MARINE MAMMAL SCIENCE, 21(3):458–475 (July 2005)

THE GUNSHOT SOUND PRODUCED BY MALE NORTH ATLANTIC RIGHT WHALES (*EUBALAENA GLACIALIS*) AND ITS POTENTIAL FUNCTION IN REPRODUCTIVE ADVERTISEMENT

SUSAN E. PARKS[1]
Woods Hole Oceanographic Institution,
Redfield 132, MS 34,
Woods Hole, Massachusetts 02543, U.S.A.
E-mail: sparks@whoi.edu

PHILIP K. HAMILTON
SCOTT D. KRAUS
Edgerton Research Laboratory,
New England Aquarium,
Central Wharf,
Boston, Massachusetts 02110, U.S.A.

PETER L. TYACK
Woods Hole Oceanographic Institution,
Redfield 132, MS 34,
Woods Hole, Massachusetts 02543, U.S.A.

ABSTRACT

North Atlantic right whales (*Eubalaena glacialis*) make a short, distinctive broadband sound that is produced internally called a Gunshot sound. This sound has been recorded in the Bay of Fundy, Canada from both single whales ($n = 9$) and social surface active groups ($n = 49$). Those single whales producing Gunshot sounds whose sex could be determined ($n = 9$) were all mature males. Gunshot sounds were produced as part of a stereotyped behavioral sequence by these individuals, including frequent head-lifts and flipper slapping at the surface. In surface active groups, Gunshot sounds were commonly recorded when males were present in the group. The rate of production of Gunshot sounds was weakly correlated with the total number of males present in the group. Given the behavioral context of Gunshot sound production, and production of the sound only by male whales, Gunshots may function in a reproductive context as an advertisement signal to attract females, an agonistic signal directed toward other males, or a combination of the two functions.

Key words: right whale, *Eubalaena glacialis*, acoustics, communication, male advertisement, Gunshot sound, surface active group, Bay of Fundy.

[1] Current mailing address: Bioacoustics Research Program, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850, U.S.A.

Male acoustic advertisement is common in the mating systems of terrestrial animals where the females are mobile and can seek out mates (Greenwood 1980). In these species, males often make signals that differ from those of females. In baleen whales, both males and females are highly mobile and the mating system is not well understood for any species. The production of distinctive sounds by males has been documented in several large whale species (Payne and McVay 1971, Tyack 1981, Weilgart and Whitehead 1988, McDonald *et al.* 2001, Croll *et al.* 2002), suggesting the possibility that males use sound in reproductive advertisement or intrasexual competition. Little behavioral information exists about sound production related to reproduction in North Atlantic right whales (Kraus and Hatch 2001, Parks 2003*a*) and no information has been published on sounds attributed to males in potentially reproductive contexts. This paper describes behavioral observations and acoustic recordings of a short, intense broadband acoustic signal produced by male North Atlantic right whales (*Eubalaena glacialis*) in the Bay of Fundy, Canada. This sound is referred to as a Gunshot sound because of its acoustic similarity to the sound of a rifle being fired.

The Gunshot sound has been mentioned in previous publications on balaenid whale species including Southern right whales (*Eubalaena australis*) (Clark 1983), North Atlantic right whales (Matthews *et al.* 2001, Laurinolli *et al.* 2003, Parks 2003*b*) and the Bowhead whale (*Balaena mysticetus*) (Würsig and Clark 1993). In Southern right whales, Gunshot sounds were recorded both from single whales and from groups (Clark 1983). The sound has been referred to as a "pulse" (Payne and Payne 1971), "underwater slap" (Clark 1983), and Gunshot (Clark 1983, Clark 1990, Würsig and Clark 1993, Matthews *et al.* 2001, Laurinolli *et al.* 2003) in previous publications. Although the Gunshot sound is acoustically similar to other impulsive sounds, such as the sounds produced from flipper slaps or lobtails (Watkins 1981, Würsig and Clark 1993), it appears to have an internal production mechanism in right whales, with no externally visible movements of flippers, flukes or jaws during the generation of the sound.

There are no published reports of behavior related to the production of this sound in North Atlantic right whales. Earlier results (Parks 2003*a*), and observations described in this paper, indicate that Gunshot sounds do not attract other right whales. Here we describe Gunshot sounds recorded from North Atlantic right whales in two behavioral contexts. These include stereotyped displays by lone adult males and surface active groups (SAGs) (Kraus and Hatch 2001) with multiple whales present.

METHODS

Behavioral Data Collection

Data were collected during summer and autumn vessel-based right whale surveys conducted by the New England Aquarium between 1990 and 2002 and surface active group behavioral observations carried out by S. Parks from 1999 to 2002 in the Bay of Fundy, Canada. The New England Aquarium surveys have been conducted since 1980 in the Bay of Fundy and focused on the identification and distribution of individual right whales in their summer and autumn habitat. Only data from 1990 to 2002 were included in this paper to reflect the survey period with the most consistent documentation of acoustic recordings and behavioral observations. When a right whale was sighted, the survey vessel would approach the whale to collect photographs, document the position of the whale, and then return to the survey transect. During these surveys, additional behavioral data were collected opportunistically, including the documentation of associations between individuals, and video and audio recordings of any behaviors considered noteworthy.

The primary behavioral interaction observed in North Atlantic right whales in the Bay of Fundy is the surface active group (SAG). These groups are defined as two or more animals interacting at the surface, less than one body length apart with frequent physical contact (Kraus and Hatch 2001). The animal at the center of the SAG around which most of the activity appears to be focused is referred to as the focal whale. These focal whales frequently roll upside-down with their bellies exposed at the surface in the center of the group. The focal whale in groups of three or more animals in the Bay of Fundy is typically female while other whales in the groups are generally males (Kraus and Hatch 2001).

Behavioral observations and acoustic recordings of SAGs were made by S. Parks from 1999 to 2002. This study involved finding right whales in SAGs and staying with the group to observe it for as long as possible. Once a group was located, photographs were taken to determine which individuals were involved in the group. Acoustic recordings were made of the sounds produced in the group. Both single hydrophone recordings (1999–2001) and 15-element hydrophone array recordings (2002) were made. Behavioral data collected included changes in group composition resulting from arrivals and departures of individual whales, the identity of the focal animal and the distance of the groups from the recording platform. Recordings of Gunshot sounds from lone whales and SAGs were made during both of these studies.

Individual Identification

Photographs were taken of head callosities, flukes, and any distinguishing body scars of whales to use for individual identification as described in Kraus *et al.* (1986). Photographs were compared to the North Atlantic right whale catalog (Hamilton and Martin 1999) by the New England Aquarium right whale research group in Boston, MA, for identification of individuals. The catalog of individuals includes information on the sex of individuals in the population based on direct observation of the genital area, long-term association with a newborn calf, and genetic typing of tissue samples (Brown *et al.* 1994). Life histories, including age and mother-offspring relatedness are known for most individuals born into the population since 1980 (Hamilton and Martin 1999). This database allowed us to determine the sex and age for the whales observed in this study. Many of the whales in the catalog were first observed as juveniles or adults, so their exact age is unknown. The estimate of age was made from the year of first sighting to provide a minimum estimate of the age of the animals. For example, a whale listed as 12+ yr of age had a 12-yr sighting history and was first sighted as a juvenile or adult. Many of the whales with minimum estimates of age may be much older than the minimum ages reported here. Although little is known about the age of sexual maturity in male right whales, the average age of first parturition for females is 9.5 yr (Kraus *et al.* 2001). For this paper, males were considered to be adult at 9 yr or older.

Acoustic Data Collection

From 1990 to 1998, single hydrophone acoustic recordings were made with a Sonotronics hydrophone and a Marantz Model PMD430 recorder with a flat frequency response from 35 Hz to 17 kHz. Video of behaviors from 1992 to 1998 were made using Sony Hi8 Handycam (Model CCD-TR81). From 1999 to 2002, single hydrophone acoustic recordings were made with an Hi-Tech HTI-94-SSQ hydrophone (frequency response 50 Hz–20 kHz, ±0.5 dB) and a TASCAM DA-P1 DAT recorder (nominal frequency response 20 Hz–20 kHz, ±0.5 dB). Additional acoustic recordings were made with the HTI hydrophone connected directly to a SONY DCR-TRV V900 MiniDV camera to provide synchronized audio and video recordings of the observed behaviors. In the single hydrophone recordings of lone whales, no other whales were visible in the immediate area during the recording period and the recorded sounds were of high intensity, suggesting that the observed individual produced all of the sounds.

In 2002 an array recording system was used to determine direction to a recorded sound consisting of a 3.75-m rigid linear array of 15 Benthos AQ-2TS hydrophones with custom preamps with 40 dB gain. The array design and pre-amps were based on an array design developed for use with killer whales (*Orcinus orca*) (Miller and Tyack 1998). The hydrophones were evenly spaced 0.25 m apart. The array was manually deployed at 5 m depth off the side of a stationary 7-m outboard vessel, the R/V *Callisto* in 2002. The array was originally designed for towing behind a vessel in motion. For this study the array was buoyed with foam spar buoys made of pipe insulation in three evenly spaced points along the length of the array. This maintained a horizontal position of the array in the water while the vessel was stationary during behavioral observations. The signal from each hydrophone was acquired through a low power (30 mW), 15-channel, computer programmable, bandpass filter with adjustable corner frequencies and gain designed by Robert B. MacCurdy, an electrical engineer at the Bioacoustic Research Program at Cornell University (CUBRP). The digital data acquisition set up consisted of a National Instruments PCMCIA DAQCard-6062E (12-bit 500 kS/s sampling) in a Dell Latitude C610 laptop using the program Chickadee developed at CUBRP. Sounds for all channels were acquired at 8 kHz sampling. The beamforming frequency cutoff was 2.5 kHz. Near real time beamforming was carried out in the field to determine the bearing to sound sources during behavioral observations. The CUBRP Matlab Time-Delay Beamformer used acoustic data from four hydrophones in the array and was developed by Kathy Dunsmore and Kurt Fristrup at Cornell University. The same software was used for later processing of saved files to confirm that observed bearings to whales agreed with the calculated bearings to the sounds.

Sound Analysis

Sound analysis was done using Cool Edit Pro (Syntrillium, Adobe). The characteristics of the signal and the rates of production were investigated from all recordings with a high signal-to-noise ratio. Measurements were taken of the number of broadband pulses present in the signal, the timing between pulses and the time between the onset of the sound and the recorded echo off the bottom.

Gunshot sounds recorded from a whale in a known position were analyzed to estimate the source level. The position of the whale was determined using the beamformer to determine bearing to the sound source and using a Leica LRG 800 laser range finder to measure range to the whale at that bearing at the surface. Received level measurements were made using custom written scripts in Matlab 6.5 (Mathworks, Natick, MA, USA). The received level at the Hi-Tech hydrophone (sensitivity −170 dB re: 1V/1 μPa) was calculated relative to a calibration signal with a known 3 kHz RMS voltage level recorded directly into the DAT recorder. Peak-to-peak (p-p) sound pressure level (dB p-p re: 1μPa) was given by the p-p amplitude difference between the signal relative and the p-p value of the calibration signal. The RMS sound pressure level (dB rms re: 1μPa) was calculated by taking the root of the mean pressure squared in a time window *T*. This duration *T* was defined by the sample fraction that generates 90% of the total cumulative energy in a window including the sound pulse (Madsen *et al.* 2004). Source Level (*SL*) and Transmission Loss (*TL*) were estimated for the *RL* of recorded calls by $SL = RL + TL$, where $TL = 20\ \log(r)$ under the assumption of spherical spreading (Urick 1983). Absorption had negligible effect (<1 dB) on the *TL* at the ranges (<500 m) and frequency (<22 kHz) in these measurements and was omitted from the final calculation of *TL*. The maximum range for *SL* measurements was 150 m while the average water depth was 180 m. The hydrophone was deployed at a depth of 5 m to approximate the depth of a whale's ear at the surface. The whales producing the sounds were at or near the surface during sound production. Both the measured *RL* and the calculated *SL* are reported in the results.

Results

Gunshot Sound Description

The Gunshot sound is a brief, intense broadband signal. Measurements were made from 20 Hz to 20 kHz with the upper frequency range limited by the recording equipment. In the Bay of Fundy there was typically an initial signal, presumably the direct path from the whale to the hydrophone, followed by what appears to be an echo with prolonged reverberation of the signal (Fig. 1). The time delay between the signal and the echo ranged in duration from 80 ms to 308 ms with an average delay of 145 ± 57 (SD) ms corresponding to the expected time for the sound to travel twice the depth of the water (120–200 m) to the recording hydrophone which was horizontally 100–500 m away from the whale at the surface assuming a speed of sound of 1,500 m/s, suggesting that the recorded echoes were reflections off the bottom.

Recordings of distant Gunshot sounds often resulted in the appearance of a single, lower frequency signal. The duration of Gunshot sounds with a single pulse averaged 35.8 ± 15 ms ($n = 226$). During calm recording conditions when the whale was within 500 m of the hydrophone, it was possible to detect two to four discrete impulse sounds produced in rapid succession (<100 ms between each pulse) making up the entire sound (Fig. 2b, c). The second or third pulse was often (124/159) more intense than the initial pulse (Fig. 2c). The signal (including 1–4 pulses) ranged in duration from 4 to 279 ms with an average duration of 52.8 ± 36.7 ms ($n = 407$). The delay between individual pulses for Gunshots containing multiple pulses ranged from 10 to 95 ms ($n = 159$, $x = 34.9 \pm 19$ ms). Eleven of the 407 inspected Gunshot sounds had a scraping sound of increasing intensity and frequency proceeding the actual broadband pulse (Fig. 2d) which seems similar to the description of the "cr-unch" sound in bowhead whales (Würsig and Clark 1993).

Gunshot sounds were typically produced singly in SAGs or in bouts of multiple Gunshot sounds by lone whales. Behavioral observations of SAGs and close observations of lone individuals indicate that the sound is produced without hitting the water's surface with a flipper or fluke. The entire body of the whale producing the Gunshot sound has been seen to vibrate or jiggle at the time of sound

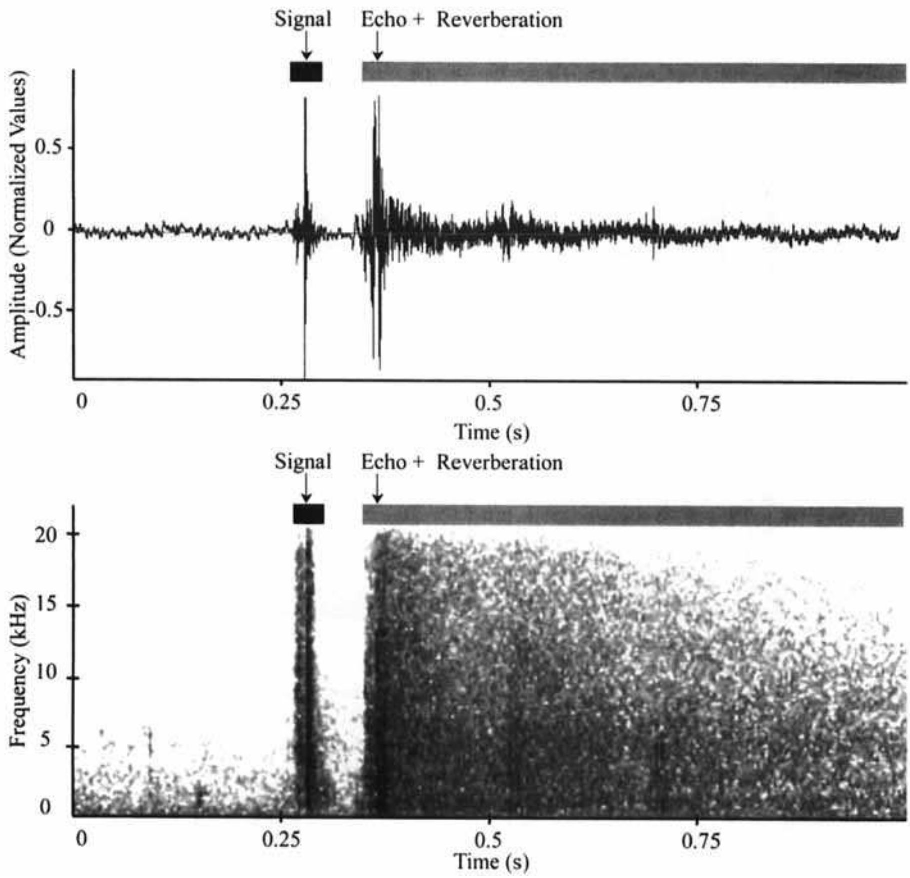

Figure 1. Example of a Gunshot sound recorded from North Atlantic right whales. The top graph shows the waveform of the recorded gunshot. The bottom graph shows the spectrogram of the same sound. This example shows a single impulse signal, followed by an echo and reverberation. The overall duration of the entire sound is 1 s. The times corresponding to each section of the call are marked with a bar showing the signal in black and the echo and reverberation in gray.

production. The best illustration of the difference between Gunshots and other externally produced impulsive sounds comes from the whales that produced both Gunshot sounds and flipper slaps or lobtails. Gunshot sounds are aurally similar to sounds made from flipper slapping (due to their short duration and broadband frequency content), but they generally have energy at higher frequencies and are louder than sounds of flipper slapping when recorded at the same distance from the sound source. Several observations of lone males producing both Gunshot sounds and flipper slaps in sequence highlight these similarities and differences (Fig. 3). The intensity of the Gunshot sound varies during production by a single animal without changes in the relative orientation of the whale to the hydrophone. Sequences of Gunshot sound production occur with lower intensity sounds produced between the most intense sounds (Fig. 4).

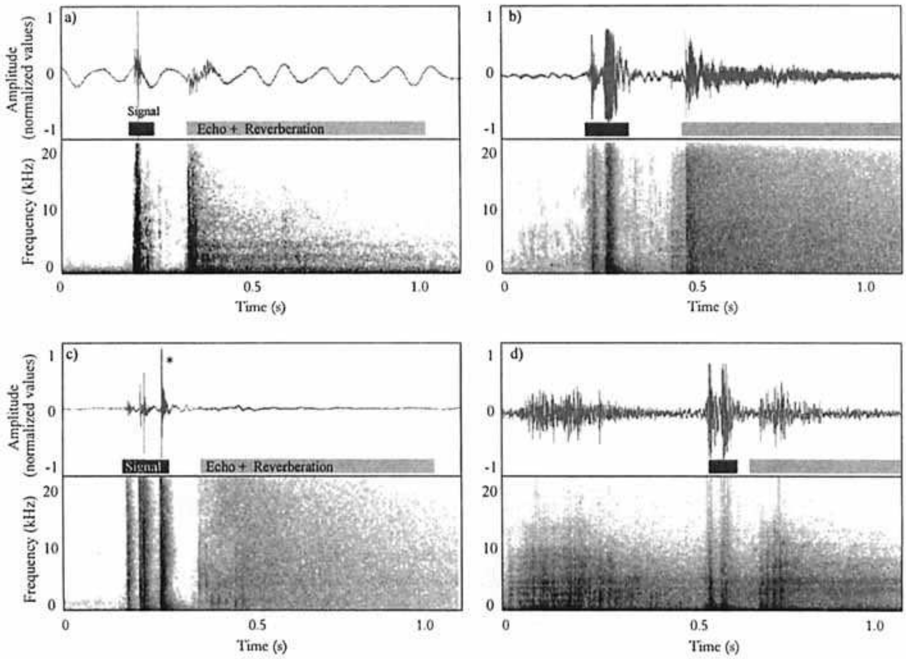

Figure 2. Example of the four types of Gunshot sounds recorded from North Atlantic right whales. Each graph shows the waveform (above) and spectrogram (below) for each signal. Panel a) illustrates a Gunshot sound with a single pulse for the signal and b) illustrates a Gunshot sound with two pulses making up the initial signal. These two types of Gunshot sounds were most common. Panel c) illustrates a Gunshot sound with three pulses in the signal, an * denotes that the intensity of the third impulse in the signal was most intense, and d) shows a two part Gunshot sound with a grating sound produced 50 ms before the signal. For each sound, the time corresponding to the signal is marked in black, and the echo and reverberation are marked in gray.

Source Level

Source level measurements were made only for Gunshot sounds recorded from a whale at a known distance from a calibrated hydrophone. This was limited to two SAG recordings, two measurements from each SAG, where the range to the SAG was known and the Gunshot sound bearing was consistent with the position of the SAG. The actual range to the sound source is likely a few m different than the reported range, due to uncertainty of the location of sound production within the whales and movements of individuals in the SAG. The calculated broadband (20 Hz–22 kHz) SL for the four measurements averaged 196 dB p-p and 189 dB rms re: 1 μPa (Table 1).

Behavioral Contexts

Nine lone male right whales were observed making Gunshot displays in the Bay of Fundy between 1992 and 2002. These nine whales were all adult and ranged in age from 12+ to 26+ yr. These whales were encountered during surveys for right

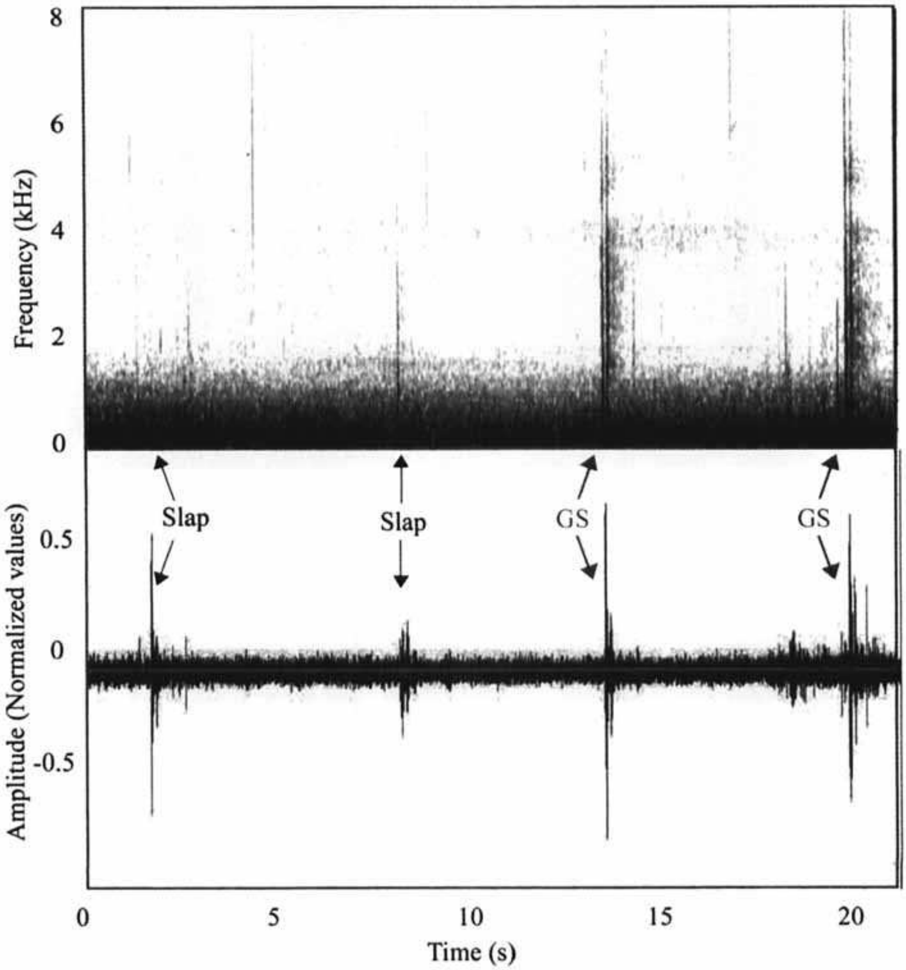

Figure 3. Spectrogram and waveform of flipper slaps and Gunshots recorded from a single whale on 8 August 1994. The flipper slap sounds are noted by the black arrows and "Slap" label. The two Gunshot sounds are noted by the gray arrows and the "GS" label. Note that the Gunshot sound has energy at higher frequencies than the flipper slaps and were generally more intense, though the whale was at the same distance from the hydrophone for production of all four sounds. Note the change in time scale for a total of 20 s for the entire sound. Only the initial signal and echo are visible for each Gunshot sound. The number of pulses in the initial signals cannot be resolved at this scale.

whales in the Bay of Fundy and their distinctive behavior led observers to collect video and acoustic data. One whale was encountered after we heard distant Gunshot sounds on the hydrophone and searched until we found a single whale in the area engaged in distinctive surface behaviors that had been associated with Gunshot sound production. This whale was a male that had been observed in a SAG with one adult female ≈2.8 km away from and 30 min prior to observations of the Gunshot production display. All nine of these males were usually located several kilometers away from other right whales sighted on that day.

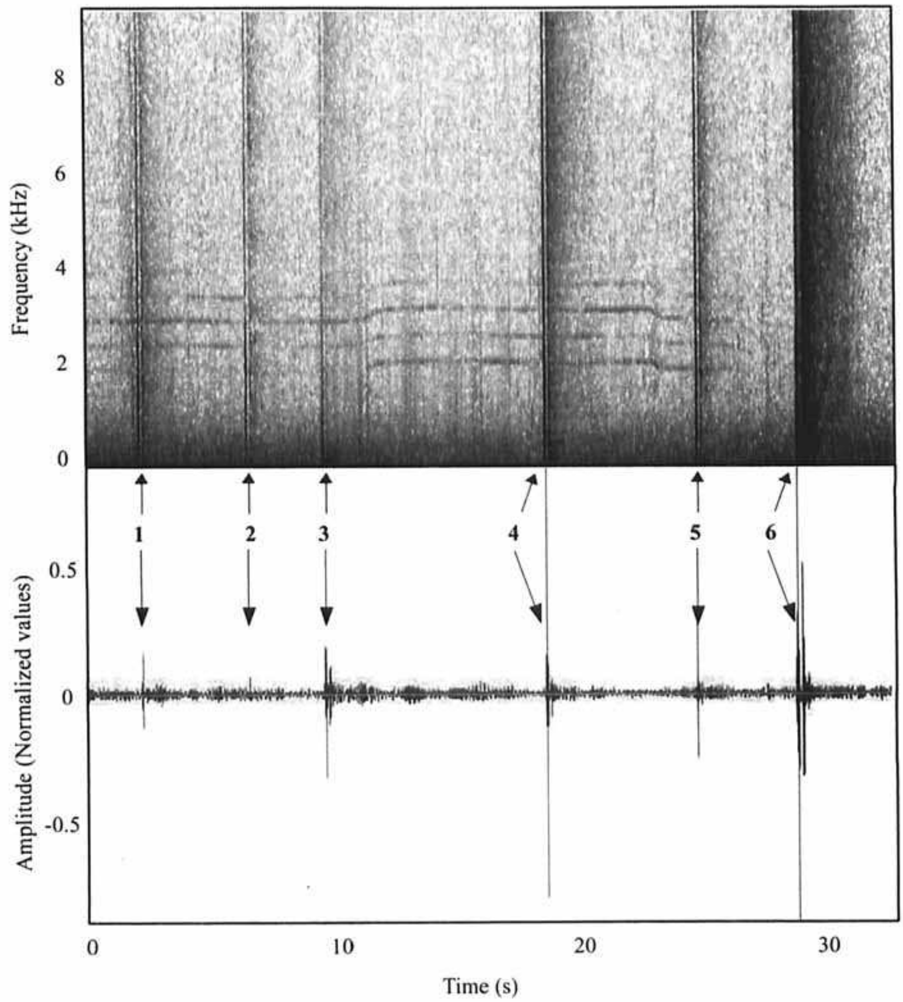

Figure 4. Spectrogram and waveform of a sequence of six Gunshot sounds recorded on 11 August 2000. Each Gunshot is labeled on the waveform. The figure shows the variation in intensity of signals produced by one whale in the same location and orientation to the hydrophone. Note the change in time scale for a total of 35 s for the entire sound. Only the initial signal and echo are visible for each Gunshot sound. The number of pulses in the initial signals can not be resolved at this scale.

Gunshots were produced primarily while the whales were at the surface, with a few produced immediately before surfacing or immediately after diving. Surfacing intervals of lone whales producing Gunshot ranged from 2 to 5 min and dives were generally short (3–10 min). No lone whale was observed to breathe at the same time that Gunshot sounds were recorded from it. Gunshot sounds were not produced by slapping the water with a flipper or a fluke. No movement of a flipper or fluke was ever observed coinciding with the production of Gunshot sounds. This included observations of whales within a body length of the platform. Occasionally

Table 1. Measurements of RL of Gunshot sounds, listing laser range to the whale producing the sounds, the measured received level (peak-to-peak and rms), and the calculated source level all given in dB re: 1 μPa.

Range to whale (m)	Measured received level (peak-to-peak | rms)	Calculated source level (peak-to-peak | rms)
131	159 | 150	201 | 192
131	147 | 143	189 | 185
70	160 | 151	197 | 188
70	159 | 152	196 | 189

the entire body of the whale was seen to shake or ripple at the time a Gunshot sound was produced.

All nine males exhibited similar surfacing behavior patterns during bouts of Gunshot sound production. The typical behavior pattern consisted of a whale at the surface either stationary or moving slowly forward, making head-lifts and a short dive before returning to the surface and repeating the sequence. All nine whales made head-lifts (ranging from one to eight head-lifts per surfacing) where the head and chin were raised out of the water with the rest of the whale's body parallel to the water's surface and then the head was rapidly pulled back into the water. Gunshot sounds were typically produced after a head-lift or while the whales were stationary at the surface. Most head-lifts were followed by very loud, intense Gunshot sounds. The sound occurred after the head was back in the water and did not result from the chin slapping the water's surface. Head-lifts were often made immediately before a dive.

Each whale showed some variation on the basic pattern of surfacing behavior. Two whales arched their peduncle out of the water prior to their dive. Four of the nine whales would flipper slap repeatedly (5–9 times) on each surfacing before rolling over and starting to produce Gunshots. In seven of nine cases, the male would raise his flukes high out of the water, with ¼–⅔ of the tailstock exposed to the air and would sink slowly beneath the surface with very little forward movement on the dive. One whale swam in slow tight circles at the surface while making occasional head-lifts. Another whale made quick tail slaps on the surface immediately before diving.

Tonal calls, including Upcalls, Downcalls, and Scream-like calls (Parks 2003*b*), were documented in all acoustic recordings of lone whales producing Gunshot sounds >5 min in duration (seven of nine observations) (Fig. 5). No other whales were visible from the recording platform during these recordings and no whales were seen to approach the whale producing the Gunshot sounds. These tonal calls coincided with the timing of the short dives of these whales and were likely produced by the same whales that produced the Gunshot sounds at the surface given the intensity of the signal and the lack of other whales sighted in the immediate vicinity.

Two of the nine individuals were observed to moan at the surface, producing a sound audible in air, similar to the mooing sound of a cow. The same sound has been described for southern right whales (Clark 1983). These Moans coincided with an exhalation through the blowholes and they were typically only audible in air with no sound recorded underwater. Occasionally these Moans were detectable both in the air and underwater.

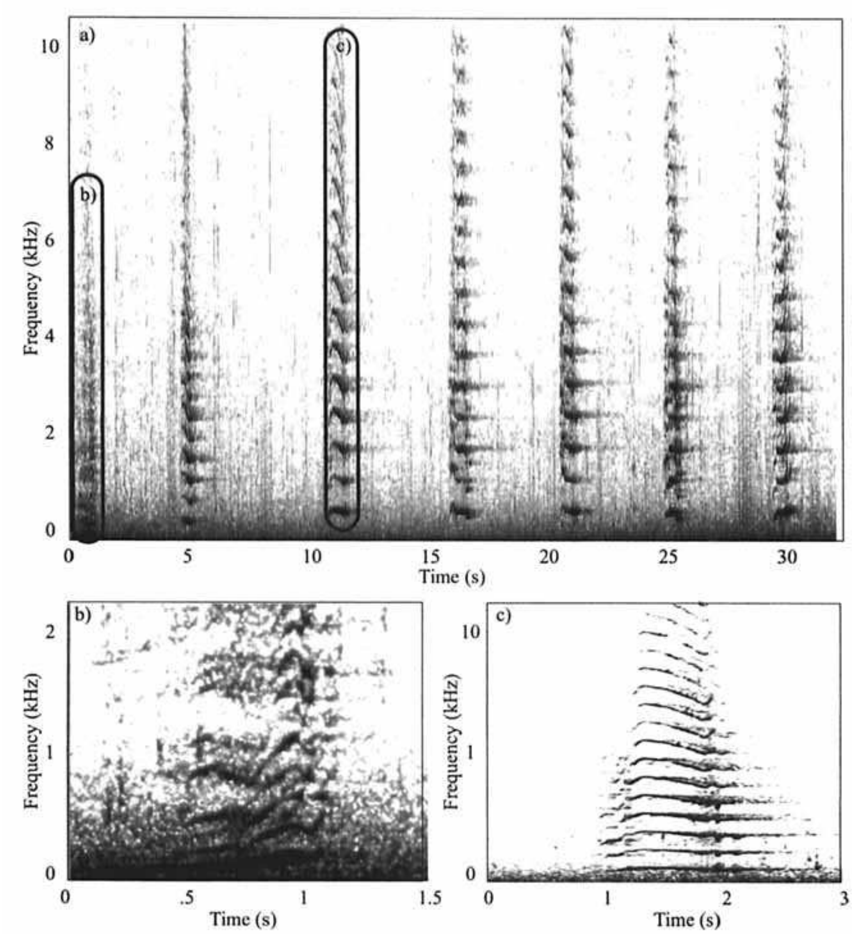

Figure 5. a) Spectrogram of tonal call production recorded on 11 August 2000. Note the first call in the sequence (b) is an Upcall with multiple harmonics. Whales produced "scream-like" calls (c), Upcalls or some combination of both while on dives between surfacings. b) and c) show a more detailed view of calls from the spectrogram a). Note the difference in frequency and time scale for each spectrogram.

Gunshot sounds were recorded from 49 SAGs with at least one male present in the group. On two occasions, no females were present in the SAG when the Gunshot sounds were produced. Video with synched hydrophone recordings were used to determine if Gunshot sounds were produced in SAGs at the same time that the focal female whale was breathing. Videos from 20 of the 49 SAGs, totaling 348 min of observation time were scored, resulting in 107 documented Gunshot sounds. The focal female was observed to breathe 232 times in the video. There were 31 instances of the focal female breathing when Gunshot sounds were being produced. Although the precise mechanism of sound production is not known for any baleen whale, the absence of any observations of individual whales simultaneously producing calls or Gunshots while breathing (Clark 1982) is taken to indicate that all sounds, other than Moans, are produced when the whales are not breathing. These observations indicate that males produce some of the Gunshot sounds in these groups, but do not exclude the possibility that females also produce Gunshot sounds in SAGs. The number of whales in the group was related to Gunshot sound production. The maximum number of Gunshots recorded per min was significantly correlated to the number of males present in the SAG ($r = 0.508$, $P = 0.025$). In small SAGs consisting of a male-female pair Gunshot sounds were uncommon and were recorded from only one out of four observed pairs. Gunshots were recorded in four of four observed male-male SAG pairs. Gunshot sounds were recorded from 44 of 49 SAGs consisting of three or more whales.

Discussion

The Gunshot Sound

The Gunshot sound is a distinctive and intense broadband sound produced by North Atlantic right whales. The observations described in this paper indicate an internal mechanism for production. Gunshot sounds have only been reported in balaenid whales, including North Atlantic right whales, southern right whales, and bowhead whales. There may be unique anatomical features of these species from the balaenid group, distinct from other baleen whale species, which could explain the production of this distinct sound.

The information on the timing of the multiple pulses of the sound, the intensity of the sound, and the production of the sound at or near the water's surface may provide clues to the mechanism of sound production. Multiple impulses were frequently recorded for the Gunshot signals (Fig. 2b–d). These multiple pulses were distinct from the secondary echo that was recorded for many of these sounds. The timing of these pulses was such that they likely represent true signals, rather than some artifact of the recording environment (*i.e.*, multipath arrivals at the hydrophone from surface or bottom reflection). Toothed whales, such as the sperm whale, produce multiple pulses within a click by multiple reflections within the sound production organ of a single initial impulse (Madsen *et al.* 2002). This does not appear to be the case for the multiple pulses of Gunshots, however, for the average interpulse interval of 35 ms is too long to be from internal reflections. Their timing is also more variable and the second or third pulse was often more intense than the initial signal even when the whale maintained the same orientation with respect to the hydrophone (Fig. 2c). This suggests that each new pulse of the Gunshot is created by an additional movement of the sound generator in right whales, rather than by internal reflections of a single sound impulse. Further studies will be needed to determine the precise production mechanism of this sound, as well as the directional characteristics of the signal.

Sex Differences in Production

Only adult male right whales have been observed producing Gunshot sounds in the Bay of Fundy, both alone and in multi-whale surface active groups (SAGs). No other whales were sighted in the vicinity of the recording platform during recording of lone males producing Gunshot sounds. In SAGs it was difficult to assign sound production to a single individual because the whales in the group are in close body contact, but males often showed behavioral cues (*i.e.*, head-lifts) coinciding with the production of Gunshot sounds. To date, there have been no observations of females producing Gunshot sounds in the North Atlantic. The sex ratio of right whales is approximately 1:1 (Brown *et al.* 1994), and both males and females are commonly sighted in the Bay of Fundy. All of the recordings of Gunshot sound production made in this study were of male right whales indicating that, at least in the Bay of Fundy, males are the predominant sex producing this sound. Clark (1983) reported a female Southern right whale producing Gunshot sounds when her calf was approached by another adult whale. This sex difference in sound use may have implications for the functional use of the sound in this species.

Potential Functions of the Gunshot Sound

There are several potential functions for an intense broadband signal such as the Gunshot sound including using the sound to stun prey; for echolocation to locate prey or other whales; or to communicate with conspecifics in social situations. The prey of right whales in the Bay of Fundy consists primarily of *Calanus finmarchicus*, a copepod (Baumgartner *et al.* 2003). It is unlikely that right whales would need to use sound to stun their relatively slow moving prey nor is there any evidence that a SL of 201 dB p-p re: 1 μPa is sufficient to affect copepods. Therefore the more plausible functions are echolocation or social communication.

Right whales could use the Gunshot sounds for echolocation. Information about the water column and bottom topography is certainly contained in the echoes and reverberation of these signals. Suggested functions of echolocation in whales include location of patches of prey, navigating by using information about the bottom topography (Tyack and Clark 2000) or locating silent whales in the area (Frazer and Mercado III 2000). Behavioral observations of whales during sound production do not support the theory that the whales are actively using the information from the Gunshot sounds for any of these echolocation purposes. The lone males producing Gunshot sounds made brief dives between surfacing intervals and spent the majority of their time at the surface. Whales producing Gunshot sounds in SAGs also spent the majority of the time at the surface and were often engaged in the SAGs for several hours. The whales do not appear to be feeding or traveling in either of these situations, making the use of the Gunshot sound to locate prey or to navigate unnecessary.

The Gunshot sounds could be used by males to locate silent female right whales by echolocation. This has been suggested as a potential function of humpback whale (*Megaptera novaeangliae*) song (Frazer and Mercado III 2000). Acousticians have questioned whether baleen whale sounds are appropriate for locating other whales (Au *et al.* 2001). Our behavioral observations also suggest echolocation of conspecifics to be an unlikely function for the Gunshot sound in the Bay of Fundy. Both male and female right whales are regularly sighted alone in the Bay of Fundy, making it impossible to distinguish gender from group or target size. Females in large groups such as SAGs would likely already be acoustically advertising their presence by scream calls (Kraus and Hatch 2001, Parks 2003*a*), eliminating the need for active echolocation on the part of a male to locate them. Females nursing calves on the summer feeding grounds have never been documented giving birth to a calf the following year (Kraus *et al.* 2001). Therefore it would not be advantageous for males to mate with females with young calves. Given these observations, it is unlikely that a male would be able to distinguish males from sexually receptive females if they used Gunshot sounds for echolocation.

The Gunshot sound likely functions for communication with other right whales. The observation that only adult male right whales have been recorded producing this sound in the Bay of Fundy has led to the hypothesis that the sound plays a role in reproduction. Reproduction is poorly understood in right whales and information on the breeding season and location for this species remains unknown (Kraus and Hatch 2001). The disproportionately large testes found in mature male right whales has been taken to indicate that sperm competition may be part of the mating system (Brownell and Ralls 1986). SAGs are also thought to play a role in reproduction and have been observed throughout the known range of the North Atlantic right whale (Kraus and Hatch 2001). Females produce calls in SAGs which attract multiple males to the group (Kraus and Hatch 2001, Parks 2003*a*). The Gunshot sound may represent a male acoustic signal used in reproductive contexts.

Use of sound in reproduction is common in many species, particularly in the marine environment where visibility is limited. A single acoustic signal can have more than one target audience. The most commonly known example is that of song in birds, where males can use song to advertise their willingness to defend territory and to attract females at the same time (Catchpole and Slater 1995). This type of dual-function acoustic signal has also been described in mammalian species, with the roaring by male red deer prior to fights thought to allow males to assess one another and to allow females to assess male quality from a distance (Clutton-Brock and Albon 1979, Clutton-Brock *et al.* 1982, McComb 1991).

Humpback whale song is the best-studied example of male advertisement for baleen whales. Humpback whale song has been well described in the literature over the past 30 yr and there have been many hypotheses proposed for its function (Payne and McVay 1971, Winn and Winn 1978, Hafner *et al.* 1979, Guinee *et al.* 1983, Payne *et al.* 1983, Cato 1991, Helweg *et al.* 1992, Frazer and Mercado III 2000). Like the right whale Gunshot sound, humpback whale song has been only been documented in males. Two major hypotheses proposed for the function humpback whale song are to attract females to the singer through male advertisement (Payne and McVay 1971, Tyack 1981) or for male-male interactions to establish dominance rankings (Darling and Bérubé 2001). The Gunshot sound may serve similar functions either as a reproductive advertisement display directed at females or as an agonistic signal directed at other males. Given the two distinct behavioral contexts of Gunshot sound production by males, both alone and in SAGs, it is possible that the sound may serve multiple functions.

The reproductive advertisement hypothesis is supported by the displays of eight different lone mature adult male right whales. The similarity in the patterns of behavior and sound production between individuals suggests that it is a common display used by multiple individuals. Even though each individual showed behaviors that were unique to his display, the overall pattern of short dives, production of a series of Gunshot sounds and the production of tonal calls, were observed for each male. Females may be able to assess male quality from a distance by listening to these sounds and use some aspect of the display, such as the tonal calls produced on the dives, for later individual recognition. A current weakness of this hypothesis is the lack of observation of females approaching these lone males. In SAGs, females may be able to assess males within a SAG by some characteristics of the Gunshot sounds that they produce in the group. The position of the males producing Gunshot sounds in the SAG relative to the location of the female is currently unknown, and a more detailed analysis of behavior in SAGs may provide more insight into this aspect of behavior.

The Gunshot sounds could also be explained as a male-male agonistic signal. Observations of Gunshot sound use in SAGs agrees with the previously proposed function as an agonistic threat sound (Clark 1983, Würsig and Clark 1993). Males in SAGs are competing to get close to the female in the center of the group, presumably for access to mating (Kraus and Hatch 2001). In this situation males may be using the Gunshot sounds to threaten other males in the group. Gunshot sounds produced by lone males may serve as acoustic displays directed at other distant males, giving indication of male quality, size or willingness to defend a particular location in space.

The Gunshot sound is very loud and therefore may function offensively to cause physical discomfort or pain for competing males. This agonistic function has been suggested for higher intensity impulsive sounds produced by dolphin (220+ dB p-p re: 1 μPa) and sperm whales (235 dB rms re: 1 μPa), both in the context of stunning prey and causing discomfort in conspecifics (Norris and Møhl 1983, Weilgart and Whitehead 1988). The main problem with this hypothesis is the use of the Gunshot sound in SAGs with females present. Unless Gunshot sounds are highly directional, the female of the group would also be subject to the painful effects of such a loud sound. The calculated SL for the Gunshot sound in this paper (185–192 dB rms re: 1 μPa) is less than the intensity of 1-s tonal signals that caused masked temporary threshold shifts in dolphins (*Tursiops truncatus*) and white whales (*Delphinapterus leucas*) (192–201 dB rms re: 1 μPa) but is comparable to levels that altered the behavioral response of the test subjects (178–196 dB rms re: 1 μPa) (Schlundt *et al.* 2000).

It seems likely that the actual function of this sound encompasses one or both of the proposed functions of male reproductive advertisement and male-male agonistic signaling. The production of Gunshot sounds may allow for female assessment of male quality and for direct agonistic acoustic threats between males. Although Gunshots have been recorded in other North Atlantic habitats, the behavioral context in which these sounds are produced outside of the Bay of Fundy remains to be determined. The Bay of Fundy is thought to be used primarily as a feeding area and the potential reproductive function of the Gunshot sound in this habitat is puzzling, unless it marks the beginning of a prolonged mating season or functions for long-term establishment of male dominance hierarchies. This would suggest that these whales can identify individuals producing the displays and remember the results of contests for months or years. The North Atlantic right whale population is very small and it is possible that individuals may exhibit seasonally aberrant behavior resulting from inbreeding or isolation of the population. Targeted behavioral research focusing on the Gunshot sound should be carried out to further describe this behavior, both in terms of production and characteristics of the sound and the behavioral role that the sound plays in right whale communication. To get a better sense of the function of the lone displays, it would be useful to follow one of these males for the entire duration of the social interactions preceding and following Gunshot displays to determine whether other whales join the male, the male joins another group of whales or if the male ends the display and moves out of the area. The geographic positioning of lone males making Gunshot displays and the distribution of other whales in relation to these whales may also help determine the function of this signal. Additional studies should include playback of these Gunshot sounds to both male and female right whales of different reproductive status to determine if there are differences in response. The description of the functional use of this sound will hopefully aid in our understanding of the social structuring in this endangered species.

Acknowledgments

These data were collected with extensive field assistance from the researchers at the New England Aquarium right whale research group. Life history data were provided with permission from the North Atlantic Right Whale Consortium. Both the field recordings and the photo identification were due in a large part to the contributions of the following people: K. Carson, J. Ciano, L.Conger, T. Fraiser, C. Harper, A. Knowlton, B. Kraus, K. Lasko, S. Martin, M. Marx, H. Pettis, and B. Pike. E. Lilly, K. Fristrup, and one anonymous reviewer provided useful comments on early versions of this paper. P. T. Madsen provided advice and assistance in the RL measurements. Funding for the surface active group research was provided by the National Fish and Wildlife Whale Conservation Fund and the Northeast Consortium. This research was conducted under U.S. permit NMFS #1014 and was approved by the WHOI Institutional Animal Care and Use Committee. This is contribution #11107 at the Woods Hole Oceanographic Institution.

Literature Cited

AU, W. W. L., A. S. FRANKEL, D. A. HELWEG AND D. H. CATO. 2001. Against the humpback whale sonar hypothesis. I.E.E.E. Journal of Oceanic Engineering 26:295–300.

BAUMGARTNER, M. F., T. V. N. COLE, R. G. CAMPBELL, G. J. TEEGARDEN AND E. G. DURBIN. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. Marine Ecology Progress Series 264:155–166.

BROWN, M. W., S. D. KRAUS, D. E. GASKIN AND B. N. WHITE. 1994. Sexual composition and analysis of reproductive females in the North Atlantic right whale, *Eubalaena glacialis*, population. Marine Mammal Science 10:252–265.

BROWNELL, R. L. J., AND K. RALLS. 1986. Potential for sperm competition in baleen whales. Report of the International Whaling Commission (Special Issue 8):97–112.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird song: Biological themes and variations. Cambridge University Press, Cambridge, England.

CATO, D. H. 1991. Songs of humpback whales: The Australian perspective. Memoirs of the Queensland Museum 30:277–290.

CLARK, C. W. 1982. The acoustic repertoire of the southern right whale, a quantitative analysis. Animal Behavior 30:1060–1071.

CLARK, C. W. 1983. Acoustic communication and behavior of the southern right whale. Pages 163–198 *in* R. S. Payne, ed. Communication and behavior in whales. Westview Press, Boulder, CO.

CLARK, C. W. 1990. Acoustic behavior of mysticete whales. Pages 571–584 *in* J. A. Thomas and R. A. Kastelein. Sensory abilities of cetaceans. Plenum Press, New York, NY.

CLUTTON-BROCK, T. H., AND S. D. ALBON. 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145–169.

CLUTTON-BROCK, T. H., F. E. GUINNESS AND S. D. ALBON. 1982. Red deer behavior and ecology of two sexes. The University of Chicago, Chicago, IL.

CROLL, D. A., C. W. CLARK, A. ACEVEDO, B. TERSHY, S. FLORES, J. GEDAMKE AND J. URBAN. 2002. Only male fin whales sing loud songs. Nature 417:809.

DARLING, J. E., AND M. BÉRUBÉ. 2001. Interactions of singing humpback whales with other males. Marine Mammal Science 17:570–584.

FRAZER, L. N., AND E. MERCADO III. 2000. A sonar model for humpback whale song. IEEE Journal of Oceanic Engineering 25:160–182.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

GUINEE, L. N., K. CHU AND E. M. DORSEY. 1983. Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). Pages 59–80 *in* R. S. Payne, ed. Communication and behavior of whales. Westview Press, Boulder, CO.

HAFNER, G. W., C. L. HAMILTON, W. W. STEINER, T. J. THOMPSON AND H. E. WINN. 1979. Signature information in the song of the humpback whale. Journal of the Acoustical Society of America 66:1–6.

HAMILTON, P. K., AND S. M. MARTIN. 1999. A catalog of identified right whales from the Western North Atlantic: 1935 to 1997. New England Aquarium, Boston, MA.

HELWEG, D. A., A. S. FRANKEL, J. R. MOBLEY AND L. M. HERMAN. 1992. Humpback whale song: Our current understanding. Pages 459–483 *in* J. A. Thomas, R. A. Kastelein and A. Y. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, NY.

KRAUS, S. D., AND J. J. HATCH. 2001. Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). The Journal of Cetacean Research and Management (Special Issue) 2:237–244.

KRAUS, S. D., K. E. MOORE, C. A. PRICE, M. J. CRONE, W. A. WATKINS, H. E. WINN AND J. H. PRESCOTT. 1986. The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Report of the International Whaling Commission (Special Issue 10):145–151.

KRAUS, S. D., P. K. HAMILTON, R. D. KENNEY, A. R. KNOWLTON AND C. K. SLAY. 2001. Reproduction parameters of the North Atlantic right whale. The Journal of Cetacean Research and Management (Special Issue) 2:231–236.

LAURINOLLI, M. H., A. E. HAY, F. DESHARNAIS AND C. T. TAGGART. 2003. Localization of North Atlantic right whale sounds in the Bay of Fundy using a sonobuoy array. Marine Mammal Science 19:708–723.

MADSEN, P. T., R. PAYNE, N. U. KRISTIANSEN, M. WAHLBERG, I. KERR AND B. MØHL. 2002. Sperm whale sound production studied with ultrasound time/depth-recording tags. The Journal of Experimental Biology 205:1899–1906.

MADSEN, P. T., I. KERR AND R. PAYNE. 2004. Source parameter estimates of echolocation clicks from wild pygmy killer whales (*Feresa attenuata*) (L). Journal of the Acoustical Society of America 116:1909–1912.

MATTHEWS, J. N., S. BROWN, D. GILLESPIE, M. JOHNSON, R. MCLANAGHAN, A. MOSCROP, D. NOWACEK, R. LEAPER, T. LEWIS AND P. TYACK. 2001. Vocalisation rates of the North Atlantic right whale (*Eubalaena glacialis*). Journal of Cetacean Research and Management 3:271–282.

MCCOMB, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. Animal Behaviour 41:79–88.

MCDONALD, M.A., J. CALAMBOKIDIS, A. M. TERANISHI AND J. A. HILDEBRAND. 2001. The acoustic calls of blue whales off California with gender data. Journal of the Acoustical Society of America 109:1728–1735.

MILLER, P. J., AND P. L. TYACK. 1998. A small towed beamforming array to identify vocalizing *resident* killer whales (*Orcinus orca*) concurrent with focal behavioral observations. Deep-Sea Research 45:1389–1405.

NORRIS, K. S., AND B. MØHL. 1983. Can odontocetes debilitate prey with sound? The American Naturalist 122:85–104.

PARKS, S. E. 2003*a*. Response of North Atlantic right whales (*Eubalaena glacialis*) to playback of calls recorded from surface active groups in both the North and South Atlantic. Marine Mammal Science 19:563–580.

PARKS, S. E. 2003*b*. Acoustic communication in the North Atlantic right whale (*Eubalaena glacialis*). Ph.D. thesis, MIT-WHOI Joint Program in Oceanography, Woods Hole, MA. 244 pp.

PAYNE, R. S., AND S. MCVAY. 1971. Songs of humpback whales. Science 173:585–597.

PAYNE, R. S., AND K. PAYNE. 1971. Underwater sounds of southern right whales. Zoologica 58:159–165.

PAYNE, K., P. TYACK AND R. PAYNE. 1983. Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. Pages 9–57 *in* R. Payne, ed. Communication and behavior of whales. Westview Press, Boulder, CO.

SCHLUNDT, C. E., J. J. FINNERAN, D. A. CARDER AND S. H. RIDGWAY. 2000. Temporary shift in masked hearing thresholds of bottlenose dolphins, *Tursiops truncatus*, and white whales, *Delphinapterus leucas*, after exposure to intense tones. Journal of the Acoustical Society of America 107:3496–3508.

TYACK, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology 8:105–116.

TYACK, P. L., AND C. W. CLARK. 2000. Communication and acoustic behavior of dolphins and whales. Pages 156–224 *in* W. W. L. Au, A. N. Popper and R. R. Fay, eds. Hearing by whales and dolphins. Springer-Verlag, New York, NY.

URICK, R. J. 1983. Principles of underwater sound. Peninsula Publishing, Los Altos, CA.

WATKINS, W. A. 1981. Activities and underwater sounds of fin whales. Scientific Reports of the Whales Research Institute, Tokyo 33:83–117.

WEILGART, L. S., AND H. WHITEHEAD. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 66:1931–1937.

WINN, H. E., AND L. K. WINN. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Marine Biology 47:97–114.

WÜRSIG, B., AND C. W. CLARK. 1993. Behavior. Pages 157–199 *in* J. J. Burns, J. J. Montague and C. J. Cowles, eds. The bowhead whale. Special Publication Number 2, The Society for Marine Mammalogy, Lawrence, KS.

Received: 1 April 2004
Accepted: 5 January 2005