Pacific and Atlantic herring produce burst pulse sounds

Ben Wilson[1,2*]**, Robert S. Batty**[3]
and Lawrence M. Dill[2]

[1]*Bamfield Marine Science Centre, Bamfield, British Columbia V0R 1B0, Canada*
[2]*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada*
[3]*Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban PA37 1QA, UK*
[*]*Author and address for correspondence: Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada (bwilson@zoology.ubc.ca).*

The commercial importance of Pacific and Atlantic herring (*Clupea pallasii* and *Clupea harengus*) has ensured that much of their biology has received attention. However, their sound production remains poorly studied. We describe the sounds made by captive wild-caught herring. Pacific herring produce distinctive bursts of pulses, termed Fast Repetitive Tick (FRT) sounds. These trains of broadband pulses (1.7–22 kHz) lasted between 0.6 s and 7.6 s. Most were produced at night; feeding regime did not affect their frequency, and fish produced FRT sounds without direct access to the air. Digestive gas or gulped air transfer to the swim bladder, therefore, do not appear to be responsible for FRT sound generation. Atlantic herring also produce FRT sounds, and video analysis showed an association with bubble expulsion from the anal duct region (i.e. from the gut or swim bladder). To the best of the authors' knowledge, sound production by such means has not previously been described. The function(s) of these sounds are unknown, but as the *per capita* rates of sound production by fish at higher densities were greater, social mediation appears likely. These sounds may have consequences for our understanding of herring behaviour and the effects of noise pollution.

Keywords: fish; sound production; sound characteristics; marine mammal; swim bladder

1. INTRODUCTION

The commercial importance of the clupeoid sub-order, particularly the Pacific and Atlantic herring (*Clupea pallasii* and *Clupea harengus*), has ensured that their biology has received considerable attention (Blaxter 1985). Sound reception in these fishes appears to be unusually well developed, implying that hearing is important to them (Blaxter & Hunter 1982). However, it is unknown which sounds their hearing structures were developed to receive. One possibility is the high-frequency sounds produced by echolocating cetaceans (Mann *et al.* 1997; Wilson & Dill

2002). Another may be sounds made by the fishes themselves.

Little is known about the acoustic emissions of herring. Described sounds fall into three categories. Incidental noises include those associated with jaw movements while feeding, and hydrodynamic sounds from moving schools (Fish & Mowbray 1970). Tonal sounds, termed 'whistles', have been detected in the vicinity of herring at night (Schwarz & Greer 1984). Pulsed sounds vary from thumps to low-frequency pressure pulses (Fish & Mowbray 1970) and, in one study of Pacific herring, include bursts of broadband pulses (Schwarz & Greer 1984).

The production mechanism and function of tonal and broadband pulsed sounds are unknown. Various sonic mechanisms are recognized in fishes but no special adaptations have been identified in herring. Because herring have no gas gland, swim bladder re-inflation is thought to occur by transferral, via the stomach, of gulped surface air (Blaxter & Batty 1984). This transferral has been described as a mechanism with potential for incidental sound production (Fish & Mowbray 1970). Although it is feasible that all herring sound production is incidental, the complexity of the tonal and pulsed sounds, coupled with the species' own hearing abilities, raise the potential for communicative function(s). The ramifications of acoustic communication by these widespread, ecologically and economically important species prompted us specifically to investigate their potential for sound production.

2. MATERIAL AND METHODS

Pacific herring (mean fork length: 170 ± 30 mm (s.d.), $n = 400$) were caught off Vancouver Island, British Columbia and held at the Bamfield Marine Science Centre. Atlantic herring were caught near Oban and held at the Dunstaffnage Marine Laboratory, Scotland (mean fork length: 208 ± 12 mm (s.d.)). Experiments on Pacific herring were carried out in two 500 l tanks. Recordings were made with a calibrated Cetacean Research Technologies C50a omnidirectional hydrophone suspended at mid-depth in each tank and connected to a DAT recorder sampling at 44.1 kHz. In-water light levels were monitored with a LI-COR spherical probe and datalogger (LI-COR LI1000). Measurements of sound pressure levels were carried out in a circular 1.86 m diameter fibreglass tank. The tank was divided with a net twine barrier to keep fishes at least 1 m from the hydrophone. For feeding trials, fishes were either deprived of food for 48 h prior to the trials or fed 28 h and 4 h before, and then every 2 h during, the trials.

To determine whether access to surface air was required for sound production, 20 Pacific herring were placed in each of two tanks. In the 'screened' tank, a rigid mesh screen was fixed below the surface to deny the fishes access to the air–water interface. In the second 'unscreened' tank, the mesh was fixed above the air–water interface. On the night following fish introduction, the number of Fast Repetitive Tick (FRT) sounds in each tank was recorded for 120 min. To examine whether the presence of predatory shark odour impacted sound production, two tanks holding herring were set side-by-side. One was fed water directly from a container holding adult dogfish (*Squalus acanthias*) at high density and the other was fed water from an unoccupied container. To observe herring during sound production, nocturnal video recordings of Atlantic herring were carried out with a camera, infrared floodlights and hydrophone, as described above. Individual fishes were not re-used in any experiments.

3. RESULTS AND DISCUSSION

The most distinctive sounds detected during our study were the trains of FRT sounds (see electronic Appendix A, available on The Royal Society's Publications Web site). The best recordings of FRT sounds came from juvenile and adult Pacific herring. FRT sounds consisted of discrete stereotyped bursts of 7–65 pulses (mean of 32, $n = 20$; figure 1) lasting 0.6–7.6 s (mean of 2.6). They
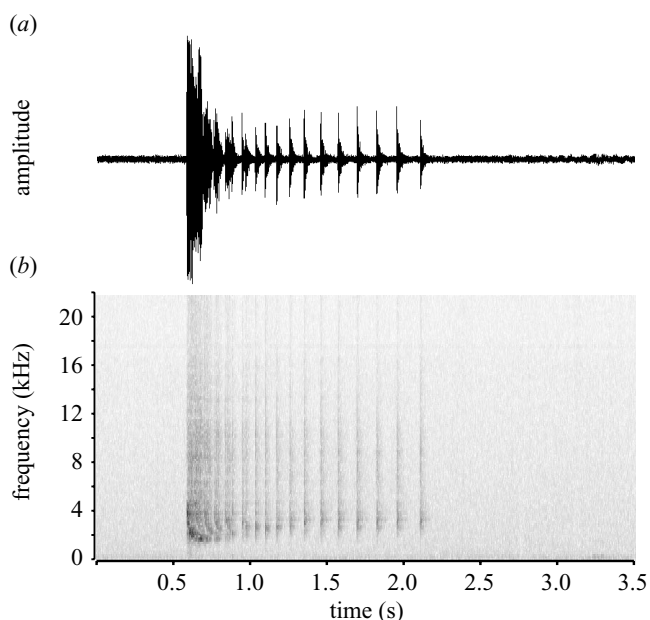
(a)

(b)

Figure 1. (*a*) Waveform and (*b*) spectrogram of a typical FRT sound. Sampling rate of 44.1 kHz. In (*b*), the fast Fourier transform length is 256, frequency resolution is 86 Hz and time resolution is 11.6 ms.

comprised a single continuous burst train rather than intermittent bursts and, within a train, the time-interval between successive pulses increased in a characteristic fashion. The pulses themselves were broadband with frequencies from 1.7 to at least 22 kHz (this study's frequency ceiling; figure 1). The spectral composition of pulses varied subtly during each FRT sound, notably in the first few pulses (figure 1). The rapid succession of pulses, smooth transition of interpulse intervals and absence of overlapping or out-of-phase pulse trains suggest that each FRT sound was produced by an individual fish. The presence of high-frequency components and absence of low frequencies makes these sounds unusual when compared with other fish sounds (Fish & Mowbray 1970). Precise measurement of the amplitude of the FRT sounds proved problematic, but from a sample of 13, a conservative measurement of sound pressure level of 143 dB re1µPa @ 1–1.8 m (peak) was recorded.

Herring at sea typically follow a diel behavioural rhythm, forming diurnal deep-water schools and nocturnal loose surface shoals (Blaxter & Parrish 1965). If some component of the process of transferring gulped surface air to the swim bladder generates the FRT sounds (Fish & Mowbray 1970) then we might expect that these sounds would be most prevalent at night. This was found to be the case. Sounds made by eight groups of 20 Pacific herring were sampled over 24 h periods. The diel distribution of FRT sounds differed significantly from random (see figure 2; $p < 0.001$) with most occurring after dark (23.00 to midnight PST). During this experiment, fed and unfed fishes produced similar numbers of FRT sounds (fed: 10; food deprived: 13).

To investigate the transfer of gulped air to swim bladder hypothesis further, we tested whether access to surface air was required for FRT sound production, using the screened and unscreened tanks described above. FRT sounds were recorded in both tanks (mean screened: 6; unscreened: 9; $n = 4$ replicate trials). We therefore conclude that access to surface air is not immediately necessary for FRT sound production. For two out of the four trials, monitoring was continued for a second and third night after fish introduction. The number of FRT sounds recorded on these nights in the screened tank was much lower (mean of 0.75), whereas in the unscreened tank they remained as numerous (mean of 9). Thus, although access to the air–water interface is not immediately necessary for FRT sound production, previous air access does appear important.

Atlantic herring also produce FRT sounds. Simultaneous nocturnal acoustic and infrared video recordings of 50 captive juvenile Atlantic herring showed that FRT sounds were temporally associated with the appearance of fine bubble streams from the anus or anal duct of individual fishes (see electronic Appendix A). The fish that produced the bubbles appeared otherwise normal during bubble emission.

It is unlikely that FRT sound generation results from swim bladder inflation with gulped or digestive gases or from buoyancy trimming subsequent to inflation. We reached this conclusion following observations that bubbles were vented from the anal duct simultaneously with the occurrence of FRT sounds and that fish denied access to the surface or deprived of food produced these sounds. Instead, we suggest that FRT sound production is associated with gas expulsion from the swim bladder via the anal duct, a form of sound production not, to our knowledge, previously described in fishes. This notion appears to be supported by the reduction in FRT sounds by fishes that have been denied access to the surface for more than one night. This is because these fishes are likely to have under-inflated swim bladders owing to previous FRT production or diffusion of gas from the swim bladder (Blaxter & Batty 1984). Although herring release gas through the anal duct in response to rapid pressure reductions (Brawn 1962), it is unclear why captive fishes in shallow tanks, other than through habit, should vent gas nocturnally to control their buoyancy. Gas venting and associated sounds might instead have other function(s).

The capacity of herring to respond to various underwater sounds is well documented (Schwarz & Greer 1984; Wilson & Dill 2002). Early studies of clupeoids indicated that their auditory range extended to 1 kHz, but more recent work has shown that they can detect sounds at higher, and in some instances considerably higher, frequencies (Mann *et al.* 2001). It is conceivable, therefore, that they can detect FRT sounds made by conspecifics, creating the potential for intraspecific communication. FRT sounds could function in mate location/choice or as alarm calls, but these possibilities are unlikely since the fishes in this study were not in breeding condition, and FRT sounds were not recorded during disturbance for tank maintenance or upon addition of predatory shark odour. Contact calls are more plausible. It is unknown how herring shoal in darkness, when their schools become scattered and less organized, but visual and olfactory cues are unlikely (Blaxter & Parrish 1965). Acoustic communication could allow fishes to maintain contact. Indeed, when different numbers of Pacific herring (1, 5, 10 and
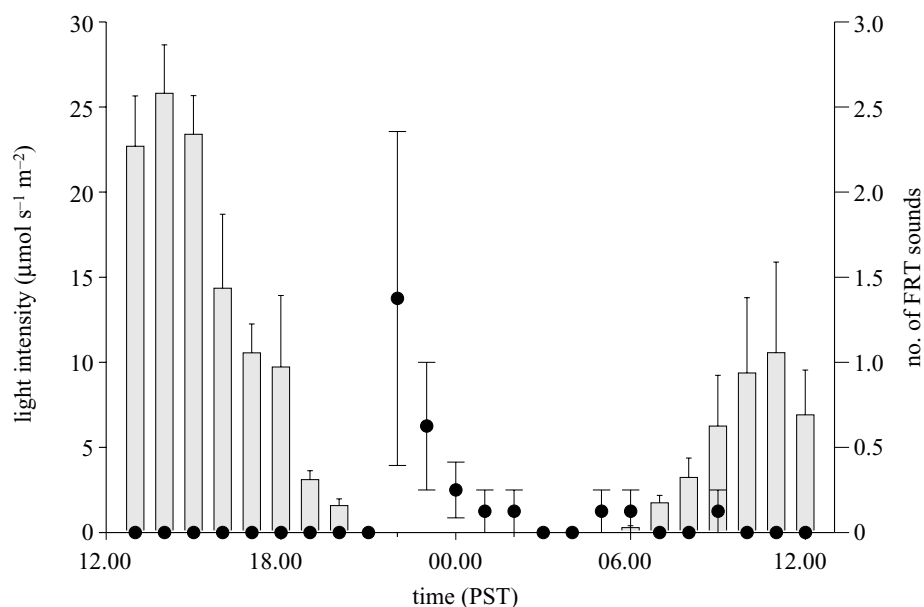
Figure 2. The occurrence of FRT sounds (solid circles) and in-tank light levels (columns). Means ± 1 s.e. The timing of FRT sounds differed significantly from random (Rayleigh test, $r = 0.85$, $p < 0.001$, $n = 8$; Batschelet 1981) during 24 h recordings in July and August 2000. The bulk of FRT sounds occurred after dark, between 23.00 and midnight PST. Recordings were made for 6 minutes every hour. No relationships were found between the occurrence of FRT sounds and oxygen saturation, temperature or salinity ($p = 0.74$, $p = 0.38$, $p = 0.60$, respectively).

30) were held overnight in 500 l tanks, the number of FRT sounds recorded increased disproportionately to the number of fishes present (mean hourly emissions *per capita*: lone fish = 0; 5 fishes = 0.02; 10 fishes = 0.12; 30 fishes = 0.17, OLS regression, $r^2 = 0.46$, $p < 0.001$, $n = 4$ per density treatment), implying that sound production is socially mediated. Calls advertising location would only be advantageous, however, if predators are unable to detect the caller. The unusual frequency structure of the FRT sounds, with most of the energy above 2 kHz, means that they are near or above the known auditory range of most predatory fishes (Fay & Simmons 1999). However, we note that they are well within the detection capabilities of marine mammals.

If herring use sounds to communicate, our understanding of the impacts of anthropogenic noise may require some re-evaluation. Regardless of function, the superficial resemblance of these sounds to those of other marine organisms may necessitate methodological modifications to ensure that herring sounds are not erroneously included in such datasets. By contrast, autonomous acoustic equipment developed to monitor odontocete occurrence (Culik *et al.* 2001) could be adapted to study the presence and abundance of herring. Finally, herring are a major dietary component of many Northern Hemisphere pinniped and cetacean species. Despite considerable efforts to understand how these predators locate prey at sea, our knowledge remains rudimentary. Given the auditory capabilities of these predators, it is conceivable that they use the distinctive herring sounds as foraging cues. Recognition of this cue could give new insight into marine mammal foraging tactics and the impacts of anthropogenic sound pollution on foraging efficiency.

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