue whales tagged in the St. Lawrence River estuary ranged along a 60 km stretch of the north shore but concentrated their feeding activity in smaller, distinct sites (Fig. 2b). All of these sites were used by >1 individual and, in 1 case, by 5 different whales. These whales were tagged at different locations and in different years, suggesting that these sites represent high-quality habitat, presumably in terms of predictable concentrations of prey as well as minimum densities, and that their use may be recurrent from year to year. Although we could not measure feeding efficiency (i.e. mouthfuls with a high concentration of food vs. less profitable ones), we assumed that blue whales did not perform feeding lunges if prey concentration did not meet a minimum threshold (Goldbogen et al. 2011). It is possible that some lunges were performed in low prey densities precisely to assess krill concentration, but overall we believe our approach allowed us to identify sites of intense feeding activity, thus yielding a better image of habitat use and quality.

Identification of these sites has obvious, direct benefits for conservation efforts in the St. Lawrence Estuary, where endangered blue whales face several threats linked to the high level of human activity (Sears & Calambokidis 2002, Beauchamp et al. 2009). Managers can choose to target these specific areas for mitigation measures, thus focusing their effort to reduce disturbance at the most important sites for feeding activity. Unfortunately, given our current sample size, we were unable to determine the relative importance of the various feeding sites. Moreover, it should be remembered that maintaining connectivity between these sites is necessary and that other equally important behaviours such as resting and socialising may be taking place in other areas.

Habitat modelling

Blue whales travelled across a wide variety of bottom topographies during the time they were tracked in the SLE. The resulting physiographic characteristics in the naïve set were spread over the entire environmental space (Fig. 3b), resulting in an incorrect model that failed to predict areas where blue whales were observed, let alone where feeding activity was taking place. This is not a problem specific to ENFA but rather a direct consequence of multimodality along environmental axes in the realised niche space. In our data set, the problem was exacerbated by the 'horseshoe' shape of selected habitat in environmental space, which drew the centroid of used habitat towards the middle of the ENFA biplot. The corresponding set of characteristics did not describe sites where blue whales were actually observed, which explained the poor performance of the resulting habitat suitability map (Fig. 3a).

This problem was partly alleviated in the feeding set, presumably because it allowed us to differentiate between locations that were actively selected versus locations that were used in transit between patches or during exploration (Beyer et al. 2010). The model had considerably higher predictive power (Fig. 4a), but still suffered from the feeding events occurring over a vast range of physiographic characteristics. The resulting map better excluded areas of low quality, but could not highlight all high-quality habitats at the same time.

Other analyses of rorqual whale habitat selection have often resulted in low explanatory power. For instance, Ingram et al. (2007) modelled finback whale distribution in the Bay of Fundy using generalised additive models (GAMs) and could explain

only 14 % of deviance. Doniol-Valcroze (2008) found similar low values for finback and humpback whales in the Gulf of St. Lawrence using conditional logistic regression. Even at a larger scale, average correct prediction rates of fin whale presence in the Mediterranean Sea using GAMs were poor (mostly <15%), although they were improved by using boosted classification trees (Panigada et al. 2008). Our results suggest that failure to identify different behaviours or to take into account the potential existence of multiple foraging habitats with different characteristics could explain the low predictive power of previous studies.

The predictive power of habitat modelling may also suffer from issues of scale. For mobile animals, habitat selection is a hierarchical process that operates at the level of the individual, involving a series of behavioural decisions about what habitat components to use, from broad spatial scales to the local micro-habitat (Wiens et al. 1986). At fine scales, whales may have already selected the SLE because it contains a mosaic of high-quality habitats, possibly in proximity to other suitable sites outside our study area, allowing them to exploit different habitats at different times, or to access other feeding sites within minimal travel distances (Orians & Wittenberger 1991). This would enable them to adapt to rapidly changing conditions in a dynamic system, for instance over diurnal, tidal and seasonal cycles (Boyd 1996).

In the present study, we only used depth and slope variables to describe whale habitat; these are commonly used as proxies for areas of higher biological productivity at broad scales and to identify sites of predictable prey concentrations at fine scales (Yen et al. 2004). These variables have been the most successful at explaining rorqual habitat use in previous studies (Ingram et al. 2007, Panigada et al. 2008). Selection for certain combinations of bathymetric features were clear in our analysis. However, the map of suitable habitats included areas that were not used by blue whales (e.g. slopes and plateaux along the south shore). Such false positives limit the applicability of modelling exercises to management efforts and the ability to extrapolate to other areas. The inclusion of dynamic features (e.g. currents, fronts) and information on krill vertical and horizontal distribution is likely necessary to discriminate between potential and actual high-quality habitats. In the absence of accurate data on krill distribution and movements, however, it is not clear which variables can be used as effective proxies of the complex interactions between 3-dimensional currents, topography and prey behaviour.

Feeding behaviour among habitat types

In our study area, feeding activity occurred over a range of distinct habitats, some of which were used preferentially at certain times of the tidal cycle. The characteristics of these habitat types and of blue whale feeding behaviour can be interpreted in the light of known mechanisms of krill aggregation, such as those reviewed by Genin (2004), some of which have been shown to occur in the SLE.

Over lower slopes, blue whales fed preferentially at flood tides and at depths of 60 to 100 m, which is in the range of the known daytime depth distribution of krill in the SLE (Harvey et al. 2009). On the upper portion of the same slopes, blue whales fed mostly during the 2 h before high tide and at slightly shallower depths. In both cases, whales could have been exploiting a mechanism of counter-upwelling depth retention proposed by Simard et al. (1986): zooplankton organisms being advected by tidally induced upwelling in an up-slope direction against the bottom contour try to maintain their depth by swimming downward, resulting in dense accumulations along slopes. This process has been described *in situ* at the end of the Laurentian Channel, at the south-western tip of our study area (Cotté & Simard 2005). This process may also be enhanced by wind-driven upwelling that occurs mostly on the north side because of prevailing westerly winds (Lavoie et al. 2000). These mechanisms could explain why blue whales were not observed feeding along the southern slope of the channel.

Blue whales fed at shallow depths over plateaux along the northern side of the SLE, mostly during ebb tide. They may have had access to large concentrations of krill trapped at shallow depths by topographic blockage, for instance during their descent at dawn (Genin 2004) or after having been advected there by upwelling currents. Theoretical models (Kramer 1988, Houston & Carbone 1992) suggest that accessibility of food at shallow depths allows diving predators to increase their feeding rate and energetic efficiency by performing short dives needing little recovery time. Recent empirical studies have shown such a relationship between the number of lunges and feeding depth (Doniol-Valcroze et al. 2011, Ware et al. 2011). Sites where krill is accessible at shallow depths may therefore be particularly attractive to foraging blue whales (Doniol-Valcroze et al. 2011).

Blue whales were also observed feeding in offshore areas at various times of the tidal cycle. This feeding behaviour, away from the shelf edge and over deep and flat bathymetry, implies other aggregation processes. Krill patches aggregated along the slopes

may drift downstream over habitats where accumulation of prey is not necessarily expected, a process described on the southern side of the SLE by Cotté & Simard (2005). Dense aggregations may also result from counter-downwelling depth retention (Franks 1992), a mechanism believed to operate in coastal areas when zooplankton organisms maintain their depth by swimming upward against downwelling currents (Genin 2004). Krill would then be expected to accumulate in Langmuir cells (Thorpe 2004) and along thermal fronts (Olson & Backus 1985). For instance, blue whales in the northern Gulf of St. Lawrence were shown to be associated with areas of strong thermal gradients (Doniol-Valcroze et al. 2007). Despite representing a relatively small proportion of feeding activity in our study, the importance of these offshore feeding areas should not be overlooked by research and management efforts.

Blue whales are known to track the vertical migration of their prey at dawn and at dusk (Calambokidis et al. 2008, Oleson et al. 2007). Our observations show that blue whales also find prey at shallow depths during daytime. Moreover, all 11 of the tagged individuals in the SLE fed in >1 type of habitat over the time that they were tracked (2 to 11 h), suggesting that they follow their prey or exploit profitable characteristics of different habitats at different times of the tidal cycle, thus painting a more complex picture of their daytime feeding behaviour than previously described.

Conclusions and recommendations

Effective conservation of marine mammals depends on accurate identification of their critical habitat. However, the mobile nature of prey in dynamic marine systems and the complex spatial structure of habitats associated with increased food availability (e.g. slopes, fronts) constitute additional challenges for habitat selection studies. Despite their short durations, our tag deployments illustrate changes in feeding depth and habitat types related to tidal phases, showing that fine-scale foraging in the marine environment by epipelagic predators can take place in a variety of habitats and that the heterogeneous characteristics of these habitats can complicate modelling efforts. Although additional research is needed to further elucidate the relationships between tides, topography and feeding behaviour, these results suggest that management efforts must acknowledge that critical habitats may be difficult to describe using simple proxies and that suitability of specific habitats can vary through time.

Acknowledgements. We thank Paul Couture for Visual-Basic programming; Robin Baird and Michel Moisan for tag development; Yves Morin, Samuel Turgeon, Daniel Lefebvre, Renaud Pintiaux, Michel Moisan, Caroline Guimont, Shawn Thompson and Jeremy Winn for help with field work; and Becky Woodward for providing access to the D-tag data. We also thank Arnaud Mosnier for his help with the bathymetry data and Ian McQuinn for advice on this project. The comments of D. Palacios and 3 anonymous reviewers greatly improved the manuscript. Funding support came from the Species at Risk and Oceans Management programs of Fisheries and Oceans Canada, and from the Saguenay–St. Lawrence Marine Park.

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*Editorial responsibility: Daniel Palacios,
Pacific Grove, California, USA*

*Submitted: January 16, 2011; Accepted: February 23, 2012
Proofs received from author(s): June 18, 2012*