The habitat preferences of marine mammals west of Scotland (UK)

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This study used classification and regression trees (CART) to investigate and compare the habitat preferences of marine mammals in this area. Data were collected in early summer (June/July) in 2004 and 2005 and the distribution of marine mammal species was compared to 10 ecogeographic variables (EGVs). Of 13 species of marine mammals sighted during the study, there were sufficient sightings to examine the habitat preferences of seven. For all species a measure of 'shelf tendency' (distance to coast or water depth) was an important variable and the species could be separated into two groups, the deep-water species and the shelf species, with little overlap between them. The occurrence of both deep-water species (long-finned pilot whales and Atlantic white-sided dolphins) was also related to dynamic variables such as sea surface temperature (SST) or primary productivity. Two of the shelf species (northern minke whales and grey seals) were only linked to topographic variables and were limited to quite specific habitats. A third species (harbour porpoise) was primarily related to topographic variables, but in the shallowest waters was also related to local variation in SST. The occurrence of the final two species (common and white-beaked dolphins) was linked to SST and local primary productivity. However, while both species preferentially occurred in areas with higher productivity, the two species differed in their preference for SST, with common dolphins preferentially occurring in warmer waters and white-beaked dolphins in colder waters.

INTRODUCTION

The waters to the west of Scotland form a heterogeneous region encompassing a large variety of potential marine mammal habitats. These include coastal shelf waters (<20 km from the coast, water depths <200 m), offshore shelf waters (>20 km from the coast, water depths <200 m), shelf edge habitat (water depths 200–1000 m between shelf and oceanic waters), oceanic waters (>1000 m deep), offshore banks (<200 m depth not connected to the continental shelf) and seamounts (Figure 1). The region also straddles the boundary between cold temperate and warm temperate waters, adding to potential combinations of marine mammal habitats. While the spatial distribution of marine mammals in this region is relatively well described (e.g. Pollock et al., 2000; Weir et al., 2001; MacLeod et al., 2003; MacLeod 2004; Reid et al, 2003), there has been little work examining and, particularly, comparing the habitat preferences of different species. This is somewhat surprising given the large amount of data on marine mammal distribution that has been collected in this region.

The habitat preferences of a species represent an important part of a species niche. A species niche can be defined as the environmental conditions that allow a local population to persist in such a way that its birth rate is equal to or greater than its death rate (Chase & Leibold 2003). As such, while a species distribution may change in the short-term as local conditions change, its niche is likely to remain unchanged, making it a relatively robust entity (Meyer et al., 2004). Therefore, an understanding of a species niche can be used to predict how a species will react to changes in its local environment over time. This is particularly important in the light of potential impacts of global climate change on marine mammals (Harwood 2001; Learmonth et al., 2006). Such changes have implications for how species interact with human activities and also for determining the best approaches to the conservation and management of marine mammal populations and species (MacLeod et al., 2005). In addition, due to the potential for competition and habitat partitioning between ecologically similar species, changes in the distribution or abundance of one species may have implications for other species that will not be foreseen unless habitat preferences of different species are understood and compared.

This study examined the distribution of marine mammals in the waters to the west of Scotland and related their occurrence to a number of components of the physical environment (topography, water temperature and primary production). Due to the circumstances of the data collection (see below), not all possible combinations of different components available within the region were surveyed. As a result, it is possible that species may have wider habitat preferences than those identified here. In addition, data collection was limited temporally to the early summer months (June/July).
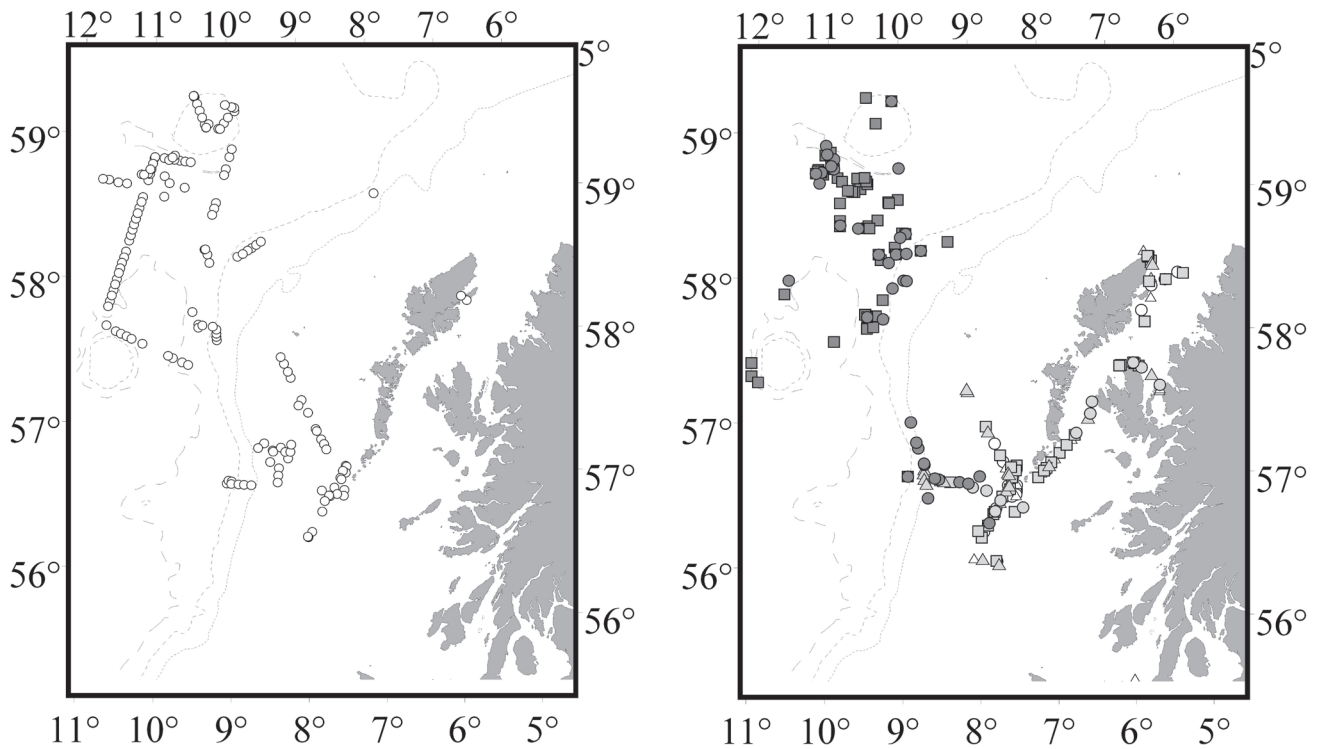
Figure 1. Study area of waters west of Scotland. Lines represent 200 m, 500 m, 1000 m, 2000 m and 3000 m depth contours. Left: absence data points used in analysis where sea state was Beaufort 2 or less and no marine mammals were seen (see Methods for details). Right: sightings data for the seven most commonly seen species. Circles: dark grey, Atlantic white-sided dolphin; light grey, common dolphin; white, white-beaked dolphin; squares: dark grey, long-finned pilot whale; light grey, harbour porpoise; white, northern minke whale; triangle, grey seal.

However, the data used in this study can still be used to make valid comparisons between species in terms of preferences for the habitats and time of year surveyed. Classification and regression trees (CART) were used to identify and compare the most important habitat preferences of marine mammal species in this area. This is the first time this approach has been applied to investigating and comparing marine mammal habitat preferences (Redfern et al., 2006). From the CART analysis, species' combinations and areas in which habitat partitioning due to competitive exclusion may be occurring in early summer were identified.

MATERIALS AND METHODS

Data collection

The data used in this study were collected in two time periods (6–17 June 2004 and 28 June to 11 July 2005) during survey work aimed at assessing and mitigating the potential affects of a new low-frequency sonar system on marine mammals during its pre-deployment sea trials. A large variety of habitats and habitat variable combinations were sampled (Figure 1). The use of data collected during such activities contains a number of inherent limitations and possible biases, particularly if the activity being undertaken results in the exclusion of animals or species from a specific habitat where they would otherwise be present, giving rise to 'false' absences within the data. Details of how these difficulties and possible biases have been taken into account and their implications for the results of this analysis are considered below.

In each year, the main vessel used for data collection (the 'research vessel') was tasked with collecting environmental data such as XBT (expendable bathythermograph) measurements, data on marine mammal occurrence and behaviour and acoustic recordings. The research vessel was not fitted with the sonar system being tested. During marine mammal surveys, data were collected by a team of trained and experienced observers (biologists with several years of experience working as marine mammal observers). Two observers were on watch at most times during daylight hours. One observer was stationed on either side of the bridge and scanned an area from directly ahead of the ship to approximately 135 degrees from the bow using low power (7×50 or 10×42) binoculars or the naked eye on a regular basis. The ship's position, along with environmental conditions such as sea state, swell height, visibility and precipitation, was recorded every 15 or 20 min. Whenever a group of marine mammals was sighted, the data recorded included the position of the ship, environmental conditions, species identification to the lowest taxonomic level possible, and group size.

The second vessel from which data were collected was the vessel transmitting the sonar (the 'source vessel'). These data were collected as part of the mitigation procedure designed for the sonar trial. In 2004, trained and experienced observers were used, while in 2005 the observers on the sonar transmission vessel had received basic training (consisting of lectures and practical experience on a specifically designed bridge simulator) in marine mammal detection and identification. The level of experience and training of these observers means that they may have missed, or failed

to identify correctly, more cryptic species such as beaked whales (Stone, 2003). This possibility was taken into account during data processing (see below). The same data were gathered by the observers on the source vessel as on the main research vessel.

Different vessels were used as the research and source vessel in each year. In 2004, the main data collection vessel was an offshore supply vessel of 54 m length. Marine mammal observations were conducted from the bridge wings at a height of approximately 9 m above sea level. In 2005, the research vessel was a 64 m long ex-East German spy trawler which had been converted into a research ship. Marine mammal observations were conducted either from the bridge wings or from the roof of the bridge, at a height of around 9 m above sea level. In 2004, the source vessel was a 90 m long merchant vessel. Marine mammal surveys were carried out from the bridge at a height of between 20 and 25 m above sea level. In 2005, the source vessel was a British warship of 133 m length. Again observations were conducted from the bridge at a height of around 20 m above sea level. In general, observations were conducted from 0600 h to at least 1800 h GMT, with each observer working for two hours followed by a one hour break.

In each year, the sonar trials were conducted over a period of several consecutive days in two separate trial areas, one in deep, oceanic waters and one in shallow, shelf waters. The same trial areas were used in each year, and data were collected throughout both the trials and the transits to, from and between each area. The research vessel also conducted additional observations in the broader trial areas prior to and after the sonar transmission period.

Data processing

Prior to data analysis, the data were separated into two components comprising: (1) marine mammal presence data consisting of the sightings data from the research and source vessels; and (2) data on survey coverage consisting of regular 15 or 20 min recordings of the research vessel's position and environmental variables. The marine mammal presence data were entered into a geographic information system (GIS) created in ESRI Arcview 3.3. For some sightings, a sequence of positions was recorded indicating that the group of animals were followed or remained close to the vessel for a prolonged period of time. For these sightings, only the first position was used for analysis to remove any element of spatial autocorrelation between multiple records from a single group of animals. For other sightings, animals were first seen from a distance and then approached to confirm species identification or to observe behaviour. For these sightings, the position closest to the animals before they reacted to the vessel was used. Precise distance and bearing measurements to sightings were not available to calculate the actual position of each group, and the ship's position was therefore used as an approximation of the actual position of the group. On almost all occasions (and all occasions where species identification could be confirmed), this distance was within 1km of the vessel. These data served as the presence data for each species in a classification tree. Sightings data from all sea states were included in the presence data since all represented habitat where a species occurred.

Classification trees also require absence data and it is important that these absence data are accurate (i.e. that they do not contain 'false' absence data). While the sighting of an animal means that it was definitely present at a specific location (and therefore using that habitat), an absence of sightings does not necessarily mean that no animals were present. For example, this could occur when the animal was not available to be detected by the observers (for example due to the fact it was underwater) or when it was present but was not detected by the observers (for example during rough weather when breaking waves can make detection of marine mammals at the surface difficult). Therefore, the types of absence data included in analyses need to be strictly controlled to reduce the level of 'false' absences in the data.

For this study, the survey coverage data collected from the research and source vessels were used as the source of absence data. However, not every position was included as an absence data point. Firstly, all survey coverage points recorded when marine mammals were present were removed from the data set. Secondly, only data collected by trained and experienced observers (see above for details) in sea state 2 or less were used as absence data points to reduce the possibility that animals were present but not detected at higher sea states or by less experienced observers. Thirdly, during periods when the vessel did not travel a substantial distance between successive ship positions, only the first recorded position was used to represent an absence point to avoid repeated sampling of the same location. Due to the possibility of avoidance of the sonar source by marine mammals, no survey coverage data recorded from the source vessel on the dates of sonar transmission were used as absence data. In addition, any data points recorded when the research vessel was in close proximity to the source vessel (<5 km) on the date of sonar transmission were removed from the data set. This resulted in a set of controlled data (with 'false' absence data minimised) that could be used as an absence data set. However, even with such data filtering, some 'false' absence data may still be retained due to the fact that marine mammals spend a proportion of their time below the surface where they cannot be detected by a visual observer. This will be particularly problematic with deep-diving species such as beaked whales that spend long periods away from the surface (Barlow & Gisiner 2006). However, this is less of an issue for shallow-diving species that spend more time at the surface, such as delphinids.

Ecogeographic variables

The occurrence of marine mammals was compared to ten ecogeographic variables (EGVs). These could be divided into three categories: topographic, temperature and productivity. The topographic variables were based on water depths obtained from two data sets. Firstly, the DIGIBATH 250 m resolution data set was used for coastal and shelf waters of <500 m depth, while for deeper offshore areas the GEBCO data set was used. These data sets were integrated and converted into a 4 km^2 grid using Arcview 3.3 GIS software. From this, grids of distance to coast, seabed slope and standard deviation of slope in a box consisting of 25 neighbouring cells centred on each grid cell were calculated using functions in Arcview. For temperature, three EGV

Table 1. *Number of sightings (N) and key variable linked to the occurrence of each species identified though CART. The preferred range of values for each variable is shown in parentheses after the name.*

Species	N	Primary variable	Secondary variable	Tertiary variable	Other important variables
Northern minke whale	15	Distance to coast (<6.9 km)	–	–	–
Harbour porpoise	37	Distance to coast (<14.6 km)	Water depth (≥60 m)	Range of SST (≥0.7 °C)	–
Common dolphin	15	Distance to coast (<42.6 km)	SST (≥12.3 °C)	Chlorophyll-*a* (≥1.03 mg l^{-1})	–
White-beaked dolphin	17	Water depth (<122 m)	Chlorophyll-*a* (≥0.56 mg l^{-1})	SST (<11.5 °C)	Distance to coast (>7.7 km), SST (<11.9 °C)
Atlantic white-sided dolphin	38	SST (>12.2 °C)	Distance to coast (≥36.6 km)	Distance to coast (≥96.6 km)	–
Long-finned pilot whale	54	Water depth (>1370 m)	Chlorophyll-*a* (≥1.12 mg l^{-1})	SST (>10.9 °C)	Water depth (<1951 m)
Grey Seal	22	Water depth (>296 m)	Standard deviation of seabed gradient (>0.3°)	–	–

grids were created. These were based on monthly composites of sea surface temperature (SST) derived from the aqua-MODIS satellite. From the monthly composites, 4 km^2 grids of SST, a standard deviation of SST grid and a range of SST grid were interpolated to match the topographic grids. These latter two grids were both calculated based on the values of grid cells in a box of 25 neighbouring grid cells around each cell and measured local variability in SST (the first the variation across all cells in the box and the second the maximum difference between any two cell values in the box). As these two variables were generally co-variable only one was used in any specific model at any one time. For productivity, grids were created of chlorophyll-*a* and standard deviation of chlorophyll-*a* concentrations. Each presence and absence data point was then assigned a value from these grids for each variable. For temperature and productivity variables, these values were specific to the year and month of the data collection. While monthly composite SST and chlorophyll-*a* concentrations will not provide information on fine-scale temporal information on habitat use decisions (e.g. reactions to daily 'weather-type' changes), they will provide information on distribution in relation to longer-term local 'climate' which may also affect habitat preferences.

Statistical analysis

Before CART analysis was conducted, the data were checked for co-variance using pair plots. For any pairs of variables with high levels of co-variance (r>0.8), only one was included in the CART. Classification trees were then created using the presence and absence data for all species of marine mammals with 10 or more sightings. CART uses a statistical approach to objectively group data into two subsets based on the specific value of one habitat variable in such a way as to produce subsets of data with the most different values for species presence (De'ath & Fabricius 2000). The splitting of the data into two subsets is repeated to produce a 'tree' consisting of a hierarchy of nodes. The top-most split is based on the value of a specific habitat variable which allows the production of subsets with the greatest difference in species presence and represents the

most important habitat variable for a species as determined by the CART analysis (the analyser has no input into where specific variables fall within the final tree). Each successive split represents the next most important variable and its key value. Pruning was applied to keep the final trees relatively simple and allow only the most important variables to be identified. All analysis was conducted using BRODGAR software (available from www.highstat.com) to implement CART using the RPART package and R version 2.3.0 (R Development Core Team 2006; Therneau & Atkinson 2006).

RESULTS

In June 2004 and June/July 2005 data were collected on a total of 22 days from the research vessel and 11 days from the source vessel. Over 250 sightings were recorded during this period and 13 species of marine mammals were identified during these sightings. Of these 13 species, there was a sufficient number of sightings (N>10) of seven to examine their habitat preferences using CART (Table 1). The remaining species were the sperm whale (*Physeter macrocephalus*), Sowerby's beaked whale (*Mesoplodon bidens*), Risso's dolphin (*Grampus griseus*), bottlenose dolphin (*Tursiops truncatus*), fin whale (*Balaenoptera physalus*) and common seal (*Phoca vitulina*). Of these six less commonly-seen species, the first four were only recorded in deeper, oceanic waters while the latter two species were only recorded over shelf waters. From a total of 1053 positions recorded to monitor survey coverage, 159 were found to be suitable for use as absence data (see above for conditions required for absence data) in CART analysis (see Figure 1).

Northern minke whale (Balaenoptera acutorostrata)

For the northern minke whale, only one of the ten variables examined was found to contribute to the final tree. This was distance from the coast (Figure 2A). Seventy-seven per cent of data points included in the analysis (i.e. presence and absence data points combined) at distances less than 6.9 km (3.6 nM) from the coast were northern minke whale sightings, while at distances greater than this only 3% of the data points were
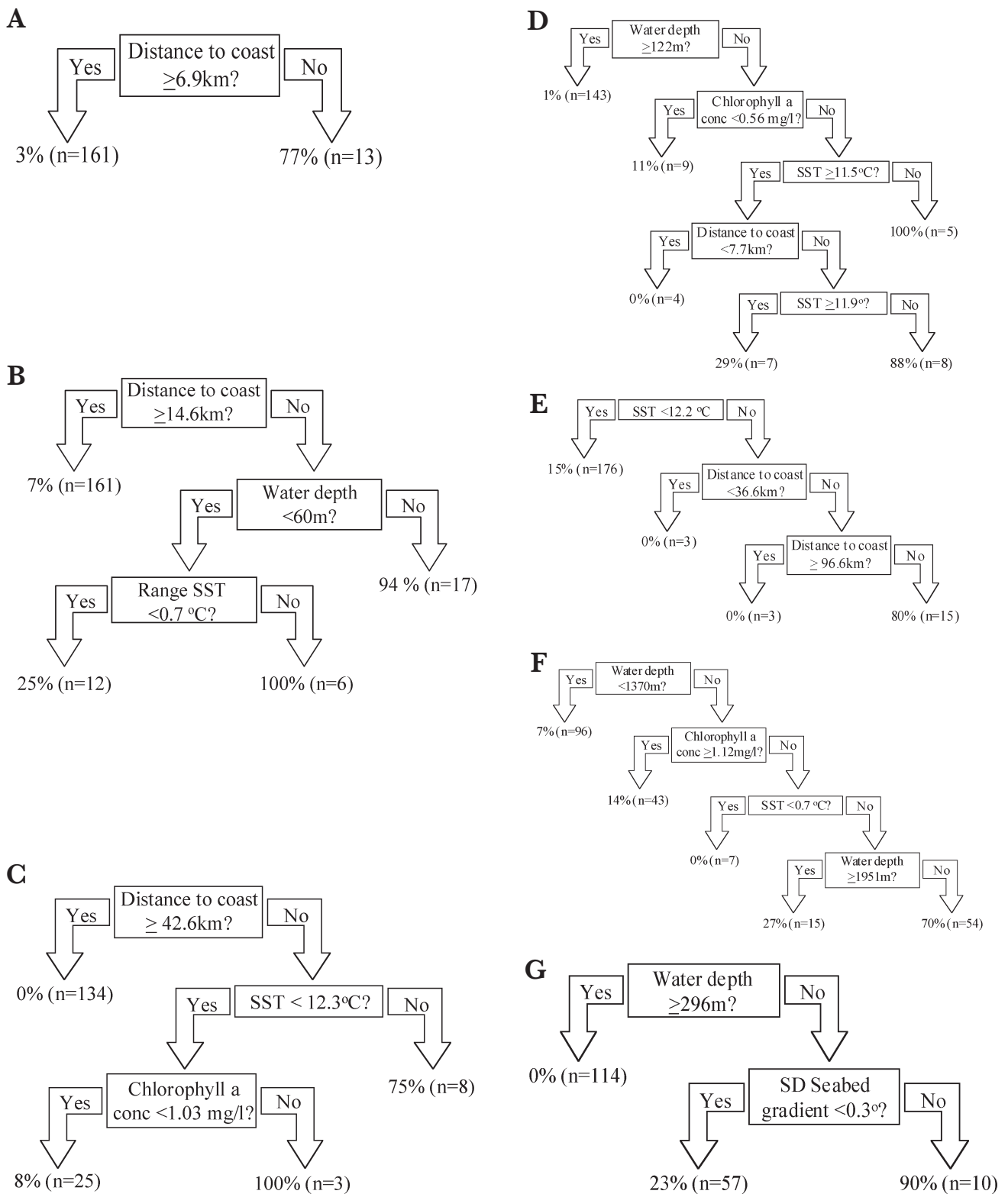
Figure 2. The classification tree of habitat preferences of the studied species. Percentages refer to the proportion of data points within specific habitat class defined by the branches of the tree which are sightings of that species. N refers to the total number of data points in that habitat class (absence and presence data points combined). (A) northern minke whale; (B) harbour porpoise; (C) common dolphin; (D) white-beaked dolphin; (E) Atlantic white-sided dolphin; (F) long-finned pilot whale; (G) grey seal.

northern minke whale sightings and 97% were absence data points. Therefore, during the early summer months off the west coast of Scotland northern minke whales are primarily a coastal species, and preferentially occur in areas closer to the coast than 6.9 km (3.6 nM).

Harbour porpoise (Phocoena phocoena)

The classification tree revealed that harbour porpoise distribution was related to three of the variables examined. These were distance from the coast, water depth and SST range (Figure 2B). The distance from the coast and depth

could both be included in this model since they are not co-variable in the study area (primarily due to the complex seabed topography and the highly complex coastline in this region). Distance from the coast was the most important variable, defining the first branch in the tree. Harbour porpoises preferentially occurred in areas closer to the coast than 14.6 km or 7.7 nm (71% of all data points closer to the coast than this comprised harbour porpoise sightings) than at greater distances (only 7% of data points were harbour porpoise sightings). Within waters <14.6 km (7.7 nM) from the coast, the next branch was defined by water depth, with a key value of 60 m. In shallower waters, only 50% of data points comprised porpoises, while 94% were porpoise sightings in waters deeper than 60 m. In the shallower waters (<60 m), the range in SST defined a third branch, with harbour porpoises preferring areas with a local range in SST >0.7°C (where 100% of the data points were harbour porpoise sightings) to areas with a smaller range in local SST (25%). Therefore, harbour porpoises were preferentially recorded in waters closer to the coast than 14.6 km (7.7 nM) and deeper than 60 m. In shallower waters close to the coast, they were preferentially recorded in water areas with more local variation in SST values.

Common dolphin (Delphinus delphis)

Distance from the coast was the most important variable of those examined related to common dolphin distribution (Figure 2C). Common dolphins were not recorded at distances >42.5 km (22.5 nM) from the coast, whereas at distances within 42.5 km (22.5 nM) of the coast 42% of the data points comprised common dolphin sightings. In these coastal waters, SST was the most important variable related to common dolphin occurrence, with a key value of 12.3°C. Common dolphins preferentially occurred in waters warmer than this (75%) rather than in waters colder than this where they comprised only 32% of data points. In coastal waters colder than 12.3°C, chlorophyll-*a* concentrations were important. At chlorophyll-*a* concentrations exceeding 1.03 mg m^{-3}, 100% of data points were common dolphin sightings, while at lower chlorophyll-*a* concentrations only 24% of data points comprised common dolphin sightings. Therefore, common dolphins preferred waters within 42 km of the coast, and within cooler water areas where they were primarily found in areas of high chlorophyll-*a* concentration.

White-beaked dolphin (Lagenorhynchus albirostris)

The most important variable related to the occurrence of white-beaked dolphins was water depth (Figure 2D).

No white-beaked dolphins were recorded in water depths >122 m, while at depths less than this 45% of data points comprised white-beaked dolphin sightings. Within these shallower waters, chlorophyll-*a* concentrations were important, with white-beaked dolphins preferring areas with chlorophyll-*a* concentrations greater than 0.56 mg m^{-3} (58%) in comparison to areas with chlorophyll-*a* concentrations less than this (only 11% of data points were white-beaked dolphin sightings). Within shallow, productive areas, white-beaked dolphins preferred waters less than 11.5°C (100%) to those warmer than this value (47%). In these warmer waters, white-beaked dolphins preferred areas that were >7.8 km (4.1 nM) from the coast and waters of <11.9°C. Therefore, white-beaked dolphins preferentially occurred in shallow waters, with higher chlorophyll-*a* concentrations and lower SST.

Atlantic white-sided dolphin (Lagenorhynchus acutus)

For Atlantic white-sided dolphins, SST was the most important variable relating to occurrence. This species occurred more frequently in areas with SST >12.2°C (57%) than in colder waters (15%; Figure 2E). Within waters >12.2°C, distance to the coast was the most important variable. No Atlantic white-sided dolphins were recorded at distances <35.6 km (18.9 nM) from the coast or >96.6 km (51.2 nM) from the coast. Between these two distances, 80% of data points were sightings of Atlantic white-sided dolphins.

Long-finned pilot whale (Globicephala melas)

Water depth was the most important variable relating to the occurrence of long-finned pilot whale sightings. The key value was 1370 m (Figure 2F). Pilot whales preferred waters deeper than this value (40%) compared with shallower waters (7%). In these deeper waters, chlorophyll-*a* was the most important variable, with only 14% of data points with values <1.12 mg m^{-3} comprising pilot whale sightings in comparison to 55% of data points at higher chlorophyll-*a* concentrations. The next most important variable was SST, with pilot whales only recorded in waters >10.9°C. In these warmer waters, more pilot whale sightings occurred over water depths of less than 1951 m (70%) than over deeper waters (27%). Therefore, pilot whales preferentially occurred in waters with higher chlorophyll-*a* concentrations, warmer SSTs and water depths of between 1370 and 1951 m.

Grey seal (Halichoerus grypus)

Two variables were related to where grey seals were recorded. These were water depth and the standard deviation of seabed slope (Figure 2G). Of these, depth was the most

Table 2. *A comparison of habitat preferences of marine mammal species for the three most commonly identified habitat variables in this study.*

Species	Shelf or deep-water	Water temperature	Primary productivity
Northern minke whale	Shelf	No preference	No preference
Harbour porpoise	Shelf	No preference	No preference
Common dolphin	Shelf	Warmer water	Higher primary productivity
White-beaked dolphin	Shelf	Cooler water	Higher primary productivity
Atlantic white-sided dolphin	Deep-water	Warmer water	No preference
Long-finned pilot whale	Deep-water	Warmer water	Higher primary productivity
Grey seal	Shelf	No preference	No preference

important. Grey seals were never recorded at locations with depths greater than 296 m, but 33% of data points with water depths less than this comprised grey seal sightings. In these shallower areas grey seals preferred areas with standard deviations in slope of greater than 0.3 degrees (90%) over areas with less variation in the slope (23%). Therefore, grey seals have a preference for shallow waters and areas where the seabed has a higher variation in slope.

DISCUSSION

The waters to the west of Scotland have a relatively high diversity of marine mammals (Evans 1992; Shrimpton & Parsons 2000; Reid et al., 2003) and 13 species of marine mammals were recorded in each survey year during this study. There were sufficient sightings to investigate the habitat preferences of seven of these species using CART. However, biases associated with the data collection with regards to coverage of all possible ranges and combinations of habitat variables means that the habitat preferences identified for individual species are not absolute. Instead, these identified preferences should be seen as relative to the ranges and combinations of habitats covered by the surveys. However, this bias does not affect the comparison of habitat preferences between the different species since it applies to the same extent to all of the species examined.

Each species examined in this study had a distinct set of habitat preferences (Table 1; Figure 2A–G). However, the seven species can be divided into several categories based on key variables affecting their distribution (Table 1). For all seven species, a measure of 'shelf tendency' (either water depth or distance to coast) was either the most important variable (representing the first branch in the tree) or the second most important variable (Table 1). This separated the species into two groups, the shelf species and the deep-water species (Table 2). The shelf species preferentially occurred near the coast or in water depths under 200 m (for northern minke whales, harbour porpoises, common dolphins and white-beaked dolphins) or over shelf and upper shelf edge waters (grey seals). In comparison, the deep-water species occurred far from the coast or in deeper waters (long-finned pilot whales and Atlantic white-sided dolphins). A similar segregation between shelf and deep-water species was also evident in the sightings of the remaining six species (see above). This suggests that the division between shelf and deep-waters is one of the most important factors in defining where species occur in this region and will have a strong influence on the composition of local marine mammal assemblages in this region. Such divisions between shelf and deep-water species are relatively common in marine mammal assemblages and have been noted in this region before (Weir et al., 2001).

Of the two offshore species, long-finned pilot whales were found in deeper waters further from the coast than Atlantic white-sided dolphins. However, in both cases dynamic variables such as elements of SST (both species) or primary production (pilot whales only) were also important in determining habitat preferences. Both species preferentially occurred in warmer waters and pilot whales preferentially occurred in areas of higher primary productivity. Therefore, in general there was a high degree of overlap in the habitat

preferences between the two species. This is consistent with other studies in this region (e.g. Weir et al., 2001) and is also confirmed by the relatively high frequency of mixed-species schools of these two species that are observed west of Scotland (Weir et al., 2001; Stone, 2003; observations during this study). However, such mixed-species schools may only occur in areas where the habitat preferences of the two species overlap (e.g. waters warmer than 12°C and in intermediate water depths and distance from the coast).

The shelf species showed a different pattern of occurrence. For two species, the northern minke whale and the grey seal, only non-dynamic topographic variables were important in determining where the species occurred (Table 1). Both of these species were limited to quite specific habitats that overlapped considerably in coastal areas (Figure 2A&G). Similarly, harbour porpoises were also primarily linked to topographic variables and had a high degree of overlap in habitat preferences with both northern minke whales and grey seals. However, dynamic variables may play a small part in determining where harbour porpoises occur in some water depths. In particular, in the shallowest water areas, harbour porpoise occurrence may be linked to the occurrence of frontal areas as indicated by a preference for areas with higher local variation in SST (Figure 2B). For the final two shelf species, the common and white-beaked dolphin, after a preference for shelf waters, dynamic variables were the most important in determining distribution (Figure 2C&D). However, while both species preferentially occurred in areas with higher primary productivity, they differed in their preference for SST (Table 2). Specifically, white-beaked dolphins preferred SSTs <12°C while common dolphins preferred SSTs higher than this figure (Figure 2C&D, Table 1). Therefore, while these two species are likely to overlap considerably with other shelf species, particularly in coastal areas, the preferences for different SSTs means that these two species will have a relatively low overlap with each other.

Of the species analysed in this study, common dolphin, white-beaked dolphin and Atlantic white-sided dolphin are the most ecologically similar. When the habitat preferences of the three dolphin species are compared, there are notable differences that are consistent with habitat partitioning. Atlantic white-sided dolphins preferred deep-water areas, white-beaked dolphins colder shelf waters and common dolphins warmer shelf waters (Table 2). In addition, the key values for these variables were very similar between species. For example, common dolphin prefer a distance to coast of <42.6 km while Atlantic white-sided dolphin prefer distance to coast greater than or equal to 36.6 km. Similarly, for the two shelf species, common dolphin prefer water temperatures of 12.3°C or more, while white-beaked dolphins prefer temperatures of <11.5°C (Table 2). Such habitat partitioning is most likely to be driven by competition for a limited, shared resource (in this case most likely prey).

The potential contribution of habitat partitioning to the composition of local marine mammal assemblages has implications for how the assemblage, as a whole, may react to environmental perturbations, either natural or anthropogenic. For example, changes in the cetacean community of north-west Scotland have been linked to changes in local climate, and in particular the occurrence

of white-beaked dolphins has declined in this region while the occurrence of common dolphins has increased as local sea temperatures have increased (MacLeod et al., 2005). The apparent habitat partitioning based on water temperature suggests that the changes in the occurrence of these two dolphin species are not linked to separate, direct, physiological impact of changes in water temperature on each species of dolphin. Instead, their response to climate change may be primarily driven by how water temperature relates to habitat partitioning between the species resulting from potential competition. Specifically, the common dolphin appears to be the dominant species in waters warmer than 12°C while the white-beaked dolphin appears to dominate cooler waters. If local water temperatures change across this threshold due to climate change, the outcome of competitive interactions between the two species may shift, resulting in the previously dominant species becoming excluded, even through the local area may remain otherwise suitable for their occurrence.

In terms of the other marine mammal species examined in this study, there was no clear evidence to suggest habitat partitioning was occurring between them. However, this does not mean that no niche partitioning occurs. It may be that habitat partitioning occurs along habitat variables not included in this study (e.g. foraging position in the water column), that potential competitors were not included in this study due to a lack of data (e.g. common seals as potential competitors of grey seals) or that partitioning occurs along niche variables not associated with habitat (e.g. prey size or mode of prey capture). This is a common issue when investigating whether niche partitioning occurs between species within a region. Unless all possible competitors are examined and all possible niche variables are compared, it may be wrongly concluded that niche partitioning is not occurring between species and that other mechanisms are responsible for the structure and composition of local marine mammal communities.

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