Seasonal distribution of minke whales Balaenoptera acutorostrata in relation to physiography and prey off the Isle of Mull, Scotland

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ABSTRACT: Sightings of minke whales Balaenoptera acutorostrata were recorded in waters off the Isle of Mull between March and November each year from 1992 to 1999. Survey effort amounted to 42,342.5 km, and 850 minke whale encounters were recorded. Data were analysed in relation to undersea topography and seabed sediment type using multiple logistic regression. The effect of potential minke whale prey distribution was inferred from maps predicting suitable habitats for the lesser sandeel Ammodytes marinus and herring Clupea harengus constructed using a Geographical Information System (GIS). Whale distribution changed with season, and this may be a response to a shift in prey preferences. In spring, sediment type was a significant predictor of whale presence and sightings predominated over mixtures of gravel/sand seabed sediments. This distribution closely matched that of the sandeel, which is dependent on suitable winter settlement grounds. Throughout summer, the distribution of the minke whale underwent considerable change. In June, minke whales were predominately distributed over the sandeel habitat, but in July they dispersed to the predicted pre-spawning herring habitat, clustering in that area by August. In the waters around Mull, shifts in prey distribution and abundance occur between March and November and are the most likely factor governing the distribution and abundance of the minke whale.

KEY WORDS: Minke whale · Bathymetry · Seabed sediment · Herring · Sandeel · Geographical Information System
pollution, and other forms of habitat degradation and loss, are potential threats to most cetaceans, including the minke whale (Parsons et al. 2000, Gill et al. 2001).

Effective management and conservation of cetaceans can be assisted through an understanding of the effects of environmental factors, including physical, chemical and biological factors, on their distribution and abundance. Knowledge of species habitat preferences can aid the establishment of protected areas (Hoek et al. 1999), improvement of population abundance estimates, interpretation of population trends (Forney 1999) and understanding the consequences of environmental shifts for long-term management. Many factors may influence the temporal and spatial distribution and abundance of cetaceans but few studies have investigated such links for minke whales. Water depth (Skov et al. 1995, Hoek et al. 1999), seabed sediment type (Naud et al. 2003), oceanographic fronts (Kasamatsu et al. 2000), sea-surface temperature (Kasamatsu et al. 2000, Hamazaki 2002) and the extent of sea ice (Kasamatsu et al. 2000) are known to influence minke whale distribution, although their relative importance varies geographically. Minke whale distribution and abundance on the feeding grounds will ultimately depend on the distribution of their prey, as has been demonstrated for other baleen whales (Whitehead & Carscadden 1985, Payne et al. 1990, Woodley & Gaskin 1996). Significant correlations between whale distribution and environmental factors may be indirect due to their influence on prey distribution. Many benthic and pelagic fishes show habitat associations throughout or during parts of their life cycle that can directly influence their survivorship and recruitment (Reay 1970, Lindholm et al. 2001, Maravelias 2001, Borja et al. 2002).

Minke whales have been described as the most ichthyophagous of the Balaenoptera (Gaskin 1982). In the North Atlantic, they are known to take a range of pelagic shoaling and demersal fish species, in particular sandeel Ammodytes sp., herring Clupea harengus, mackerel Scomber scombrus, capelin Mallotus villosus, cod Gadus morhua and haddock Melanogrammus aeglefinus (Jonsgård 1982, Nordsøy & Blox 1992, Haug et al. 1995a,b). The feeding habits of most baleen whales can be categorised as skimming, swallowing or both (Hoezel et al. 1989). Minke whales are a typical swallowing species and engulf prey concentrated in shoals, which they chase and herd from below (Hoezel et al. 1989) or locate below feeding birds (Hoezel et al. 1989, Gill et al. 2000). The lesser sandeel A. marinus and herring are prey of the minke whale in British waters (Nordsøy & Blox 1992) and these species are known to exhibit habitat preferences in terms of bathymetry and seabed sediment type. Sandeel prefer shallow waters and seabed sediments of coarse sand and fine gravel (Macer 1966, Reay 1970, Wright & Begg 1997). The relative abundance of herring is influenced by temperature, seabed substrate, depth and by boundaries between water masses that enhance local production and food availability (Maravelias 1997, 2000). Maravelias et al. (2000) showed that aggregations of pre-spawning herring in the northern North Sea preferred zooplankton-rich waters at depths between 100 and 150 m. Spawning herring favour gravel beds, generally within 30 to 50 km of the coast (Saville & Bailey 1980, Blaxter 1990).

Waters surrounding the Inner Hebrides off the west coast of Scotland, UK, accommodate a minke whale population in which most individuals are seasonally resident (Gill 1994) and in which some may reside year-round. Data collected by a tour operator in coastal waters of the Isle of Mull, Coll and the Small Isles off western Scotland (Fig. 1) between 1992 and 1999 were analysed to investigate the seasonal and spatial distribution of the minke whale in relation to depth, slope and seabed sediment type. In the absence of fisheries data, the influence of sandeel and herring distribution, inferred from maps of potential distribution predicted from known associations of these species with bathymetry and sediment type, is also discussed.

Part of these data (1993 to 1995) collected by the same tour operator were previously analysed by Leaper et al. (1997) to assess the relative abundance and distribution of minke whales. The potential for bias in such data sets is strong because tour operators tend to travel to areas thought to have high densities of whales. Leaper et al. (1997) divided the survey area into blocks for analysis. The purpose of the stratification was to determine the largest block size such that prior knowledge of the locations in which the whales were last found did not allow them to be found more easily in the block on subsequent trips. With a 4 km-square block, overdispersion caused by clumping of sightings was evident in only 3% of all blocks surveyed; this was considered the maximum size of block free of bias due to prior knowledge of whale locations. This study further showed that minke whale distribution changed significantly with season. These results form the basis of the temporal and spatial stratification for this analysis.

**MATERIALS AND METHODS**

**Data collection.** Data were collected in coastal waters off the Isle of Mull, the Small Isles and Coll (~56°20’ to 57°N and 6° to 6°40’W) (Fig. 1) between March and November each year from 1992 to 1999. The data were collected on board the 12 m motor vessel ‘Alpha Beta’ run by an experienced tour operator, who had been running cetacean sighting trips in the area since 1989.
Cetacean sightings, search effort (measured as distance travelled by the boat) and environmental variables were recorded by the tour operator (the vessel skipper) using Logger software (IFAW 1994) run on a personal computer in the wheelhouse. The skipper made observations from the wheelhouse (2 m eye height), an additional trained observer was on the flying bridge (4.5 m eye height) and a varying number of passengers observed from seats on the observation deck (3 m eye height). Surveying was carried out in Beaufort sea states of ≤4.

Data on survey effort was collected and included the position of the vessel (NMEA 0183 serial interface between the laptop computer and the vessel Global Positioning System, GPS), start and end time of trips, and the search status throughout each trip. The search status detailed whether the observers were actively searching for whales (on effort) or not (off effort). The GPS position was updated every 5 min so that the cruise track of the vessel could be plotted. Environmental data, including wind speed, wind direction and Beaufort sea state, were recorded in Logger by the skipper. Logger data were updated at regular intervals (environment) or as they changed (effort and environment). The program provided an audible prompt when the input of the environmental data was due.

When a cetacean was sighted, the time of the first sighting cue, the GPS position and visual estimates of sighting angle and bearing were recorded in Logger. The skipper entered additional information on species and certainty of identification, group size and composition (such as the presence of calves), behaviour and associations between species and sea birds.

Environmental data. Admiralty charts of the survey area were digitised using the Geographical Information System (GIS) ArcInfo 8 to produce digital terrain models of seabed slope and bathymetry. A digital map of sediment classes in the survey area was obtained from the British Geological Survey. The sediment types were reclassified: (1) $S_1 = $ gravelly sand, sandy gravel, (2) $S_2 = $ mud/sand/gravel, gravel/mud/sand, (3) $S_3 = $ mud, sandy mud, (4) $S_4 = $ mud/sand, sand and (5) $S_5 = $ rock. All data were imported into a GIS, ArcView 3.2 (ESRI 1999) to form the basic environmental coverages on which analyses with the minke whale sighting data were based.

The environmental coverages were used to make maps of potential habitat for sandeel and pre-spawning and spawning herring. Sandeel habitat was defined as shallow waters (20 to 60 m) and sediments of coarse sand and fine gravel (Macer 1966, Reay 1970, Wright & Begg 1997). Pre-spawning herring habitat was defined as water depths of 100 to 150 m (Maravelias et al. 2000) and spawning herring habitat as areas of gravel seabed sediments (Saville & Bailey 1980, Blaxter 1990). Using this information, the digital bathymetry and sediment data were queried using ArcView, and 3 further coverages of potential sandeel habitat and attractive areas to pre-spawning and spawning herring were produced.

Data analysis. All data from 1992 to 1999 were used in the analysis, with the exception of that collected in 1996, which were considered unreliable due to problems with the GPS and Logger.

Only positive identifications of minke whales and sightings recorded during survey effort were used in the analysis. The sightings and survey effort data were pooled over years and stratified both spatially and temporally. We defined 3 seasons: (1) spring (March, April and May), (2) summer (June, July and August), and (3) autumn (September, October and November). Spatial stratification of the survey area was used to aid visual identification of 'high use' areas by minke whales and limit bias caused by the searching behaviour of the tour operator (Leaper et al. 1997). For this study, a 2 km-square grid (4 km²) was created throughout the survey area and the data were analysed on this spatial scale. A smaller grid than suggested by Leaper et al. (1997) was used so that relationships between minke whales and environmental features on a finer scale could be investigated. Changes in seasonal distribution of the minke
whale were investigated through the estimation of an
encounter rate (number of sightings km\(^{-1}\) surveyed,
\(n\ \text{km}^{-1}\)) within each 2 km square-grid and for each
season, and was mapped using ArcView.
To investigate the relationship between minke whale
distribution and environmental parameters, each
square of the 2 km grid was assigned a value for the fol-
lowing parameters: MD = mean depth (m); MIND = min-
imum depth (m); MAXD = maximum depth (m); SDD = 
standard deviation depth (m) (a measure of variability
within a grid square); MS = mean slope (%); MINS = 
minimum slope (%); MAXS = maximum slope (%); SDS = 
standard deviation slope (%); and \(S_{1-5}\) = dominant 
seabed sediment type. The survey effort (\(E\)) in each grid
square was also included in the analysis as a continuous
variable to account for the varying survey effort.

General linear models (GLMs) can be used to fit non-
normally distributed data by expression of an appropri-
ate link function (McCullagh & Nelder 1989). Logistic
regression (Collet 1991) was used to examine the im-
portance of the environmental parameters on the distri-
bution of minke whales. The encounter rate for each
grid square was categorised as either 0 or 1, signifying
presence or absence of whales, respectively. Logistic
regression models the probability of whale presence in
a grid square given the environmental parameters. The
logistic transformation (the link function) of a success
probability \(p\) is log(\(p/(1 – p)\)), written as:

\[
\logit(p) = \beta_0 + \beta_1 x_{i_1} + \beta_2 x_{i_2} + \ldots + \beta_k x_{i_k}
\]

for \(k\) explanatory variables \((x_{i_1}, x_{i_2} \ldots x_{i_k})\) associated
with that observation. On rearrangement of this equa-
tion and given \(h_i = \sum b_j x_{i_j} \ldots\)

\[
p_i = \frac{e^{h_i}}{1 + e^{h_i}}
\]

The data were overdispersed and a scale parameter
was estimated for each model. Each environmental pre-
dictor variable was modelled in turn, and the significant
variables were used to build a full model using forward
selection procedures. The significance of additional
variables was assessed using an analysis of deviance
(Collet 1991) against the critical values of a \(\chi^2\) distribu-
tion (\(\alpha = 0.05\)). Single variables significant at the 10%
level were also initially retained in the model. The residual deviance was used
as a measure of model fit; the smaller
the deviance the better the fit of the model. The residual deviance of the fi-
nal model, scaled for the estimated dis-
"
Fig. 2. *Balaenoptera acutorostrata*. Survey effort, as distance travelled (on a 2 km grid) in study area during spring (top), summer (middle) and autumn (bottom).

Fig. 3. *Balaenoptera acutorostrata*. Encounter rates (sightings km⁻¹) of minke whales during spring (top), summer (middle) and autumn (bottom).
with a noticeable shift in distribution from the area between North Coll and Ardnamurchan in spring to the channel between Ardnamurchan headland and the Small Isles (Rhum, Muck and Eigg) in autumn. Environmental factors and ultimately prey distribution may be influencing this. Behaviour consistent with feeding activity, such as lunges through fish shoals, was observed during 27.5% of the minke whale encounters. During all seasons, the variable that on its own had the greatest predictive power was the amount of survey effort (E). Subsequent environmental parameters were fitted allowing for the effects of survey effort. Sediment type was also significant in all seasons (Table 2).

During spring, a further 3 variables, MAXS, MS and SDS were, singly, significant predictors of the presence of whales (Table 2). However, a 2-term model containing just E and S was the best fit of the data ($\chi^2$, $p = 0.492$): \[
\logit(p)_{MW_{spring}} = \beta + \beta_1 E + \beta_2 S
\]

where $\beta$ is a constant and $\beta_1$ and $\beta_2$ are parameter estimates for survey effort and sediment class. The parameter estimates (Table 3) show that S1, gravelly sand, seabed sediment, is the strongest predictor of the presence of a minke whale within any grid square compared to other sediments. Sediments of mud/sand/gravel (S2) are also an important predictor, but to a lesser extent than S1. Seabed sediment is likely to have an indirect influence on minke whale distribution, possibly through its influence on sandeel distribution. Fig. 4 shows the distribution of minke whale sightings

### Table 2. Significant environmental variables predicting presence of minke whales *Balaenoptera acutorostrata* (logistic regression).

D: residual deviance; S1 to S5: seabed types (see second subsection of ‘Materials and methods’ for details)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Antilog $\beta$</th>
<th>df</th>
<th>D</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.072</td>
<td>299</td>
<td>250.1</td>
<td>0.436</td>
</tr>
<tr>
<td>Effort (E)</td>
<td>1.004</td>
<td>298</td>
<td>178.1</td>
<td>0.000</td>
</tr>
<tr>
<td>Sediment (S)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>1.000</td>
<td></td>
<td></td>
<td>1.000</td>
</tr>
<tr>
<td>S2</td>
<td>0.300</td>
<td></td>
<td></td>
<td>0.877</td>
</tr>
<tr>
<td>S3</td>
<td>0.000</td>
<td>295</td>
<td>188.3</td>
<td>0.000</td>
</tr>
<tr>
<td>S4</td>
<td>0.000</td>
<td></td>
<td></td>
<td>0.629</td>
</tr>
<tr>
<td>S5</td>
<td>0.105</td>
<td></td>
<td></td>
<td>0.059</td>
</tr>
<tr>
<td>Mean depth (MD)</td>
<td>1.014</td>
<td></td>
<td>441</td>
<td>529.6</td>
</tr>
<tr>
<td>Min. depth (MIND)</td>
<td>1.012</td>
<td></td>
<td>443</td>
<td>537.4</td>
</tr>
<tr>
<td>Max. depth (MAXD)</td>
<td>1.006</td>
<td></td>
<td>441</td>
<td>539.3</td>
</tr>
<tr>
<td>Standard deviation depths (SDD)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean slope (MS)</td>
<td>0.853</td>
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<td>298</td>
<td>244.5</td>
</tr>
<tr>
<td>Min. slope</td>
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<td>298</td>
<td>243.8</td>
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<tr>
<td>Max. slope</td>
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<td></td>
<td>298</td>
<td>244.5</td>
</tr>
<tr>
<td>E × MD</td>
<td>1.001</td>
<td></td>
<td>433</td>
<td>328.4</td>
</tr>
<tr>
<td>E × MIND</td>
<td>1.001</td>
<td></td>
<td>433</td>
<td>351.1</td>
</tr>
<tr>
<td>E × S</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>1.000</td>
<td></td>
<td></td>
<td>1.015</td>
</tr>
<tr>
<td>S2</td>
<td>1.017</td>
<td></td>
<td></td>
<td>430</td>
</tr>
<tr>
<td>S3</td>
<td>1.050</td>
<td></td>
<td></td>
<td>346.3</td>
</tr>
<tr>
<td>S4</td>
<td>0.992</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S × MD</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>S1</td>
<td>1.000</td>
<td></td>
<td></td>
<td>1.000</td>
</tr>
<tr>
<td>S2</td>
<td>0.961</td>
<td></td>
<td></td>
<td>430</td>
</tr>
<tr>
<td>S3</td>
<td>0.977</td>
<td></td>
<td></td>
<td>359.3</td>
</tr>
<tr>
<td>S4</td>
<td>1.042</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SDD × MS</td>
<td>0.987</td>
<td></td>
<td>276</td>
<td>202.4</td>
</tr>
<tr>
<td>MAXD × MS</td>
<td>0.997</td>
<td></td>
<td>276</td>
<td>203.9</td>
</tr>
<tr>
<td>MAXD × SDD</td>
<td>0.999</td>
<td></td>
<td>276</td>
<td>204.4</td>
</tr>
</tbody>
</table>
during spring in relation to predicted sandeel habitat. The majority of the sightings are within a single sediment type (gravelly sand) and within depths of less than 60 m.

A number of environmental variables were, singly, significant predictors of minke whale occurrence during the summer (Table 2). In addition to E and S, MINS, MD, MIND and MAXD were significant. MAXD and MD were strongly correlated (p < 0.001) and, as the less significant predictor variable, MAXD was therefore eliminated from further analysis. At the 5% level, 3 interaction terms, E with S, MD and MIND, were also significant. The interaction between E and MD was the most significant and only the interaction between E and S was significant when added to this. The final model (χ², p = 0.504) was:

\[
\text{logit}(p)_{\text{MWsummer}} = \beta + \beta_1 E + \beta_2 S + \beta_3 MD + \beta_4 E \times MD + \beta_5 E \times S
\]

Of the dominant sediment types, the probability of minke whale presence was greatest in areas of mud/sand/gravel mixtures (S2). Deeper waters also increased the probability of whale occurrence (Table 3). During summer, particularly July, a number of known prey species, such as sprat *Sprattus sprattus* and mackerel, are abundant in the survey area. The range of environmental variables which, used singly, were significant predictors of whale presence may indicate that minke whales do not have a strong habitat (and therefore prey) preference during summer. Alternatively, the patterns of whale distribution between June and August (Fig. 5) could be explained in terms of a shift in prey preference from sandeel at the beginning of summer to herring towards the end of the season.

| Table 3. Summary of parameter estimates for final multiple logistic regression models of significant variables for each season |
|-------------------|------------------|------------------|
| Variables         | Spring (SE)      | Summer (SE)      | Autumn (SE)     |
| Constant          | 0.106 (0.258)    | 0.311 (0.352)    | 0.015 (0.618)   |
| Effort            | 1.029 (0.004)    | 0.991 (0.004)    | 1.025 (0.004)   |
| Dominant sediment |                  |                  |                  |
| S1                | 1.000            | 1.000            | 1.000           |
| S2                | 0.700 (0.579)    | 2.754 (0.679)    | 0.001 (9.33)    |
| S3                | 0.000 (10.2)     | 1.112 (0.461)    | 2.863 (0.373)   |
| S4                | 0.000 (13.3)     | 0.801 (0.544)    | 1.481 (0.464)   |
| S5                | 0.164 (0.520)    | 0.121 (0.550)    | 0.215 (0.707)   |
| Mean depth        | 0.987 (0.069)    |                  |                  |
| SDD               | 1.142 (0.036)    |                  |                  |
| Mean slope        | 1.271 (0.143)    |                  |                  |
| SDD × MS          | 0.987 (0.005)    |                  |                  |
| E × MD            | 1.001 (0.000)    |                  |                  |
| E × S             |                  |                  |                  |
| S1                | 1.000            |                  |                  |
| S2                | 0.980 (0.015)    |                  |                  |
| S3                | 0.999 (0.010)    |                  |                  |
| S4                | 1.024 (0.014)    |                  |                  |
| S5                | 1.010 (0.004)    |                  |                  |

Fig. 4. *Balaenoptera acutorostrata*. Minke whale sightings during spring as a function of predicted sandeel habitat.
During autumn, SDD, MAXD, MD and MS were significant predictors of minke whale presence in addition to E and S. There were 3 significant interactions: MAXD and both SDD and MS, and SDD and MS (Table 2). The interaction between SDD and MS was the most significant and the 2 other interactions did not reduce the deviance significantly when added to the model, and were thus eliminated. The final model ($\chi^2, p = 0.488$) was:

$$\text{logit}(p)_{\text{MWautumn}} = \beta + \beta_1E + \beta_2S + \beta_3SDD + \beta_4MS + \beta_5SDD \times MS$$

The parameter estimates (Table 3) indicate that the probability of encountering a minke whale was increased in areas with mud or sandy mud sediments ($S_3$) and where SDD and MS was greater, perhaps indicative of areas of variable seabed topography. Most autumn sightings with minke whales were in areas predicted to be suitable for pre-spawning herring (Fig. 6) and thus predation by minke whales on this species in autumn is a possible explanation for the spatial distribution of whales. Feeding on bait balls of juvenile herring has been observed during September in the survey area (A. Gill pers. comm.).

**DISCUSSION**

A shift in the spatial and temporal distribution of the minke whale was apparent in the Hebridean waters off the Isle of Mull (Fig. 3). In spring, minke whales were distributed predominantly between Ardnamurchan and Coll. During summer, the whales appeared to disperse over a wider area extending as a ‘corridor’ of higher encounter rates between the north of Coll and the east of Muck and Eigg. Finally, a concentration of whales southeast of Muck and Eigg predominated in...
the autumn, with a few scattered areas of high encounters in the southern region of the Treshnish Isles. The encounter rates suggest that the relative abundance of the minke whale reaches a peak during the end of summer and beginning of autumn annually.

Minke whales are present off the Island of Mull and wider Inner Hebrides throughout summer, the main feeding season for baleen whales. During this period, their distribution changes, and this may be a response to changing prey availability. The minke whale diet is flexible, varying spatially and temporally. A strong correlation exists between prey availability and minke whale diet (Haug et al. 1995, Tamura & Fujise 2002).

In spring, the environmental variable with the most influence on the presence of minke whales was sediment type, in particular gravel/sand mixtures, with small quantities of mud and rock. The distribution of whale sightings compared well with the expected inferred distribution of sandeels during the spring (Fig. 4). Sandeels are a schooling fish, are of high calorific value (Hislop et al. 1991) and are eaten by a range of marine predators. Sandeels burrow into the seabed from October to early April, with the exception of a short period between December and January when they emerge to spawn. Sandeel distribution is restricted by their dependence on suitable settlement grounds and the most favourable sediments include clean, coarse sands or fine gravel (Reay 1970). In the North Sea, Ammodytes marinus is most abundant in depths of 20 to 40 m (Macer 1966). During April and May, 1-group and older sandeels emerge from the seabed to feed in the water column. They retreat to the sediment as a form of defence, which binds them to the sediments from which they emerged. The 0-group sandeels disperse over wider areas than the older age classes (P. J. Wright pers. comm.). Therefore, during spring, sandeels are available in the water column as prey to minke whales. The local sandeel fishery coincides with this timing, starting in April and finishing in mid-July (H. Allen pers. comm.). Minke whales off the Mingan Islands in the Gulf of St. Lawrence were sighted more frequently over sand dunes, where their 2 main prey items, sandeels and spawning capelin, were abundant (Naud et al. 2003). A link between sandeel distribution and other marine predators has been established, including the common guillemot Uria aalge (Wright & Begg 1997), the humpback whale Megaptera novaeangliae (Payne et al. 1986) and the fin whale Balaenoptera physalus (Overholtz & Nicolas 1979).

The summer distribution of minke whales may represent a shift in dietary preference from one prey to another as the season progresses. The whales are distributed widely in the research area; this may be a response to increased prey availability, with 2 abundant species, sandeels and herring, dominating the diet in early and late summer, respectively. Stockin et al. (2001) noted significant differences in the surfacing intervals of minke whales off Mull between April and October. This was interpreted as a result of changes in the foraging strategies of minke whales during this period. The spatial distribution of whale sightings appears to correlate with the likely sandeel distribution in June and the pre-spawning herring habitat in August (Fig. 5). During July, many prey species are abundant and minke whales may not have strong prey preferences at this time, as reflected in the range of single environmental predictor variables significant for the summer season.

The distribution of whales during August, southeast of the islands of Muck and Eigg, is maintained into the autumn (September to November) and is possibly linked to a continuation of feeding on pre-spawning herring. The waters of the Inner Hebrides are nursery grounds for herring, but minke whales target certain age classes (Haug et al. 2003) and may only feed on schools that have reached a certain threshold density. Small prey that occurs in dense schools is probably easier to catch. The energy density of herring, like other fish species, varies seasonally but reaches a peak in September (Mårtensson et al. 1996). Off Mull, herring form large schools and spawn during late August through October, but begin to congregate near the spawning grounds about 2 mo before this time. They move to deeper, cooler waters below the thermocline and undertake diurnal vertical migrations. Their daily migration may be a response to that of Calanus finmarchicus, their main food, which also moves into deeper, cooler waters beneath the thermocline during summer and autumn (Maravelias & Reid 1997). This may explain the preference of minke whales for deeper waters east of Muck during late summer and autumn (Fig. 6). Herring also school in areas of increased productivity (Maravelias et al. 2000). Increased mixing in the vicinity of the Small Isles occurs due to the confluence of fresher coastal water north of Ardnamurchan and close to the south coast of Skye, with the coastal current as this travels northeast. Additionally, the surrounding islands, headlands and channels increase mixing and may enhance productivity in this area (Pingree & Maddock 1985). Topographic fronts can also form in the lee of islands and headlands and are often the location of enhanced primary and secondary production (Simpson et al. 1982). The final model of the autumn data highlighted the significance of areas of high topographic relief. Variation seabed topography can also enhance productivity. The predominance of herring in the minke whale diet in areas of the NE Atlantic is well known (Nordøy & Blix 1992, Mårtensson et al. 1996, Lindstrøm et al. 1999).
The apparent increase in group sizes in autumn may be a response to the abundant prey and large school sizes of herring.

The searching behaviour of the tour boat is a potential source of bias in these data. As a commercial venture, the boat tends to search areas where cetaceans have been encountered before. The importance of this variable was reflected in the significance of survey effort in each grid square in all models. Attempts to limit this bias were made by modelling environmental variables to allow for the effects of survey effort. The index of abundance was also chosen such that survey effort was the denominator of the encounter rate; whereby relative abundance between grid squares would be comparable. Finally, the data were spatially stratified on the basis of the results presented in Leaper et al. (1997) to minimise bias caused by searching behaviour of the tour operator.

This study suggests that 2 areas contained concentrations of minke whales for most of the tour operator’s season. The area north of Coll had relatively high encounter rates throughout spring and summer. It did not seem to be of importance in autumn; however survey effort was low in this season. The area between Muck and Ardnamurchan was used throughout summer, but in particular during autumn. On this basis, these 2 areas may be considered as being of particular importance to minke whales in this area, a conclusion also drawn by Leaper et al. (1997). Evidence of territoriality in minke whales was proposed by Dorsey (1983) from studies of identified minke whales in the coastal waters of Washington State. The whales formed 3 distinct groups and each occupied a ‘home-range’ which adjoined but did not overlap with the ranges of the other groups of whales. Future research of the habitat use of identified minke whales in the Mull area could be used to investigate whether the 2 high-use areas identified represent core ranges for different, but consistent, groups of minke whales during the tour operator’s season. However, the photo-identification catalogue for this area is relatively small, with few re-sightings, and currently does not allow such analysis. Alternatively, differences in the arrival time and usage of the area around Mull for feeding may vary with changing proportions of age and sex classes from spring to autumn, explaining the observed changes in distribution. The results from marking experiments off Svalbard and Norway have shown that females arrive at the feeding grounds before males (Christensen & Rørvik 1980). In the Antarctic, females generally occur at higher latitudes than males during the feeding season (Ohsumi & Masaki 1975).

At present there are limited threats to minke whales in these waters, but increased understanding of this species ecology could be important in the future. Comparable studies on minke whales and environmental variables in the wider Hebridean waters would be of use in determining on a wider geographical scale the stability of those environmental parameters identified as important in this study.

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