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Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles

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The vocal repertoire of many delphinid odontocetes includes narrowband tonal whistles used mainly for communication. The aim of this study was to describe the whistle repertoire of short-beaked common dolphins, *Delphinus delphis*, recorded in the Celtic Sea between May and August 2005. The 1835 whistles recorded were classified into six broad categories and 30 sub-types, of which simple upsweeps and downsweeps were the most common. Furthermore, the parameters duration, inflections, steps and various frequency variables were measured. The whistles covered a frequency span from 3.56 kHz to 23.51 kHz and had durations between 0.05 and 2.02 seconds. Whistle parameters varied with behavioural context, group size and between encounters. The whistle repertoire of Celtic Sea common dolphins was compared to that of *D. delphis* from the Western Approaches of the English Channel, recorded during a survey between January and March 2004. The relative abundances of the broad whistle types did not differ between the two locations, but most whistle parameters were significantly different: almost all frequency variables measured were significantly higher in English Channel whistles. This may indicate some degree of population structuring of short-beaked common dolphins around Britain. Alternatively, the common dolphins in the English Channel may have shifted the frequencies of their vocalizations up to avoid masking by low-frequency ambient noise produced by high levels of vessel traffic in this area.

INTRODUCTION

The vocalizations of toothed whales (odontocetes) are generally grouped into three types: short pulsed sounds that are used in echolocation, less distinct burst pulse calls (sometimes described as cries, barks, grunts or squeals as their high pulse repetition rate makes them audible to humans) and narrowband tonal whistles (Richardson et al., 1995). The latter two seem to be used mainly for communication, but most studies have focused on whistles rather than burst pulse sounds because whistles are largely in the audible or sonic range and easier to record and analyse (Au, 2000).

Whistles are narrowband tonal calls with durations up to a few seconds and fundamental frequencies that typically fall between 5 and 20 kHz. They are frequency modulated and usually described based on spectrogram views of their time–frequency contours (Richardson et al., 1995). Contour categories commonly used are unmodulated constant frequency whistles, upsweeps, downsweeps, U-shapes (or concave), inverted U-shapes (or convex), or wavering sinusoidal whistles. However, repertoires are often more complex and may include intermediate types between those categories, as well as whistles that consist of repeated types or a combination of different types. Also, whistle contours may not be continuous but may contain breaks (Richardson et al., 1995).

The whistle repertoires of odontocetes show great variability between different species, different geographically separate populations, different groups within populations, or even between individuals. Rendell et al. (1999) compared the whistle characteristics of five odontocetes, the false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*), long-finned pilot whale (*G. melas*), white-beaked dolphin (*Lagenorhynchus albirostris*) and Risso's dolphin (*Grampus griseus*). They found significant differences of whistle parameters, especially mean call frequency, between most species and it was possible to classify whistles to the correct species in more than double the cases than would be expected by chance alone.

The characteristics of vocal repertoires not only differ between species but also to varying degrees within species. Morisaka et al. (2005a) found that three populations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Japan had different whistle characteristics. Frequency parameters were the most important variables to discriminate between populations while within population variability was higher for the parameters duration and number of inflections (Morisaka et al., 2005a). Similarly, the whistles of tucuxi dolphins (*Sotalia fluviatilis*) in Brazil have most variation in duration and number of inflections, but differences between geographically separate populations were mostly caused by frequency parameters (Azevedo & Van Sluys, 2005). Also, this study reported that variation was greater between populations that were geographically further apart than between adjacent populations. The variation in whistle characteristics between different species or populations, which is usually variation in frequency parameters, is likely to be the result of physiological or environmental factors such as body size or ambient background noise (Rendell et al., 1999; Morisaka et al., 2005a,b). Some odontocetes, for example, show variation in frequencies of their echolocation clicks (observed in *Delphinapterus leucas*) or whistles (observed in *Globicephala* spp. and *Tursiops aduncus*) related to varying background noise levels in different locations (Rendell et al., 1999; Tyack, 2000; Morisaka et al., 2005b). Within populations, parameters such as duration or number of inflections or steps are usually more variable and these variations may carry information about individual identity or behaviour (Rendell et al., 1999; Morisaka et al., 2005a).

Generally, dolphins and other species that live in fluid societies of changing groups tend to show much variation in the whistle repertoire at the level of individuals, while those that live in stable groups usually do not have individually distinct whistles but they have group-distinct repertoires often referred to as dialects (Tyack, 1986). The best-known example of dialects in an odontocete species is that of the killer whale (*Orcinus orca*). Killer whales spend their lives in stable matrilineal groups which associate on a regular basis with particular other closely-related matrilineal groups. These associating matrilines form a pod and have a distinct repertoire of discrete calls that is unique to each pod. These pod-specific vocalizations probably facilitate group cohesion, recognition and coordinated behaviour within pods (Ford, 1991).

Rather than this type of group-specific repertoire, many dolphin species have whistles that are unique to individual animals. The concept of 'signature whistles' was first introduced by Caldwell & Caldwell (1965) who recorded five captive bottlenose dolphins and found that each animal had a specific whistle which, with slight variations in intensity or duration but always the same contour, made up over 90% of that individual's vocalizations. Since cetaceans are highly mobile and live in an environment where visibility is limited, individual-specific calls are useful for maintaining contact between animals which frequently separate over distances that make vision unreliable (Tyack, 2000).

As odontocete whistles and burst pulse calls are thought to have primarily a social function, they can be expected to show some variation depending on behavioural context. Herzing (1996) described the underwater behaviour and vocalizations of Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins in the Bahamas. She found associations between certain types of sounds and certain behavioural contexts. For example, signature whistles were produced by spotted dolphins during reunions of mother–calf pairs, during alloparental care and during courtship behaviours. 'Excitement vocalizations' occurred during distress or excitement, particularly in calves. 'Squawks' were related to aggressive encounters or sexual play, both within or between the two species, and 'screams', 'barks' and 'synchronized squawks' were all associated with agonistic and aggressive behaviour of males between or within species (Herzing, 1996).

Common dolphins (*Delphinus* spp., family Delphinidae) are considered to be of high abundance with a worldwide distribution. Many different populations seem to exist which often show varying morphological characteristics. Two distinct species are now widely recognized: the short-beaked common dolphin (*Delphinus delphis*, Linnaeus 1758) and the long-beaked common dolphin (*D. capensis*, Gray 1828) (Perrin, 2002). Around the British Isles, the short-beaked common dolphin is regularly found in the southern Irish Sea and the Celtic Deep area, in the Western Approaches to the English Channel, around the Inner Hebrides and west of Ireland (Evans, 1998). In the Celtic Sea, *D. delphis* abundance has been estimated at 75,450 animals (with a 95% confidence interval of 23,000–249,000) (Hammond et al., 2002). In the Western Approaches to the English Channel area the abundance estimate is 9708 animals (95% CI=4799–19,639; with potentially large bias caused by responsive movement by the animals) (De Boer et al., 2005). The short-beaked common dolphin is a very gregarious species that is usually encountered in large schools which can reach sizes of thousands of animals (Perrin, 2002). These large schools are often structured, with several subgroups of around 20–30 animals (Perrin, 2002). A small mean school size of 11 individuals has been reported in the Celtic Sea (Hammond et al., 2002).

Common dolphins are highly vocal animals. Like most delphinids they produce echolocation click trains, burst pulse sounds and whistles. Their calls have been described as 'chirps' with dominant frequencies between 8 and 14 kHz, 'barks' with low dominant frequencies below 3 kHz and whistles that cover a dominant frequency range from 2 to 18 kHz (based on recordings of captive *D. delphis* made by Caldwell & Caldwell (1968) as quoted in Richardson et al., 1995). Oswald et al. (2003) described the whistle characteristics of short- and long-beaked common dolphins in the eastern tropical Pacific Ocean. Short-beaked common dolphin whistles had a mean beginning frequency of 9.8 kHz, mean end frequency of 11.4 kHz, mean minimum and maximum frequencies of 7.4 and 13.6 kHz respectively, a mean frequency range of 6.3 kHz, and a mean duration of 0.8 s. Their average number of inflection points was 1.2 and they had on average 1 step within their contours (see Figure 1 for an illustration of the different parameters measured). The frequency parameters of long-beaked common dolphin whistles were consistently slightly higher with mean beginning and end frequencies of 10.1 and 14.1 kHz respectively, mean minimum and maximum frequencies of 7.7 and 15.5 kHz respectively and a mean frequency range of 7.9 kHz. Mean duration was minimally shorter than in short-beaked common dolphins, at 0.7 s and the degree of complexity or frequency modulation was slightly higher, described by means of 1.3 inflection points and 1.5 steps per whistle (Oswald et al., 2003).

Wakefield (2001) identified 18 different types of whistles with varying degrees of frequency modulation in the repertoire of short-beaked common dolphins in the Celtic and Irish Seas, including the six broad types generally used in studies of whistle repertoires (constant, upsweep, downsweep, convex, concave and sinusoidal). Simple upsweeps, downsweeps and constant frequency whistles were the three most common types (in that order) and whistles ranged in frequency from 4.7 to 20.3 kHz. Wakefield (2001) also found that during periods of intense background noise from seismic surveying, whistle frequencies of common dolphins were significantly

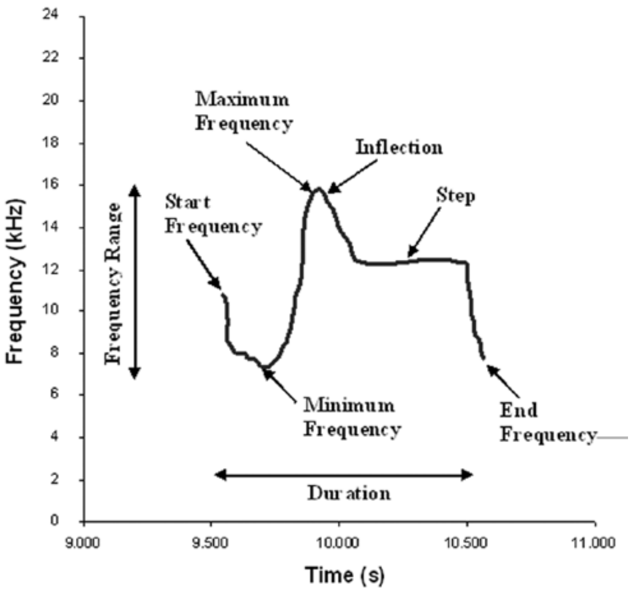

Figure 1. Whistle contour illustrating parameters measured.

higher and the vocalization rate increased. Scullion (2004) also recorded short-beaked common dolphins in the Celtic Sea and found a slightly wider whistle frequency range from 3.4 to 21.0 kHz. Whistles had durations between 0.017 and 2.148 s and 20 different whistle types were determined, with upsweeps again being the most often recorded type (Scullion, 2004).

The purpose of this study was to describe the whistle repertoire of short-beaked common dolphins, *Delphinus delphis* (hereafter common dolphins), in the Celtic Sea and to compare this repertoire to that of common dolphins in the English Channel. The aim was to explore variation in the vocalizations of common dolphins between different geographical locations. Such variation may be an indicator of structuring and a possible existence of sub-populations within the range of what appears to be a single population. The population structure of common dolphins in the north-east Atlantic is currently a matter of considerable conservation interest because of the high levels of by-catch reported to the south of the UK (De Boer et al., 2005).

MATERIALS AND METHODS

Celtic Sea field work

Four line-transect surveys were conducted in the Celtic Sea, over the Celtic Deep between May and August 2005. The survey area was situated between 51°30'N and 52°00'N latitude and 005°30'W and 006°20'W longitude (Figure 2) and the platforms were two chartered vessels, of 12 m and about 15 m length.

Visual observers recorded information for all cetacean sightings. Behaviour of the animals sighted was subjectively categorized as: (1) travelling (fast directed swimming); (2) foraging (rapid movements, changing directions, diving behaviour, sometimes fish chasing was observed); (3) socializing (group staying in one general area without obvious travelling or foraging; breaching/leaping and other aerial behaviour); and/or (4) bow-riding (approaching the vessel to swim in the bow wave or stern wake).

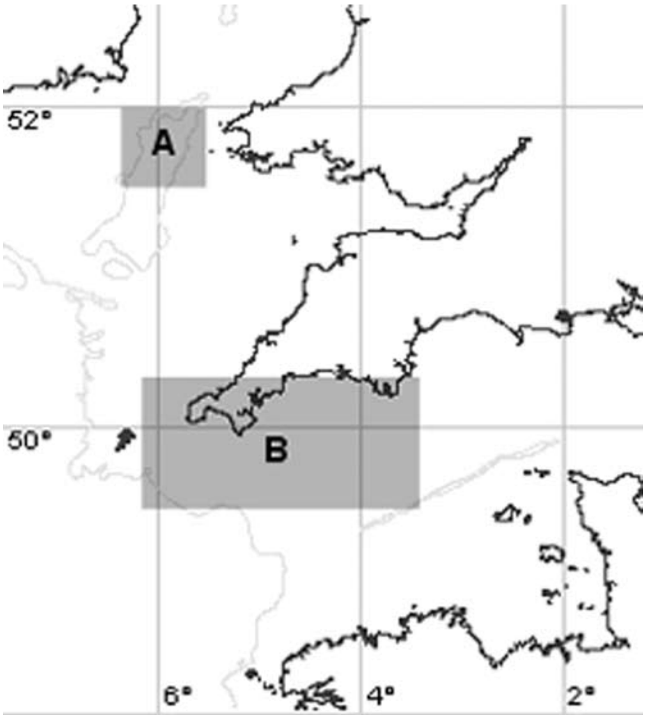

Figure 2. Map of the two survey areas in (A) the Celtic Sea and (B) in the Western Approaches of the English Channel.

Acoustic recordings were made continuously throughout the surveys, using hydrophones based upon the Benthos AQ-4 transducer towed behind the vessel travelling at a speed of around 8–10 knots. The hydrophones were connected to a 3 kHz high pass filter and then to a Sony TCD-D8 digital audio tape (DAT) recorder with a flat frequency response from 20 Hz to 22 kHz.

English Channel field work

Line-transect surveys were conducted in the Western Approaches of the English Channel between February and March 2004. The platform was a 72.3 m research vessel travelling at average speeds of 5–9 knots. The survey area was situated between 49°20'N to 50°20'N and 003°26'W to 006°10'W (Figure 2). Visual observations of cetacean sightings and environmental information were recorded. Acoustic recordings were made using a stereo hydrophone array. Data were recorded directly onto a laptop computer onboard with a sampling rate of 96 kHz.

Computer analysis

For the analysis, only recordings made during visual sightings of common dolphins (with no other odontocete species present) were used. These were imported into the computer software MATLAB, version 5.2 (The MathWorks, Inc.) in which the time–frequency contours of whistles were traced and saved as strings of time/frequency coordinates. Harmonics were not included in the analysis. To avoid oversampling particular groups of animals or individuals, a maximum of 100 whistles from each encounter were traced. Each continuous contour was treated as one whistle. For each whistle, 11 parameters were determined (Figure 1; Table 1). Based on the overall shape of the contour, whistles were subjectively grouped into separate schematic whistle types.

Table 1. *The eleven parameters determined for each common dolphin whistle.*

Parameter	Abbreviation	Description
Duration		Time duration (s) of the whistle (end time minus start time)
Start frequency	SF	Frequency (Hz) at the start point of the whistle
End frequency	EF	Frequency (Hz) at the end point of the whistle
Minimum frequency	MinF	Frequency (Hz) at the lowest point of the whistle
Maximum frequency	MaxF	Frequency (Hz) at the highest point of the whistle
Mean frequency	MeanF	Average frequency (Hz) of all points marked along the whistle
Frequency gradient	FG	Overall gradient/steepness (Hz/s) of the rise or fall of the whistle, calculated as: FG=(EF−SF)/Duration
Absolute frequency gradient	AFG	Absolute value of FG, removing positive/negative sign
Frequency range	FR	Range of frequencies (Hz) spanned by the whistle, calculated as: FR=MaxF−MinF
Inflections		Turning points where frequency modulation or slope of the whistle changes from falling to rising or rising to falling frequency
Steps		Periods of constant frequency between two periods of the same frequency modulation, i.e. two periods of rising or two periods of falling frequency

Using the Celtic Sea whistles only, we analysed whether whistle parameters and/or relative proportions of the whistle types were statistically correlated to group size (number of dolphins) and/or behaviour, and whether they differed significantly between individual encounters. A random sub-sample of Celtic Sea whistles were then compared to the English Channel whistles to determine whether whistle characteristics or types varied significantly between the two locations.

RESULTS

Celtic Sea whistle characteristics

A total of 57.5 h of acoustic recordings, encompassing 43 common dolphin encounters, was made in the Celtic Sea. From these recordings 1835 common dolphin whistles were analysed. Table 2 shows the minimum, maximum and mean values for each of the 11 whistle parameters measured of those 1835 Celtic Sea whistles.

Categorizing whistles into types, a system was created consisting of the six major whistle types commonly used in other studies that describe the overall general appearance of the whistle: constant frequency, upsweep, downsweep, convex, concave and sine. These were further split into sub-types depending on the degree of modulation of this general type (Figure 3). Upsweeps were the most common general whistle type, accounting for 31.0% of the Celtic Sea whistles, followed by downsweeps which made up 26.5%, constant frequency whistles which described 14.3%, convex and concave whistles which made up 11.7% and 9.3% respectively and, lastly, sine whistles which accounted for 7.3% (Figure 4). Further classification into sub-types showed that generally the simpler sub-types were more common than the more modulated ones.

Relationship between Celtic Sea whistle characteristics and encounters, behaviour and group size

The Kruskal–Wallis test showed that the means of all whistle variables were significantly different between encounters (at $P<0.001$). Furthermore, most parameters (except for FG and AFG) had significantly different means for the different survey days (at $P<0.05$). Whistle types were also significantly correlated with survey days ($\chi^2=83.090$; df=25; $P<0.001$).

Non-parametric Mann–Whitney *U*-tests were used to determine the influence of each behaviour category on the whistle characteristics. No significant differences were found in the means of any whistle variable between encounters where bow-riding was recorded and encounters where no

Table 2. *Means and ranges (in parentheses) for the parameters measured of common dolphin whistles in the Celtic Sea and English Channel.*

	Celtic Sea	English Channel
Duration (s)	0.646 (0.048–2.017)	0.643 (0.093–1.886)
Start frequency (Hz) *	12025 (3555–23514)	12641 (5017–27945)
End frequency (Hz) *	11971 (4071–22271)	12476 (4519–26124)
Minimum frequency (Hz) *	9447 (3555–19492)	9801 (4519–21080)
Maximum frequency (Hz) *	14685 (5740–23514)	15835 (8160–27945)
Mean frequency (Hz) *	11889 (4763–20377)	12669 (5757–22249)
Frequency gradient (Hz/s)	376 (−52544–72372)	509 (−44241–41157)
Absolute frequency gradient (Hz/s) *	6971 (0–72372)	8363 (0–44241)
Frequency range (Hz) *	5238 (117–17227)	6034 (121–20513)
Inflections *	0.64 (0–10)	0.56 (0–6)
Steps	0.13 (0–3)	0.10 (0–3)

*, marks those that were significantly different between the two locations.

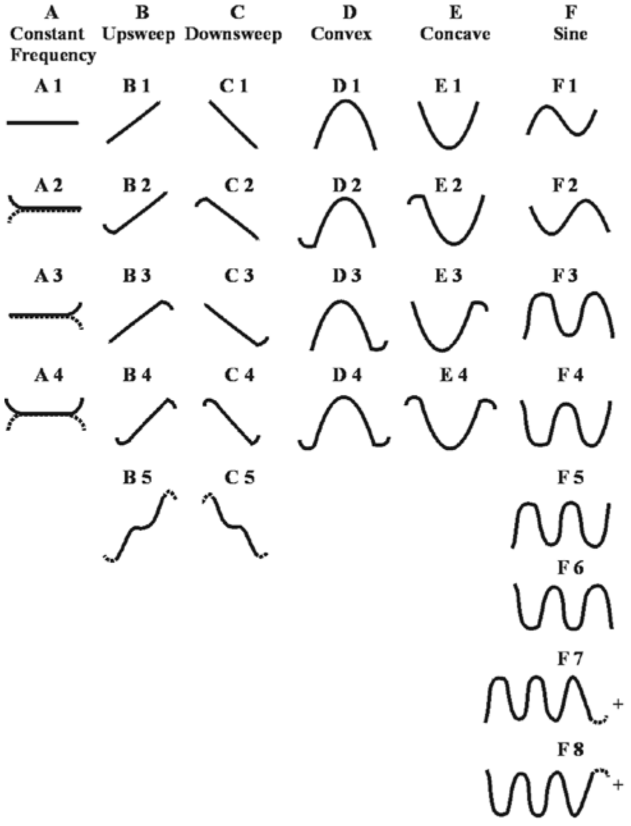

Figure 3. Idealized contours of the different whistle types.

bow-riding was observed. Mean MaxF and FR were lower when dolphins were travelling than when they were not (for MaxF: $Z=-2.214$; $N=1826$; $P<0.05$; for FR: $Z=-1.973$; $N=1826$; $P<0.05$) and whistles had on average more steps when travelling occurred ($Z=-2.627$; $N=1826$; $P<0.05$). Significantly more steps were also found when foraging was observed than when no foraging occurred ($Z=-3.573$; $N=1826$; $P<0.001$). When dolphins were socializing, mean duration of whistles was significantly longer ($Z=-3.393$; $N=1826$; $P=0.001$), mean MinF was higher ($Z=-2.584$; $N=1826$; $P<0.05$) and the whistles had on average fewer inflections ($Z=-2.136$; $N=1826$; $P<0.05$). The proportions of general whistle types were significantly correlated with whether the animals were foraging or not ($\chi^2=11.188$; df=5; $P<0.05$) and whether they were socializing ($\chi^2=22.448$; df=5; $P<0.001$). All behaviours were significantly correlated to the proportions of each of the 30 sub-types of whistles (at $P<0.05$).

The largest group size observed during a common dolphin encounter in the Celtic Sea (of those later included in the analysis) was estimated at over 128 and the smallest was one, with an average group size of 23 animals. For the analysis, group sizes were pooled together into the categories <5, 5–10, 11–20, 21–50, 51–100 and >100. Non-parametric Kruskal–Wallis tests showed that only the mean frequency gradient (FG) was significantly different between group sizes ($\chi^2=12.180$; df=5; $P<0.05$). While the absolute value of the frequency gradient was not significantly different, FG was positive for groups of 5–10 animals (so on average the whistles of those groups had a rising slope) while for groups of >50 animals it was negative (so whistles were overall falling in frequency). For the other group sizes FG had an intermediate distribution around zero. However, cross-tabulation and Pearson's chi-square analyses found no significant correlations between group sizes and whistle type ($\chi^2=33.385$; df=25; $P>0.05$).

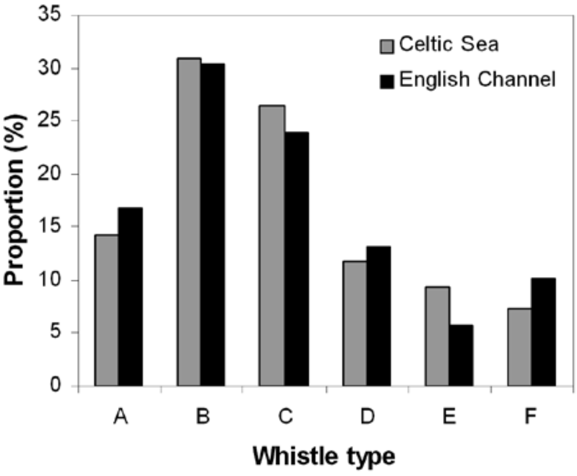

Figure 4. Proportional frequencies (%) of each broad whistle type in the 1835 sampled whistles of common dolphins in the Celtic Sea (grey) and the 435 sampled whistles from the English Channel (black). A, Constant frequency; B, upsweep; C, downsweep; D, convex; E, concave; F, sine.

English Channel whistle characteristics

From the English Channel recordings, a total of 435 whistles was analysed (Table 2). Similarly to the whistles recorded from the Celtic Sea, out of the overall whistle types of English Channel whistles, the upsweep was most frequent making up a proportion of 30.3%. The next common whistle types were the downsweep (23.9%) and the constant frequency type (16.8%), followed by the convex and sine types which accounted for 13.1% and 10.1% respectively. Unlike in the Celtic Sea, the least common whistle type in the English Channel was the concave type which only represented 5.7% of the total (Figure 4). Again, similarly to the whistles from the Celtic Sea, within each of the six broad types of English Channel whistles, the least modulated sub-types were most frequent.

Celtic Sea versus English Channel whistle comparisons

A random subset of 435 Celtic Sea whistles was taken for comparison with the 435 English Channel whistles. Significant differences between the two locations were found in the means of SF ($t=-2.033$; df=852.646; $P<0.05$), EF ($t=-2.131$; df=842.580; $P<0.05$), MinF ($t=-2.303$; df=868; $P<0.05$), MaxF ($t=-4.839$; df=868; $P<0.001$), MeanF ($t=-4.911$; df=858.321; $P<0.001$), AFG ($t=-3.179$; df=840.974; $P<0.05$), FR ($t=-3.073$; df=868; $P<0.05$) and inflections ($t=2.863$; df=829.402; $P<0.05$). In other words, the means of all variables except for duration, frequency gradient and steps were significantly different between the two locations (Table 2). For all the frequency-related variables in which differences were determined, the English Channel whistles consistently had higher mean frequency values than those from the Celtic Sea (Figure 5). The mean number of

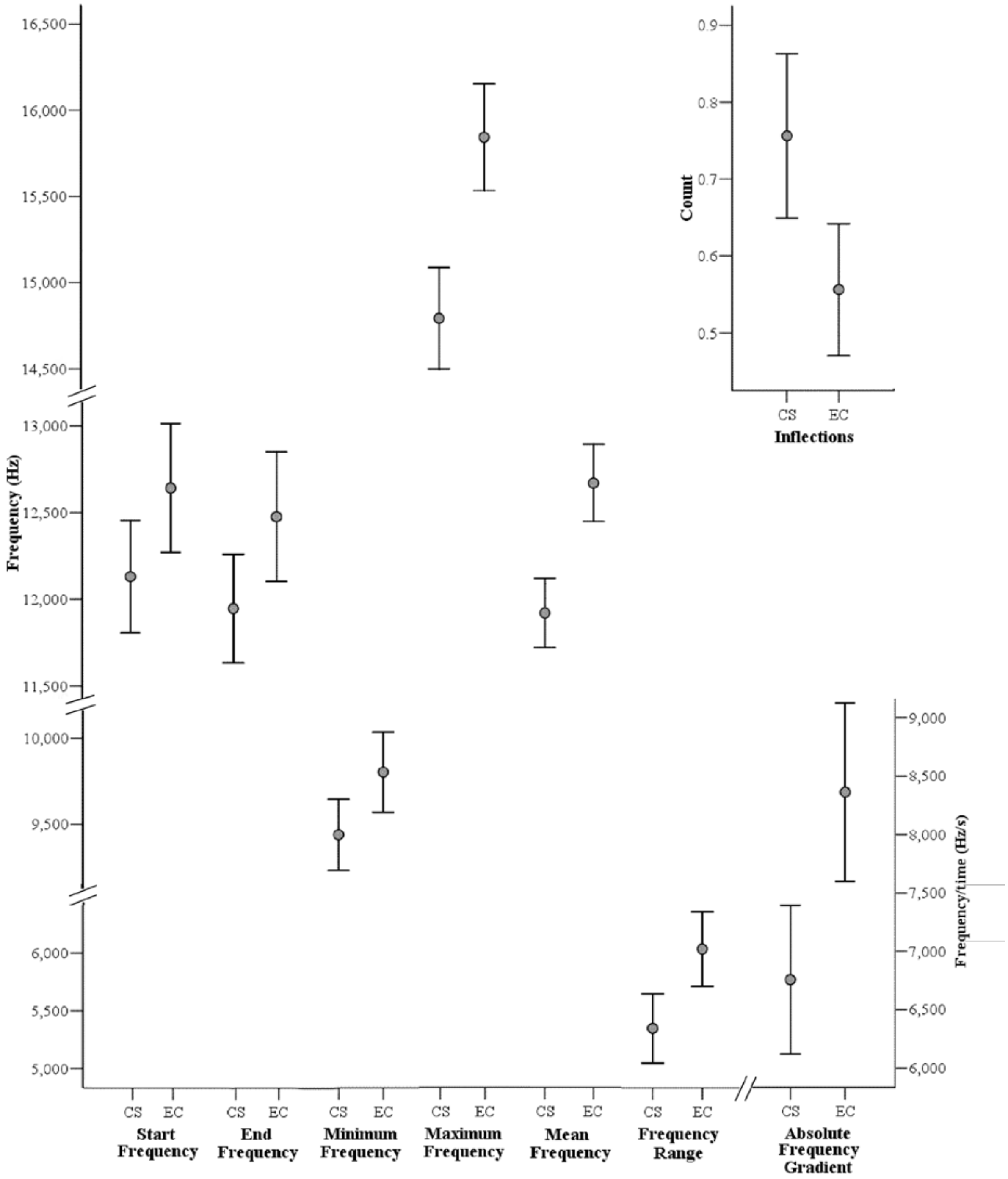

Figure 5. Means and 95% confidence intervals of significantly different frequency parameters and inflections (inset) by location. CS, Celtic Sea; EC, English Channel.

inflections was higher for Celtic Sea whistles (Figure 5). The broad whistle type was not significantly correlated to the sampling location (χ^2=10.295; df=5; P>0.05).

DISCUSSION

The 1835 whistles recorded from common dolphins in the Celtic Sea covered a frequency span from 3.56 kHz to 23.51 kHz, with most whistles occurring between 9 and 15 kHz. The shortest recorded whistle was 0.05 s long and the longest lasted 2.02 s with a mean of 0.65 s. Common dolphin whistles in the Celtic Sea were of a relatively simple structure as the average whistle had no or only one inflection and no steps. This was further shown by the relative abundance of whistle types. The simplest sub-types were the most common within each broad whistle type. Overall, the upsweep was the most frequent type, followed by the downsweep. The whistle parameters measured for the Celtic Sea common dolphin whistles were similar to those described by Wakefield (2001) in the same general study area, based on recordings of common dolphins from September to December 1994. The means of frequency parameters of whistles from Wakefield (2001) and the present Celtic Sea data were all within 1 kHz of each other except for maximum frequency which was 2 kHz higher in the present study. Mean duration was also slightly longer in the present study. Overall, the whistle characteristics were consistent between Celtic Sea recordings from autumn/winter 1994 and summer 2005 (Wakefield, 2001 and present study, respectively).

All of the whistle parameters measured showed statistically significant differences between different encounters. It is likely that these were caused by differences related to the recording context, such as behaviour, group size, or the presence and possible over-sampling of individual-specific vocalizations such as signature whistles (Oswald et al., 2003). Behaviour as well as group size were significantly correlated to some whistle characteristics but no strong overall patterns were apparent so, while they do influence certain whistle parameters, these factors alone may not account for all the variation between different encounters. The other possible factor is high variation between individuals. This would be expected if the majority of the vocalizations of each animal were signature whistles. Caldwell & Caldwell (1965) determined that over 90% of the calls of captive bottlenose dolphins were highly stereotyped whistles specific to each individual. It is not known how much of the whistle repertoire of free-ranging common dolphins consists of signature whistles. During the analysis of the present study, highly stereotyped whistles that were repeated several times in close succession were encountered, which were probably signature whistles. However, the majority of whistles were not clearly recognizable as such. Also, the finding that the simplest whistle sub-types, that is simple upsweeps, downsweeps or constant whistles without much further modulation, were the most frequent types recorded, suggests that a large part of the repertoire of common dolphins in the Celtic Sea consists of non-signature whistles. A major problem with acoustic studies of wild cetaceans, and possibly the main reason for the high variance between encounters, is the non-independence of data. Currently it is very difficult to determine which individual from a pod of dolphins is vocalizing, therefore it is likely that recordings often include more than one whistle from each individual and it cannot be guaranteed that each whistle used in the analysis is from a different animal (Oswald et al., 2003). This should be kept in mind when examining the results of this and other acoustic studies of social cetaceans.

The comparison between the common dolphin whistles recorded in the English Channel and a random sub-sample of the Celtic Sea whistles found significant differences in the number of inflections, as well as all frequency parameters except from mean frequency gradient (Table 2; Figure 5). The significant differences between almost all frequency parameters seem to indicate variation caused by geographical separation of the common dolphins of these two locations, since frequency parameters have generally been found to vary mostly between, rather than within, (sub-)populations (Azevedo & Van Sluys, 2005; Morisaka et al., 2005a).

It has to be considered in this case, that the recording sampling rates varied between the two locations, that is, in the Celtic Sea, frequencies were recorded up to 24 kHz while in the English Channel, the upper bandwidth limit was 48 kHz. Thus, whistles higher than 24 kHz would have been missed in the Celtic Sea, but recorded and analysed in the English Channel. This may have increased the mean values of English Channel data, which were indeed higher for all frequency parameters in the English Channel than in the Celtic Sea. The highest frequency measured of an English Channel whistle was 27.945 kHz, which certainly would have been cut off by the Celtic Sea recording equipment. In the Celtic Sea, the highest frequency was 23.514 kHz, close to the bandwidth limit of the equipment. However, out of the 435 analysed English Channel whistles, only five had maximum frequencies above 24 kHz, so it is unlikely that these five whistles significantly influenced the mean value of 435 whistles. Also, the parameter minimum frequency, which was significantly different as well, should not have been influenced by the upper bandwidth limit. Oswald et al. (2004) compared the whistles of four dolphin species, including *Delphinus delphis*, recorded with different bandwidths. They found that increasing the upper bandwidth limit only had a significant effect on maximum and ending frequency. Furthermore, increasing the upper bandwidth limit to over 24 kHz only resulted in minor changes in whistle variables and correct classification between species, compared to increasing it from 20 to 24 kHz. They concluded that 24 kHz seems to be a sufficient upper bandwidth limit to describe the majority of dolphin whistles (Oswald et al., 2004).

Another possible problem related to methodology is that different vessels were used to make the recordings in the different locations. In the Celtic Sea, two vessels of 12–15 m length were used whereas the platform for the English Channel surveys was a considerably larger 72 m vessel. It can be expected that these different sizes of vessels cause very different noise levels and frequencies underwater and it is conceivable that the dolphins reacted directly to the survey boat and shifted their frequencies. Alternatively, the different noise levels may have influenced the quality of the recordings at different frequencies. To exclude these possible biases more recordings would have to be made using the same equipment and survey vessel in both locations.

Differences between the whistle characteristics of the same species in separate locations may be caused by several different factors. Firstly, the two locations may be used differently by the animals; for example, one might be used as a feeding ground and the other as a breeding/resting/socializing area. Thus, different behaviours in the two areas might cause variation in the whistle characteristics. Intraspecific behavioural variation is usually reflected in differences of parameters such as duration, inflections and steps, as these are more freely modulated by the animals (Rendell et al., 1999; Morisaka et al., 2005a). While the mean number of inflections was significantly lower in English Channel whistles than in Celtic Sea whistles, duration and steps were not significantly different. Furthermore, different behaviours (travelling, socializing, foraging and bow-riding) were all observed in common dolphins during the Celtic Sea surveys and were only found to influence certain whistle parameters, including duration, inflections and steps but not consistently all frequency parameters as was found for the between-location comparison. Differences in frequency parameters are usually associated with variation between species or between populations rather than behavioural contexts within populations, as these frequency characteristics are generally related to anatomical variables such as body size or to environmental factors such as ambient noise levels (Rendell et al., 1999; Morisaka et al., 2005a). To the authors' knowledge, no differences in body size or other anatomical features related to sound production have been reported for the common dolphins in the Celtic Sea and English Channel. A study by Mirimin et al. (2005) examining the genetic relationship of common dolphins in the Celtic Sea and the English Channel found no genetic differentiation between these two locations, based on the analysis of 14 microsatellite loci. Thus the common dolphins in the two surveyed areas seem to belong to the same genetic population. However, it is possible that some sub-structuring may exist, as different subunits of a genetic population may have differing life strategies. If these common dolphins are separate sub-populations, this would have implications on management strategies. In the Western Approaches to the English Channel area, common dolphins experience high mortality rates caused by incidental catches in fishing gear (De Boer et al., 2005). These by-catch levels are large enough to pose a risk of local depletion of the species in this area, which is considered an important habitat during the winter season (De Boer et al., 2005).

The consistently higher mean frequency parameters of English Channel whistles compared to those from the Celtic Sea may also be related to differences in the background noise levels in the two areas. The English Channel and its Western Approaches are an area of intense fishing effort by English as well as French trawl fisheries (De Boer et al., 2005). Furthermore, there are several ferry lines regularly crossing the Channel and many trade vessels pass through it. This can be expected to cause considerable background noise. As ship noises are mostly low in frequencies, dolphins may shift the frequencies of their vocalizations up to avoid/reduce masking, a phenomenon called the acoustic niche hypothesis (Richardson et al., 1995; Morisaka et al., 2005b). Wakefield (2001) found that Celtic Sea common dolphins whistled at higher frequencies when exposed to high background noise levels during seismic surveying. This avoidance of masking by background noise seems a plausible explanation for the higher frequency parameters in the whistles of English Channel common dolphins. Further studies analysing this in more detail and measuring the source levels and frequencies of background noise in the two locations are needed to confirm this hypothesis.

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