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Spatial scale and environmental determinants in minke whale habitat use and foraging

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ABSTRACT: Because pelagic prey concentrations are patchy in both space and time, predators such as marine mammals require high degrees of flexibility in their habitat use. We tested the hypothesis that minke whales *Balaenoptera acutorostrata* adjust their habitat use during the feeding season at different spatial scales: their overall distribution should be determined by broad-scale oceanographic features, while foraging activity at finer scales should be dictated by short-term changes in habitat conditions. Results from generalized additive models indicate that minke whale distribution off the west coast of Scotland is dependent largely on temporally variable parameters (sea surface temperature in spring, chlorophyll concentration in autumn), in addition to depth and topography. However, fine-scale foraging behaviour was dictated by the strength and direction of tidal currents. Seasonal distribution patterns according to environmental parameters were largely consistent between 2 different spatial scales, and over a time period of 15 yr. Significantly higher sighting rates occurred in areas of predicted sandeel *Ammodytes marinus* presence in spring, but not during the rest of the summer, while in August and September, prey samples from the core study area consisted almost entirely of sprat *Sprattus sprattus*. The low energetic cost of swimming in minke whales and their ability to switch between different prey according to their seasonal availability thus appears to allow them to readily respond to temporal changes in pelagic prey concentrations at different scales. This occurs through a distribution influenced by temporally variable parameters (temperature and chlorophyll concentration), combined with adjustments in foraging activity dependent on variable conditions at fine spatial scales (tides).

KEY WORDS: Habitat modelling · *Balaenoptera acutorostrata* · Prey distribution · North Atlantic · Baleen whale · Cetacean · Hebrides

INTRODUCTION

Patterns of habitat use in an organism relative to its size and mobility are ultimately influenced by the availability of resources. In natural habitats, physical environmental parameters often determine where and when prey are likely to be aggregated (e.g. Simard et al. 2002) (predator knowledge of this would reduce travelling time between high-density patches of prey), or can be caught most efficiently (thereby reducing handling time). Within the constraints of its mobility, a predator would therefore be expected to adjust its spatial and temporal habitat use at different scales. At large to intermediate scales, finding areas of high prey density is essential, whereas at finer scales, the optimal times and/or locations for efficient capture of prey should be selected.

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In the marine environment, suitable feeding locations for predators are patchy in both space and time and are influenced by a combination of static (e.g. water depth, bottom topography or sediment type) and temporally variable (e.g. water temperature or currents) physical environmental parameters, which influence biological processes at lower trophic levels. Pelagic predators have thus evolved to be highly mobile searchers, and some perform seasonal feeding migrations across vast distances of ocean (e.g. McKeown 1984, Baker et al. 1986, Shillinger et al. 2008). In baleen whales, breeding and feeding are both spatially and temporally segregated: breeding often occurs at lower latitudes during the winter months and feeding at higher latitudes during summer (Evans & Stirling 2001, Stevick et al. 2002). Their distribution and abundance in an area during summer is therefore most likely a direct reflection of the availability, density and quality of their prey, which makes them well suited for a study on the influence of spatial and temporal factors on foraging behaviour.

The minke whale *Balaenoptera acutorostrata* shows seasonal site fidelity to summer feeding grounds (Dorsey 1983, Dorsey et al. 1990, Gill & Fairbairns 1995), and Hoelzel et al. (1989) documented individual foraging specializations, which were associated with different habitat types. Minke whales feed on a wide range of shoaling fish, as well as krill, and appear to be able to adjust their diet to regional and seasonal changes in prey abundance (Jonsgård 1982, Lydersen et al. 1991, Haug et al. 1995, 2002, Lindstrøm et al. 1997, Neve 2000, Olsen & Holst 2001).

Several environmental parameters may simultaneously determine changes in local prey distribution and abundance for cetaceans and other marine predators either in the short or long term. For example, variable seafloor topography, especially when combined with strong currents, can cause increased vertical mixing of water masses (Pingree & Griffiths 1978), bringing nutrient-rich, cold bottom water into the photic zone and thus facilitating phytoplankton growth (e.g. Valiela 1995). Such areas of upwelling can represent important feeding habitat for a variety of cetacean species (e.g. Evans 1990, Baumgartner 1997). Tidal currents through deep channels or around headlands, on the other hand, can have the effect of concentrating prey, and in some areas are known to influence the local distribution of cetaceans (Mendes et al. 2002, Simard et al. 2002, Hastie et al. 2004, Cotté & Simard 2005, Chenoweth et al. 2011) or their foraging behaviour (Evans & Borges 1996, Pierpoint 2008). Bottom sediment type can influence the distribution of some shoaling fish such as herring *Clupea harengus* (Maravelias 1999) and sandeel *Ammodytes marinus* (Wright et al. 1998, 2000, Holland et al. 2005), which are important prey for several cetacean species including the minke whale (Lydersen et al. 1991, Haug et al. 1995, 2002, Lindstrøm et al. 1997, 2002, Neve 2000, Olsen & Holst 2001, Pierce et al. 2004). Different fish species also show preferences for particular temperature ranges that reflect either their own physiological adaptations or the occurrence of their zooplankton prey (Southward et al. 1988), which in turn may influence the distribution of predators such as seabirds and cetaceans (Evans 1990). Finally, when direct prey data are not readily available, remotely sensed chlorophyll concentrations can serve as a good proxy for primary productivity and, thus, as an indirect indicator of feeding conditions for species feeding at lower trophic levels, such as baleen whales (e.g. Smith et al. 1986, Thiele et al. 2000, Panigada et al. 2008). While the distribution of numerous marine predators has successfully been linked to different environmental parameters, few attempts have been made to include data on prey distribution alongside static and dynamic physical variables in habitat models and to compare results at different scales between distributional data and fine-scale tracks of individual animals (Guinet et al. 2001, Cotté et al. 2009).

In this study we investigated the spatial and temporal environmental factors that correlate to patterns of distribution and foraging activity in the minke whale. We tested the hypothesis (at 2 spatial resolutions) that seasonal distribution patterns should be determined by broad-scale geographic, oceanographic and biological features (such as mean depth, sea surface temperature [SST] and chlorophyll concentration), while foraging intensity at a fine geographic scale should be determined by local topography and short-term changes in habitat conditions, such as tidal direction and flow.

MATERIALS AND METHODS

Habitat models

The study area was located in the Hebrides on the west coast of Scotland, UK (Fig. 1), an extensive shelf area with a varied topography dominated by depths of <200 m and a convoluted coastline with numerous islands that leads to highly variable tidal flows (Ellett 1979, Ellett & Edwards 1983). Harbour porpoise *Phocoena phocoena* and minke whale are the 2 most commonly recorded cetacean species in the region.

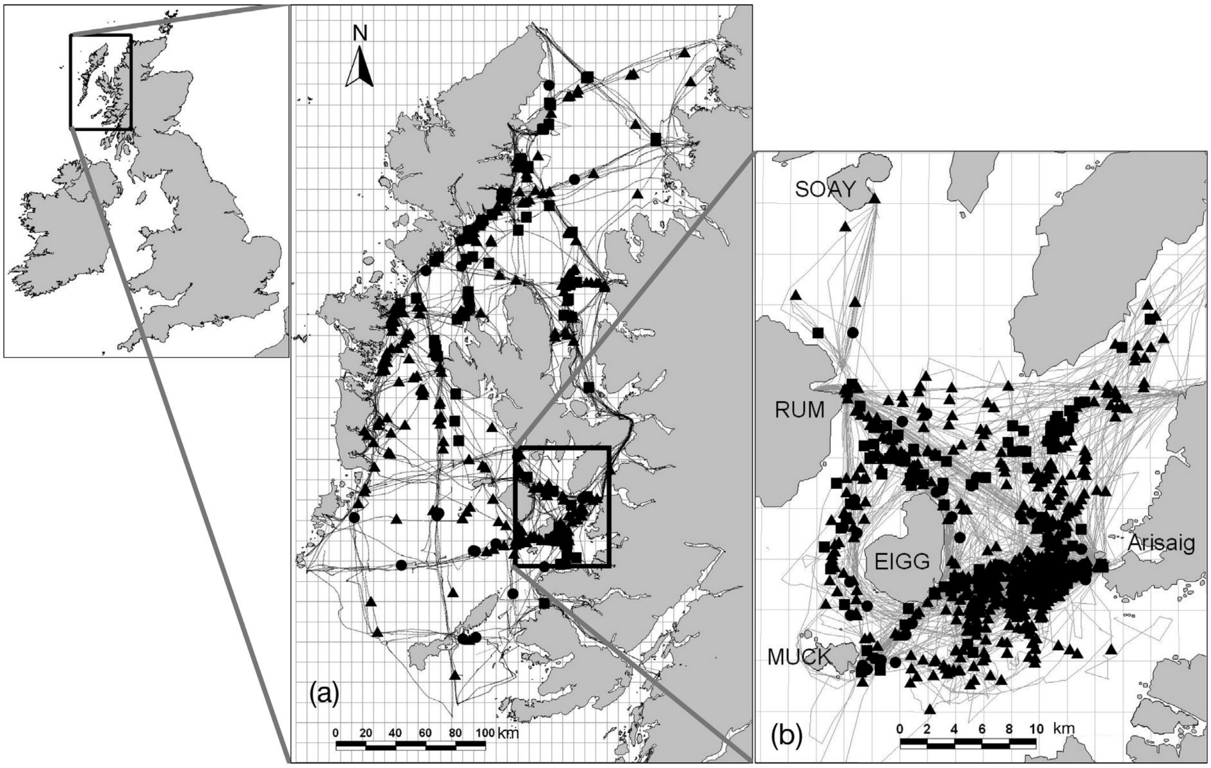


Fig. 1. Study area (a) over the entire eastern Hebrides (1993–2002) and (b) core study area around the Small Isles (1998–2007). Circles along survey routes represent sightings during early (May/June), squares during mid (July), and triangles during late (August/September) season. Grid cells in the background indicate (a) 4′ and (b) 2′ cells on which analyses were based

Minke whales are present between May and October, but their numbers peak between July and September (Boran et al. 1999).

Survey data were collected from 3 main vessels (platforms): (1) the ketch 'Marguerite Explorer' (length = 20.3 m, speed = 5 to 8 knots [kn], eye height = 4 m), from which 5 to 20 d line-transect and ad libitum surveys (the latter was combined with commercial wildlife watching charters, i.e. with standard recording protocols in place, but not on preplanned transect lines) were conducted over the entire eastern Hebrides during summer months (June to September) between 1993 and 2002 (although no month received coverage in every year); (2) the ferry MV 'Sheerwater' (length = 14 m, speed = 10 kn, eye height = 3.5 m; simultaneously used for wildlife watching en route), which operated daily in our core study area between Arisaig and the islands of Eigg, Muck, Rum (i.e. the Small Isles) and Soay (Fig. 1b) from May to September, covering the time period between August 2003 and September 2007 for the purpose of this study; and (3) 'Gwen' (length = 5 m, speed = 6 to 8 kn, eye height = 2 m) and a variety of vessels of similar size to either 'Gwen' or MV 'Sheerwater' which were used for dedicated minke whale fieldwork (including focal sampling of individuals) in the core study area for 2 to 7 wk each year in summer between August 2003 and July 2007. Data from surveys conducted with the 'Marguerite Explorer' were also included in the analysis of the core study area for months during which more than 10 h were spent around the Small Isles (August 1998 and 2002, September 1999 and July 2001).

Survey effort from platforms (1) and (3) was conducted by 2 to 3 dedicated experienced observers, including at least one of the authors. Notes were taken on preprinted recording forms every 15 to 30 min and at every change in direction, speed or environmental conditions. Effort records consisted of time, date, position (latitude and longitude), vessel speed and direction and sea state. Effort from platform (2) was conducted by R. Dyer and recorded as departure and arrival time at each harbour, from which time to specific waypoints was later calculated based on detailed 5 min effort recordings taken from the ferry during a total of 3 wk in August 2002 and 2003. Minke whale sightings were recorded on a standardised form from all platforms and we noted group size, time, position and behaviour/surfacing type (i.e. 'normal, fast or slow surfacing': whale swimming at normal, fast or slow speed, respectively, with the usual surface roll; 'high arch': whale arching its back before diving, indicating a longer dive; 'lunge': surface lunge with distended throat grooves, often with fish visible above the surface).

The most important environmental parameter influencing sighting efficiency for marine mammals is sea state, especially when observing from low platforms (Buckland et al. 1993, Evans & Wang 2002, Hammond et al. 2002, Reid et al. 2003, Evans & Hammond 2004, Marubini et al. 2009). A correction factor for survey effort was therefore applied to observations above sea state 0 for each of the 3 main platforms (since observer height varied between vessels) by dividing sighting rates at each higher sea state by the sighting rate at sea state 0. For additional boats, the appropriate correction factor was applied by using the most similar-sized platform. The duration of each effort leg was then divided by the appropriate correction factor for sea state to be included as an explanatory variable in each model.

Using the ArcView extension cr_tools, the study area was divided into grid cells at 2 spatial scales: 4′ latitude × 4′ longitude resolution for analysis of the sightings data over the entire eastern Hebrides, and 2′ latitude × 2′ longitude for the core study area (Fig. 1). The 2′ cells for the Small Isles were chosen as the finest resolution that still allowed for some deviation from the normal straight route by MV 'Sheerwater', which would otherwise have resulted in erroneous assignment of some survey segments to cells at finer resolutions. On the other hand, an analysis of the 'Marguerite Explorer' data based on a grid size of 2′ for the entire eastern Hebrides had resulted in coverage of each cell that was too low and thus inflated sighting rates. The 4′ cells were therefore chosen as the finest resolution for the larger study area, which still ensured representative sighting rates per cell given the lower coverage by comparison with the core study area.

Cell areas were calculated with the XTools extension in ArcView. Areas covered by land were excluded from each cell by combining cell and land polygons and subsequently deleting all land fragments from the total cell area. A British National Grid Transverse Mercator projection, centred on the study area (57° N, 6° W) and with chart datum set to WGS84 (as on the GPS) was used for all calculations within ArcView. Both map and distance units were set to metres.

Effort records were linked to sightings and subsequently cut into segments of 1 min duration by using a macro in Microsoft Excel. Based on the position of its mid-point, each 1 min effort segment was then assigned to its corresponding cell at both spatial resolutions by using an additional macro. Cell summaries were calculated for all environmental parameters and linked to effort records (Table 1).

To avoid overlooking possible changes in minke whale habitat preference through the season due to uneven temporal distribution of sighting rates, separate distribution models were derived for early (May and June), mid (July) and late (August and September) season for both the entire eastern Hebrides and the core study area, resulting in a total of 6 models.

Minke whale sighting rates per cell were modelled with generalized additive models (GAMs; Hastie & Tibshirani 1990), implemented in the mgcv library (Wood 2004, 2006) with the freeware R (R Development Core Team 2006). In comparison with generalized linear models (GLMs) or parametric linear regression, GAMs have the advantage of letting the data dictate how the shape of the dependent variable is affected by each covariate by fitting nonparametric smoother terms. They have therefore been widely applied in fisheries (e.g. Augustin et al. 1998, Maravelias 1999, Beare et al. 2002) and more recently in marine mammal studies (e.g. Bradshaw et al. 2004, Hastie et al. 2005, Panigada et al. 2008) for modelling species distribution and habitat preferences, where the relationship between explanatory and dependent variables is not expected to be linear.

Owing to an excess of zero values in the dependent variable 'sighting rate', overdispersion in the residuals was detected in 4 of the 6 separate analyses when applying models with a Poisson distribution. The overdispersion in the residuals was accounted for by applying a quasi-Poisson GAM, which provided more realistic estimates of the variance and thus significance of each smoother in the model. The residuals of the 2 spring models showed minimal overdispersion (dispersion parameter < 1.1), and minke whale sighting rates at both spatial scales for spring were therefore refitted with a Poisson distribution. Thin plate regression splines were used as penalized regression smoothers for all models. The amount of smoothing (i.e. the degrees of freedom) for each continuous explanatory variable was estimated automatically by using generalized cross-validation (GCV), but with the maximum df set to 4 to avoid overfitting. Model selection was performed in a stepwise backward procedure by minimising the unbiased risk estimator (UBRE) score (for Poisson models) and GCV score (for quasi-Poisson models), respectively (Craven & Wahba 1979, Wood 2006). For quasi-Poisson models, the deviance explained was used for

Table 1. Details of environmental variables used in models. For a detailed description of data processing methods, see Anderwald (2009). H: entire eastern Hebrides; C: core study area; nd: no data. TIN: Triangular Integrated Network; AVHRR: Advanced Very High Resolution Radiometer; NEODAAS: NERC Earth Observation Data Acquisition and Analysis Service; MODIS = Moderate Resolution Imaging Spectroradiometer; UKHO = UK Hydrographic Office; SST: sea surface temperature; GAM: generalized additive model

Environmental variable	Area	Source	Resolution/years covered	Methods
Bathymetry	H	Digbath250 NW Scotland (British Geological Survey)	1:250 000, converted to 200 m grid	TIN, then conversion to 200 m and 70 m grids; mean depth per cell calculated with ArcView extensions 3D-Analyst and Spatial Analyst 3.3
	C	Authors' own depth soundings and nautical chart (Digbath250 inadequate for core study area)	70 m grid	
Slope	H, C	Derived from bathymetry data at same resolution as depth via Surface-Menu in Spatial Analyst; mean and maximum per cell		
SST	H, C	AVHRR[a] (via NEODAAS)	1.1 km^2; monthly composites 1993–2007	Spatial join (ArcView 3.3) with mid-points of 1 min effort segments, then averaged for all segments per cell
Chl *a*	H	nd[b]	–	–
	C	SeaWiFS, MODIS Aqua (both via NEODAAS)	1.3 km^2, (Sep 1997–2004), 1.1 km^2 (May 2005–Sep 2007); monthly composites	Same as for SST
Tidal current	H	TotalTide (UKHO)	22 ports and 26 tidal diamonds within study area	Spatial join with mid-points of 1 min effort segments, then averaged for all segments per cell (split for each hour of tidal cycle [spring and neap])
	C	High resolution (<200 m) 3-dimensional (3D) hydrodynamic model forced by tidal velocity and elevation from a regional model (POL CS20)[c] (TotalTide inadequate for core study area)	0.5' for each hour of tidal cycle (spring and neap)	
Sandeel occurrence	H	GAM prediction, based on relationship between measured densities from day grab and silt and gravel content of seabed sediment (Wright et al. 2000)	Prediction points assigned to each 4' cell	$x \leq 0.3$ = unlikely, $0.3 < x \leq 0.7$ = probable, $x > 0.7$ = very likely; fourth category for cells with no prediction points. Maximum probability of occurrence per cell
	C	nd[d]	–	–

[a] Excluded for July (for both H and C) owing to missing data caused by cloud cover in most years. Cloud cover also prevented the use of composites at finer temporal resolutions (weekly or daily) for both SST and chl *a*

[b] Included only in C, since no data were available at appropriate resolution before September 1997

[c] No relationship was found between tidal current and distribution of minke whales in original models (Anderwald 2009). Cell summaries therefore recalculated without subdivision according to 2 × 13 h of tidal cycle in order to achieve more representative sighting rates per cell, and to alleviate problem of zero inflation

[d] Excluded owing to low number of prediction points in C; no quantitative data on distribution of other potential prey species were available

model selection in addition to the GCV score. Nonsignificant variables were retained in the model if they contributed to minimizing the UBRE or GCV score and (in the latter case) increased the deviance explained. Residuals of the final models were plotted against each explanatory variable to check for residual patterns. Since the data were divided into 3 separate models per season, the significance values of each explanatory variable in the final models were Bonferroni-corrected and provided a new p-value of 0.0167.

Exploratory analysis included Spearman's rank correlation coefficients and pair-plots to check for both linear and (based on pair-plots) nonlinear correlations between continuous explanatory variables (Table 2). Sea state corrected time spent on effort and kilometres travelled per cell were included as correction factors in all models to account for biases in spatial and temporal coverage of different cells. Since the same amount of effort with respect to time spent watching and distance travelled in a cell with reduced sea area (i.e. adjoining land) results in better coverage than an equivalent amount of effort in a cell entirely covered by sea, cell area covered by sea was included as an additional correction factor.

Inclusion of the MV 'Sheerwater' data in the core study area resulted in strong correlations (Spearman's r_S: $0.788 < r_S < 0.927$) between the correction variables 'sea state corrected time' and 'length of survey track' per cell. The 2 variables could therefore not be included in the same model. The decision on which parameter to include was based on which improved the model the most (i.e. led to a greater decrease in the UBRE or GCV score and increase in explained deviance). For the May/June and August/September models, this was the number of sea state corrected hours; for the July model, it was the distance travelled per cell. No strong correlations were found between any of the other selected explanatory variables ($r_S < 0.6$).

Table 2. Environmental variables (see Table 1 for data collection details and sources) selected for use in the habitat models following exploratory analysis. Dependent variable: sighting rate (no. of ind. h^{-1}) per cell (per year, month, tidal state and hour of the tidal cycle)

Explanatory variable	Category No./unit	Category Description	Used at scale
Factors			
Year	2 to 8		H,C
Month	2	For May/June & August/September models	H,C
Tide	2	Spring, neap	H,C
Sandeel occurrence	4	Unlikely, probable, very likely, no data[a]	H
Smooth terms			
Mean SST[b]	°C		H,C
Mean chlorophyll	mg m^{-3}		C
Mean depth	m		H,C
Mean slope	°		H
Max. slope	°		C
Tidal current	knots		H,C
Mean difference between high and low water at nearest harbour	m		H
Sea state corrected time spent per cell	min		H,C
Length of survey track per cell	km		H,C
Area per cell covered by sea	ha		H,C

[a] According to Wright et al. (2000); see Table 1 for definitions

[b] Excluded from models for July owing to missing data

Tracks of individuals

The aim of the second analysis was to investigate which environmental parameters determined minke whale behaviour — notably foraging (including feeding and searching) versus travelling — to help characterize foraging habitat in the context of distributional data. Individual whales were followed for as long as possible, while recording their surfacing times to the nearest second, their position and surfacing type ('normal or fast surfacing' or 'high arch' before dive, 'surface feeding': lunge with distended throat grooves, fish often visible). Any possibilities of missed surfacings were noted and those dives were subsequently excluded from analysis. All whales were followed at a distance of 30 to 100 m, taking care to remain on as constant a course and speed as possible in order to avoid influencing the focal animal's behaviour or dive pattern.

The study area around the Small Isles was divided into cells of 0.5′ latitude × 0.5′ longitude (Fig. 2), and the surfacing positions of individual whales were linked to the same environmental parameters as the 1 min effort segments for the habitat models covering the core study area (Table 1). The direction of the tidal current was included as an additional categorical explanatory variable.

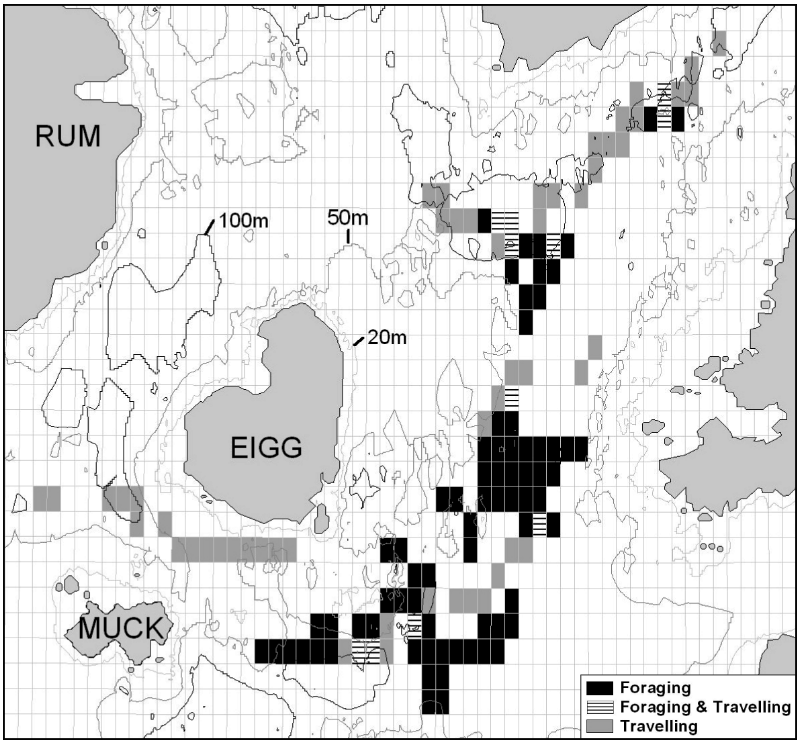


Fig. 2. Distribution of 0.5′ cells used by minke whales *Balaenoptera acutorostrata* for foraging, travelling or both, based on focal follow data within the core study area

Owing to the variability in dive patterns between individuals and the possibility of whales switching between different behaviours during a focal follow (the period when an individual is followed for an extended period of time), no attempt was made to distinguish between foraging and travelling whales in the field. Instead, foraging or travelling behaviour was assigned based on the plotted track line of each individual. According to area-restricted search, an animal increases the turning rate in its search path after food intake, and thus remains longer in high-density prey patches (Tinbergen et al. 1967, Kareiva & Odell 1987, Walsh 1996, Fauchald & Tveraa 2003). It was therefore assumed that foraging whales would, on average, spend more time in a given area compared with those travelling and thus moving in a more direct line. The number of 0.5′ cells covered by the track line of each focal follow was therefore divided by its duration, giving a rate of 'number of cells visited per hour'. The resulting frequency distribution of the number of cells visited per hour roughly divided individuals into 2 groups (data not shown): whales moving at a rate of <5 cells h^{-1} were classed as foraging, whereas whales that covered >10 cells h^{-1} were classed as travelling. The tracks of individuals moving at intermediate rates of 5 to 10 cells h^{-1} were visually inspected for a possible switch between foraging and travelling, based on a change from moving in a straight line to fine-scale use of cells combined with an abrupt change in the direction of movement. All other tracks within this category were classed as foraging. These assumptions were then validated independently by checking that any surfacings associated with feeding behaviour only occurred during focal follows classed as foraging.

Typical breathing sequences in minke whales consist of 3 to 6 short dives followed by one longer dive (typically 3 to 13 min; see Gunnlaugsson 1989, Joyce et al. 1990, Anderwald et al. 2008). However, only longer dives (i.e. not within a breathing sequence) are likely to be relevant in determining the foraging path and behaviour of individuals. The cut-off value between breathing sequences and potential foraging dives was determined by a marked decline in overall frequencies of dive duration (found to be at 50 s, Anderwald 2009). Only surfacing positions preceding dives of >50 s in duration, and part of focal follows lasting at least 30 min or including at least 10 dives of >50 s each, were therefore considered for the analysis.

To reduce the risk of spatial auto-correlation, the analysis was based on grid cells rather than single dives: all long dives (i.e. >50 s) of an individual within a 0.5′ cell were summarized and the resulting means of the continuous explanatory variables included in the model. This resulted in each cell being represented only once per individual per day (Fig. 2). A GAM with a binomial error distribution indicated approximately linear relationships between the continuous explanatory variables and the response variable. The model was therefore refitted with a logistic regression. Before including the environmental parameters into the GLM, a univariate ANOVA with 'Behaviour' (forage versus travel) as the explanatory variable was performed for each continuous parameter in turn in order to examine its residual pattern. A natural log transformation of chlorophyll *a* (chl *a*), maximum slope and tidal current data ensured that the residuals of all 3 parameters followed a Poisson distribution, while SST and mean depth did not require transformation. All explanatory variables were simultaneously included in the logistic regression, and model selection was performed in a stepwise backward manner first by applying Akaike's information criterion (AIC; Burnham & Anderson 2002) and then the deviance test.

RESULTS

Habitat models

A total of 356 minke whale sightings (comprising 409 individuals) during 1515 h of survey effort were included in the analysis from the 'Marguerite Explorer' data over the entire eastern Hebrides between 1993 and 2002 (Fig. 1a). Survey effort around the Small Isles amounted to a total of 2326 h with 765 minke whale sightings between 1998 and 2007 (Fig. 1b). Of these, data from MV 'Sheerwater' between 2003 and 2007 contributed 1688 h (72.5 %) and 376 (49 %) sightings; dedicated field work from 'Gwen' and other vessels between 2003 and 2007 accounted for 572 h (24.5 %) and 342 (45 %) sightings, and data from 'Marguerite Explorer' between 1998 and 2002 provided 66 h (3 %) of effort and 47 (6 %) sightings. Highest sighting rates from all platforms occurred during July and August.

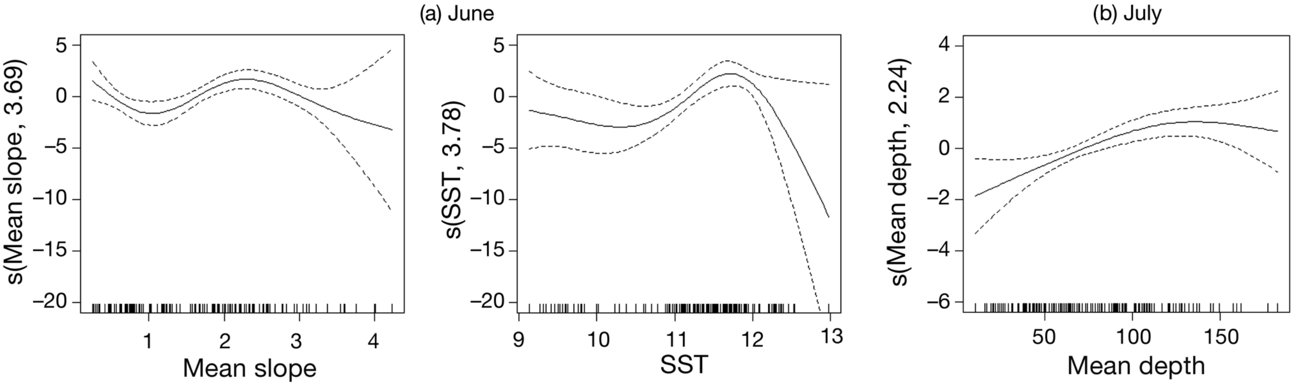
Minke whale sighting rates from the 2 independent sources — MV 'Sheerwater' and dedicated fieldwork from 'Gwen' (and other vessels during 2003 to 2007) — were positively correlated for all months of simultaneous data collection within the core study area (Spearman's correlation: $r_S = 0.803$, $p = 0.009$). Sighting rates along the ferry route could therefore be viewed as representative of the whole area around the Small Isles, so the data sets were pooled.

Entire eastern Hebrides

A common feature among all 3 seasonal models for the entire eastern Hebrides was that none of the tidal parameters used was relevant in determining minke whale sighting rates per cell (Table 3). Although retained in some models for better fit, they were not

Table 3. Summaries for final generalized additive models for data from 'Marguerite Explorer'; 4′ cells over entire study area. –: parameter not included in final model; na: not applicable for model in question. $^{*}p < 0.0167$ (Bonferroni correction: 0.05/3), $^{**}p < 0.005$, $^{***}p < 0.001$

	June 1995, 2000 (n = 174)	July 1993, 1994, 1998 (n = 212)	August and September 1993–1994, 1996–1997, 2002 (n = 738)
Parametric coefficients		**Estimate (±SE)**	
Intercept	−6.283 (±1.031)***	−1.629 (±0.360)***	−2.625 (±0.459)***
Year:		–	
2000 (vs. 1995)	3.860 (±1.465)*	na	na
1994 (vs. 1993)	na	na	1.614 (±0.461)***
1996 (vs. 1993)	na	na	1.680 (±0.454)***
1997 (vs. 1993)	na	na	2.021 (±0.481)***
2002 (vs. 1993)	na	na	1.856 (±0.554)***
Month: September (vs. August)	na	na	−0.611 (±0.254)*
Sandeel probability:			
Probable (vs. unlikely)	3.091 (±0.839)***	−8.654 (±52.14)	–
Very likely (vs. unlikely)	2.777 (±0.778)***	−0.284 (±0.500)	–
No data (vs. unlikely)	0.661 (±0.868)	0.116 (±0.311)	–
Spring vs. neap tide	0.803 (±0.610)	0.449 (±0.554)	−0.828 (±0.377)
Smooth terms		**X^2 (estimated df)**	
Depth (mean)	–	10.320 (1.91)*	20.084 (3.68)***
Slope (mean)	15.875 (3.77)**	–	9.959 (3.70)
SST	15.507 (3.81)**	na	21.343 (3.83)***
Tidal height difference	–	6.111 (2.51)	4.127 (1.82)
Tidal current	–	–	1.546 (2.58)
Duration (sea state corrected)	–	6.545 (2.41)	31.523 (2.42)***
Distance (km) travelled per cell	2.265 (1.82)	5.552 (2.95)	3.302 (1.49)
Cell area	3.566 (2.48)	0.896 (1)	–
Dispersion parameter	na	1.451	1.585
Deviance explained	64.2 %	26.1 %	29.1 %


(a) June

(b) July

(c) August & September

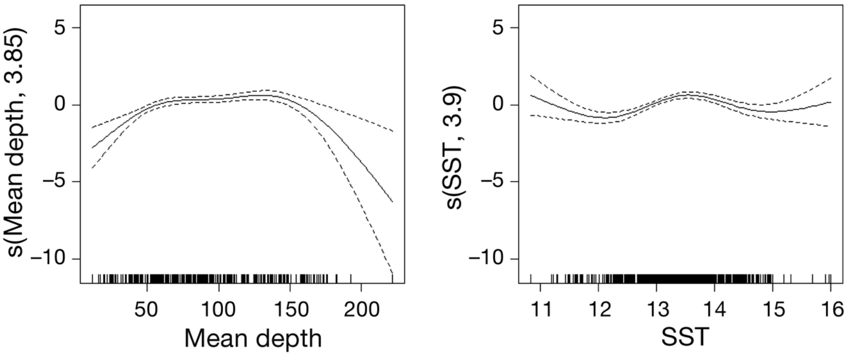


Fig. 3. Generalized additive model smoothing curves for significant environmental parameters (after Bonferroni correction) on minke whale *Balaenoptera acutorostrata* sighting rates (ind. h^{-1}) per cell for the 3 seasonal models over the entire eastern Hebrides (smoothers for correction terms not shown). Broken lines represent 2 × SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the *y*-axis. Vertical dashes on the *x*-axis represent the distribution of the explanatory variable

significant when corrected for other explanatory variables. In June, minke whale sighting rates were significantly higher in cells with ‘probable’ and ‘very likely’ sandeel occurrence compared with cells with ‘unlikely’ sandeel presence, whereas there was no difference between cells with ‘unlikely’ sandeel occurrence and no prediction points (Table 3). For July, sandeel occurrence was still retained in the model for better fit even though it was no longer significant, and for August/September, this factor was removed from the model altogether (Table 3), which indicated that sandeels are important to minke whales only early in the season.

Smooth terms also showed differences in their relevance between months. Seafloor topography only played a role for the month of June, when whales showed a preference for intermediate slopes of around 2 to 2.5° (Fig. 3a). During summer and autumn, however, depth better explained minke whale distribution. Sighting rates increased with water depth (from 50 to 60 m and above, reaching a plateau at 110 to 120 m; Fig. 3b) in July, when depth was the only significant continuous variable in the model. During August/September, the smoothing curve for depth exhibited an overall bell-shaped form, showing a broad preference by whales for waters of 50 to 150 m deep (Fig. 3c). SST was important in explaining minke whale distribution during both June and August/September. During June, the whales showed a preference for temperatures at the higher end of the scale at around 11.5 to 12°C (Fig. 3a), and in August/September for intermediate values between 13 and 14°C (Fig. 3c).

The model that best explained minke whale distribution over the whole of the Hebrides was for June and accounted for 64.2% of the deviance. The models for July and August/September, on the other hand, only explained 26.1 and 29.1% of the deviance, respectively, despite the high number of explanatory variables retained in the latter (Table 3).

Core study area

While the factor ‘year’ was irrelevant for spring, significantly more whales were seen per unit effort spent in the month of July in 2004 and 2007 compared with 2001. By contrast, there was a large and significant decline in sighting rates during August/September for the years 2005 to 2007 compared with 1998 (Table 4).

The smoothing curve for depth in July showed the same shape as for the same month in the model for the entire eastern Hebrides; both reached a plateau at around 100 m (Fig. 4b). For August/September, the shape of the depth curve was similar, but reached a peak at 70 to 80 m and remained level up to 100 m

Table 4. Summaries for final generalized additive models for core study area around the Small Isles, based on 2′ cells. max.: maximum; –: parameter not included in final model; na: not applicable for model in question. $^{*}p < 0.0167$ (Bonferroni correction: 0.05/3), $^{**}p < 0.005$, $^{***}p < 0.001$

	May and June 2004–07 (n = 440)	July 2001, 2004–07 (n = 305)	August and September 1998–99, 2002–07 (n = 814)
Parametric coefficients	**Estimate (±SE)**		
Intercept	−2.688 (±0.211)***	−2.954 (±0.694)***	−0.035 (±0.297)
Year:	–		
2004 (vs. 2001)	na	2.767 (±0.696)***	na
2005 (vs. 2001)	na	−0.733(± 1.116)	na
2006 (vs. 2001)	na	1.716 (±0.718)	na
2007 (vs. 2001)	na	1.742 (±0.699)*	na
1999 (vs. 1998)	na	na	1.017 (±0.444)
2002 (vs. 1998)	na	na	−0.045 (±0.399)
2003 (vs. 1998)	na	na	−0.209 (±0.421)
2004 (vs. 1998)	na	na	0.096 (±0.301)
2005 (vs. 1998)	na	na	−2.504 (±0.575)***
2006 (vs. 1998)	na	na	−2.524 (± 0.510)***
2007 (vs. 1998)	na	na	−2.607 (± 0.684)***
Month: September (vs. August)	–	na	−0.772 (±0.222)***
Spring vs. neap tide	–	–	0.165 (±0.143)
Smooth terms	**X^2 (equivalent df)**		
Depth (mean)	6.627 (3.17)	29.879 (2.28)***	32.181 (2.66)***
Slope (max.)	1.211 (1.50)	16.497 (2.43)***	5.123 (1)
SST	11.942 (2.71)*	–	0.768 (1)
Chl *a*	0.395 (1)	–	16.455 (3.31)***
Duration (sea state corrected)	2.385 (2.47)	–	11.859 (1)***
Distance (km) travelled per cell	–	7.391 (1)*	–
Cell area	–	8.157 (3.51)	–
Dispersion parameter	na	2.712	2.275
Deviance explained	14.9%	46.3%	41.6%

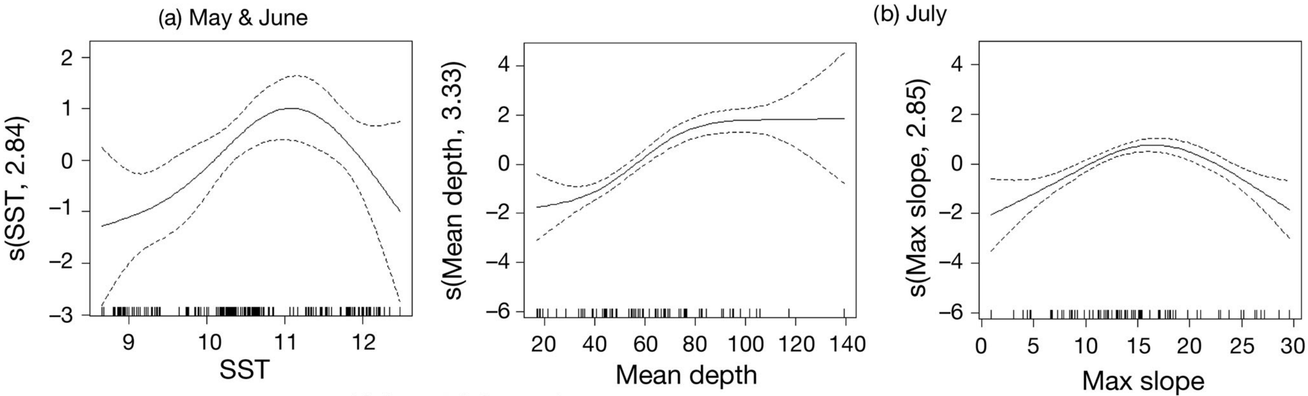
(Fig. 4c). This depth range coincides with a deep channel between Arisaig and the Isle of Eigg (Fig. 2). Topography only affected minke whale sighting rates during the month of July, during which the maximum slope showed a bell-shaped form around a peak of 15 to 17° (Fig. 4b).

Both temporally variable continuous parameters (SST and chlorophyll) were important predictors of relative minke whale abundance at particular stages of the season. SST was the only significant variable in the May/June model, when whales showed a preference for water temperatures around 11°C (Table 4, Fig. 4a). In contrast to the entire eastern Hebrides, however, SST was not significant in the Small Isles model for August/September. Instead, chlorophyll concentration (data for which had not been available for the earlier years of coverage) played a highly significant role in determining minke whale sighting rates during the latter part of the season: numbers of whales per unit effort showed a steady increase from a chl *a* concentration of 1 mg m^{-3} to a peak at 3 mg m^{-3} (Fig. 4c).

The explanatory power of the 3 seasonal models was reversed for the Small Isles compared with the entire eastern Hebrides. The spring model, in which SST was the only significant variable, explained only 14.9% of the deviance, making it the poorest of all 6 models. On the other hand, both the July and August/September models performed better for the Small Isles than for the whole area, with 46.3% of the deviance explained for July and 41.6% for August/September, respectively (Table 4).

Tracks of individuals

A total of 26 track lines fulfilled the duration criterion of at least 30 min or the inclusion of at least 10 dives of >50 s per dive. Based on their track lines (i.e. the number of cells visited per unit time), the behaviour during 19 focal follows (73%) was classed as foraging, and 4 focal follows (15%) were classed as travelling. Three sequences (12%) appeared to include a transition between foraging and travelling or vice



(c) August & September

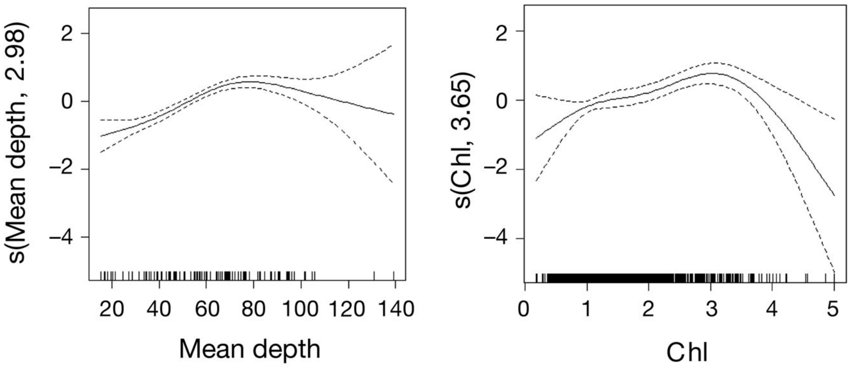


Fig. 4. Generalized additive model smoothing curves for significant parameters (after Bonferroni correction) on minke whale *Balaenoptera acutorostrata* sighting rates (ind. h^{-1}) per cell for the 3 seasonal models covering the core study area around the Small Isles (smoothers for correction terms not shown). Broken lines represent SE ranges around the main effects. The degrees of freedom for each smoothing curve are indicated on the *y*-axis. Vertical dashes on the *x*-axis represent the distribution of the explanatory variable

versa, based on an abrupt change in the direction of the whales' movement combined with a switch from moving in a straight line to a more unpredictable course in which fewer cells were visited per unit time.

The duration of successful focal follow sequences ranged from 26 min to 2 h 54 min, which amounted to a total of 1552 recorded dives (32.4 h), 593 of which exceeded 50 s. The maximum dive time for which any possibility of a missed surfacing could be excluded was 10 min 10 s (Table 5). Sixteen individuals could be identified during focal follows by using photo-identification. Of these, only 1 individual was followed on 2 consecutive days (S06 in 2006; Table 5); focal follows of all other identified individuals were confined to a single day.

The only significant parameters included in the final logistic regression model were direction and strength of tidal current (Table 6): minke whales were more likely to forage in areas of strong tidal currents (regression coefficient = 1.1713, SE = 0.3722; Fig. 5), and travelling was more likely in areas in which the current flow was in a north-westerly direction as opposed to an easterly (the reference level) direction (regression coefficient = –3.0781, SE = 1.2268). The model including both tidal strength and direction explained almost half of the total variance in the data (Nagelkerke $R^2 = 0.458$).

DISCUSSION

As expected for a highly mobile baleen whale, habitat modelling results indicated that minke whale distribution on the west coast of Scotland during the summer feeding season was influenced simultaneously by both fixed and temporally variable environmental parameters that are thought to determine the spatial and temporal availability of pelagic prey concentrations. However, the relative importance of these variables changed through the season, both over the entire eastern Hebrides and within the smaller core study area around the Small Isles. Despite the differences in spatial scale (4′ versus 2′), coverage (the entire eastern Hebrides with a large area and relatively low temporal coverage, and the Small Isles with extensive temporal coverage) and study period (large area from 1993 to 2002, and Small Isles from 1998 to 2007 but mainly 2003 to 2007), the GAM results for each part of the season were surprisingly consistent between the entire eastern Hebrides and the core study area. This suggests that the findings for minke whale habitat use within a comparatively small but high-density area are generally applicable for the species across the entire west coast of Scotland and over an extended time period (15 yr).

Table 5. Summaries of minke whale *Balaenoptera acutorostrata* focal follows conducted around the Small Isles between 2003 and 2007. Max.: maximum; ID: identification; f: foraging; t: travelling

Individual no.	Individual identification	Date (d.mo.yr)	Start time (h)	End time (h)	Duration (min)	Max. dive time (s)	No. surfacings	No. dives > 50 s
1 f	Unidentified	4.8.2003	16:47	17:13	26	242	21	10
2 f	Unidentified	4.8.2003	19:27	20:15	48	250	47	19
3 t	Unidentified	5.8.2003	19:28	20:03	35	335	26	10
4 f	Unidentified	6.8.2003	10:49	11:29	40	167	35	10
5 f	Unidentified	7.8.2003	10:44	11:48	64	320	49	24
6 f	F02	10.8.2003	11:49	12:59	70	422	39	17
8 f/t	F03	11.8.2003	11:44	14:32	168	420	106	50
9 f	F05	11.8.2003	15:53	16:42	49	343	47	17
10 f	N06	11.8.2003	17:38	18:26	48	280	35	14
11 f	S05	12.8.2003	10:44	11:11	27	124	31	14
12 f	W02	12.8.2003	12:38	13:16	38	202	40	12
13 f	N17	12.8.2003	13:16 14:12	13:31 15:41	104	279	72	42
14 f	F04	12.8.2003	16:25	18:26	120	228	95	38
15 t	S01	22.8.2004	11:41 12:08	11:51 13:29	91	360	103	33
16 t	Unidentified	22.8.2004	18:26	19:11	45	150	30	22
18 t	B01	31.8.2004	12:09	13:41	92	335	47	21
20 f/t	Unidentified	10.9.2004	14:58	16:23	85	435	41	19
22 f	F15	9.8.2005	08:58	09:42	44	277	27	9
23 f	Unidentified	11.8.2005	08:57	11:05	128	463	107	37
24 f	F14	11.8.2005	16:28	17:07	39	255	32	12
25 f	Unidentified	14.8.2005	18:43	19:34	51	333	43	12
26 f	N23	4.9.2005	17:56	20:06	130	430	127	28
27 f	S06	11.8.2006	15:51	16:53	62	251	43	22
f/t		12.8.2006 12.8.2006	11:48 14:24	13:59 15:07	174	389	168	52
28 f	F19	20.7.2007	13:35	15:49	134	610	125	41
30 f	F26	23.7.2007	10:41	11:12	31	380	16	8
Mean ± SD					75 ± 44	318 ± 109	60 ± 40	23 ± 13
Total					32.4 h		1552	593

Table 6. Final model of logistic regression on minke whale *Balaenoptera acutorostrata* behaviour (foraging versus travelling). AIC: Akaike's information criterion

Parameters included	df	Deviance	AIC	Likelihood ratio	p
Current direction and strength		164.373	180.373		
Strength	1	175.689	189.689	11.316	<0.001
Direction	6	223.853	227.853	59.480	<0.001

During the month of June, sighting rates of minke whales were significantly higher in 4′ cells with 'probable' or 'very likely' sandeel occurrence by comparison with cells where sandeel presence was 'unlikely'. In contrast, this relationship did not apply later in the season, which suggests that sandeels are only important in minke whale diet during spring. This period coincides with the main growth phase of sandeels where they have been studied in the Irish (Cameron 1959) and North Seas (Pedersen et al. 1999) when the fish are active in the water column feeding on zooplankton. These results quantitatively support the hypothesis of a change in diet between early and late seasons as suggested by Macleod et al. (2004), who based their findings on a qualitative comparison between information from the literature on sandeel and herring habitat with their minke whale distribution models that were restricted to fixed physical environmental parameters. However, Macleod et al.'s (2004) hypothesis of prespawning herring being the main prey during August and September was not corroborated by prey sampling around the Small Isles in the same months, 96% (n = 26) of which consisted of sprat (Anderwald 2009). The majority of minke whale surface feeding activity in the area during this time of year occurs in the presence of multi-species flocks of seabirds (auks, kittiwakes *Rissa tridactyla*, gulls *Larus* spp. and Manx

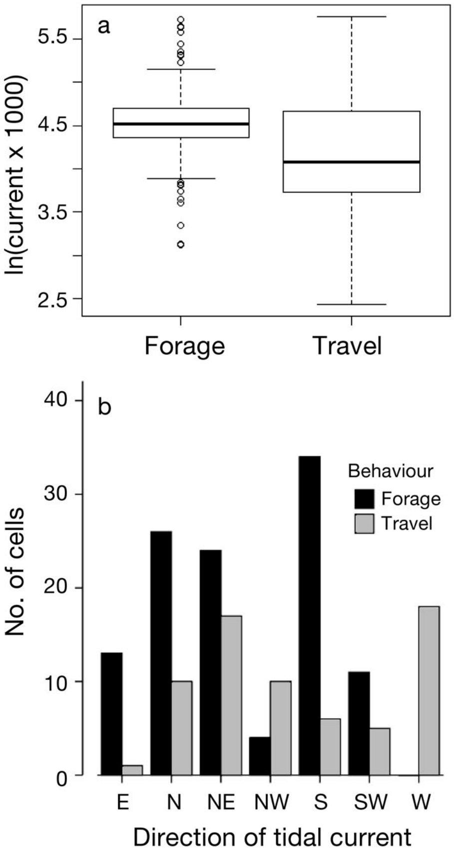


Fig. 5. Minke whale *Balaenoptera acutorostrata* foraging and travelling behaviour in relation to the only 2 parameters retained in the final logistic regression model: (a) current speed (m s^{-1} × 1000), and (b) direction of tidal current. Boxplots show median (thick line), interquartile range (IQR, box), median ± 1.5 × IQR (whiskers) and outliers (circles)

shearwaters *Puffinus puffinus*) that apparently take the same prey as the whales (Anderwald et al. 2011). Prespawning (i.e. adult) herring would be too large for any of these bird species to catch, and fish scales compatible with the size of adult herring were never found in either whale or seabird feeding locations during August and September 2003 and 2004.

The role of sandeel in minke whale diet in the earlier part of the season was further supported by the important contribution of SST towards explaining relative minke whale abundance during spring in the present models, both for the Small Isles (where it was the only significant parameter for May/June) and the entire eastern Hebrides. Minke whale sighting rates showed a peak towards the higher end of the spring temperature scale at around 11 to 12°C. In the laboratory, Winslade (1974) demonstrated that swimming activity of sandeels increased when temperature was increased from 5 to 10°C, thus making them more readily available to predators in the water column at higher temperatures. Similarly, in the field, van der Kooij et al. (2008) found that peak sandeel abundance occurred at temperatures around 9°C. Although sandeels do not fully enter their overwintering phase until September or October, during which time they remain buried in the sand, their abundance in the water column steeply declines in July and August, which is evident from changes in commercial catches (Pedersen et al. 1999) and their lower availability to surface feeding seabirds (Wanless et al. 2004). This seasonal reduction in sandeel density within the water column probably explains why they appear to become less important to the whales. The observed temperature preferences of minke whales during spring would therefore be consistent with those water temperatures in which sandeels are more active during this time of year, even when allowing for the fact that SST (as measured in the present study) is somewhat higher than seafloor temperature (most relevant for sandeel activity) if the water is stratified. Around the Dogger Bank in the North Sea, average differences between surface and seafloor temperatures at up to ca. 60 m depth were mostly below 0.5°C, and the greatest difference between seafloor temperatures at depths of 10 to 60 m during spring was <3°C (van der Kooij et al. 2008).

A recent dietary study of common guillemots *Uria aalge* on the west coast of Scotland during the breeding season (Anderson 2008) identified sandeels as the main prey being fed to chicks at some of the major colonies, and the same seasonal changes in distribution with respect to sandeel occurrence as observed for minke whales, have previously been found for common guillemots across Scotland (Wright & Begg 1997). Since sandeel presence is unlikely over most of the core study area around the Small Isles (Wright et al. 2000), this could explain the low numbers of minke whale sightings in this region during spring, followed by a movement into the area only later on in the season (Fig. 1b; see also Leaper et al. 1997, Macleod et al. 2004) when the whales appear to be feeding mainly on sprat (Anderwald 2009). Indeed, the model for May/June for the Small Isles explained only 14.9% of the deviance (making it the poorest model of all) compared with 64.2% of the deviance explained for the entire eastern Hebrides, which included the likelihood of sandeel presence as an explanatory variable. If minke whales can use water temperature to assess an area with respect to its likely productivity for sandeels in the water column, this could explain why the relative abundance of minke whales around the Small Isles in spring seemed to be dictated entirely by SST.

A dependence on sprat in August/September would then explain the significant effect of phytoplankton concentration (as indicated by chl *a* concentration) in the GAM for the area around the Small Isles that occurred precisely during this part of the season. Since sprat fast during winter (Lee & Ramster 1981), late summer and early autumn would be a crucial time for them to increase their fat reserves, and it would therefore make sense for them to aggregate in areas of high phytoplankton concentrations, and thus presumably high copepod abundance, at this time of year.

The strong effects of temporally variable environmental parameters (SST and phytoplankton concentration) on minke whale distribution in the habitat models for the west coast of Scotland appear to have more general applicability: they are consistent with large between-year shifts in the distribution of minke whales according to the fluctuating location of the Polar Front in the Barents Sea (Bjørge 2001), where the species feeds on different prey (Haug et al. 1995, 2002); Extreme differences in sighting rates between years have also been reported from the Gulf of St. Lawrence in eastern Canada (U. Tscherter pers. comm.). By contrast, tidal parameters had no influence on overall minke whale distribution, but instead showed a significant effect on foraging versus travelling behaviour at the finest spatial scale investigated in which whales exploited stronger currents within a relatively narrow range for foraging. The lack of a relationship between tidal parameters and the distribution of whales was surprising considering that minke whales are often associated with tidally active areas (Johnston et al. 2005, Ingram et al. 2007, Baumgartner 2008). However, given the extreme variations in current strength in one and the same location throughout the tidal cycle, it seems plausible that this parameter is most likely to influence minke whale behaviour in a particular area at a fine spatial scale rather than their overall distribution at the scales measured in the present study.

Because minke whales have a low energetic cost of swimming (Blix & Folkow 1995), exploiting dynamic environmental conditions at both small and large spatial scales in order to locate prey patches would seem to be energetically profitable. In this context, the combined results of the habitat models and logistic regression on foraging versus travelling behaviour are also consistent with the spatial scales of the different environmental parameters. If the combination of depth, topography, temperature and phytoplankton concentration (i.e. the variables that were important in the habitat models) makes an area worth visiting, foraging behaviour at the local scale can then be fine-tuned according to parameters that change over a matter of hours, but in a predictable manner, such as occurs with tidal currents. These patterns of habitat use indicate that minke whales respond at appropriate scales to changes in both spatial and temporal factors relevant for determining prey distribution and abundance.

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