

# Echolocation constraints of Daubenton's Bat foraging over water

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## Summary

1. Daubenton's Bats (*Myotis daubentonii*) foraging over a stream concentrated their activity over calm surfaces, avoiding an adjacent area with small ripples (< 3 cm high). Aerial insects were most abundant over the ripples, so insect distribution could not explain why the bats avoided this area.

2. The bats flew low over water and always ( $N = 22$ ) directed the head forwards, presumably emitting the echolocation beam parallel to the surface, thus minimizing clutter. At an angle of incidence of 30° there was significantly more clutter from the rippled water.

3. The ripples produced ultrasonic noises in the form of transient pulses at an average rate of 6.2 per second. In the present case, such pulses were common enough potentially to interfere with target detection by the bats. Transient noises and echo clutter from moving ripples may be the principal reason why bats generally avoid foraging low over turbulent water.

4. The target strength of a potential insect prey at the water surface and the source levels of the bats' searching signals were measured to use in estimating the echo level at the bat when it detects the prey. The echo level at detection (+ 38 dB sound pressure level) was about the same as the clutter level extrapolated to the detection distance. This suggests that Daubenton's Bat operates at very low signal-to-noise ratios when foraging for insects near the water surface.

*Key-words:* Echo clutter, noise, predation, source levels, ultrasound

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## Introduction

The air above bodies of water is usually rich in insects and therefore constitutes an important feeding habitat for many species of bats. Several species of *Myotis* including *M. daubentonii* and *M. lucifugus* typically concentrate their foraging activity just above the water surface. *Myotis daubentonii* may also gaff insects floating at the surface (Kalko & Schnitzler 1989a). The air space above water is usually open with little disturbing clutter, and bats prefer to forage over calm waters in bays, over small lakes or pools and above smooth running waters in streams, normally avoiding surfaces with waves or ripples (Wallin 1961; Nyholm 1965; Fenton & Bell 1979; Fenton, Merriam & Holroyd 1983; Jones & Rayner 1988).

Echoes from small insects are faint and may be masked by clutter, extraneous echoes from vegetation or noise in the environment: this can force bats to operate at low signal-to-noise ratios in order to detect targets (Møhl 1988). von Frenckell & Barclay (1987) hypothesized that bats (*M. lucifugus*) tend to avoid

turbulent water because ultrasonic noise and clutter echoes from the ripples prevent efficient hunting by echolocation. Mackey & Barclay (1989) tested this hypothesis, using artificial clutter and playback of noise. The artificial clutter objects they used were large (10–40 cm in diameter and 3–20 cm high) and stationary, and the noise level over the turbulent water was high (79 dB sound pressure level relative to 20 µPa), indicating that the stream was quite rough. They did not report the clutter level from the artificial clutter or from the water surface.

We have observed that *M. daubentonii* tends to avoid running water surfaces even with very small ripples. Hence, to extend the work of von Frenckell & Barclay (1987) and Mackey & Barclay (1989), the noise and clutter levels over calm and gently rippling surfaces of a small stream regularly used by this species were measured and insect densities correlated with the activity of bats. The results allow us to suggest mechanisms by which noise and clutter from the rippled water may interfere with the echolocation of the bats.

## Materials and methods

### DESCRIPTION OF THE STUDY SITE

The study was made at the upper reach of the Tidån river system in southern Sweden (57°53'N; 13°38'E) 24 July to 31 August 1996. The study site was a small (5–10 m wide, about 0.5 m deep) stream, ≈ 200 m long, connecting two oligotrophic lakes and surrounded by deciduous woodland and pasture (the site has been described in more detail earlier; Rydell 1986). The observations and experiments were made within 50 m along the stream; in a 15-m section of gently turbulent water and along adjacent sections of calm, slow-flowing water upstream and downstream. The bank of the upstream calm water section consisted of stone walls (about 1 m high) and this section also had an old stone bridge crossing it. The rippled section and the downstream calm water section had lower banks, naturally covered by herbaceous vegetation and a few rocks. All sections of the stream were bordered by old deciduous trees and thus partly shaded by the overhanging branches. The largest ripples in the middle of the turbulent section had amplitudes of 2–3 cm (measured with a ruler) with distances of 5–10 cm between the tops.

### RECORDING BAT ACTIVITY

The flight activity of *Myotis daubentonii* was estimated at the three sites (calm water upstream, ripples and calm water downstream, respectively), by counting bat passes, using a D-960 bat detector (Pettersson Elektronik AB, Uppsala, Sweden), directed out over the water. A small torch light was also aimed across the stream, to facilitate visual observations in cases when there were many bats and their passes were hard to separate by the sound alone. Counts were made during one 5-min period at each sampling site during each of 10 evenings, starting 1–2 h after sunset. The order by which the sites were sampled was alternated from day to day. The sampling of bat activity took 18–20 min each night, including the three 5-min counts and movements between the sites.

### ESTIMATING INSECT DENSITY

Estimates of the relative aerial insect density at the three sampling sites were obtained by taking flash photographs, and counting the white dots on the projected slides, each dot representing a flying insect (Rydell 1992). We used a 34 × 36 mm camera (Nikkormat, Nikon, Japan) with a short tele lens (Nikkor 2.5/105 mm, Nikon, Japan), a flash (Metz 60 CT-4 Metz-Werke GmbH & Co KG, Fürth/Bay., Germany) and 50 ASA colour slide film (Fujichrome Velvia, Fuji, Japan). The aperture was  $f = 16$ . The lens was focused at 2 m throughout and was directed horizontally out over the water. Three photographs were taken at each sampling site during each evening, with

the camera at 0.5 m, 1.0 m and 2.5 m above the water surface; hence 81 pictures were taken in total (the photo equipment failed during one of the 10 evenings that bats were counted). At the focal distance (2 m), the two lower pictures (with the camera at 0.5 and 1.0 m) overlapped by ≈ 20%.

The counts for the three different heights were pooled when comparing the insect density of the three sampling sites. Likewise, when comparing the density between the three heights, the counts were pooled across the three sampling sites (disregarding the overlap). The photographs were taken during approximately 10 min immediately preceding the bat counts. Insect size or taxonomic identity was not accounted for.

### DETERMINATION OF SOURCE LEVELS

Three 1/4-inch (6-mm) Brüel & Kjær (B & K, Naerum, Denmark) microphones (type 4135, protective grid removed, preamplifier B & K 2633) were used in a 50-cm long horizontal linear array. The signals from the three microphones were amplified by 40 dB (B & K 2804 and WB 1057), high-pass filtered (13 kHz, custom-made filters), and recorded simultaneously on three channels of a Racal Store 4 Racal, Bergisch Gladbach, Germany high-speed tape recorder (762 mm second<sup>-1</sup>). The fourth channel (FM channel) was used for comments. The microphone array was placed ≈ 20 cm above the water surface, the approximate flight altitude of *M. daubentonii* (Kalko & Schnitzler 1989a). The 1/4-inch microphone has a flat frequency response up to 140 kHz (± 3 dB), and the frequency response of the Racal operated at 762 mm s<sup>-1</sup> is flat up to 150 kHz (± 2 dB). Thus the 1/4-inch microphone set the upper frequency response of the system. The recording system was calibrated using a B & K 4230 calibrator giving a 1-kHz tone at + 94-dB sound pressure level (SPL) relative to 20 µPa root mean square (RMS). All acoustic amplitudes are given in dB SPL (RMS).

The difference in relative arrival times of a bat echolocation call to the three microphones was used for calculating the distance to the bat. In a linear array this places the bat on a circle with its centre on and perpendicular to the long axis of the array. However, this gives only two out of three coordinates. The third was estimated from comments on the tape. The relative arrival times were found by cross-correlating a signal on one channel with the same signal recorded on the two other channels. For cross-correlation the three channels were digitized simultaneously using a CED (Cambridge Electronic Design, Cambridge, UK) 1401 A/D converter with a commercial program (CED MassRam 2.01). The analogue to digital sampling rate for each channel was 355 552 Hz (no anti-aliasing filter). Cross-correlations and distance calculations were made using custom-written programs. The error in calculating the distance to a source increases with decreasing angle to the array

line (e.g. bats outside the length of the array). Signals from bats only within the length of the array plus 10 cm on each side were therefore used.

The 1/4-inch B & K microphones measured sound perpendicular to the membrane correctly, but underestimated sound parallel to the membrane by 8 dB at 50 kHz and 15 dB at 80 kHz (Brüel & Kjær 1982). Because of the directional properties of the microphone and the restricted sound beam from the bat (Mogensen & Møhl 1979), only signals from bats coming directly towards the microphones were used for calculating the source level. Furthermore, signals were used only if they did not overload the system and if they were from bats flying alone.

As there was no control over the flight paths or head orientations of the bats, the criteria for signals that could be used for calculating the source level were hard to fulfil and only five signals from three sequences could be used from the 40 min of recordings containing hundreds of signals. The source levels are given in dB SPL (RMS) at 10 cm. The RMS measure was chosen, since the signals recorded from *M. daubentonii* contained interference caused by surface reflections (Kalko & Schnitzler 1989b). This interference can give problems in determining peak equivalent (pe) levels, which are commonly used to express source levels in field studies.

#### MEASURING CLUTTER ECHOES AND NOISE

Short (130 ms) clicks from an electrostatic loudspeaker (diameter 60 mm) were used as probe signals. The clicks were generated by short-circuiting the polarizing voltage of the loudspeaker for 7 ms, and had a -6 dB bandwidth extending from 10 kHz to 37 kHz with a peak at 22 kHz (Fig. 3a). They were repeated at a rate of 50 per second and had a free-field sound level of 90 dB SPL (RMS) at 1 m. When the clicks were measured at a hard surface (such as water), the level increased by about 2 dB.

The loudspeaker was mounted on a tripod 14–20 cm above the water surface and tilted at angles of 8°, 9°, 13°, 24°, 29° and 30° from the horizontal. Distances from the loudspeaker to the water surface varied between 23 and 109 cm, depending on the height above the water and the angle. A table tennis ball or a dead insect (a stonefly, Plecoptera) attached to a thin rod was placed at the water surface in line with the loudspeaker to serve as targets. The table tennis ball was used to determine the time delay between an emitted click and the returning echo. The ball and rod were then removed in order to record clutter echoes from the water surface.

Echoes were recorded with a 1/4-inch B & K microphone (protective grid removed) placed 100 mm from the centre of the electrostatic loudspeaker with the membranes parallel. The microphone signal was amplified 40 dB and recorded on one track of a Racal Store 4. The system was calibrated using the B & K 4230 calibrator. The ambient noise was also recorded

about 15 cm above the rippled and smooth water with the same setup. The noise floor of our recording system was about +55 dB SPL.

Recordings of clutter echoes, noise and calibrating signals were digitized at a sampling rate of 352 800 Hz (no anti-aliasing filters). The 12-bit binary files were digitally bandpass filtered between 13 and 130 kHz. The RMS voltage of the clutter was measured in a 2-ms time window encompassing the expected echoes (see Fig. 2). BatSound (Pettersson Elektronik AB, Uppsala, Sweden) was used to display amplitude spectra (512 point FFT, rectangular window) of clutter echoes (Fig. 3), and the time and spectrogram traces of noise (Fig. 4).

#### STATISTICS

The aerial insect density decreased considerably half way through the study due to a passing cold front, and the statistical distribution therefore became strongly skewed and bimodal. The change in the weather also affected the activity of bats, although this effect was less dramatic. Insect densities and bat activity were therefore analysed using non-parametric statistics (Siegel 1956). For the acoustic analyses a two-tailed Student's *t*-test was used.

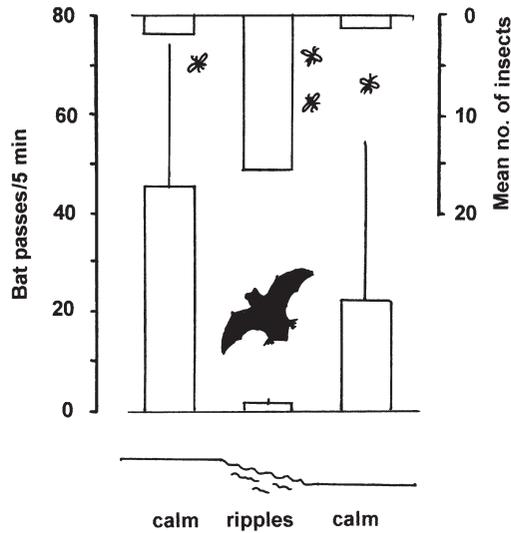
#### PHOTOGRAPHY OF FORAGING BATS

Foraging *M. daubentonii* were photographed close up, using an infrared beam across the stream under the stone bridge, a flash (Metz 60 CT-4) on each side and a camera (either a 24 × 36 mm Nikkormat with a 105-mm lens or a 6 × 6 cm Hasselblad 1000F (Hasselblad AB, Göteborg, Sweden) with a 120-mm lens) on a tripod. Breaking the beam triggered one of the flashes while the other flash was triggered by the first. The camera was prefocused at 1.5 m (the distance to the beam) and was kept with open shutter ( $f = 11$ ) until the frame was exposed by a flash. The film was either 100 ASA slide film (Kodak Ektachrome or Fujichrome Provia) or 400 ASA black and white (Kodak Tri-X). The photography was made either during 1988–92 or in September 1996, after the experiments were completed. Hence, the photography did not interfere with the other observations and experiments.

## Results

#### HABITAT SELECTION AND BEHAVIOUR OF BATS

On average, the bat activity, as measured by the number of bat passes per 5-min period, was as much as 20–40 times higher over the calm water sections than over the section with ripples (Kruskal–Wallis one-way analysis of variance (ANOVA); KW = 16.7,  $df = 2$ ,  $P < 0.0001$ ; Fig. 1). In fact, only 10 commuting passes were recorded over the ripples (one per



**Fig. 1.** Activity of *Myotis daubentonii* (mean and SD) over three adjacent sections of a stream and the corresponding mean aerial insect densities (the variation is not shown by error bars because the distribution was strongly bimodal; see text). Bat passes were counted during 30 5-min periods ( $N = 10$  evenings; one count at each of the three sections each evening) using a bat detector. Insect densities were measured from 81 flash photographs taken over the stream on the same evenings ( $N = 9$  evenings; one photograph at each of three heights).

sample on average), and the bats made no attempt to capture insects during any of these passes. This was in contrast to what they did over the calm water, where feeding buzzes always were heard frequently. When passing over the ripples, they also flew much higher (0.5–1 m) than they normally did over the calm water sections (< 0.5 m).

Twenty-two close-up photographs of *M. daubentonii* foraging over the upstream calm water section were obtained. In all cases the bats held their heads approximately in line with the body horizontally, with the mouth directed forwards, indicating that they emitted the echolocation calls roughly parallel to the surface of the water.

#### AERIAL INSECT DENSITY

The insect density varied considerably from night to night, with total counts (eight nights, three sites and three frames per site) between 0 and 89 insects (0–23 at the upper calm section, 0–78 at the rippled section and 0–7 at the lower calm section). The total number of insects counted was 190.

Differences in the density of insects in the air could not explain the differential use of the three sections by the bats, since there was no indication that the insect density was lower over the section with ripples compared with the two calm water sections (Kruskal–Wallis ANOVA;  $KW = 2.2$ ,  $df = 2$ ,  $P = 0.33$ ; Fig. 1). On the contrary, during six of the eight evenings, the section with ripples had higher insect

density than any of the two calm water sections, while it was equal on one evening and lower on one. When comparing the sections pairwise using Wilcoxon's matched pairs signed ranks tests, the insect density turned out to be significantly higher over the rippled section, where the bats did not feed, both when this section was compared with the upstream calm section ( $T + = 25$ ,  $P < 0.05$ ,  $N = 8$ ) and with the downstream calm section ( $T + = 26$ ,  $P < 0.05$ ,  $N = 8$ ).

The insects were concentrated near the water. Their density was highest at the lowest level (0.5 m) on seven of the eight nights, which is significant ( $P < 0.05$ ) by sign test. On average 83% of the insects were found at this level above the surface, while 14% were found at 1 m and 3% at 2.5 m. There was no indication that the insects flew higher over the ripples, where 12% of the insects occurred at 1 m or higher, as compared with the calm water sections, where 26% occurred at 1 m or higher. Hence, although the insect density was always highest near the water surface, they flew on average slightly but significantly higher over the calm water than over the rippled water ( $\chi^2 = 3.74$ ,  $df = 1$ ,  $P < 0.05$ ).

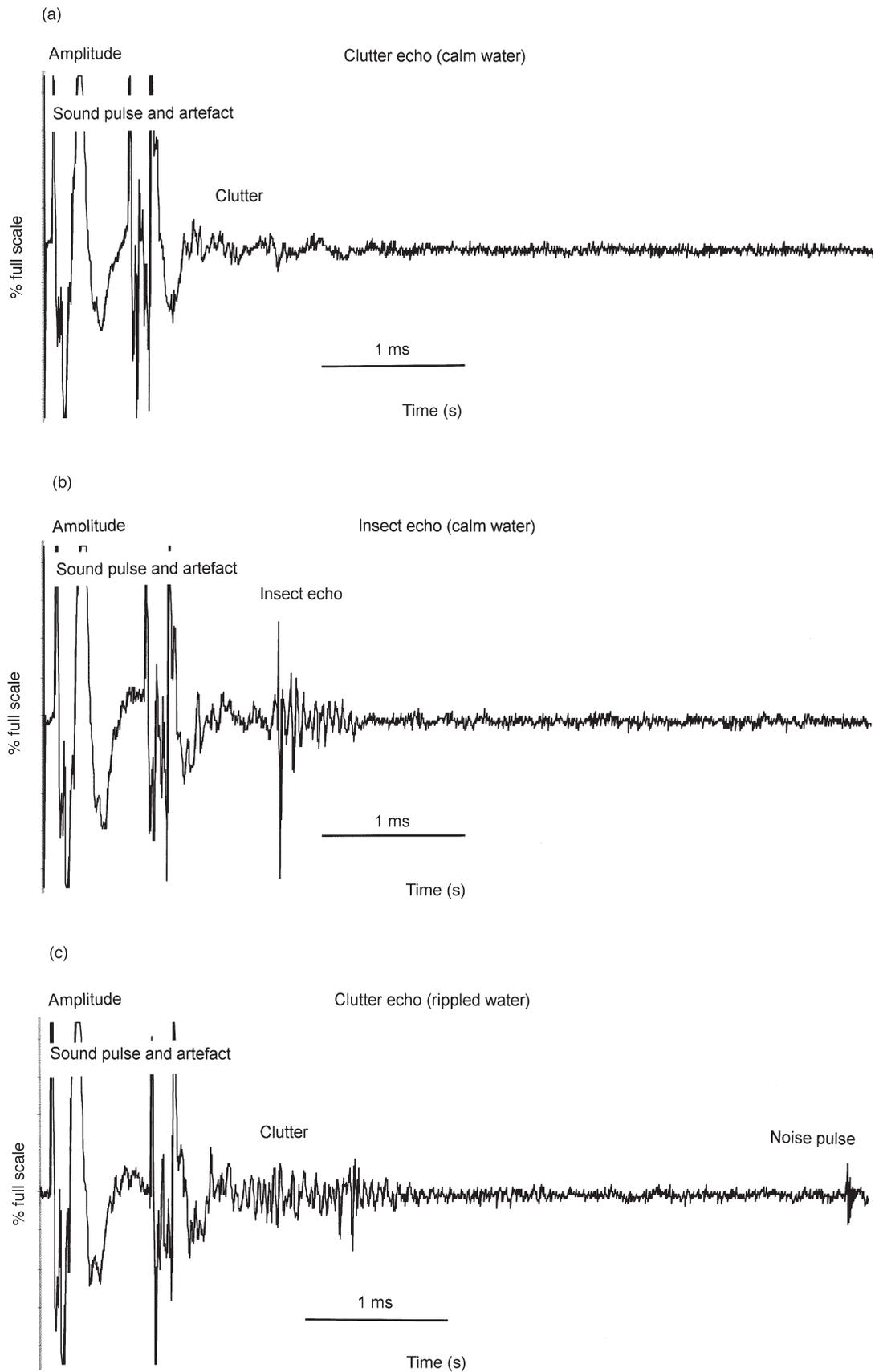
#### ECHOLOCATION CALLS AND INTENSITY (SOURCE LEVEL)

The bats (*M. daubentonii*) at our site used echolocation calls similar to those reported by Kalko & Schnitzler (1989a). Searching signals had durations of 3–6 ms with frequencies in the first harmonic ranging from 105 to 24 kHz ( $N = 26$  signals from 12 samples). Accurate measurements were difficult to obtain because of interference between the direct signal and that reflected from the water surface.

Only five met the criteria for determining source levels. No signals were free from interference owing to overlap of the direct signal and the same signal reflected from the water surface. The interference appeared as amplitude modulations of individual signals (Kalko & Schnitzler 1989b), and made it difficult to measure a peak value. Consequently, the RMS measure for the duration of the signal was used, which ranged from 4 to 5 ms. The source levels (at 10 cm) for the five signals were: 103, 106, 109, 110 and 113 dB SPL (RMS). The RMS measurement is –9 dB relative to a peak-to-peak measurement.

#### CLUTTER ECHOES, INSECT ECHOES AND NOISE

Clutter from rippled water was recorded at angles of incidence of 15° or greater and from smooth water at 24° or greater. The RMS voltages of clutter echoes were measured at angles of 29° and 30° above rippled and smooth water, respectively. Figure 2 (a) and (c) shows the transmitted click followed by an artefact echo from the immediate vicinity (probably from our setup), clutter echoes and noise from the smooth and rippled water, respectively. The clutter level from the rippled water was  $61.1 \pm 0.1$  dB SPL ( $N = 9$ ) at 24 cm



**Fig. 2.** Amplitude/time traces of clutter and insect echoes. (a) A transmitted click (130 ms) followed by an artefact echo (probably from our setup), clutter echoes from the surface of calm water followed by noise ( $N = 9$  samples). The distance between the loudspeaker and the microphone and the water surface is 23 cm. (b) Like (a) but shows an echo from a stonefly (wing span 24 mm) mounted with the wings spread at the calm water surface; distance is 30 cm from the microphone ( $N = 9$ ). (c) Clutter echoes from rippled water and later a noise pulse; the distance is 24 cm ( $N = 9$ ).

while that from the smooth water was  $60.5 \pm 0.1$  dB SPL ( $N = 9$ ) at 23 cm. The difference was significant ( $t = 16.74$ ,  $df = 16$ ,  $P < 0.001$ ). The target strength (defined as the echo sound pressure in dB at 1 m minus the incident sound pressure in dB, Møhl 1988) of the clutter from the rippled water was about  $-54$  dB while that from the smooth water was about  $-55$  dB.

Spectral characteristics of the clutter are shown in Fig. 3(b)–(f). The spectra and energy of clutter from smooth water was fairly consistent from sample to sample. In 11 of 15 samples the spectral energy fell between 10 and 30 kHz, and two of these are shown in Fig. 3(b) and (c). The spectra and energy of clutter from rippled water varied from sample to sample and in 11 of 15 samples the spectral energy fell between 10 and 40 kHz. Three samples are shown in Fig. 3(d)–(f). The spectral characteristics of the incident sound are shown in Fig. 3(a).

Figure 2(b) shows the echoes from a stonefly (wing span of 24 mm) near the surface of smooth water with the wings spread and at a distance of 30 cm directly in front of the loudspeaker. The echo level was  $62.66 \pm 0.14$  dB SPL ( $N = 9$ ). The target strength of this relatively large insect was about  $-47$  dB. Figure 2(a) shows a recording similar to that shown in Fig. 2(b), but with the insect removed.

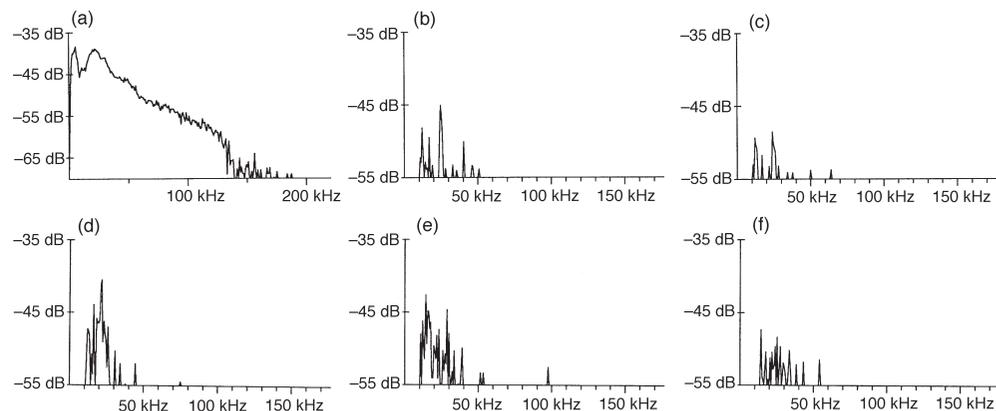
The noise level of our recording system was near that of the ambient noise measured above the water. Short broadband noises were recorded over rippled water. Figure 4 shows time traces and spectrograms of a recording over rippled water with noise pulses (Fig. 4a) and, for comparison, also over calm water, where such noise pulses were absent (Fig. 4b). The noise pulses were common (6.2 per second of amplitudes greater than twice the background noise measured over a 9-s sample), and were probably produced by the action of water flowing over submerged stones near the surface.

## Discussion

The horizontal and vertical distribution of foraging bats over the water was not related to the distribution of the prey, only to the presence of calm water. Indeed, although the insect density was highest over the ripples, not a single feeding attempt was observed there. The bats apparently used the rippled section only as a flyway when moving between the two calm water sections. The ripples, which probably were much smaller than those in the studies of von Frenckell & Barclay (1987) and Mackey & Barclay (1989), because the noise level was much lower, thus had a dramatic effect on the behaviour of the bats.

The lower insect numbers over the calm water sections compared with the rippled section, and the relatively low density at the lowest level over the calm water, indicate that the bats reduced the density of insects immediately over the calm water surface by predation. Alternatively, the insects might have responded behaviourally by moving both vertically and horizontally from the calm water surfaces towards areas where the predation risk was lower. Since we did not collect and identify the insects, we cannot say if they originally emerged from the calm or the rippled water.

Like von Frenckell & Barclay (1987) and Mackey & Barclay (1989) we believe that *M. daubentonii* were hindered from feeding over the turbulent surface by some physical characteristics of the latter, presumably clutter and/or noise produced by the ripples. The clutter level encountered by a bat above a water surface presumably varies with the angle of incidence, with smaller angles giving less pronounced clutter. *Myotis daubentonii* flies on average 16 cm over the water surface when foraging and detects prey at an average distance of 128 cm (Kalko & Schnitzler 1989a). This means that the bats project



**Fig. 3.** Spectral characteristics of incident sound (a) and clutter (b–f). The clutter was recorded under identical conditions except that the recording made from the smooth water (b and c) was at an angle of  $29^\circ$  and a distance of 30 cm ( $N = 15$  samples) while that from the rippled water (d–f) was recorded at an angle of  $15^\circ$  and a distance of 57 cm ( $N = 15$ ). The beginning of the FFT window (512 points) was placed just before the clutter echo. The incident sound was not filtered, but the clutter was digitally band pass filtered (13–130 kHz).

the echolocation signals at an angle of  $\approx 7^\circ$  to the water surface on average, when detecting prey there. In practice this angle can be considered as a maximum, however, because at least some prey are detected in the air above the surface, i.e. at even lower angles of incidence (Kalko & Schnitzler 1989a). Furthermore, our photographs showed that the bats usually directed the head forwards, not obliquely downwards, and therefore probably emitted the echolocation beam almost parallel to the water (near  $0^\circ$ ). Since the beam width is about  $80^\circ$  (Mogensen & Møhl 1979) the bats presumably perceive echoes even when the signals are projected straight ahead and may thus be able to distinguish smooth from rippled water. Minimizing the incidence angle is presumably a strategy used by bats to

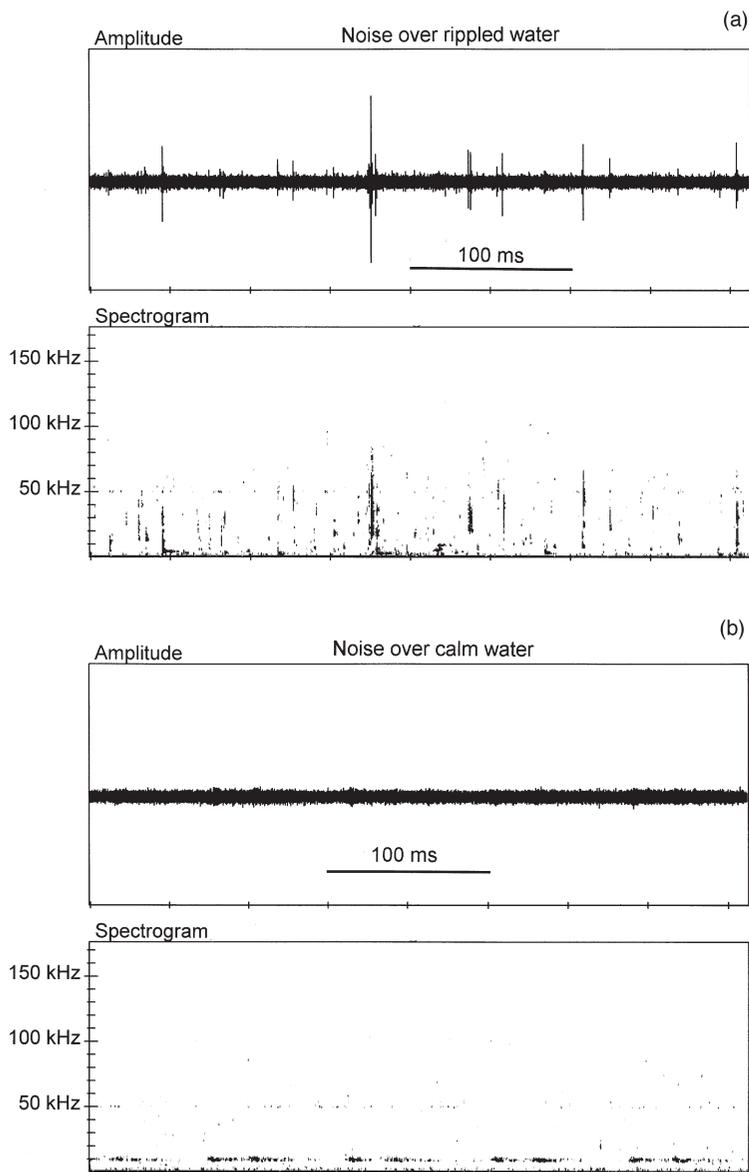
minimize the clutter from the water surface, and thus improve the signal-to-noise ratio of the echoes, and thereby detection of chironomids and other small Diptera, which constitute the bulk of the prey of *M. daubentonii* (Swift & Racey 1983). However, this strategy would appear less effective over rippled water, where clutter echoes are generally stronger than those from smooth water and continually change in amplitude and spectral characteristics. The clutter from moving ripples would have a greater tendency of masking the echoes from prey at the water surface.

The ambient noise levels over rippled and calm surfaces could not be measured, because of limitations in our equipment, but the bats presumably can hear such differences. Based on audiograms of other vespertilionid bat species, e.g. *Eptesicus fuscus* (Moss & Schnitzler 1995), the hearing sensitivity of *M. daubentonii* may perhaps surpass our system by as much as 20–40 dB. Thus the overall difference in noise level between rippled and calm water could have affected the bats' choice of foraging habitat, although we were unable to show this. On the other hand, it seems very likely that the brief ultrasonic noise pulses from the ripples may have interfered with the bats' echolocation, since they were similar to echoes from insects. These pulses were common and the chance that one would coincide with the bats' detection window (Kalko & Schnitzler 1993), and therefore being mistaken for an insect echo, is high ( $\approx 60\%$ ). The transient noise pulses and the clutter from the moving wave fronts may together complicate target detection for the bats and seriously affect their foraging efficiency over ripples. We cannot evaluate the relative importance of noise and clutter in this respect, however.

With our data and those of Kalko & Schnitzler (1989a), the level of the echo that is detected by foraging *M. daubentonii* can be estimated using the following relationship:

$$EL = (SL + TS) - [20 \log_{10}(DD/1) \times 2] - [2 \times ATT \times (DD - 1)], \quad \text{eqn 1}$$

where EL is the echo level at detection, SL the source level of the bat's signal (90 dB SPL at 1 m), TS the target strength of the insect at the water surface ( $-47$  dB at 1 m, using the stone fly), DD the detection distance (128 cm) and ATT the atmospheric attenuation ( $0.87$  dB  $m^{-1}$  at 45 kHz). The beam width of the 40-kHz component of *M. daubentonii* is about  $80^\circ$  ( $-3$  dB points, Mogensen & Møhl 1979). Solving for eqn 1, the echo level at detection will be  $+38$  dB SPL. This value, which probably is a maximum, fits with the range of thresholds for echo detection in laboratory experiments, which extend from 0 to 59 dB SPL for various species of bats under various conditions (Moss & Schnitzler 1995). Since the target strength of small insects would be similar to that of the clutter, *M. daubentonii* probably



**Fig. 4.** Amplitude/time traces (above) and spectrograms (below) of recordings made (a) over rippled water, containing short, ultrasonic noise pulses, and (b) over calm water. Each trace shows 400 ms taken from 9-s samples.

operates at low signal-to-noise ratios when foraging near the water surface.

Few measurements of signal source levels from bats flying outdoors have been made, since obtaining these estimates is not a trivial task. *Myotis septentrionalis* uses weak echolocation signals when gleaning prey from surfaces, but much stronger ones (102 dB peak equivalent (pe) SPL measured at 10 cm) when they hunt prey on the wing (Miller & Treat 1993). Examples of bats hunting flying insects in open areas include *Craseonycteris thonglongyai* and *Myotis siligorensis*, two very small species that use source levels of 100–115 dB pe SPL (Surlykke *et al.* 1993), and *Eptesicus fuscus* and *E. serotinus*, larger bats that use 120–125 dB pe SPL (Roeder 1966; Jensen & Miller 1997). One might perhaps expect *M. daubentonii* to use source levels comparable to those of gleaning bats since it hunts near the water surface. However, the low angle of incidence (about 7°) means that most of the signal energy will reflect away from the bat, and this probably explains why *M. daubentonii* can use high source levels (about 110 dB SPL RMS).

Our results largely confirm the conclusions of von Freneckell & Barclay (1987) and Mackey & Barclay (1989), namely that bats (*M. lucifugus*) avoid turbulent water because their foraging efficiency is impaired over ripples by clutter and/or noise. However, Mackey & Barclay (1989) used stationary Styrofoam blocks on the water surface as 'clutter', thus simulating rocks rather than water ripples. Ripples, in contrast to stationary objects, constantly change the position back and forth, altering the shape of the reflecting surface and thus give rise to a more complicated form of clutter. The experiment of Mackey & Barclay (1989) is therefore not directly comparable to our situation.

It remains possible that the bats avoided the ripples partly because of the risk of colliding with the moving waves and thus getting wet or because of manoeuvrability constraints close to the moving water. However, this seems unlikely to be a general explanation for the almost total avoidance of the rippled section in our case, considering that the highest ripples were only 2–3 cm high (10–20% of the average flight height). The fact that adjacent areas of even smaller ripples were also consistently avoided by the bats also speaks against this explanation. The ripples are continually moving in an irregular pattern that probably makes it difficult for the bat to determine the range to prey on the water surface.

Minimization of the incidence angle of the echolocation beam against the surface is probably critical for *M. daubentonii* and other bats that feed over water, and the bats therefore probably fly as low as they can, without dipping the wings into the water. The shortened wingbeats, typical of *M. daubentonii* and other species that fly low over water, may further enhance this objective.

## Acknowledgements

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