Fine-scale habitat selection by white-beaked and common dolphins in the Minch (Scotland, UK): evidence for interspecific competition or coexistence?

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A decline in white-beaked dolphins Lagenorhynchus albirostris *had been reported in the Minch (Scotland, UK) since the 1990s, coinciding with an increasing occurrence of short-beaked common dolphins* Delphinus delphis. *This has led to suggestions that rising seawater temperatures are causing* D. delphis *to out-compete and exclude* L. albirostris *in this region. A total of 793 km (66.3 hours) of survey data were collected in the Minch during August 2007, to examine fine-scale habitat selection by* L. albirostris *and* D. delphis *and investigate whether their ecological overlap is sufficient to result in interspecific competition and/or habitat partitioning. Ten sightings of* L. albirostris *(70 animals) were recorded in a relatively small spatial area in the northern Minch. In contrast, the eleven sightings of* D. delphis *(1486 animals) were more widely distributed. The relative abundance per 1/4 ICES rectangle ranged from 0.41 to 0.53 animals/km for* L. albirostris *and 0.13 to 6.68 animals/km for* D. delphis. *The mean group size and group body mass were higher for* D. delphis *than for* L. albirostris *indicating* D. delphis *as the dominant delphinid in the Minch during August.* Lagenorhynchus albirostris *occurred in waters significantly deeper and further from shore than* D. delphis, *suggesting interspecific differences in preferred habitat. Most dolphin schools were recorded as foraging/feeding. Behaviour and seabird associations indicated that the two species differed in diet and/or foraging strategy, with* L. albirostris *foraging sub-surface and* D. delphis *exhibiting surface-feeding with associated gannets* Morus bassanus. *This is consistent with published information on the stomach contents of Scottish animals. The results suggest that there are subtle differences in habitat selection and diet between these two species, which may enable* L. albirostris *and* D. delphis *to coexist in the Minch. Whether these differences result from niche partitioning arising from previous/ongoing interspecific competition or are the result of genuine differences in the habitat preferences of each species, remains unclear.*

INTRODUCTION

Sightings and long-term stranding data indicate that changes in the cetacean community of the Minch, located off north-western Scotland (Figure 1), may have occurred in recent years (MacLeod *et al.*, 2005). Regular survey work since the early 1980s identified year-round concentrations of white-beaked dolphins *Lagenorhynchus albirostris* Gray, 1846 in the Minch, particularly in the waters north of 58°N (Northridge *et al.*, 1995; Macleod, 2001; Weir *et al.*, 2001; Reid *et al.*, 2003). In contrast, the short-beaked common dolphin *Delphinus delphis* Linnaeus, 1758 was historically uncommon in the Minch, with only a small number of sightings documented between the 1980s and early 2000s (Macleod, 2001; Weir *et al.*, 2001; Reid *et al.*, 2003).

Recently, MacLeod *et al.* (2005) reported a marked increase in the occurrence of *D. delphis* off the west coast of Scotland, with a corresponding decline in *L. albirostris*. An increase in local seawater temperature has been proposed as the cause of these changes (MacLeod *et al.*, 2005), and sea-surface temperatures of 12°C (MacLeod *et al.*, 2007) and 13–14°C (MacLeod *et al.*, 2008) respectively, have been proposed as the threshold water temperatures at which *D. delphis* replaces *L. albirostris* in the region.

At least three potential temperature-related explanations for the changes in relative occurrence of *D. delphis* and *L. albirostris* have been proposed (MacLeod *et al.*, 2005, 2007, 2008): (1) one or both species are limited (lethally or energetically) by their physiological tolerance of water temperature; (2) temperature influences the outcome of interspecific competition between the two species; and (3) temperature affects the distribution of preferred prey species.

Although *D. delphis* typically occurs in warm water (Evans, 1994) while *L. albirostris* inhabits cold waters (Reeves *et al.*, 1999), both species occur at temperatures either side of the

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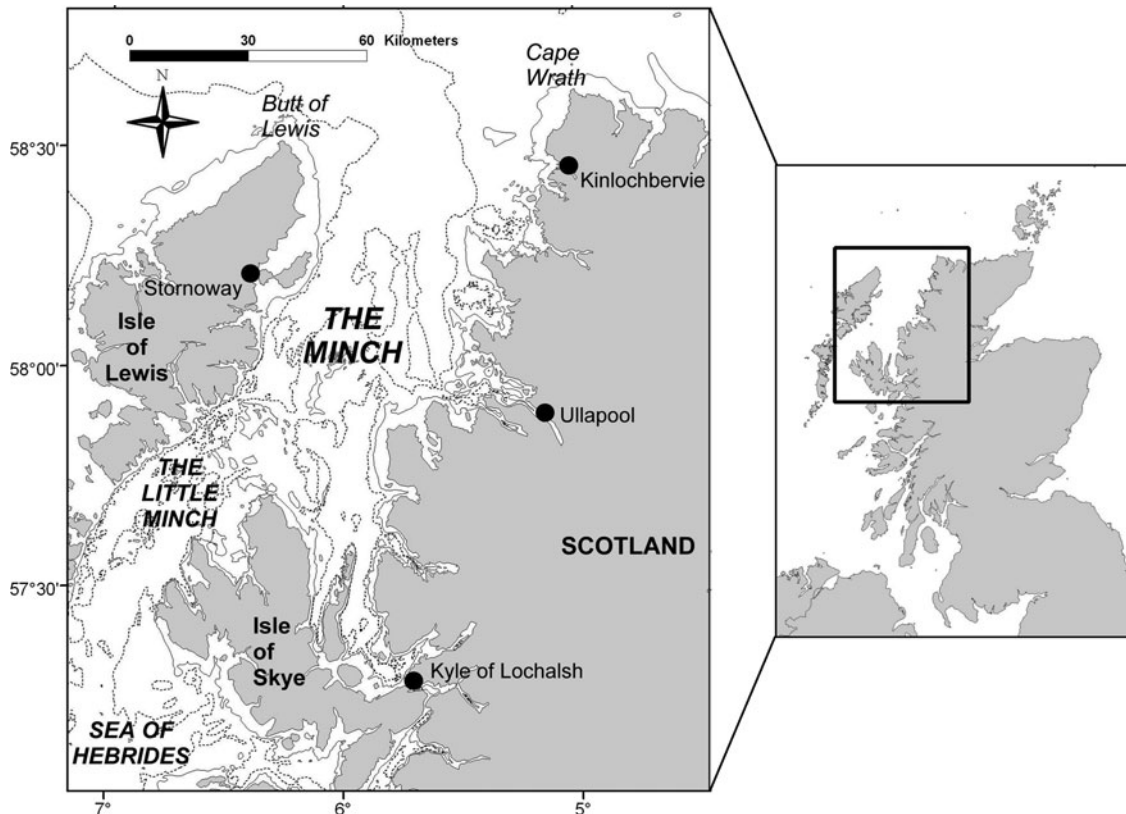Email: Caroline.Weir@ketosecology.co.uk

Fig. 1. Location of the study area off north-western Scotland, showing the 50 and 100 m depth isobaths.

threshold water temperatures identified by MacLeod *et al.* (2007, 2008) and neither should be directly physiologically limited by these temperature values off west Scotland (Macleod *et al.*, 2008). Neumann (2001) suggested that although seasonal changes in the distribution of *D. delphis* in New Zealand waters were related to sea-surface temperature, this was best explained by the impact of sea-surface temperature upon their prey species. However, Macleod *et al.* (2008) suggest that the distributions of *D. delphis* and *L. albirostris* are unlikely to reflect temperature-limitations of preferred prey, since both species take a range of prey species that occur throughout north-western Europe. Niche partitioning resulting from interspecific competition has, therefore, been suggested as the most plausible explanation for the observed temperature-related distributions, with *D. delphis* dominating in warmer water and *L. albirostris* dominating in cooler water (MacLeod *et al.*, 2007, 2008).

Where similar species co-exist, careful analysis usually reveals that apparently shared resources are divided through each species occupying different physical locations (i.e. habitat partitioning) or by differences in diet (i.e. dietary divergence) (Bearzi, 2005a; Friedlaender *et al.*, 2006). Habitat partitioning has been shown to occur between delphinid species, for example, by species demonstrating temporal segregation (Gowans & Whitehead, 1995), inhabiting different water depths (Griffin & Griffin, 2003) or seabed topography (Gowans & Whitehead, 1995), or occupying different inshore or offshore habitat (Bearzi, 2005b). However, determining whether apparent habitat partitioning is due to the effects of interspecific competition (past or present) or whether it results from differences in the fundamental

niches preferred by different species is difficult. Therefore, assessing whether interspecific competition with *D. delphis* is related to the decline of *L. albirostris* in the Minch is complex. Addressing this issue initially requires comparative analysis of the habitat and foraging behaviour of the two species in this area, to determine the level of overlap in their ecology.

Although the foraging ecology of *D. delphis* has been widely documented, relatively little is known about that of *L. albirostris*. Both species have opportunistic diets, taking a range of prey species including small, pelagic schooling fish and cephalopods (Evans, 1994; Reeves *et al.*, 1999; Stockin, 2008). While *D. delphis* is primarily an epipelagic predator (Pusineri *et al.*, 2007), *L. albirostris* also forages demersally and takes larger prey items found nearer to the seabed such as gadoids, octopus and benthic crustaceans (Reeves *et al.*, 1999; Canning *et al.*, 2008).

While a range of individual and coordinated feeding strategies are exhibited by *D. delphis* (Neumann & Orams, 2003), the carouseling of shoaling fish at the water surface is the most frequently reported *Delphinus* feeding technique (Gallo Reynoso, 1991; Neumann & Orams, 2003; Stockin, 2008) and is also observed in other small cetaceans that feed on pelagic shoaling prey, e.g. dusky dolphins *Lagenorhynchus obscurus* (Würsig & Würsig, 1980) and Atlantic spotted dolphins *Stenella frontalis* (Fertl & Würsig, 1995). Coordinated surface herding of prey has also been observed in *L. albirostris* in Scottish waters (Evans, 1980). However, *L. albirostris* may also forage along the seabed for benthic prey (Reeves *et al.*, 1999). Dolphins feeding on, or close to, the seabed typically occur in small groups with foraging behaviour indicated by

repeated dives in varying directions in a particular location (Bearzi *et al.*, 1999). Dolphins feeding on shoaling fish are often associated with seabirds as a result of the concentration of shared prey at the surface (Evans, 1980). Surface-feeding *Delphinus* are often associated with seabirds of the Sulidae family (Gallo Reynoso, 1991; Neumann & Orams, 2003), and seabird associations may therefore provide an indication of the prey species that dolphins are feeding on (Evans, 1980).

This study examined the fine-scale habitat selection of *L. albirostris* and *D. delphis* in the Minch during August 2007, and assessed the extent to which the niches occupied by these two species overlap at this time of year.

MATERIALS AND METHODS

The study area

The study area comprised the waters of the Minch (Figure 1), which is a 35–60 km wide stretch of water located between the west Scottish mainland and the Isle of Lewis. Water depth in this area rarely exceeds 130 m. The study area was divided into 11 1/4 ICES (International Council for the Exploration of the Sea) rectangles (15′ latitude by 30′ longitude) (Figure 3), to facilitate comparisons with previous survey work in the Minch (e.g. Weir *et al.*, 2001; Reid *et al.*, 2003).

Survey methods

The survey platform was a 16 m ketch operated by the Hebridean Whale and Dolphin Trust (HWDT). During the survey, two dedicated cetacean observers were positioned on the port and starboard sides of the vessel to maintain a continuous watch for cetaceans within the 90° area of water on their side (from the beam to the bow of the vessel), using a combination of naked eye and binoculars. A third person was present on deck as a dedicated data logger. The vessel route was determined at the start of each day, based on prevailing weather conditions and aiming to acquire greatest spatial coverage. Two modes of survey effort were utilized: (1) Search Effort, when observers were actively searching for cetaceans; and (2) Encounter Effort, when cetaceans were being followed for data collection. The vessel position was continually recorded at 1-minute intervals using a handheld Garmin 76CSx GPS. Relevant environmental data (Beaufort sea state, swell height, precipitation and visibility) were recorded at the start of each watch and at each change thereafter. Whenever cetaceans were sighted, data including the vessel position, species, group size and composition, behaviour and seabird associations were recorded. Behaviour was recorded in broad categories as: (1) feed/forage, to describe any effort to capture and consume prey including repetitive prolonged dives in one location, prey pursuit and/or fish capture; (2) travel, comprising either slow or fast directional movement; (3) social, where animals engage in body contact including breaching, play and/or mating; and (4) rest/mill, where animals exhibit inactive non-directional slow movements within the same location. Specific behaviours such as breaching and bow-riding were noted on an ad hoc basis. Seabirds were considered to be associated when they circled directly overhead of, and tracked the movements of, a dolphin school. As seabird dietary preferences are relatively

well known for Scottish waters, this allowed inferences to be drawn about the types and species of prey on which associated cetacean species were foraging. Cetaceans were classified into adults, juveniles and calves where possible, using the following criteria: individuals that appeared full grown were recorded as 'adult', individuals obviously smaller than full-grown (75% adult size) were treated as 'juveniles', and small animals with foetal folds or otherwise clearly born that year judging by their small size and close association with an adult, were treated as 'calves'.

Water depth for each sighting was recorded using the vessel's ST60 Autohelm echosounder which operated at between 90 and 120 kHz. For a small number (N = 2) of sightings where the echosounder was not working, the water depth was calculated using a geographical information system (GIS) created in ArcView 3.2. Data on water depth were extracted from the British Geological Society Digbath 250 m resolution data set, and a triangular integrated network (TIN) continuous surface was created from this depth contour data set to calculate the depth at the location of each sighting.

Throughout the survey a Minilog 8-bit data logger (www.vemco.com) was deployed at a fixed depth of 0.8 m below the water surface and programmed to record sea-surface temperature (SST) at 1-minute intervals. The Minilog had a temperature recording range of −5 to 35°C, with 0.2°C resolution and accuracy of 0.3°C.

Data analysis

To compensate for differences in the amount of survey coverage in each 1/4 ICES rectangle, an index of relative abundance (individuals per km trackline) was used to analyse dolphin occurrence, using only those data collected during Search Effort status and in Beaufort sea state ≤4. The relationship between each dolphin species was investigated with respect to three habitat parameters: (1) SST; (2) water depth; and (3) distance from the shore (as a measure of coastal or pelagic tendency). The distance from shore was calculated for each sighting using the 3D Analyst extension in ArcView GIS software to create a grid of distance from the coast and a purpose-designed script to subsequently calculate the distance.

All sightings were used to calculate the mean habitat parameters for each dolphin species, and Mann–Whitney U-tests were used to test for differences between the two species in mean group size (using best estimates of group size), water depth, SST and distance from shore. The parameters determining the relative occurrences of the two species were examined using a classification tree produced using the Brodgar interface for R statistical software (see MacLeod *et al.*, 2008). The SST, water depth and distance from shore of the sightings were entered as explanatory variables.

RESULTS

Survey effort

A total of 793.0 km (66.3 hours) of survey data was collected, of which 93% were collected in Beaufort sea states ≤4. The majority of effort (668.6 km; 84%) was spent in Search

Effort mode, while 124.3 km was spent in Encounter Effort mode. Survey effort was distributed across most of the Minch (Figure 2), with data collected in ten of the eleven target 1/4 ICES rectangles. The amount of data collected in Beaufort sea states ≤4 varied from 20 to 119 km per 1/4 ICES rectangle. The SST during the survey varied from 11.5 to 14.9°C.

Distribution, relative abundance and group composition

There were a total of 10 sightings of *L. albirostris* during the survey comprising a best estimate of 70 animals. Eleven sightings of *D. delphis* were recorded, comprising an estimated 1486 animals. Sightings of *L. albirostris* and *D. delphis* in relation to the survey track are shown in Figure 2. *Lagenorhynchus albirostris* sightings were restricted to a relatively small spatial area in the central northern portion of the Minch. In contrast, *D. delphis* was distributed widely across the Minch. Using the definitions of Bearzi (2005a) *L. albirostris* and *D. delphis* exhibited both broad and direct sympatry within the Minch during August 2007, occurring together in the wider Minch region and also overlapping on a finer spatial scale. For example, on four occasions *L. albirostris* and *D. delphis* were sighted within 10 km of each other (Table 1), meaning that 40% of all *L. albirostris* sightings occurred in spatial proximity to *D. delphis*. However, the

Table 1. Spatial proximity of *Lagenorhynchus albirostris* and *Delphinus delphis* sightings in the Minch.

Date	*L. albirostris* sighting no.	*D. delphis* sighting no.	Time span between sightings	Spatial distance between sightings (km)
5/08/2007	20	21	0 hour 19 minutes	0.35
05/08/07	22	21	0 hour 17 minutes	2.73
08/08/07	35	37	1 hour 15 minutes	9.50
08/08/07	39	37	0 hour 24 minutes	5.55

two species were never encountered in mixed-species schools or directly interacting with one another.

The overall relative abundance of *D. delphis* (1.81 animals/km) was higher than *L. albirostris* (0.09 animals/km) in the Minch. *Lagenorhynchus albirostris* occurred in only two of the surveyed 1/4 ICES rectangles, at relative abundance of 0.53 and 0.41 respectively (Figure 3A). *Delphinus delphis* was recorded within five 1/4 ICES rectangles, at relative abundance varying from 0.13 to 6.68 individuals/km (Figure 3B).

The mean group size of *D. delphis* (x = 135.1, N = 11, range = 3–450, SD = 143.09) was significantly higher than that of *L. albirostris* (x = 7.0, N = 10, range = 2–12, SD = 4.14) (Mann–Whitney *U*-test, U = 17.5, P = 0.006). The mean group body masses of 12,159 kg and 1575 kg respectively (Table 2) indicate that *D. delphis* was more numerous
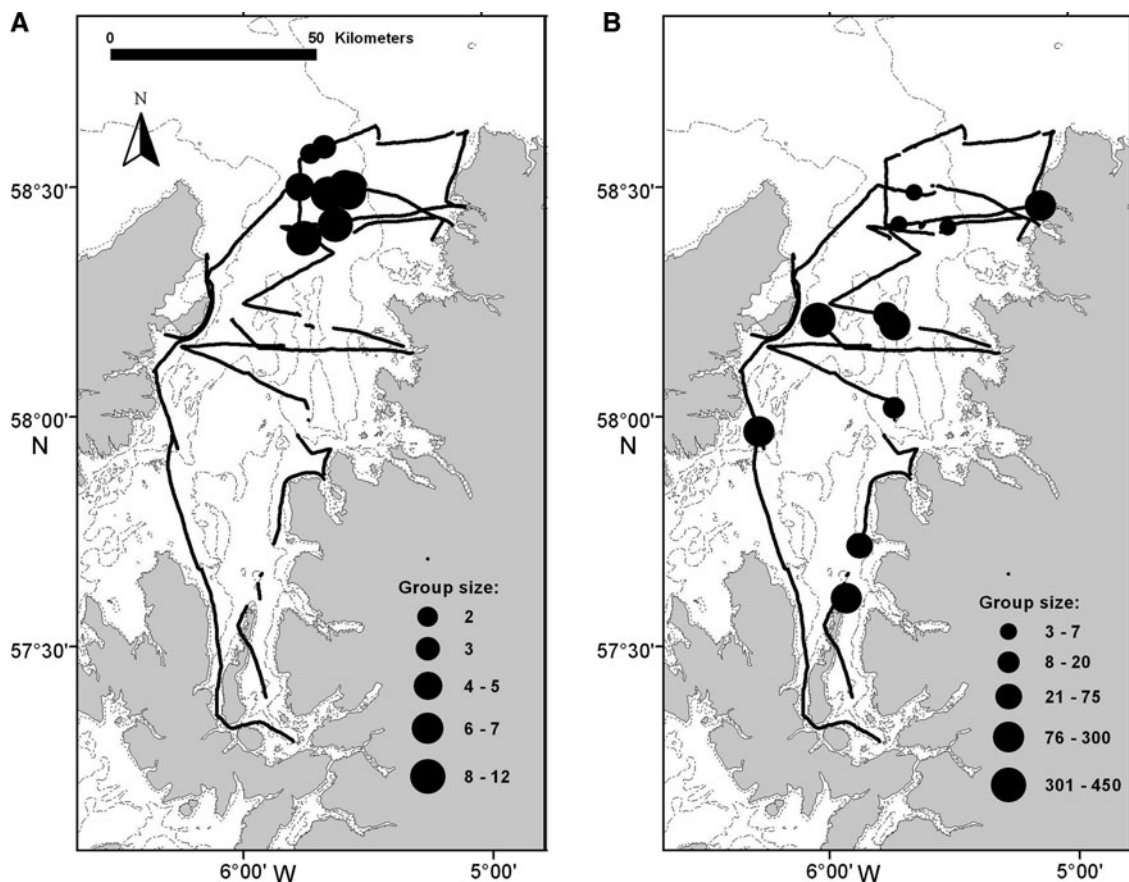

Fig. 2. Location of survey effort (Search Effort data, all sea states), showing (A) *Lagenorhynchus albirostris* sightings (N = 10) and (B) *Delphinus delphis* sightings (N = 11) in the Minch.
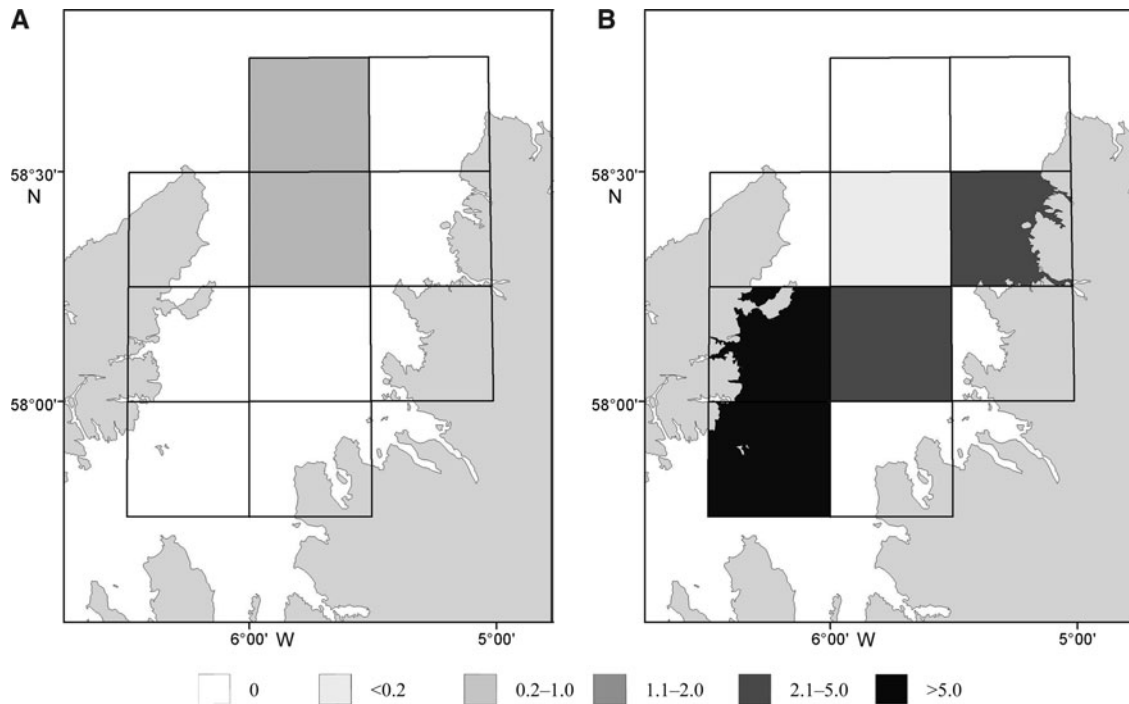
Fig. 3. Relative abundance (indiv/km) of (A) *L. albirostris* and (B) *D. delphis* in the Minch.

(both numerically and by overall biomass) than *L. albirostris*, and was the dominant delphinid species inhabiting the Minch during August 2007.

Of the ten *L. albirostris* sightings, two groups comprised adult animals only, seven groups were of mixed adult and immature animals (six groups with calves and one group containing a juvenile), and one group could not be aged. Group composition was not recorded during three *D. delphis* sightings. One small group of three animals consisted of adults only. Although the large group size recorded during *D. delphis* sightings precluded accurate estimation of group composition, calves were present in the remaining seven schools.

Habitat preferences

The mean habitat parameters measured for *D. delphis* and *L. albirostris* sightings are shown in Figure 4 and summarized in Table 2. *Lagenorhynchus albirostris* was recorded in a rather narrow water temperature range varying between 13.2 and 13.5°C ($x = 13.4$°C, N = 10, SD = 0.12). Sea-surface temperature at the location of *D. delphis* sightings varied from

Table 2. Comparison of *Lagenorhynchus albirostris* and *Delphinus delphis* parameters potentially related to interspecific competition. Data are findings of the present study unless otherwise referenced.

	L. albirostris	*D. delphis*
Habitat parameters (means)		
Distance from shore (km)	25.8	13.3
Water depth (m)	122.5	116.3
Sea-surface temperature (°C)	13.4	13.5
Biological parameters (means)		
Adult body length (m)	2.6 (2.5–2.7)[1]	2.0 (1.6–2.6)[1]
Adult body weight (kg)	225[2]	90[3]
Group size	7.0	135.1
Group body mass (kg)[4]	1575	12,159
Dietary parameters		
Main prey species documented in Scottish waters	*Merlangius merlangus*[6,7]	*Ammodytes* sp.[6]
	Melanogrammus aeglefinus[7]	*Eledone cirrhosa*[6]
	Gadus morhua[7]	*Scomber scombrus*[8]
	Eledone cirrhosa[6]	*Merlangius merlangus*[8]
		Clupea harengus[8,9]
Main prey size-class taken (total body length in mm)	155–285[7]	20–300[10]
Likely foraging level[5]	Demersal	Epipelagic

[1]Evans, 1987; [2]Sigurjónsson & Víkingsson, 1997; [3]Lahaye *et al.*, 2005; [4]calculated as mean group size multiplied by mean body weight; [5]based on prey species taken; [6]Santos *et al.*, 1994; [7]Canning *et al.*, 2008; [8]MacLeod *et al.*, 2008; [9]Embling *et al.*, 2005; [10]Pusineri *et al.*, 2007.
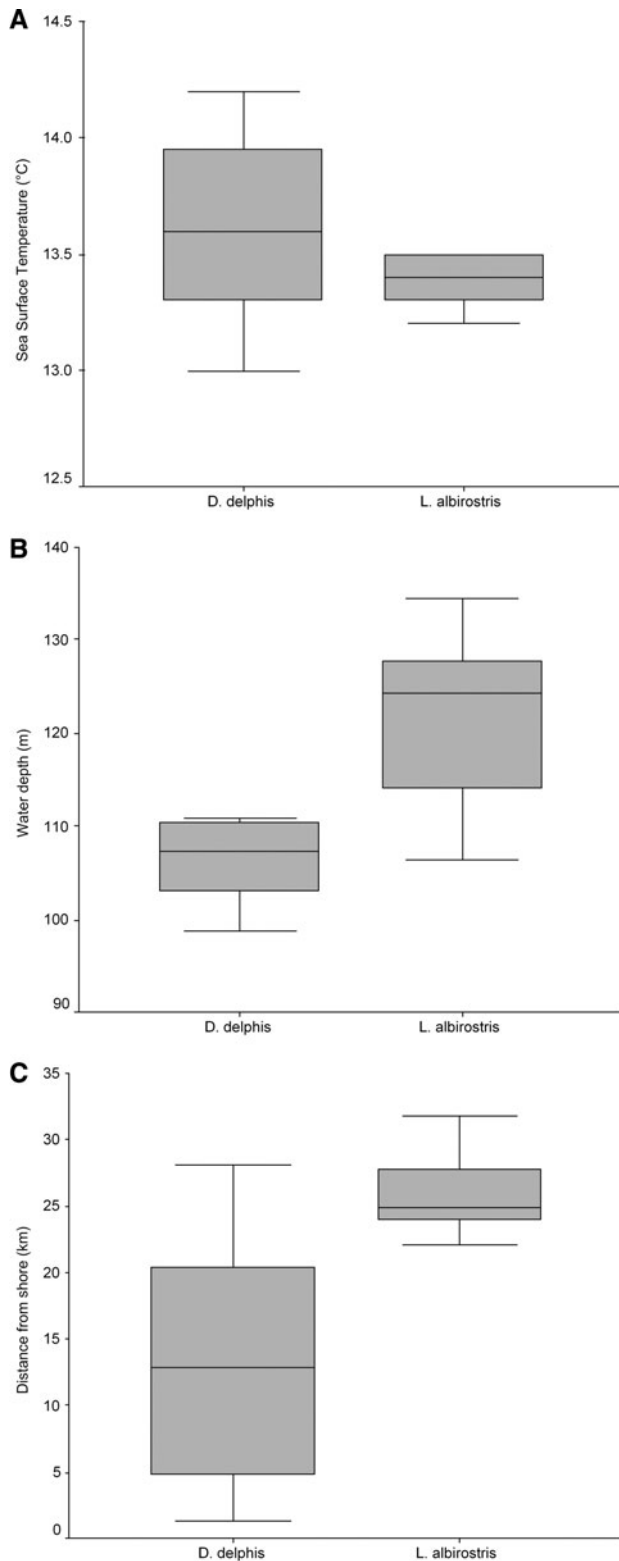
Fig. 4. Habitat parameters (outliers removed) of *Lagenorhynchus albirostris* and *Delphinus delphis* sightings: (A) sea-surface temperature; (B) water depth; and (C) distance from shore.

12.0 to 14.2°C ($x = 13.5$°C, N = 11, SD = 0.65). There was no significant difference between the mean water temperature of *D. delphis* and *L. albirostris* sightings (Mann–Whitney *U*-test, U = 41.0, P = 0.349) .

The depth-range of *L. albirostris* sightings varied from 106.5 to 134.5 m ($x = 122.5$ m, N = 10, SD = 8.67). *Delphinus delphis* sightings occurred in a wider water depth-range of 70.1 to 240.2 m ($x = 116.3$ m, N = 11, SD = 43.01). Both species exhibited a preference for deeper waters, with no sightings in waters of less than 70 m. However, the mean water depth differed significantly between the two species (Mann–Whitney *U*-test, U = 71.0, P = 0.006), with *L. albirostris* inhabiting deeper waters than *D. delphis*.

The distance from shore of *L. albirostris* sightings ranged from 22 to 32 km ($x = 25.8$ km, N = 10, SD = 2.92). This area is approximately mid-way across the Minch, indicating that white-beaked dolphins preferentially inhabited open waters located outside of the immediate coastal zone. The distance from shore of *D. delphis* sightings ranged from 1 to 28 km ($x = 13.3$ km, N = 11, SD = 9.75). *Lagenorhynchus albirostris* sightings occurred significantly further offshore than *D. delphis* (Mann–Whitney *U*-test, U = 15.0, P = 0.004).

Classification tree analysis revealed that distance from shore was the most important habitat parameter (of those examined) determining the relative occurrence of the two species (Figure 5), with all sightings recorded <21.77 km from shore comprising *D. delphis*. Of sightings occuring further from shore, water depth was the most important habitat parameter, with only *L. albirostris* occurring in depth exceeding 122 m (Figure 5).

Behaviour and seabird associations

Behaviour categories were assigned to six sightings of *L. albirostris*, comprising two travelling schools and four groups that were feed/foraging. The remaining sightings were either seen too briefly to determine behaviour (N = 1) or involved animals that appeared suddenly close to the vessel and whose undisturbed behaviour was therefore unknown (N = 3). Feed/forage behaviour was recorded in nine of the 11 *D. delphis* sightings, while two schools were travelling. No seabirds were obviously associated with *L. albirostris*. However, the nine feeding schools of *D. delphis* were all accompanied by conspicuous large (up to several hundred) flocks of northern gannets *Morus bassanus*.

DISCUSSION

Although based on a relatively small number of sightings which were recorded during a single month (and at the warmest time) of the year, the results provide several insights into the current status of *L. albirostris* and *D. delphis* in the Minch and their potential interactions. As demonstrated by MacLeod *et al.* (2005) and the results of this study, there is little doubt that *D. delphis* has increased in occurrence off the west coast of Scotland since studies during the 1980s and 1990s (Macleod, 2001; Weir *et al.*, 2001; Reid *et al.*, 2003), and now comprises the dominant delphinid species in the region (at least during the summer months).

MacLeod *et al.* (2005) suggested that as the occurrence of *D. delphis* has increased in north-western Scotland in recent years, *L. albirostris* has declined. The results from August 2007 do not disagree with this finding, since *L. albirostris*
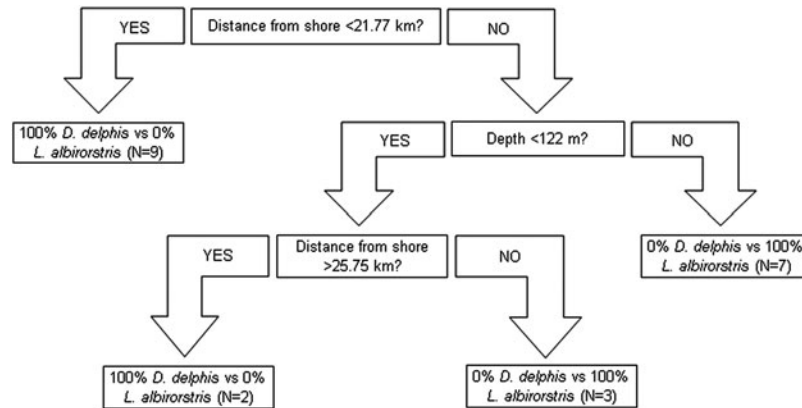
Fig. 5. A classification tree of the occurrence of *Lagenorhynchus albirostris* and *Delphinus delphis* in relation to sea-surface temperature, water depth and distance from the coast.

showed a contracted distribution range within the Minch compared to studies in the 1980s and 1990s (e.g. Weir *et al.*, 2001; Reid *et al.*, 2003). However, those studies used compilations of year-round data, and it is unclear whether *L. albirostris* exhibited seasonal changes in distribution over that time period. It is possible that the summer range of *L. albirostris* has always been more contracted than the winter range, potentially related, for example, to seasonal movements related to the summer calving period or to the large sea-surface temperature changes of around 6°C that occur in the Minch during the year (Gillibrand *et al.*, 2003). Although the spatial range of *L. albirostris* might possibly have contracted since the 1980s and 1990s, the relative abundance within the two 1/4 ICES rectangles they were recorded in was considerably higher than that recorded in earlier decades (Weir *et al.*, 2001) suggesting that reasonable numbers still occur in the region. Therefore, this study was unable to conclude whether there has, or has not been, a decline in *L. albirostris* within the Minch since the 1980s, even though a marked increase in *D. delphis* over this time frame is clearly evident.

The results of the study suggest that habitat partitioning occurred between *L. albirostris* and *D. delphis* in the Minch during August 2007. Although there was some overlap, *L. albirostris* occurred in significantly deeper water located further from the coast than *D. delphis*. The few sightings of *D. delphis* that did occur in deep water close to the location of *L. albirostris* sightings all comprised small groups of fewer than ten animals, with the larger schools of *D. delphis* occurring close to the coast and/or further south than *L. albirostris* sightings (Figure 2). Identifying whether interspecific competition between the two species is responsible for these differences is not straightforward, since habitat partitioning could occur both as a direct result of competition (i.e. both species having to share the available resources), but would also occur if the two species were sufficiently different ecologically to avoid competition occurring in the first instance (i.e. each species already occupied different niches within the Minch irrelevant of the presence of the other). Regardless of the mechanism, the results suggest that both species may be able to coexist within the Minch by occupying slightly different habitats.

Interestingly, the current study did not find a significant difference in SST between *L. albirostris* and *D. delphis* during August 2007, with both species occurring in similar mean water temperatures of 13.4°C and 13.5°C respectively. This is particularly notable given that the survey occurred during late summer when SST peaks in the Minch (Gillibrand *et al.*, 2003), likely producing some of the warmest water temperatures that white-beaked dolphins experience in this region. Using year-round data measured *in situ* off north-western Scotland, Macleod (2001) also noted that *L. albirostris* and *D. delphis* occurred at similar mean water temperatures (SST values of 11.7 and 11°C respectively). These studies using fine-scale temperature data-sets do not reveal temperature-related habitat partitioning between *L. albirostris* and *D. delphis* as reported in previous studies using coarser-scale satellite-derived temperature data (e.g. MacLeod *et al.*, 2005, 2007). However, the results are not necessarily contradictory.

For example, using 4 km² monthly summer composites of SST data for June and July 2004/2005, MacLeod *et al.* (2007) identified a key threshold SST value of 12°C for the change in dominance between the cold water *L. albirostris* and the warmer water *D. delphis*. However, they did not define a temperature at which *D. delphis* would exclude *L. albirostris*, and it might be relevant that most data in that study were collected to the south-west of the Western Isles in rather different habitat from the Minch. Using a UK and Ireland-wide dataset (1983–1998) analysed against monthly SST data with a resolution of 1° longitude by 1° latitude, MacLeod *et al.* (2008) reported a switch in dominance between the two species at temperatures of 13.4°C. However, there was evidence of a transitional temperature range between 13 and 14°C where neither species was dominant. This is consistent with the co-occurrence of *D. delphis* and *L. albirostris* at temperatures of around 13°C identified in this study.

Similarly, it is possible that the SST-related partitioning revealed by the larger-scale studies is a consequence of the wider distribution range limits of *L. albirostris* and *D. delphis* as determined by their (or their prey species) physiological tolerance of water temperatures, while the finer-scale analysis revealed that *L. albirostris* and *D. delphis* can overlap in certain SST ranges by partitioning other niches, in this case water depth and distance from shore. The water temperatures tolerated by *L. albirostris* and *D. delphis* extend well beyond the temperature range examined during August 2007. For example, Macleod (2001) found that *L. albirostris* sightings occurred over a large SST range of 7.5–14.8°C, which was the largest temperature range of any of the cetacean species

studied off north-western Scotland. MacLeod *et al.* (2008) report *L. albirostris* in 8.1–17.2°C in UK and Irish waters. In the UK, *D. delphis* can occur in water temperatures spanning 8.1–18.5°C (MacLeod *et al.*, 2008), and the species is clearly capable of inhabiting the cooler waters found in the Minch. However, during the spring months (March to May) SST within the Minch decreases to around 8°C (Gillibrand *et al.*, 2003) which is clearly towards the lower end of the temperature scale inhabited by *D. delphis* in the UK (MacLeod *et al.*, 2008). The occurrence of *D. delphis* in the Minch may therefore be expected to show strong seasonality.

The second potential method by which two or more delphinid species may co-occur within a region is via dietary divergence (Bearzi, 2005a). For example, cetaceans may share the same habitat but feed: (1) on different prey species (Saulitis *et al.*, 2000); (2) on different size-classes of the same prey species (Friedlaender *et al.*, 2006); (3) on the same prey but at different locations in the water column (Friedlaender *et al.*, 2006); or (4) on the same prey but at different times of day (Perrin *et al.*, 1973).

There is relatively little information regarding the prey taken by *L. albirostris* and *D. delphis* in Scottish waters, although Santos *et al.* (1994) suggest that both are opportunistic feeders that select prey on the basis of local abundance rather than having a preferred target species. The stomach contents of three white-beaked dolphins from Scottish coastal waters in the early 1990s showed the largest prey range of any small odontocete species examined, containing fish (particularly whiting *Merlangius merlangus*) and octopus *Eledone cirrhosa* (Santos *et al.*, 1994). More recently, an analysis of the stomach contents of 22 white-beaked dolphins from Scottish waters between 1992 and 2003 found that fish, particularly haddock *Melanogrammus aeglefinus* (43%), whiting (24%) and cod *Gadus morhua* (11%), comprised over 95% of the total reconstructed weight of the diet (Canning *et al.*, 2008; Table 2), although only two of these specimens originated from the west coast of Scotland. Fewer data are available for *D. delphis* in Scottish waters, but a single specimen examined in the early 1990s contained sandeels (*Ammodytes* sp.) (Santos *et al.*, 1994), while unidentified gadoids, mackerel *Scomber scombrus*, whiting and herring *Clupea harengus* were identified in *D. delphis* stomachs during more recent studies (Embling *et al.*, 2005; MacLeod *et al.*, 2008; Table 2). While *L. albirostris* and *D. delphis* do show overlap in their diet in Scottish waters (notably gadoid species), there are also some differences such as the higher amount of cod in *L. albirostris* diet, and the occurrence of mackerel and herring in the diet of *D. delphis*. Bearzi (2005a) notes that even a small difference in prey preference can be sufficient to support the feeding requirements of more than one species of sympatric dolphin.

The stomach contents of *L. albirostris* and *D. delphis* stranded in Scotland also provide insight into the foraging strategies adopted by these two species. Species such as gadoids and octopus which appear in the diet of *L. albirostris* mainly inhabit areas on, or close to, the seabed, indicating that *L. albirostris* may be predominantly a demersal predator. This is also indicated by the neritic waters that *L. albirostris* inhabits worldwide. In contrast, *D. delphis* is considered to be an epipelagic predator, occupying both neritic and pelagic habitat types where they prey opportunistically on small shoaling fish species within the upper water column (Brophy, 2003; Pusineri *et al.*, 2007). The presence of mackerel and herring in the diet of this species in Scotland is also supportive of a more pelagic foraging strategy by *D. delphis*. Further support for differences in foraging strategy was indicated by the interspecific differences in seabird associations, with most *D. delphis* sightings occurring in association with northern gannets, while no such associations were seen with *L. albirostris*. In Scottish waters, gannets feed predominantly on pelagic fish such as mackerel, herring, sprat *Sprattus sprattus* and sandeel *Ammodytes marinus*, while gadoids (haddock, whiting and cod) are of lower importance (Hamer *et al.*, 2000). Associations between *D. delphis* and northern gannets are therefore likely to result from both species feeding on the same prey species (Evans, 1980), most probably shoaling fish close to the water surface. Neumann & Orams (2003) observed that feeding *D. delphis* in New Zealand were frequently associated with Australasian gannets *Morus serrator*, while Gallo Reynoso (1991) noted associations between *Delphinus* and boobies *Sula* sp. in the Gulf of California. Both studies concluded that the association was based on common prey species. Associations might also be expected between *L. albirostris* and *D. delphis* if they were preying on similar species, since mixed-species schools are predominantly formed in response to either increased foraging efficiency or predator avoidance (Stensland *et al.*, 2003). In the absence of regular predators in the Minch study area, foraging advantages may represent the primary drive for the formation of species associations. Mixed-species feeding schools of *Delphinus* and other *Lagenorhynchus* species have been recorded, for example off New Zealand with dusky dolphins (Würsig *et al.*, 2007) and off California with the Pacific white-sided dolphin *L. obliquidens* (Brown & Norris, 1956). The fact that *D. delphis* and *L. albirostris* have not been recorded in mixed species aggregations in the Minch further supports the notion that the two species feed on different prey items.

MacLeod *et al.* (2008) considered that the temperature preferences of prey species were unlikely to drive the apparent difference in water temperature between *L. albirostris* and *D. delphis*, since their prey species are found throughout the shelf waters of north-western Europe. However, the spatial distributions of haddock, whiting and cod, some of the main species on which *L. albirostris* feeds in Scottish waters, are largely determined by SST and salinity (Albert, 1994; O'Brien *et al.*, 2000; Zheng *et al.*, 2001). Clearly, increasing water temperatures are likely to result in changes in occurrence of these fish populations. Fish recruitment may also be affected by increasing seawater temperatures, with some studies predicting a decrease in gadoids and an increase in herring stock productivity (Cook & Heath, 2005; Rose, 2005; Brunel & Boucher, 2007). It therefore seems possible that changing fish stocks related to warming seawater temperatures may be at least partially responsible for changes in occurrence of *L. albirostris* and *D. delphis* in the Minch.

To conclude, MacLeod *et al.* (2008) considered that *L. albirostris* and *D. delphis* are sufficiently ecologically-similar to result in interspecific competition, sharing relatively similar habitat preferences and diet. The results of this study and available information on the diet of the species in Scottish waters suggest that subtle differences in habitat preferences and foraging behaviour may be sufficient to facilitate coexistence between the two species in the Minch during the late summer. The data indicate that adult *L. albirostris* have around 2.5 times larger body mass, occur in significantly

smaller group-sizes, occur further offshore and in deeper water, take different prey species and feed at different levels in the water column than *D. delphis* (Table 2). Therefore, although *D. delphis* is increasing within the Minch, probably due to warming sea temperatures (MacLeod *et al.*, 2005), the increase in *D. delphis* might not be directly related to reported declines in *L. albirostris*.

However, the relationship between *L. albirostris*, *D. delphis* and their environment is complex and more data are required on the other habitat parameters (e.g. salinity, turbidity, seabed substrate type, seabed slope and productivity), at a wider range of SST, and on the seasonality, diet and biology (e.g. foraging depth) of both species in order to clarify these interactions. Furthermore, the habitat preferences exhibited by cetacean species may be driven by a complex interaction of factors including behavioural patterns, biological requirements and environmental conditions (Ersts & Rosenbaum, 2003). For example, off Patagonia *L. obscurus* used shallow water for rest behaviour and deep water when travelling (Garaffo *et al.*, 2007), while around Hawaii the spinner dolphin *Stenella longirostris* uses coastal habitat for rest and socializing during the day and moves offshore for night-time foraging (Lammers, 2004). Differences in group composition may also impact upon habitat use. For example several species of cetacean are known to use shallower water when accompanied by calves, such as humpback whales *Megaptera novaeangliae* in Madagascar (Ersts & Rosenbaum, 2003), *L. obscurus* off Patagonia (Garaffo *et al.*, 2007) and *D. delphis* in the Mediterranean (Cañadas & Hammond, 2008). Habitat comparisons between *L. albirostris* and *D. delphis* in the Minch using only particular behavioural and group composition categories were not possible given the relatively small dataset, but future such analyses would allow a finer-scale examination of habitat use in addition to the habitat selection analysis presented here.

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