

RESPONSE OF NORTH ATLANTIC RIGHT WHALES
(*EUBALAENA GLACIALIS*) TO PLAYBACK OF
CALLS RECORDED FROM SURFACE ACTIVE
GROUPS IN BOTH THE NORTH AND
SOUTH ATLANTIC

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ABSTRACT

The surface active group (SAG) is the most obvious social interaction of the North Atlantic right whale (*Eubalaena glacialis*). SAGs are typically composed of an adult female with two or more males engaged in social behavior near the surface. Distinct calls, believed to be produced by the female, are associated with these groups. Calls recorded from three North Atlantic right whale SAGs and three South Atlantic right whale (*Eubalaena australis*) SAGs were played back to North Atlantic right whales to determine if these sounds are sufficient to attract males to the groups. Playbacks of gunshot sounds produced by North Atlantic right whales were used as a control stimulus. Thirty-six trials were carried out from 1999 to 2001 in the Bay of Fundy, Canada. Whales approached 27 of 31 SAG playbacks and 0 of 5 gunshot playbacks. Where sex was determined ($n = 28$), all approaches to North Atlantic SAG recordings were by males. Individuals ($n = 22$) of all age and sex classes approached South Atlantic SAG playbacks. These trials indicate that SAG calls from both populations are sufficient to attract right whales to SAGs and that males and females respond differently to stimuli from the North Atlantic. The difference in response to North and South Atlantic SAG stimuli was unexpected. Novelty, species differences in calls, and different seasonal or behavioral context for the recorded stimuli may be responsible for the differences in response.

Key words: reproduction, *Eubalaena glacialis*, right whale, playback, baleen whale, surface active group.

The North Atlantic right whale (*Eubalaena glacialis*) population migrates along the east coast of the United States from northern waters in the Gulf of Maine in the spring and summer to the waters off the states of Florida and Georgia in the winter (Winn *et al.* 1986). Despite protection from whaling for the past 60 yr, current estimates indicate that fewer than 300 North Atlantic right whales remain

(Knowlton *et al.* 1994, IWC 2001), making them one of the most endangered large whale species in the world. All individuals in the population can be identified based on individually distinctive external features, such as callosity patterns on the head or scars on the body and tail (Kraus *et al.* 1986). Long-term studies relying on photographic identification of individuals have provided data on many life history parameters for individuals in the population and reproductive history for all females born since 1980 (Kraus *et al.* 2001, Brown *et al.* 1994). Demographic information this detailed is rare for a baleen whale species; it enables studies of behavioral interactions among known individuals in a wild population. Each summer up to two-thirds of the known population of North Atlantic right whales congregate in the Bay of Fundy, Canada, to feed (23–199 individuals from 1980–1998, IWC 2001; with 173, 154, and 123 for 1999, 2000, and 2001, respectively, Right Whale Consortium data catalog¹). The high concentration of known individuals in a small area makes this an ideal location to study social behavior.

Little is known about reproductive behavior in the right whale or any other baleen whale species. Observations of social groups in several species of coastal baleen whale indicate possible similarities in social and sexual behavior. In particular, distinctive sounds have been associated with surface active groups in North Atlantic right, South Atlantic right (*Eubalaena australis*), bowhead (*Balaena mysticetus*), gray (*Eschrichtius robustus*), and humpback (*Megaptera novaeangliae*) whales (Clark 1983, Norris *et al.* 1983, Silber 1986, Würsig and Clark 1993, Kraus and Hatch 2001).

Male right whales have disproportionately large testes (900+ kg, Omura *et al.* 1969): the largest for any mammal and the largest as a percentage of body weight for any baleen whale (Brownell and Ralls 1986). Large testis size has been linked to sperm competition in a variety of mammalian species (*e.g.*, Harcourt *et al.* 1981, Kenagy and Trombulak 1986, Møller 1989), suggesting that sperm competition plays a role in right whale reproduction (Brownell and Ralls 1986). One of the most obvious social groupings of North Atlantic right whales, surface active groups (SAGs), often involves a single adult female, referred to as the focal female, surrounded by up to 34 males maneuvering to approach the female (Kraus and Hatch 2001). Observations of behavior in the SAGs support the theory for sperm competition, as the interactions between males in the groups are generally only mildly aggressive and multiple males have been observed to achieve intromission with the same female in these groups (Brownell and Ralls 1986). Adult males appear to be highly motivated to join these groups and can detect and locate them from great distances. Male right whales have been observed joining these groups by swimming rapidly from up to 8 km away at speeds up to 15 km/h (Kraus and Hatch 2001). The adult sex ratio of this population is close to 1:1 (Brown *et al.* 1994), but the calving interval for females is approximately 4 yr, so there are potentially four adult males for every receptive female during the mating season. The intercalving interval in this population has increased from an average of 3.7 yr during 1980–1992 to over 5 yr during 1993–1998 (Kraus *et al.* 2001), further widening the sex ratio between sexually receptive females and males. All of these characteristics suggest that sperm competition and possibly female incitation of male-male competition may characterize the reproduction in this endangered species.

¹ Right Whale Consortium data catalog is maintained by the New England Aquarium, Right Whale Research Group, Boston, MA.

Particular calls are associated with SAGs in North Atlantic right whales. Calls recorded by the New England Aquarium from eight SAGs in the 1980s lasted from 0.5 to 2.8 sec, ranged in frequency from 400 to 3,200 Hz, and occurred, on average, at a rate of 12 per min (Kraus and Hatch 2001). An example of sounds recorded from a surface active group in the Bay of Fundy in 2000 by the author is shown in Figure 1. These bouts of high rates of calling are typically broken up by periods of silence, often associated with the entire group diving beneath the surface for periods of 10 min or more. It is likely that approaching whales use the sounds produced in these groups to locate them. Indirect evidence suggests that the SAG calls are produced by the focal female to attract males, thereby increasing the number of males competing for access to the female. The evidence for this includes: on all recordings of SAGs in which only a single female was present, single SAG calls were heard only alone and never simultaneously, no instances of calls being made while the focal female whale was breathing, and the cessation of call production with the departure of the focal female (Kraus and Hatch 2001). Although calls are thought to be produced by only one individual within each SAG, the fundamental frequency, duration, and modulation of individual calls are variable (Fig. 1b, c).

Observational evidence suggests that male North Atlantic right whales produce gunshot-like sounds. This sound has yet to be recorded from female North Atlantic right whales. Little background information exists for this behavior in right whales. Gunshot sounds, characterized by a very short intense broadband cracking sound usually followed by a strong echo off the bottom in the Bay of Fundy (Fig. 1d), have been recorded in SAGs and from lone male animals in the population. In SAGs, multiple animals appear to be making gunshot sounds as they overlap calls and/or other gunshot sounds. These sounds are produced by whales that are either alone or in SAGs without any visible flipper or fluke movement, and they are acoustically distinct from flipper slaps, lobtailing, or breaching. A similar sound has been documented both in southern right whales and bowhead whales (Clark 1983, Würsig and Clark 1993), and it has been suggested that the sound is produced in agonistic displays (Clark 1983). Gunshot sounds produced by lone animals in the Bay of Fundy do not appear to attract any other right whales. Recordings of gunshot sounds being produced by lone males ($n = 3$), coupled with the observation of gunshot sounds in surface active groups with multiple males competing for access to a centralized female ($n = 31$), suggest that the gunshot sound functions as a threat or agonistic display. Unlike calls that have been recorded only in SAGs, gunshot sounds are produced during two very different social states (lone males *vs.* whales in a SAG), therefore these sounds should be a less reliable cue that a SAG is taking place.

Playback experiments have been used to study many different aspects of communication and behavior in marine mammals over the past three decades, including playbacks of natural sounds to southern right whales (Clark and Clark 1980), humpbacks (Tyack 1983, Frankel *et al.* 1995), and gray whales (Cummings and Thompson 1971). Playbacks of sounds recorded from SAGs to North Atlantic right whales make it possible to confirm that the sounds in the groups attract other whales. Sexually mature males appear to be highly motivated to approach SAGs with females and are predicted to approach any sound that might indicate the presence of such a group. Females are predicted to not approach playbacks of SAG calls. It is possible that males locate these groups by detecting a variety of sounds associated with SAGs, such as calls, gunshot sounds, and loud, audible underwater blow sounds. The purpose of this experiment was to determine if the calls produced

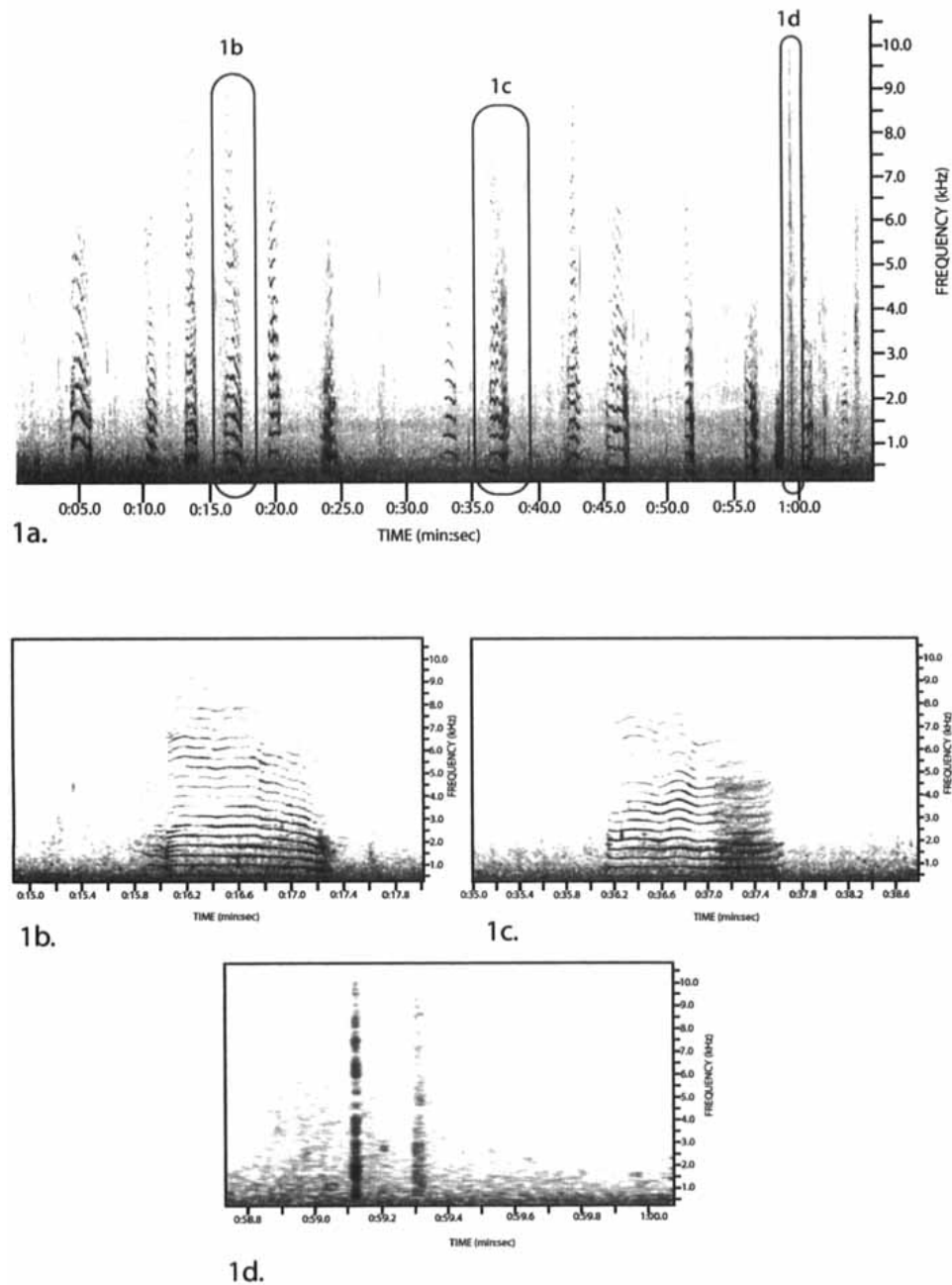


Figure 1. Four spectrograms showing examples of North Atlantic right whale surface active group calls: (a) a sequence of right whale calls and gunshot sounds recorded from a North Atlantic right whale surface active group in August 2000, (b) one call from the sequence shown in (a), (c) another call from the sequence shown in (a) to illustrate the variability of calls believed to be produced by one individual from a single surface active group, and (d) a gunshot sound taken from the sequence of calls in (a) to illustrate the presence of these sounds in surface active groups.

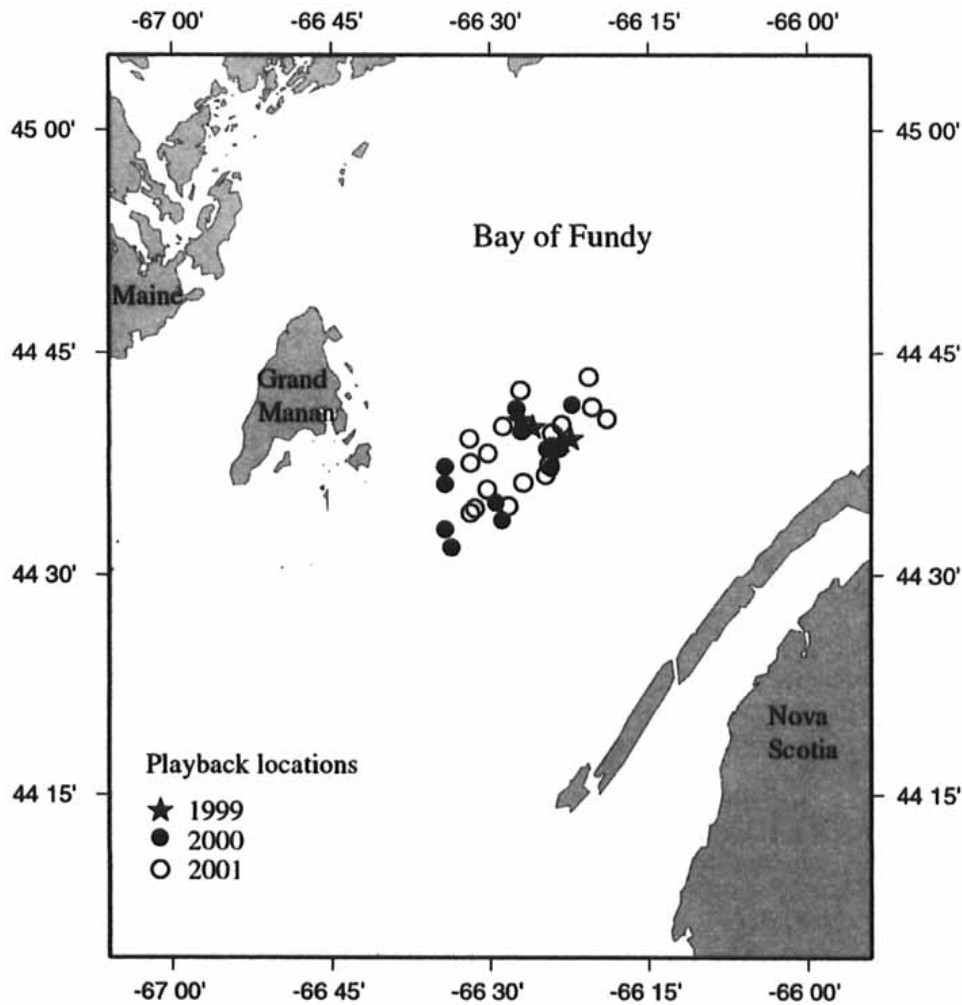


Figure 2. Bay of Fundy locations of playbacks between 1999 and 2001.

in SAGs are sufficient to attract males to these groups without additional acoustic cues. To test if this is the case, playback trials using only calls from SAGs or only gunshot sounds were conducted. Gunshot sounds are produced both in SAGs and by lone animals, so the gunshot playbacks were designed to determine if right whales would approach any sound associated with a SAG, even one that is not a reliable indicator of a SAG. If the SAG calls are the primary cue which adult males use to detect a SAG, few or no animals would be expected to approach the gunshot sound playbacks.

METHODS

Location

Playback trials were carried out in the Bay of Fundy, Canada, east of Grand Manan Island (Fig. 2) from July through September in 1999, 2000, and 2001. The

playbacks were conducted only when two or more right whales were visible from the playback platform.

Playback Platforms

Playbacks were carried out on four separate platforms. The two primary platforms were a 4.5-m rigid hull inflatable, the R/V *Bonita* (1999 and 2000), and the 22-m R/V *Stellwagen* (2001). A 7-m rigid hull inflatable boat (27 August 2000) and the 14-m F/V *Black-B* (26 July 2000) were each used for one day of playback trials in 2000. All vessels were shut down and drifting during the playback experiment.

Stimuli

Three classes of stimuli were used: (1) calls from North Atlantic right whale surface active groups (NARW-SAGs) recorded in the Bay of Fundy and Brown's Bank by the New England Aquarium from the mid-1980s to early 1990s with all broadband gunshot sounds removed (NARW, Fig. 1a–c), (2) calls from South Atlantic right whale surface active groups (SARW-SAGs) recorded in Argentina in the late 1970s by Christopher W. Clark, with all broadband gunshot sounds removed, and (3) broadband gunshot sounds recorded from a lone North Atlantic right whale male in the Bay of Fundy in 2000 (NAGS, Fig. 1d).

Few high-quality recordings of SAGs were available for North Atlantic right whales at the start of this study, therefore playback stimuli recorded from South Atlantic right whales were used to increase the number of high-quality stimulus tapes available for the experiment. The NARW-SAG calls were similar to the SARW-SAG calls in terms of types of calls, frequency range, and time interval between calls. However, all NARW-SAG recordings used were made on the feeding grounds in summer, whereas all SARW-SAG recordings were made on the calving/nursery ground in Patagonia during the austral winter, covering different extremes of the annual migratory path in these two right whale populations. During preliminary trials in 1999, a single 15-min stimulus of NARW-SAG calls (NARW2) was used. In 2000 six 20-min stimuli (3 NARW, 3 SARW) were used. In 2001 seven 20-min stimuli were used, including the six from 2000 with the addition of the NAGS stimuli.

Equipment

The frequency bandwidth characteristics of the equipment used for the sound playback were selected to match the natural stimuli as closely as possible. Two TASCAM DA-P1 DAT recorders (nominal frequency response 20 Hz–20 kHz) were used both to play and monitor the playback stimuli. A single Hi-Tech HTI-94-SSQ hydrophone (nominal frequency response 2 Hz–20 kHz) was used to monitor the playback stimuli while they were being broadcast and to record any sounds produced by whales near the playback vessel. Two amplifiers were used. In 1999 and 2000 a U.S. Acoustics 2 × 300 W car stereo amplifier was used. In 2001 a Rockford-Fosgate Punch 800 amplifier was used. Both amplifiers were powered by a 12-V marine battery and provided the same output voltage (~100 V rms for the calls) to the transducer. The stimuli were projected with a U.S. Navy Sound Reference Laboratory J-11 transducer (Nominal frequency response 20 Hz–20 kHz, flat frequency response 50 Hz–4 kHz).

Projector Source Level

The transducer had a maximum broadband source level of 163 dB re 1 μPa at 1 m for all stimuli types (bandwidth was approximately 30 Hz–20 kHz). Calculated maximum source level was approximately 160 dB re 1 μPa at 1 m for each stimulus. An estimate of the range at which transmission loss reduced the signal to equal ambient background noise levels at 250 Hz was 10 km from the source—assuming spherical spreading (Urick 1983), and ambient noise level of 80 dB re 1 $\mu\text{Pa}^2/\text{Hz}$, following short-term recordings made in the Bay of Fundy in 1999² that are in agreement with Wenz (1962) for areas with normal to heavy ship traffic. The transducer was deployed at a depth of 10 m. Average water depth was 200 m.

Playback Protocol

Each playback trial was divided into three observation periods: pre-, during, and post-playback. Throughout each of these periods visual observations were made from the playback vessel to determine the right whale distribution and general behavior in the area (e.g., SAGs, traveling single whales, mother-calf pairs). The maximum range of the visible horizon varied from 4.5 km (height of eye 1.5 m) to 10.5 km (height of eye 7.6 m) on different platforms. Approaching whales could often be seen at 4–5 km because they often swam rapidly at the surface, lifting their flukes frequently for shallow dives. Acoustic recordings were made with a single hydrophone during each of the three observation periods to monitor acoustic activity of whales around the playback vessel and to monitor the playback stimuli. During the preliminary 1999 trials the three observation periods were each 15 min. In 2000 and 2001 each period was increased to 20 min to allow more time for distant whales to reach the playback vessel. Visual observers measured the bearing, heading, and range (estimated by observers trained with a laser range finder) to all right whales seen at the surface before the playback to determine right whale distribution in the area. The same data were collected during the playback and post-playback periods. There were three levels of response to the playbacks. A no-response score “0” was given for a trial where all observed whales either did not change heading or were farther from the playback vessel at the end of the playback than at the start. A moderate, level-one response score “1” was given for trials where at least one whale approached to within 500 m of the playback vessel during the playback or post-playback periods. A strong, level-two response score “2” was given for trials where at least one whale swam rapidly to within one right whale body length of the playback vessel during the playback or post-playback periods.

On any given day in 2000 and 2001, playback stimuli were presented in a random order predetermined at the beginning of the field season. Observations were conducted from the playback vessel so it was not possible to have observers blind to the playback condition and observers could hear the transmission of the playback sounds through the hull in 1999 and 2000. Only SAG stimuli were presented in 1999 and 2000. However, although observers knew when a playback was taking place, they did not know which type of stimulus was being played, and therefore their observations should not be biased.

² Personal communication from F. Desharnais, DRDC Atlantic, Rapidly Deployable Systems Group, P. O. Box 1012, Dartmouth, NS, Canada, October 2002.

Photographs to identify individuals were taken of all animals that approached the playback vessel closely enough to obtain clear images of distinguishing features ($n = 52$). In some cases no whales approached the vessel closely enough for clear photographs. This was particularly a problem in 1999 and 2000 when the playback platform was usually a small inflatable that was low to the water. In 1999, 2000, and 2001, photographs of non-responding individuals were collected opportunistically from other research vessels in the area during playback trials ($n = 69$). These photo-identifications of non-responding individuals, while not systematically collected, allow us to compare which animals responded or did not respond during each playback trial.

The playback location was selected by finding a place with at least two right whales visible from the playback vessel. This was to ensure that at least two individuals were within range to hear the playback. This experiment differed from more traditional playback studies because there was no single focal subject followed throughout the playback trial. Due to the difficulties of working with baleen whales at sea, the age, sex class, and total number of potential responders within hearing range of the playback were unknown. The paradigm of these playback experiments was such that a yes/no (0 *vs.* 1 or 2) criteria for each trial (not each individual) was the basis for testing the significance of differences in response to different stimuli. This yes/no criterion was based on observations from similar playback experiments to South Atlantic right whales (Clark and Clark 1980) and humpback whales (Tyack 1983). Differences in response to different stimuli were tested using Fischer's exact probability test (Hinkle and Wiersma 1998). The prediction was that primarily adult males would approach the playbacks of SAG calls. The limitation of this design is that lack of obvious approach may be a function of lack of adequate exposure to the stimuli, due to noise or distance from the source, rather than an active choice on the part of a whale. The overwhelming strength of response from individual whales, coupled with opportunistic identification of whales within presumed hearing range of the playback, indicate that some juveniles and adults of both sexes had the opportunity to respond to at least one trial of each stimuli.

RESULTS

Response to the Playbacks

Thirty-six playback trials were conducted. The playback of calls from surface active groups (SAGs) elicited swimming approaches that were similar to those of whales approaching actual SAGs. Figure 3 shows an example of observations collected during a NARW-SAG playback trial. All six SAG playback stimuli from the North Atlantic (NARW-SAG 1–3) and the South Atlantic (SARW-SAG 1–3) elicited level-two responses on at least one occasion, during which whales charged the playback platform (high speed surface swimming, directly at the playback vessel) and swam under the boat. Overall, at least one whale approached the playback vessel in 27 of 31 playback trials of SAG calls (Fig. 4a). The NARW-SAG stimuli elicited approach responses on 16 of 18 trials and the SARW-SAG stimuli elicited approach responses on 11 of 13 trials. There was no significant difference in the proportion of trials with approaches for the NARW and SARW SAG stimuli: Fisher exact probability test, $P = 0.57$ (Fig. 4a). No individuals approached any of the five playbacks of the gunshot sounds (NAGS)

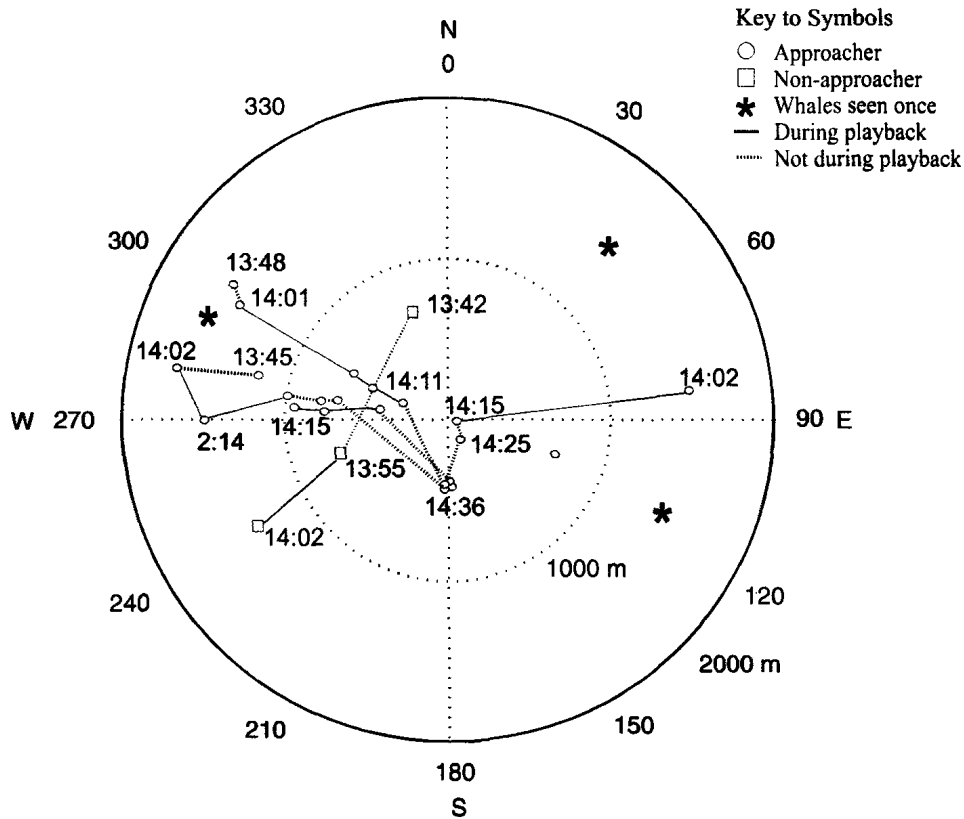


Figure 3. Sighting positions and tracks of individual whales ($n = 8$) seen within 2,000 m of the playback vessel (center of the plot) during the playback trial on 31 August 2000. The trial started at 1339. The playback started at 1359 and lasted until 1419. Dashed or solid lines are used to connect sightings for which there was a high level of confidence that the sightings were of the same individual. Sightings made during pre- and post-playback periods are shown by dashed lines. Sightings made during the playback are shown by solid lines. Four whales approached the playback vessel during this trial but only two were positively identified. All four joined together and formed a short-lived SAG off the playback vessel at 1436.

(Table 1), indicating a significant difference in response to SAG and gunshot sound playbacks ($P < 0.0003$) (Fig. 4b).

An average of 2.1 ± 1.9 SD, (range 0–6) individuals approached the playback vessel while as many as 17 right whales were seen before a playback commenced (Table 1). Many whales exposed to the playbacks did not show any clear evidence of response. For the NARW-SAG stimuli, most of these individuals were calves, adult females, or juvenile males (Table 2). For every playback stimulus, there were individuals that did not respond and these individuals were often closer to the playback vessel at the start of the playback than the whales that did approach the vessel.

In the typical level-one response, whales approached the playback slowly, often taking most of the 20-min playback session to come within 500 m of the playback vessel. Other whales approached the vessel subsurface after diving at least 1 km

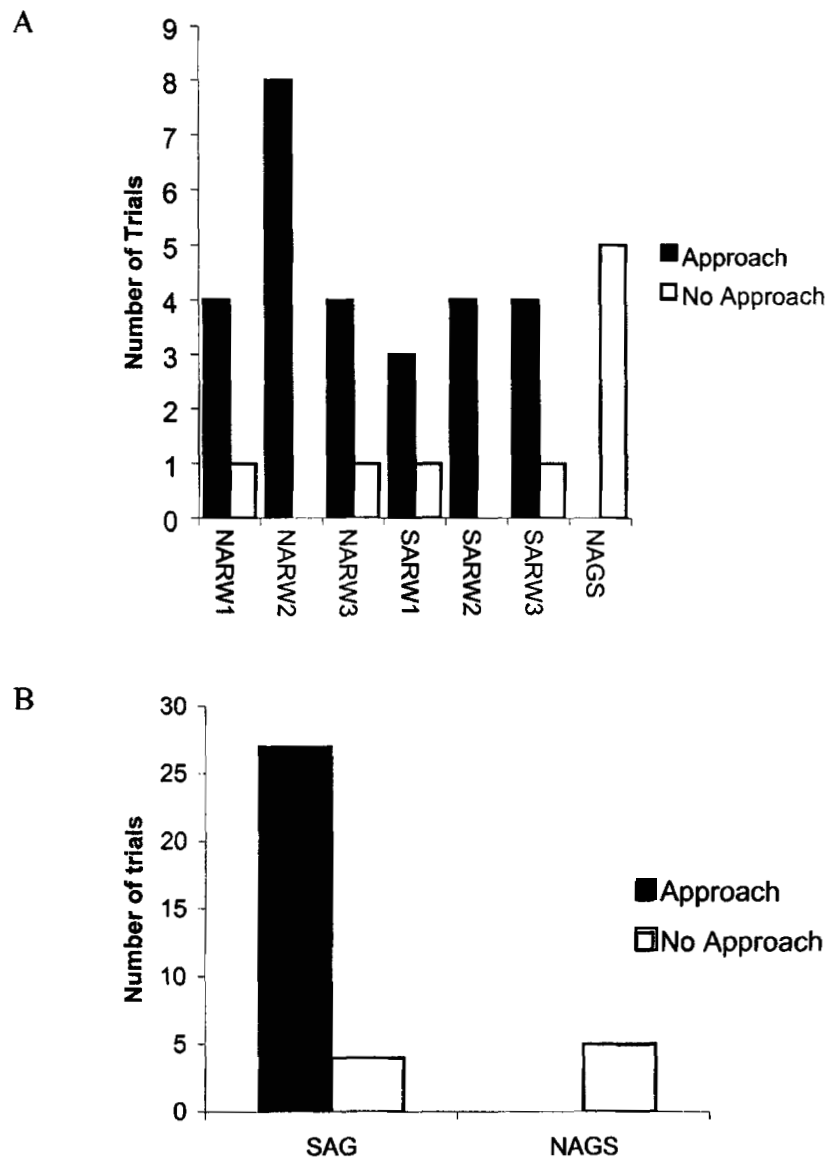


Figure 4. (A) Approach response *vs.* no approach response observed in each trial for each of the seven stimuli presented for playback. There was no significant difference between any of the SAG playback stimuli. (B) Approach response *vs.* no approach response to SAG ($n = 31$) and gunshot ($n = 5$) playbacks (NAGS). The difference in approach *vs.* no approach between SAG and gunshot stimuli was significant ($P = 0.0003$).

away. Similar approaches have been seen to actual SAGs with whales positioned near the SAG for a period of time before joining the group. For the level-2 response, whales would commonly approach the boat by “racing diving,” a term used to describe whales traveling at relatively high speeds near the surface, making repeated shallow dives with flukes raised at an angle of about 45° after each blow. A “racing

diving" whale was easy to distinguish from other whales because of its high rate of travel, frequently raised flukes, and directed straight line path of travel towards the playback vessel. Several approaching whales ($n = 18$) were observed swimming directly under the playback vessel during the trial. On two occasions whales bumped into the transducer and released a cloud of bubbles next to the boat.

Differential Response Between Sexes

Individual identification made it possible to determine the age and sex for many of the whales involved in each playback trial. There appears to be differences in the types of individuals that showed response for all three classes of stimuli (NARW-SAG, SARW-SAG, NAGS). Only the NARW-SAG calls elicited differential response between the sexes. Most whales approaching NARW-SAG sounds were adult males and no known females were observed to approach these stimuli (Table 2a). For the 16 cases when the sex of a "racing diving" approaching whale could be determined for the NARW-SAG playbacks, it was always male. Ten adult females were identified during NARW-SAG playbacks but none approached the playback vessel (Table 2a). All age and sex classes were observed to approach the SARW-SAG sounds (Table 2b). Most notably, six adult females approached the SARW-SAG sounds but none approached the NARW-SAG sounds. Females were observed "racing diving" during SARW-SAG playbacks on three occasions. The observed response in the field was comparable for both NARW-SAG and SARW-SAG playbacks. It was only later when the identity of individuals was determined by photo analysis that the differences emerged. No whales approached the playbacks of gunshot sounds even though whales of all age and sex classes were documented in the area during these playbacks (Table 1).

DISCUSSION

Playbacks of calls recorded from surface active groups (SAGs) were predicted to attract North Atlantic right whales based on observations of right whale behavior in SAGs in the Bay of Fundy. If SAGs with a single focal female function for reproduction then one would expect males to be the primary responders to SAG playbacks. All identified individuals of known sex seen approaching actual SAGs have been adult males (Kraus and Hatch 2001).

The responses to all three NARW-SAG stimuli support the initial prediction that NARW-SAG calls are what attract adult male North Atlantic right whales to SAGs. The overwhelmingly strong response to these playbacks, often involving very rapid surface swimming and persistent searching (swimming back and forth over a small area around the playback vessel) within 500 m from the sound source for up to 20 min after the end of the playback by adult males ($n = 2$), or adults of unknown sex ($n = 1$), support the idea that the calls produced in SAGs do attract the males that join these groups. Whales that were identified as not approaching the NARW-SAG stimuli were predominantly female (Table 2A). This result also corresponds with observations in the field, where fewer juvenile males or adult females are seen in the typical SAG containing a mature focal female. None of the whales that approached the playbacks produced SAG calls. The only sounds recorded near the playback vessel on the single monitoring hydrophone after (or during) playbacks were gunshot sounds or up-calls, which are

Table 1. Level of response and identity of all known approachers and non-approachers for each playback trial over the past three years. The date, stimulus type, level of response, number of whales seen from the playback vessel during a trial, the number of whales that approached the playback vessel during a trial, the age and sex of whales that approached the playback vessel and age and sex of identified whales that did not approach the playback vessel are given in the table. For the identity columns, information about sex and age is given. M = Male, F = Female, U = Unknown sex, A = Adult (>8 yr), J = Juvenile (<9 yr), C = Calf (<1 yr), U = Unknown age.

Date	Stimulus	Response level (0-2)	Number of whales seen during playback	Number of whales approaching playback vessel	Sex/age of identified approaching whales	Sex/age of identified non-approaching whales
7/31/2001	NAGS	0	9	0		1FA, 1FJ, 1UC
8/9/2001	NAGS	0	5	0		1UC
8/11/2001	NAGS	0	11	0		4FA, 1FJ, 1MA, 1MJ, 1UC
8/14/2001	NAGS	0	13	0		2FA, 2UC
8/19/2001	NAGS	0	17	0		5FA, 2UU, 1UC
7/15/2000	NARW1	1	3	2	1MA, 1MJ	
8/29/2000	NARW1	2	10	1	1MA	
8/31/2000	NARW1	2	6	2	2MA	
7/21/2001	NARW1	0	8	0		2FA, 3UC
8/1/2001	NARW1	1	12	1		1FA, 1FJ, 2UC
7/21/1999	NARW2	1	4	2		
8/20/1999	NARW2	2	4	3	2MA, 1UA	
8/20/1999	NARW2	2	1	1	1UA	
8/20/1999	NARW2	2	2	2	1MA, 1MU	
8/20/1999	NARW2	2	3	3	3MA	
7/15/2000	NARW2	2	3	1		
8/27/2000	NARW2	2	3	1	1MA	
8/11/2001	NARW2	2	16	5	4MA	1FA, 2MA, 1MJ, 1UC
7/26/2000	NARW3	1	10	2	1MA, 1UA	2FA, 1MU, 1UU
8/29/2000	NARW3	1	15	7	5MA, 1MJ	
8/31/2000	NARW3	1	5	1		
7/27/2001	NARW3	0	8	0		1FA, 2MA, 2UC
8/4/2001	NARW3	2	15	7	4MA	3FA, 1UC

Table 1. Continued.

Date	Stimulus	Response level (0-2)	Number of whales seen during playback	Number of whales approaching playback vessel	Sex/age of identified approaching whales	Sex/age of identified non-approaching whales
7/26/2000	SARW1	1	6	5	1FA, 1FJ, 1MA, 1MJ, 1MU	
7/27/2001	SARW1	1	13	3	1MA, 1MU	1FA, 1FJ, 1MA, 3MJ, 1UC
8/14/2001	SARW1	0	15	0		1FA, 1FJ, 1MA, 3MJ, 1UC
8/24/2001	SARW1	2	7	1	1MA	
8/29/2000	SARW2	1	1	1	1MA	
7/28/2001	SARW2	1	12	3	2UC	1FA, 1MA, 1UC
8/11/2001	SARW2	2	10	2	1FA	
8/19/2001	SARW2	2	15	5	2FA, 1MA, 2UC	2UU
7/26/2000	SARW3	1	6	1	1UA	
8/31/2000	SARW3	2	6	1	1FA	
7/29/2001	SARW3	0	6	0		1FA
8/11/2001	SARW3	1	14	3	1UA	2FA, 1FJ, 1MA
8/25/2001	SARW3	1	11	2	1FA, 1UC	

Table 2. Summary of the age and sex of whales approaching and not approaching the playback vessel during A) NARW-SAG B) SARW-SAG playbacks. Adults are >8 yr.

A

	Whales approaching NARW-SAG			Whales not approaching NARW-SAG		
	Male	Female	Unknown sex	Male	Female	Unknown sex
Adult	25	0	3	4	10	0
Juvenile	2	0	0	1	1	0
Calf	0	0	0	0	0	9
Unknown	1	0	0	1	0	1

B

	Whales approaching SARW-SAG			Whales not approaching SARW-SAG		
	Male	Female	Unknown sex	Male	Female	Unknown sex
Adult	5	6	2	3	5	0
Juvenile	1	1	0	3	2	0
Calf	0	0	5	0	0	3
Unknown	2	0	0	0	0	2

considered to be a form of contact call in the South Atlantic right whale repertoire (Clark 1983).

The results from the gunshot sound playbacks indicate that right whales do not approach every type of right whale sound stimulus projected to them. Only a single gunshot sound stimulus was used; so whether this response generalizes to this class of signal remains uncertain. Although gunshot sounds are typically recorded from SAGs, it appears that the calls recorded from NARW-SAGs are alone sufficient to attract males. The gunshot sounds often overlap with other gunshot sounds and calls, suggesting that more than one animal in the SAGs produce these sounds. It is, therefore, most likely that males in SAGs produce gunshot sounds as more seem to be heard with an increasing number of males present in SAGs (Parks, unpublished data) and all observed lone animals producing these gunshot sounds in the Bay of Fundy ($n = 3$) have been male. A male hearing gunshot sounds may only know that other males are interacting, with no guarantee that a female is involved. One NARW-SAG playback resulted in four approaching whales coming together and forming a brief 10–15 min SAG approximately 300 m off the playback vessel (Fig. 3). Only two of the animals approached the vessel closely enough to be positively identified, and both of these were adult males. The hydrophone recordings made during and after this playback picked up only very loud gunshot sounds, presumably produced by a whale or whales close to the vessel. No other whales were visible from the playback platform at that time and it is probable, given the sex of whales approaching other NARW stimuli that this SAG consisted only of males.

The SARW-SAG trials produced the most unexpected results from this experiment. All age and sex classes were seen to approach during these trials (Table 2b). The SARW playback stimuli were selected to increase the number of stimuli tapes. They were high-quality recordings with very similar call types and call rates to

those made from NARW-SAGs. The predictions for these playbacks were the same as those for NARW-SAG playbacks. However, these results document a clear difference in response by North Atlantic right whales to North and South Atlantic right whale SAG sounds. There are several possible reasons for the observed differences in response. The first possibility is that the calls of these two species differ enough so as not to be recognized by North Atlantic right whales as right whale calls. Secondly, if right whales recognize the calls of specific individuals, then the calls from the SARW-SAGs were from individual whales that were completely unknown to the North Atlantic right whale population. In both cases, the novelty of these stimuli might attract attention from any member of the North Atlantic right whale population. A third potential explanation for the difference is that these recordings were made from the calving grounds of a SARW population which has a different demographic structure and behavioral context than that seen on the feeding grounds in the North Atlantic. SAGs have been observed in all known habitats for the North Atlantic right whale and in eight months of the year (Kraus and Hatch 2001), but it is unclear whether the SAGs in different habitats serve the same social or reproductive function, and sounds produced by SAGs outside of the Gulf of Maine during the summer months have not been recorded for this species. SAGs on the calving ground might serve a different function and differences in frequency, call modulation, or some other factor might signal this difference to right whales in both the North and South Atlantic.

Lower levels of response (0 and 1) were observed during the month of July than in August or September. Playbacks in July elicited fewer approaches than those carried out in August or September (of the four SAG playbacks with no clear response, three were conducted in July). Males appeared to be making increased effort to get to SAGs as the summer season in the Bay of Fundy progressed. More individuals were seen approaching both playbacks and actual SAGs by “racing diving” in late August than in July (Table 1), and SAG size has been shown to increase throughout the summer months (Kraus and Hatch 2001).

There are limitations to any playback experiments to North Atlantic right whales. The detailed demographic information is primarily available because this is a highly endangered species, with fewer than 300 individuals left in the entire population. While this detailed demographic information increases insight into the response of individuals, it comes with the cost of having few potential test subjects in a small population. The large proportion of the North Atlantic right whale population that congregates on the summer feeding grounds where these playbacks were conducted compounds this problem. The source level and frequency range of the playback suggest that it may be audible above ambient noise for approximately 10 km from the source. There are times in the Bay of Fundy when the whales are all feeding in a very small geographic area; as a result, at these times, up to a quarter of the entire population could potentially be exposed to each playback trial. Therefore, after the first trial of each stimulus, it is not possible to ensure lack of previous exposure to the playback. The North Atlantic playback recordings were made on the same feeding grounds, meaning that a large proportion of the population may have been exposed to the actual sounds during the original SAG. While the playbacks occurred 8–15 yr after the original event, the signals may still be familiar to whales in the population if the signals are individually distinctive. Some individual males (*e.g.*, Catalog ID #1304 and #1901) approached the same stimuli (NARW2 and NARW3, respectively) on more than one occasion, which may be a random consequence of the whale being in the right place at the right time, or it

may indicate higher motivation in these individuals for the calls recorded from a particular SAG. The results from these playback trials cannot be evaluated without taking these factors into account. Efforts were made throughout this experiment to (1) limit the number of playbacks made on a given day, (2) conduct playbacks throughout the season (because the population in the bay changes during the season), and (3) use several different examples of stimuli for each class of signal of interest. Aside from the first playback trials of the SARW-SAG stimuli, there is the possibility that all potential test subjects may have had previous exposure to the stimulus being presented. However, if SAG sounds signal mating opportunities for males, then one should expect strong selection against habituation.

This playback experiment demonstrates that calls produced by right whales in SAGs do have behavioral significance to individuals. Adult males show the strongest responses to playbacks of NARW-SAG calls, which was predicted by observations of behavior in real SAGs. The approach to SAG sounds by adult males supports the assumption that females produce the calls in SAGs. The difference in the age and sex composition of the whales that approached the SARW-SAG calls demonstrates that behaviorally significant variation exists in response to this broad class of sounds. Finally, the responses of whales to these playbacks indicate that right whales have the ability to accurately locate a sound source and remember where the sound source was for at least 20 min after the broadcast of sound stops. These results suggest that further studies of right whales' perceptual and cognitive abilities may be warranted. Playback trials, coupled with newly developed tagging methods (Johnson and Tyack 2003), can be used to look at fine scale motor response and record the received level of a signal to address hearing and detection abilities of individual free-ranging whales.

ACKNOWLEDGMENTS

The data used in this paper were collected with the assistance of numerous research staff and volunteers. Sincere thanks to everyone involved in the data collection and setup; D. Allen, N. Biassoni, A. Boccencelli, M. Brown, C. Carson, J. Ciano, C. Clark, L. Conger, S. Ensign, T. Fraiser, A. Frankel, I. Greene, P. Hamilton, A. Knowlton, B. Kraus, M. Johnson, A. Loer, R. MacCurdy, S. Martin, M. Marx, J. Matthews, R. McLanaghan, A. Moscrop, S. Nowacek, D. Nowacek, J. Partan, H. Pettis, E. Pike, A. Shapiro, K. A. Shorter, C. Slay, A. Vanderlaan, and D. Waples. A. Solow provided valuable advice on statistical analysis. R. Weir provided assistance with figures. C. Clark, K. Fristrup, E. Lilly, R. Thomas, P. Tyack, and one anonymous reviewer made helpful comments on earlier versions of this paper. Special thanks to C. Clark, K. Fristrup, S. Kraus, P. Tyack, and everyone in the New England Aquarium Right Whale office for invaluable support, advice, and encouragement throughout this project. Funding for the fieldwork was provided by the International Fund for Animal Welfare, Northeast Consortium (UNH), Office of Naval Research, and the U.S. National Marine Fisheries Service. S. Parks was supported by a NDSEG Fellowship. 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 # 10659 of the Woods Hole Oceanographic Institution.

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Received: 29 May 2002

Accepted: 14 November 2002