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ORIGINAL PAPER

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Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland

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Abstract This study measured SPLs of whistles of wild bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, Scotland, and estimated their active space, i.e. the distance at which another dolphin can perceive the whistle of a conspecific. Whistling dolphins were localized with a dispersed hydrophone array by comparing differences in the times of arrival of a whistle at different hydrophones. The mean source level for whistles was 158 ± 0.6 dB re. 1 μPa. The maximum was 169 dB re. 1 μPa. The active space of these whistles was calculated taking into account transmission loss, ambient noise, the critical ratios and the auditory sensitivity of this species. The estimated radius of the active space of unmodulated whistles between 3.5 kHz and 10 kHz produced at maximum source level ranged from 20 km to 25 km in a habitat of 10 m depth and at sea state 0. At sea state 4 it ranged from 14 km to 22 km. For whistles of 12 kHz it dropped to 1.5–4 km. The results suggest that whistles can be used to maintain group cohesion over large distances but also that dolphins that researchers consider to belong to separate groups might be in acoustic contact.

Key words Source level · Active space · *Tursiops truncatus* · Acoustic communication · Whistles

Abbreviations *rms* root mean square · *SL* source level · *SPL* sound pressure level re. 1 μPa · *TM* transmission loss

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Introduction

Most calibrated measurements of dolphin sounds have concentrated on echolocation clicks (review in Au 1993). We know that bottlenose dolphins (*Tursiops truncatus*) can produce clicks with a peak-to-peak source level of up to 228 dB re. 1 μPa (Au et al. 1974) and that they can detect a water-filled steel sphere of diameter 7.6 cm over a distance of up to 110 m (in Kaneohe Bay, Hawaii; Au and Snyder 1980). In contrast, we know very little about the source levels of dolphin whistles. This is somewhat surprising since only with this information could we calculate the effective range of dolphin whistles. This range is also called the active space of the whistle, i.e. the volume around the sound source in which the sound amplitude is high enough for a conspecific to perceive and recognize the sound.

From behavioral studies we know that dolphins use whistles to maintain group cohesion (Janik and Slater 1998) and to communicate over long distances (Janik 1997), but we do not know how long these distances can be. Only few studies have described source levels and the active space of animal signals. Between red-winged blackbirds (*Agelaius phoeniceus*), songs can be used over distances up to 189 m (Brenowitz 1982) while the active space of grey-cheeked mangabey (*Cercocebus albigena*) chorused grunts can reach 1951 m (Brown 1989). Sound transmission in water, however, is more effective than in air and, as a result, active spaces of marine animal signals with comparable source levels should be much larger. The question of how far from the source whistles can be heard by another dolphin is important for three reasons. First, it determines the maximum separation distances at which two individuals can theoretically still be in acoustic contact. Second, it defines the space within which other animals exposed to a sound can intercept the signal or eavesdrop on an interaction. Additional information on animal density would allow one to calculate the possible number of recipients. Third, it provides important information on the biological background noise caused by other dolphins that a dolphin is exposed to. The number of vocalizing conspecifics within acoustic range limits the active space of a signal given at the same time.

To calculate the radius of the active space, we need to know the source levels produced by an animal, the background noise levels in the environment, the extent to which sound is attenuated over distance, and the critical signal-to-noise ratio that is required for a sound to be audible to the animal. Psychophysical studies have revealed both the hearing abilities (Johnson 1967) and the critical ratios for masking of sounds (Johnson 1968) in bottlenose dolphins. Underwater sound transmission over short distances has also been studied intensively (review in Richardson et al. 1995). Together with information on the ambient noise, source level measurements would therefore enable us to predict the distance over which dolphins could stay in acoustic contact.

How do we obtain reliable measurements of source levels of dolphin whistles? In echolocation studies, animals trained to detect distant targets adjust their source levels to what is presumed to be close to the maximum levels (Au 1993). Even if a trained animal is taken to sea, a calibrated hydrophone can be placed close to it and the animal can be held stationary during recording to obtain source levels. Similarly, in the study of dolphin whistles we could train an individual to increase the amplitude of its whistles to find out maximum levels. This would give us a conservative estimate of what animals are capable of, but since these are social signals the animal might not produce its maximum levels even if rewarded in a conditioning procedure. To investigate what source levels are used in the wild we are limited to purely observational studies. Since it is often not possible to get within one meter of a wild animal (the reference distance for source levels), sound pressure levels (SPLs) at greater distances must be used to calculate source levels. But since ambient noise limits the sensitivity of a transducer to distant sounds, even this approach requires one to get close to moving animals without producing noise that would compromise the measurement. Furthermore, to calculate source levels from measured SPLs exact information on the distance between dolphin and transducer is needed. These obstacles in the study of wild dolphins explain why we know so little about this subject.

In this study, I measured SPLs of dolphin whistles in the Moray Firth, Scotland, using an area in which animals occurred at predictable times of the day. The use of a hydrophone array enabled the sound source position to be localized. With this information the source levels as well as the acoustic range of these signals were calculated.

Materials and methods

Recordings were conducted in the Kessock Channel of the Moray Firth, Scotland, (57° 30′ 7″ N, 4° 14′ 37″ W) when bottlenose dolphins were present. Dolphins were recorded over 3 weeks in July 1996. All recordings were carried out in sea state 0 or 1. Water depth in the study area ranges from 4 m to 20 m and the bottom consists primarily of mud.

The measuring equipment consisted of a Brüel & Kjaer 8103 hydrophone connected to a Brüel & Kjaer 2635 preamplifier This equipment was calibrated by Brüel & Kjaer, UK, 2 weeks before recordings were started. Sounds were recorded on a Nagra IV-S tape recorder. The frequency response of this system was 30–20000 Hz (± 1 dB) at a tape speed of 38.1 cm s^{-1}. Sound pressure level recordings were conducted from a small inflatable dinghy anchored in the channel (Fig. 1) using the sensitivity dial-in feature of the conditioning charge amplifier according to directions in the hydrophone manual. A calibration signal of 1 V root mean square (rms) was recorded at the start of each tape using the internal reference oscillator of the preamplifier. Recording levels were adjusted prior to the recording of the calibration signal. If an adjustment was required it was indicated by knocking on the hydrophone. Following such an adjustment another calibration signal was recorded. Recordings between a knock and the new calibration signal were not used in the analysis.

To measure distances from the recording point to the vocalizing animal, sounds were also recorded with a hydrophone array. This array consisted of three High Tech SSQ94 hydrophones that were arranged in a triangle across the channel (Fig. 1). Inter-hydrophone distances were 208 m, 513 m, and 560 m. Each hydrophone was equipped with a Micron TX-101 transmitter. Radio signals were received with three separate Yaesu FRG 9600 receivers at a recording station on the North shore. All three channels were recorded on a Fostex 380S multitrack tape recorder to preserve differences in times of arrival of the same sound on different hydrophones. The frequency response of the localization equipment was 50–18000 Hz (± 3 dB).

The position of animals was determined by using SIGNAL software (Engineering Design, Belmont, USA). First, the difference in the time of arrival of the same sound at two hydrophones was measured by cross-correlating the signals from each pair of hydrophones. In the second step the time delays were used to calculate a hyperbola of possible source positions for each pair of hydrophones. The point at which all three hyperbolas intersect then provides the position of the sound source. Only sounds from close to the array were used, where the localization error was small (median error = 6.6 m, maximum error = 13 m). For more details on the localization setup and calibration results of this array see Janik et al. (2000). The position of the dinghy from which SPLs were recorded was also determined by passive acoustic localization. Two hammers were banged together underwater as a localization signal for the hydrophone array. All distances between the

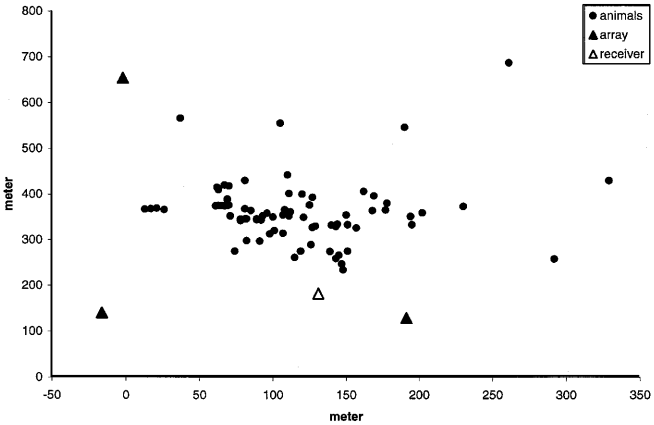

Fig. 1 Overhead view of the study area with locations of hydrophones and of all dolphins whose whistles were used. *Triangles* indicate the positions of the recording hydrophones. The *open triangle* indicates the position of the calibrated recording system. Each *dot* represents the location of one calling individual

measuring hydrophone and the calling dolphin given here were calculated by subtracting the maximum error of 13 m twice from the originally calculated distance, since both locations were determined by acoustic localization. This leads to a conservative estimate of source levels. Since ambient noise levels were below the lower limit of the dynamic range of the B & K 8103 hydrophone, data from Long Island Sound (Knudsen et al. 1948) were used to determine the active space of dolphin whistles.

To calculate pressure levels, the signals recorded on the Nagra tape recorder were analyzed with SIGNAL software. Sound pressure levels were determined by using the ANSI sound level meter incorporated in the SIGNAL software (envelope averaging time 125 ms). Before measurements were taken, signals were digitized with a sampling frequency of 50 kHz and then digitally filtered with a high-pass filter in SIGNAL to exclude low-frequency background noise. Thus, all measurements include all harmonics of the whistle up to 20 kHz, the upper frequency limit of the Nagra recording system. All decibel values given are referenced to 1 μPa.

Transmission loss (TL) from the source to the receiver was calculated using the equation presented by Richardson et al. (1995), which was derived from the Marsh and Schulkin (1962) model for shallow-water transmission:

$$TL = 15\log r + \alpha r + a_{\mathrm{T}}\left(\frac{r}{H} - 1\right) + 5\log H + 60 - k_{\mathrm{L}} \quad (1)$$

where r is the range in km, α is the absorption coefficient of seawater, a_{T} is the shallow-water attenuation coefficient, H is water depth in meters, and k_{L} represents a near-field anomaly. The values for k_{L} and a_{T} can be taken from tables in Marsh and Schulkin (1962), and $\alpha = 0.036f^{1.5}$ (dB km^{-1}), where f is the frequency in kHz. This equation works well for sloping bottom conditions if the value for H is the average of the depth at the source and the receiver (Richardson et al. 1995). However, note that the model assumes that sender and receiver are in the middle of the water column. Figure 2 shows the transmission loss at sea state 0 for selected frequencies as calculated with this equation. Water depth was set to 10 m which was the average depth of the area. The error of the equation at a frequency of 2.8 kHz is about 4 dB at a range of 2.7 km (Marsh and Schulkin 1962). Errors for higher frequencies at shorter ranges were not measured in Marsh and Schulkin's study. I compared the results of this empirically derived equation with a parabolic equation model following Jensen et al. (1994) for the same ideal habitat. It revealed that the computer model estimated transmission loss to be even lower in the middle of the water column. However, to give conservative estimates of the active space of dolphin whistles I chose to use the empirically derived equation rather than the more theoretical computer model.

To determine the minimum and mean frequency of bottlenose dolphin whistles in the Moray Firth, 500 randomly chosen whistles from 6 non-successive days were analyzed. Frequency measures were taken every 10 ms along the fundamental frequency of each whistle as described in Janik et al. (1994). Using these measurements the mean frequency and the minimum frequency for each whistle were calculated.

Results

To calculate SPLs, a signal had to be received by all four hydrophones, so that the source location could be determined. Due to the poor sensitivity of the Brüel & Kjaer hydrophone this criterion was fulfilled for only 103 whistles in the total recording time of 21 h 38 min. The locations of the animals involved are shown in Fig. 1. The distribution of rms SPLs measured from the animals is presented in Fig. 3a. The maximum SPL measured was 130 dB and the mean (±standard deviation, SD) was 114 ± 5.8 dB. Figure 3b shows the distribution of source levels calculated from measured SPLs using the source-receiver distances as determined by the passive acoustic localization. Transmission loss was calculated for a frequency of 9 kHz, which corresponds to the mean frequency of dolphin whistles (taken from frequency measurements of the fundamental frequency every 10 ms) in the Moray Firth (Fig. 4). The maximum source level was 169 dB and the mean (±SD) was 158 ± 6.4 dB. The animal that emitted the loudest whistle was 77 m away from the measurement hydrophone. This whistle is shown in Fig. 5. To investigate the contribution of the fundamental frequency to this source level, the whistle in Fig. 5 was digitally filtered for a second measurement with a low-pass filter in SIGNAL to remove the upper harmonics. The cut-off frequency was 11 kHz except for the brief modulation at 0.5 s which was filtered at 17 kHz. The SPL measurement for this filtered whistle resulted in a source level of only 1 dB below that of the unfiltered whistle. However, since the whistle has a mean frequency of less than 8 kHz the values for k_{L} and a_{T} in the calculation of the transmission loss have to be adjusted accordingly. This led to a decrease in transmission loss of 1 dB, resulting in a 169-dB source level for the filtered whistle. Thus, the maximum source level measured in this study represents the energy that could be found in the fundamental frequency of this whistle.

To determine whether only whistles from very loud animals could be analyzed or whether the mean source levels actually represented the mean levels used by animals I also localized the source of 23 quieter whistles that occurred before or after a whistle of which the SPL was measured. In 13 cases the quieter whistles were from the same position as the whistles that were measured, and in 8 cases they were from further away. Only in one case was the quieter animal closer to the hydrophone. Thus, it can be concluded that the sample represents calls with high source levels compared to the mean source levels produced by bottlenose dolphins in the area.

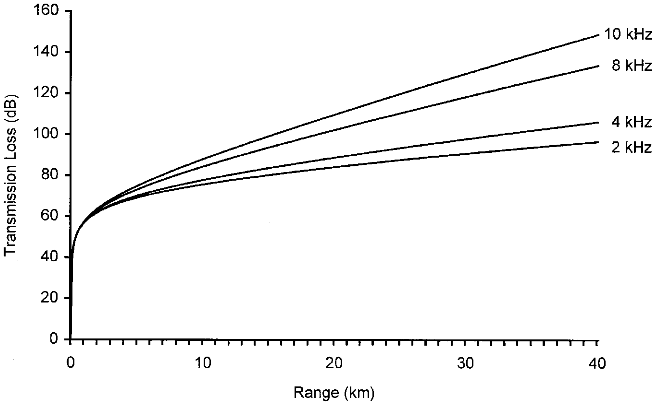

Fig. 2 Underwater transmission loss of pure-tone signals for selected frequencies in a homogeneous habitat of 10 m water depth with mud substrate in sea state 0 as calculated by the equation presented by Richardson et al. (1995), derived from a model by Marsh and Schulkin (1962)

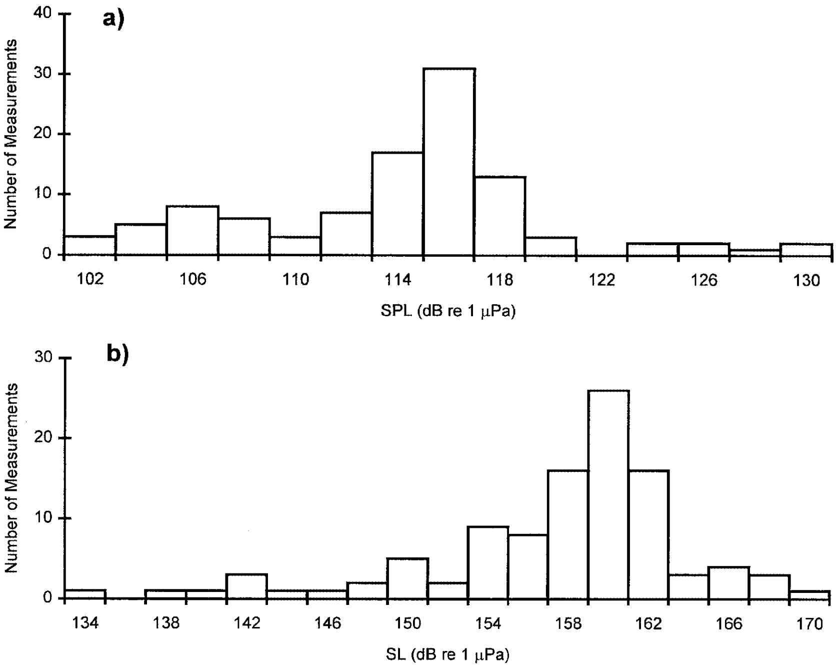

Fig. 3a, b Sound pressure levels (SPLs) of whistles ($n = 104$) before and after correction for distance. **a** SPL received at the calibrated recording system. **b** Source levels (SL) calculated from **a** by using distance information from the passive acoustic localization

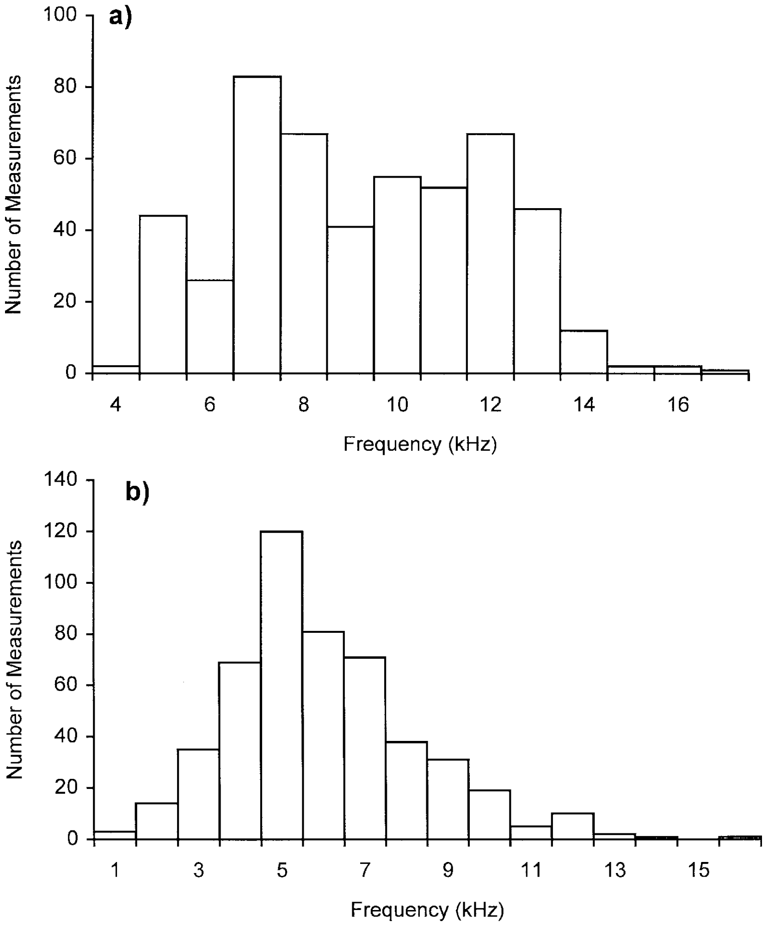

Fig. 4 The distribution of **a** the mean (taken from frequency measurements of the fundamental frequency every 10 ms) and **b** minimum frequency of 500 randomly chosen whistles from bottlenose dolphins in the Moray Firth

To estimate the active space of dolphin whistles we, furthermore, need information on the ambient masking noise for whistles and the acoustic sensitivity and critical ratios of the animals. Here, I present active space calculations for sea states 0 and 4. Sea state 0 means no waves with the water being totally flat, while sea state 4 corresponds to moderate waves with some spray. These waves are caused by wind speeds of approximately

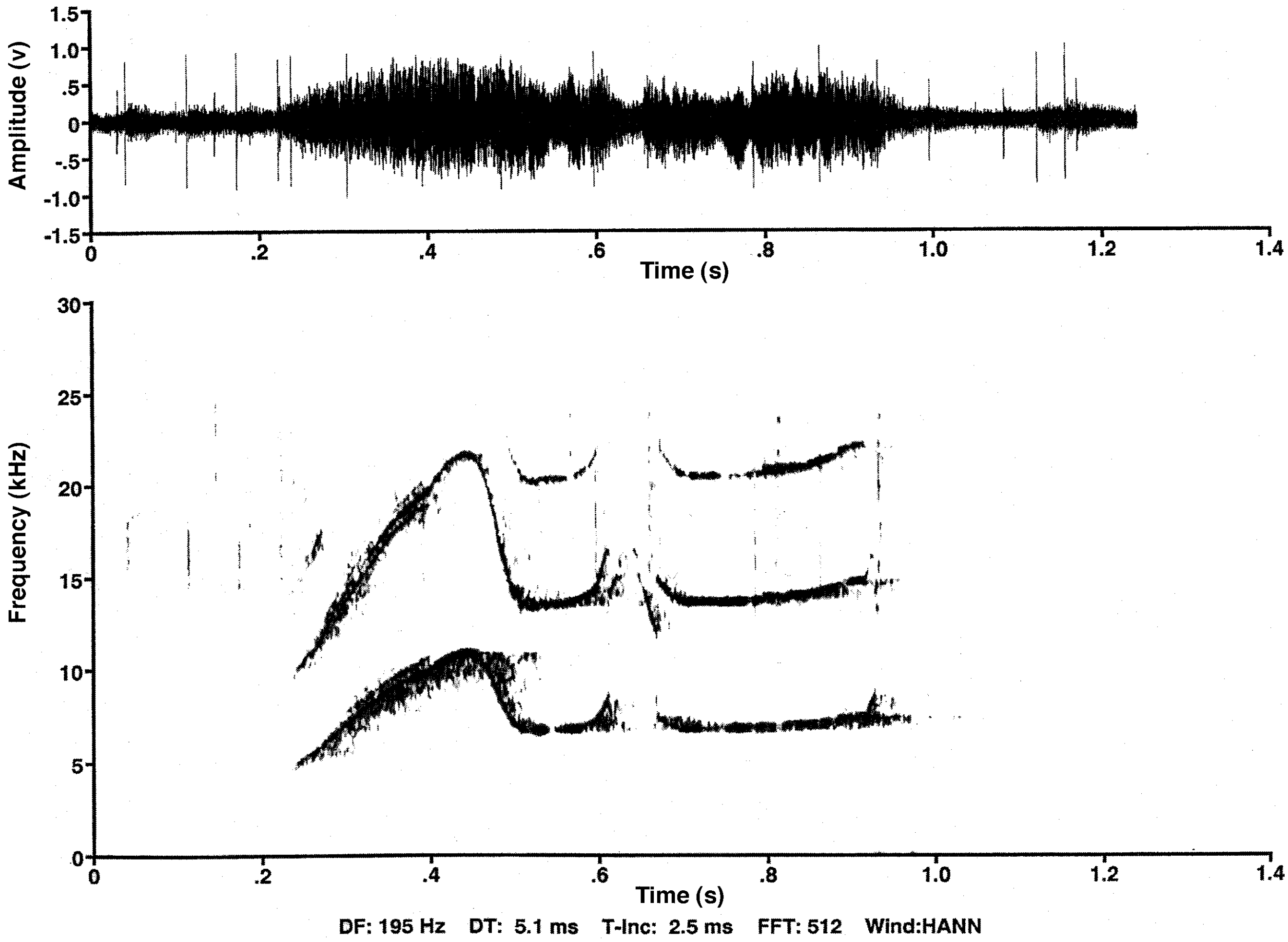

Fig. 5 Waveform and frequency spectrogram of the whistle with the highest source level (169 dB re. 1 μPa)

8–10 m s^{-1}. The ambient noise in the study area at sea state 0 was below the electrical noise of the B & K equipment. For the calculation of the active space I therefore used data from Knudsen et al. (1948) from Long Island Sound. For sea state 0 these lay between 28 dB at 12 kHz and 51 dB at 1 kHz, and for sea state 4 between 40 dB at 12 kHz and 66 dB at 1 kHz. Information on auditory thresholds and critical ratios was taken from studies carried out by Johnson (1967, 1968). If several measurements were presented by Johnson I used their mean. Critical ratios of the bottlenose dolphins have only been reported in the range at and above 5 kHz. For the calculation below 5 kHz, I used critical ratios of the beluga whale (*Delphinapterus leucas*) instead (Johnson et al. 1989). In the frequency range above 5 kHz these are slightly lower than those of the bottlenose dolphin. I calculated the active space of unmodulated whistles in the range 1–12 kHz in a 10-m-deep homogeneous habitat at sea state 0 and sea state 4. A mud bottom was assumed for this calculation since this corresponds to the situation in the Moray Firth. Transmission loss was calculated using the equation presented above, except for the 12-kHz whistle for which transmission loss data from Urick (1983) were used. Figure 6 shows the estimated active space of unmodulated whistles with the maximum source level (169 dB) and the mean value found in this study (158 dB) at sea state 0 and 4. The largest active space can be achieved by producing a 2-kHz whistle with the maximum source level. However, it is doubtful whether bottlenose dolphins can produce 2-kHz whistles at a source level of 169 dB. The 10th percentile of the minimum frequencies measured from 500 whistles in this study was 3.5 kHz (Fig. 4). The estimated radius of the active space of unmodulated whistles between 3.5 kHz and 10 kHz produced at maximum source level ranged from 20 km to 25 km in a habitat of 10 m depth and at sea state 0. At sea state 4 it ranged from 14 km to 22 km. For the mean source levels at sea state 4 it lay between 9 km and 14 km. For whistles of 12 kHz the radius of the active space dropped to between 1.5 km and 4 km depending on sea state. Given the actual mean frequency of the maximum source level whistle of 8 kHz it can probably be detected over up to 20.4 km in sea state 0 and over 17.5 km in sea state 4. The following steps have led to the estimate at sea state 0. At 8 kHz the ambient noise at sea state 0 was 34 dB re. 1 $\mu Pa^2/Hz$ (Urick 1983). The critical ratio (i.e., the amount by which a pure-tone signal must exceed the spectrum level background noise

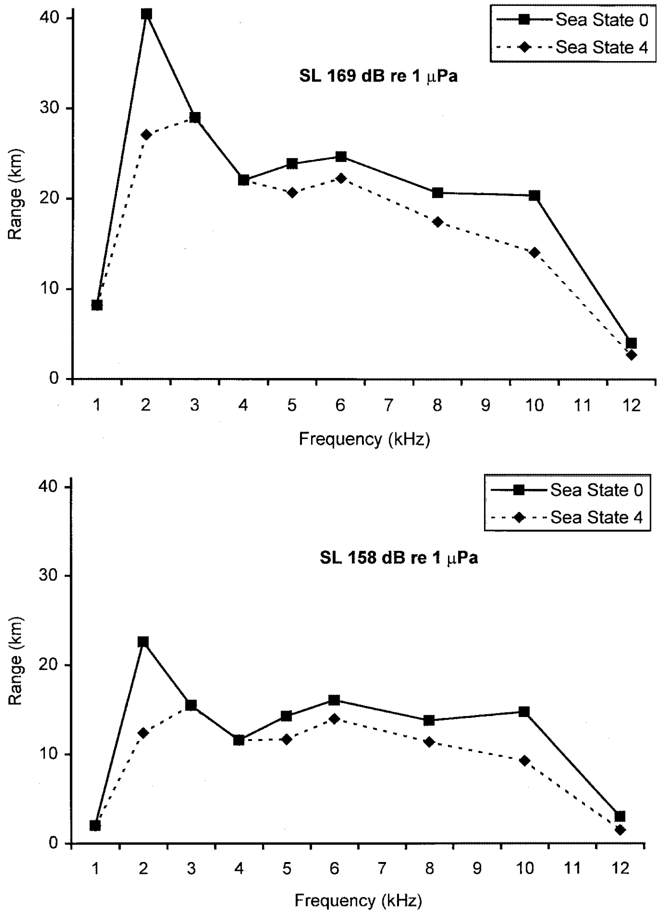

Fig. 6a, b Estimated radius of active space of unmodulated dolphin whistles at different frequencies in a homogeneous habitat of 10 m depth at sea state 0 and 4. **a** Whistles produced at maximum SL of 169 dB re. 1 μPa. **b** Whistles produced at mean SL of 158 dB re. 1 μPa. Transmission loss was calculated following Marsh and Schulkin (1962) and Urick (1983). Ambient noise was taken from Knudsen et al. (1948). Data for auditory thresholds and critical ratios of *Tursiops truncatus* were taken from Johnson (1967, 1968)

to be audible) of the bottlenose dolphin at 8 kHz is 25 dB (Johnson 1968). Therefore, a whistle had to have at least 59 dB to be perceivable by a conspecific. The auditory threshold of the bottlenose dolphin at 8 kHz lies at 66 dB (Johnson 1967). Thus, the active space is limited by the auditory threshold and not by the critical ratio in this case [note that the noise in the dolphin's critical band of one-sixth octave (Johnson 1968) around 8 kHz amounts to just about 65 dB at sea state 0, which is probably not audible to a dolphin]. The transmission loss for a signal of 8 kHz at 20.4 km is 103 dB (Fig. 2). If we subtract this transmission loss from the source level of 169 dB, we get 66 dB, which corresponds to the threshold at which the dolphin could perceive this signal due to its auditory threshold.

The active space between 1 kHz and 10 kHz at sea state 0 was limited by the auditory threshold of the bottlenose dolphin rather than the critical ratios. Thus, even though low frequencies experience less transmission loss the active space drops sharply below 2 kHz. At 12 kHz the active space was limited by the critical ratio of the bottlenose dolphin. However, this was different in the noisier sea state 4 condition, when the critical ratios limited the active space at 2 kHz and between 5 kHz and 12 kHz. Since transmission loss increases with frequency, the radius of the active space showed a drastic decrease beyond 10 kHz in all conditions.

Discussion

This study is the first to measure source levels of whistles in wild bottlenose dolphins and to estimate the active space of these signals. The only other study that has measured source levels of wild dolphins reported whistle levels of 109–125 dB for spinner dolphins, *Stenella longirostris* (Watkins and Schevill 1974). Bottlenose dolphins in this study produced source levels well above these values. However, the sampling period of Watkins and Schevill's study was very short and only looked at much smaller animals while they were resting during the day. The animals in this study were much larger, very active and feeding was frequently observed while recordings were made. Whistle source levels that have been measured from captive bottlenose dolphins ranged from 110 dB to at least 140 dB (Tyack 1985). An upper limit could not be given since source levels were measured with a vocalight attached to the dolphin's head and this did not respond to levels beyond 140 dB.

The absolute range of a given sound can vary according to environmental factors like ambient noise, temperature gradients, obstacles in the sound path or bottom characteristics. In the Moray Firth, especially at our study site which was a 500-m-wide channel, the active space is most certainly limited by the geography of the shoreline and by the presence of very shallow areas near the shore. The maximum range could only be achieved in the more open waters of the outer firth. Another factor that could affect active space is the directionality of a signal. Whistles seem to be relatively omnidirectional but even a moderate directionality could lead to different maximum transmission ranges at the caudal and the rostral end of the animal.

The calculation of the active space at different frequencies revealed that there is a strong peak at 2 kHz. Bottlenose dolphin whistles usually have their lowest frequency above 2 kHz, but non-whistle vocalizations can be found at around 2 kHz. At sea state 0 the active space in this frequency band is limited by the auditory threshold of the dolphin rather than the critical ratio. At higher sea states, the critical ratio becomes the limiting factor for the auditory system.

There are two main problems with the acoustic range derived from measurements such as those presented here. One problem lies with the calculation of the transmission loss in shallow-water habitat. Underwater transmission loss is a complex phenomenon and the approximation that can be achieved by using empirically derived equations is related to the acoustic topography of the area.

Acoustic transmission characteristics of different shallow water areas do not vary as much as those of terrestrial habitats, but it is still important to consider regional variations. Strong currents, varying water depths or obstacles in the sound path can drastically limit the range of an underwater signal. Furthermore, the model used here assumes that the caller and the receiver are in the middle of the water column. Transmission loss is much higher near the surface or the bottom of the water column. The second problem concerns the transmission of information in a whistle. Animal signals carry different sorts of information. If we assume that individual identity, for example, is the most important one for dolphins, we need to know which parameters encode identity and how well they are transmitted. Our current knowledge suggests that identity is primarily encoded in the overall contour of the fundamental frequency of a whistle (Caldwell et al. 1990; Janik and Slater 1998). Even though signature whistles without much frequency modulation can be found in dolphins (Caldwell et al. 1990), this is not usually the case. In more modulated whistles lower frequency parts of the contour will be transmitted further than those of higher frequency. Janik (1999a) showed that the identification of signature whistles was strongly affected if certain parameters were excluded by the classification method. However, bottlenose dolphins are able to identify a familiar whistle even if only a part of it is presented to them (Caldwell et al. 1990). If identity is encoded in the overall pattern of the modulation of the fundamental frequency, further behavioral studies are needed to show what parameters are crucial for identification and at what distance different whistles can still be told apart by a dolphin. Only then will we be able to give more detailed estimates of the actual active space of a dolphin whistle.

At this point we cannot be sure whether the large active space of dolphin whistles is just a by-product of the ideal transmission characteristics in water or whether they are relevant in their social behavior. We do not know over what distances individuals monitor each other's position acoustically or whether individuals eavesdrop on acoustic interactions and make use of the acquired information. This study has shown that animals that observers of surface behavior would consider to be in separate groups could form a social unit through acoustic contact. Thus, the current definitions of a social group that marine mammalogists use in the field could give a false picture of which animals are actually associated. This has also been suggested by Payne and Webb (1971) who estimated the range of fin whale vocalizations. A definition of group size that is based on distances between animals observed from a boat is more likely to be a problem in open waters where sound transmission is not limited by shallow banks or land, but again, this depends on how dolphins make use of the active space of whistles.

Apart from the implications for the distances over which animals can stay in touch acoustically, this large range is also likely to affect the design of a communication system. A dolphin is exposed to the calls of all animals present within its acoustic range. Thus, a large active space results in a high masking noise for whistles simply because other dolphins use the same frequency range for their whistles. It would be interesting to combine information on animal density, active space and calling rates for different species to test whether an increased noise level in the frequency band used for communication affects the design of a group cohesion mechanism in social animals. The large estimated active space for dolphins described here certainly supports the idea that they are exposed to increased background noise levels and that this could have contributed to the evolution of very distinctive, and thus probably learned, signature whistles to maintain acoustic contact between particular individuals (Janik 1999b).

Finally, it is important to notice that ambient noise data in this study were from conditions without any ship, industrial or human sonar noise nearby. Even a standard depth finder can produce source levels at the bandwidth of dolphin whistles that equal or exceed those measured in this study (Richardson et al. 1995); thus, they can cut the active space dramatically. This should be considered if guidelines for noise pollution are developed or if researchers use motor boats to study dolphins.

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References

Au WWL (1993) The sonar of dolphins. Springer, Berlin Heidelberg New York

Au WWL, Snyder KJ (1980) Long-range target detection in open waters by an echolocating Atlantic bottlenose dolphin (*Tursiops truncatus*). J Acoust Soc Am 68: 1077–1084

Au WWL, Floyd RW, Penner RH, Murchison AE (1974) Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. J Acoust Soc Am 56: 1280–1290

Brenowitz EA (1982) The active space of red-winged blackbird song. J Comp Physiol A 147: 511–522

Brown CH (1989) The active space of blue monkey and grey-cheeked mangabey vocalizations. Anim Behav 37: 1023–1034

Caldwell MC, Caldwell DK, Tyack PL (1990) Review of the signature-whistle-hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 199–234

Janik VM (1997) Whistle matching in wild bottlenose dolphins. J Acoust Soc Am 101: 3136

Janik VM (1999a) Pitfalls in the categorization of behavior: a comparison of dolphin whistle classification methods. Anim Behav 57: 133–143

Janik VM (1999b) Origins and implications of vocal learning in bottlenose dolphins. In: Box HO, Gibson KR (eds) Mammalian social learning: comparative and ecological perspectives. Cambridge University Press, Cambridge, pp 308–326

Janik VM, Slater PJB (1998) Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Anim Behav 56: 829–838

Janik VM, Dehnhardt G, Todt D (1994) Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. Behav Ecol Sociobiol 35: 243–248

Janik VM, Van Parijs S, Thompson PM (2000) A two-dimensional acoustic localization system for marine mammals. Mar Mammal Sci 16: 437–447

Jensen FB, Kuperman WA, Porter MB, Schmidt H (1994) Computational ocean acoustics. AIP Press, New York

Johnson CS (1967) Sound detection thresholds in marine mammals. In: Tavolga WN (ed) Marine bio-acoustics, vol 2. Pergamon Press, Oxford, pp 247–255

Johnson CS (1968) Masked tonal thresholds in the bottlenosed porpoise. J Acoust Soc Am 44: 965–967

Johnson CS, McManus MW, Skaar D (1989) Masked tonal hearing thresholds in the beluga whale. J Acoust Soc Am 85: 2651–2654

Knudsen VO, Alford RS, Emling JW (1948) Underwater ambient noise. J Mar Res 7: 410–429

Marsh HW, Schulkin M (1962) Shallow-water transmission. J Acoust Soc Am 34: 863–864

Payne R, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales. Ann NY Acad Sci 188: 110–141

Richardson WJ, Greene CR Jr, Malme CI, Thomson DH (1995) Marine mammals and noise. Academic Press, San Diego

Tyack PL (1985) An optical telemetry device to identify which dolphin produces a sound. J Acoust Soc Am 78: 1892–1895

Urick RJ (1983) Principles of underwater sound, 3rd edn. McGraw-Hill, New York

Watkins WA, Schevill WE (1974) Listening to Hawaiian spinner porpoises, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. J Mammal 55: 319–328