Vol. 15: 63–76, 2011
doi: 10.3354/esr00368

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published online October 21

# Sound production behavior of individual North Atlantic right whales: implications for passive acoustic monitoring

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ABSTRACT: Passive acoustic monitoring is being used to detect vocalizing marine mammals. Data on call types and individual rates of sound production are necessary to use passive acoustics to identify species, assess individual detectability, and estimate the number of individuals present. The present study describes the sound production behavior of endangered North Atlantic right whales *Eubalaena glacialis* in the Bay of Fundy, Canada, during July and August, recorded with suction cup archival tags (Dtag) in 2000 to 2002 and 2005. The Dtag simultaneously recorded acoustic data from a hydrophone along with the depth and orientation of the whale. Over 168 h of acoustic data were obtained from 46 tag deployments (35 ind.), with an average attachment duration of 4.5 h. The rate of sound production was variable, ranging from 0 to 200 calls $h^{-1}$ (mean ± SD: 6.4 ± 29.8 calls $h^{-1}$), with 28 of the 46 tagged whales producing no calls (corresponding to 69/168 h of data). Right whale sounds from any whale in the area were recorded on most tag records, indicating that aggregations of whales may be detected more reliably than individuals. Calling rates were highest during surface activity and traveling and lowest during foraging and logging behavior. Whales of both sexes and all age-classes produced upcalls and other tonal calls, and 1 adult male produced gunshot sounds. The present study provides insight from the largest extant collection of recordings of individual North Atlantic right whales into the acoustic detectability of individual right whales and demonstrates that the behavioral state is the primary factor affecting calling rate.

KEY WORDS: North Atlantic right whale · *Eubalaena* · Sound production · Passive acoustic detection · Tags



## INTRODUCTION

Sound production of baleen whales has been studied extensively over the past 50 yr, and call types have been described for most species (Tyack & Clark 2000). However, due to difficulties in sampling subsurface behaviors, less is known about individual rates of sound production and the behavioral context of vocalizing whales. Several methods have been utilized to overcome this limitation, including sound source localization coupled with surface visual observations (Clark 1980, Gedamke et al. 2001, Croll et al. 2002, Parks & Tyack 2005) and, more recently, attachment of tags capable of sampling both the acoustic and physical behavior of the tagged whale underwater (Johnson & Tyack 2003, Oleson et al. 2007a, Stimpert et al. 2007). These tools make it possible to determine the behavioral context of sound production, as well as the timing of calls from individuals and the trends in calling behavior based on

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age, sex, and/or time of day. These data are necessary to interpret passive acoustic recordings used to detect and monitor populations of marine mammals.

Visual surveys often detect only a small portion of the marine mammals in an area, are limited to daylight hours, and are strongly influenced by animal behavior and weather conditions (Mellinger & Barlow 2003). Passive acoustic detection of marine mammals can complement and, in some cases, offer advantages over traditional visual surveys. Provided that their calls are distinctive and well characterized, the probability of detecting vocal species of marine mammals is increased by using sound recordings in addition to or, in some cases, instead of visual surveys (Mellinger et al. 2007a), and several surveys for baleen whales have successfully combined both methods (Clark & Fristrup 1997, Swartz et al. 2003, Wade et al. 2006, Oleson et al. 2007b). Autonomous acoustic recorders are also an economical long-term tool for monitoring habitat usage by vocalizing marine species even during weather when vessels cannot go to sea. One major limitation of passive acoustic monitoring is that animals must be vocalizing to be detected. Understanding the calling behavior, including call types, behavioral function of sounds, and call rates, is important for assessing the effectiveness of passive acoustic monitoring in detecting a particular species in a particular habitat area.

The North Atlantic right whale *Eubalaena glacialis* is a highly endangered species of baleen whale, with fewer than 473 remaining in the western North Atlantic (Kraus et al. 2005). Mortality from collisions with vessels and entanglement with fishing gear are thought to play an important role in limiting the recovery of this species (Knowlton & Kraus 2001). Passive acoustic monitoring has been proposed to help determine when North Atlantic right whales are present in an area (Clark et al. 2007) and has been implemented as a real-time management tool for the North Atlantic right whale near major shipping lanes (Van Parijs et al. 2009). Data on the sound production behavior of individuals are needed to better understand the effectiveness and limitations of passive acoustic monitoring for right whales in specific habitat areas. The North Atlantic right whale population has been studied intensely for >30 yr, resulting in rich life-history data, including age and sex, for most individuals in the population (Kraus & Rolland 2007). This makes it possible to study the variability in behavior by age- or sex-class in this species. For example, differences in vocal activity by age- and sex-class could result in variable probabilities of passive acoustic detection.

There have been several studies of the sound production behavior of right whales using hydrophone recordings (Schevill et al. 1962, Payne & Payne 1971, Cummings et al. 1972, Clark 1982, 1983, Vanderlaan et al. 2003, Mellinger et al. 2004, Parks & Tyack 2005, Parks et al. 2005, Munger et al. 2008). A study from 1999 to 2000 of the vocalization rates of North Atlantic right whales combined data from towed hydrophone recordings of groups of right whales and from acoustic recording tag data collected from 10 whales to describe the call rates, depths, and diel trends in sound production (Matthews et al. 2001). Their study demonstrated that the call rate of right whales was correlated with the number of whales in the vicinity, with the highest call rates being recordings from aggregations of 10 whales or more. A more recent study found no correlation between the number of calls detected and the number of right whales detected in Cape Cod Bay through a comprehensive aerial survey (Clark et al. 2010). The results from these 2 studies suggest that individual or seasonal differences in behavior may be an important factor influencing passive acoustic detection of right whales.

A correlation between sound production types and rates and the level of social activity has been shown in southern right whales *Eubalaena australis* (Clark 1982). Similarly, differences in sound production behavior by males and females (Parks & Tyack 2005, Parks et al. 2005) and by season (Van Parijs et al. 2009) have been documented in North Atlantic right whales. These studies indicate that the calling rate of individual right whales is highly variable, being related to behavioral state, social activities, and to the age- and sex-class of the whales. Estimates of calling rates as a function of these factors are currently unavailable for North Atlantic right whales, making it difficult to assess the performance of passive acoustic monitoring as a management tool. The objective of the current study is to quantify the calling rates of individual North Atlantic right whales in one of their critical habitats, the Bay of Fundy, Canada, using behavioral state, age-, and sex-class as co-variates. The study is based on 46 deployments of sound and movement recording tags on 35 different North Atlantic right whales. Tagging took place over 4 yr during the July to August season of maximum abundance of whales in the Bay of Fundy. The results provide the first description of individual calling rates and types, interpreted by behaviour and life-history, and will inform passive acoustic monitoring efforts for this highly endangered species.

## MATERIALS AND METHODS

### Tag data

Data were collected from North Atlantic right whales *Eubalaena glacialis* in 2000, 2001, 2002, and 2005 in the Bay of Fundy, Canada, during the months of July and August using suction-cup-attached multi-sensor digital recording tags (Dtags; Johnson & Tyack 2003). Tags were attached to whales, and behavioral observations were carried out following the protocols described in Nowacek et al. (2001, 2004). The Dtag sampled acoustic data at 16 kHz (2000, 2001), 32 kHz (2002), or 96 kHz (2005), with either a 12 bit (2000 to 2002) or 16 bit (2005) analog-to-digital converter. Acoustic data were internally high-pass filtered with a single pole filter at 400 Hz to prevent flow noise from saturating the acoustic recordings, resulting in a gradual reduction of intensity below 400 Hz (6 dB octave$^{-1}$). Additional sensor data, including depth and heading of the whale, were collected at 23.5 Hz (2000 to 2002) or 50 Hz (2005), and decimated to a sample rate of 5.88 Hz (2000 to 2002) or 5 Hz (2005). The pressure data from the depth sensor were converted to meters using calibration values with an accuracy of ±2 m.

### Identification of individuals

Right whales can be individually identified by distinctive roughened skin patches called callosities found on the top and sides of their heads (Kraus et al. 1986). A catalog of individually identified North Atlantic right whales, including sex, age or age-class (adult or juvenile), and reproductive and sighting histories is maintained by the North Atlantic right whale consortium (Hamilton & Martin 1999). In the current study, photographs were taken of the head and any distinctive body markings for each whale tagged in the study and compared to the catalog images by the New England Aquarium right whale research group to identify unique individuals and obtain sex and age information.

### Determination of behavioral states

A combination of visual focal follows of the tagged whale and tag sensor data were used to assign the behavior of the tagged whale into 1 of 4 behavioral states (Altmann 1974) throughout the period of tag attachment. The 4 categories used were: (1) foraging, defined by fluke-out dives with extended flat-bottom profiles that maximized time at depth; (2) traveling, defined by consistent straight-line travel with shallow or brief v-shaped dives and consistent fluking activity; (3) surface activity, defined by prolonged periods at the surface with variable heading and repeated side rolling and fluking activity; and (4) logging, defined by prolonged periods at the surface with little or no fluking activity and no directed movement (Fig. 1). The dive profiles corresponding to these behavioral states are consistent with the description of diving behavior of right whales in the Bay of Fundy in Baumgartner & Mate (2003).

### Call detection and measurements

#### Call types

The tag acoustic records were inspected using custom Matlab (Mathworks Inc. 2002) scripts and the Matlab-based Xbat (http://xbat.org) program. Right whale sounds were detected through a combination of visual inspection of spectrograms and listening to the audio record from the tag. The duration and minimum and peak frequencies were measured for each call using Xbat. Call types were assigned to categories previously described for the Bay of Fundy (Parks & Tyack 2005), with all non-stereotyped tonal sounds combined into a general class labeled 'tonal'.

#### Assignment of calls to tagged whales

The goal of the present study was to describe variability in individual call production. To this end, a conservative approach was taken in assigning calls to the tagged whale. An initial assessment was based on the signal-to-noise ratio (SNR) of the recorded call, absence of reverberation within the call, and presence of high-frequency harmonic components (as in Matthews et al. 2001). If a high-intensity call, SNR ratio typically >10 dB, calculated as broadband SNR (root-mean-square [RMS] of signal + noise/RMS of preceding noise), was recorded on the tag and the tagged whale was visually assessed to be >5 body lengths from any other right whale, the call was definitively assigned to the tagged whale. In several cases, the tagged whale joined another individual or a surface-active group with multiple individuals (Kraus & Hatch 2001). These events were detected through a combination of visual observations, tag orientation data, and/or detection of audible blow sounds in the

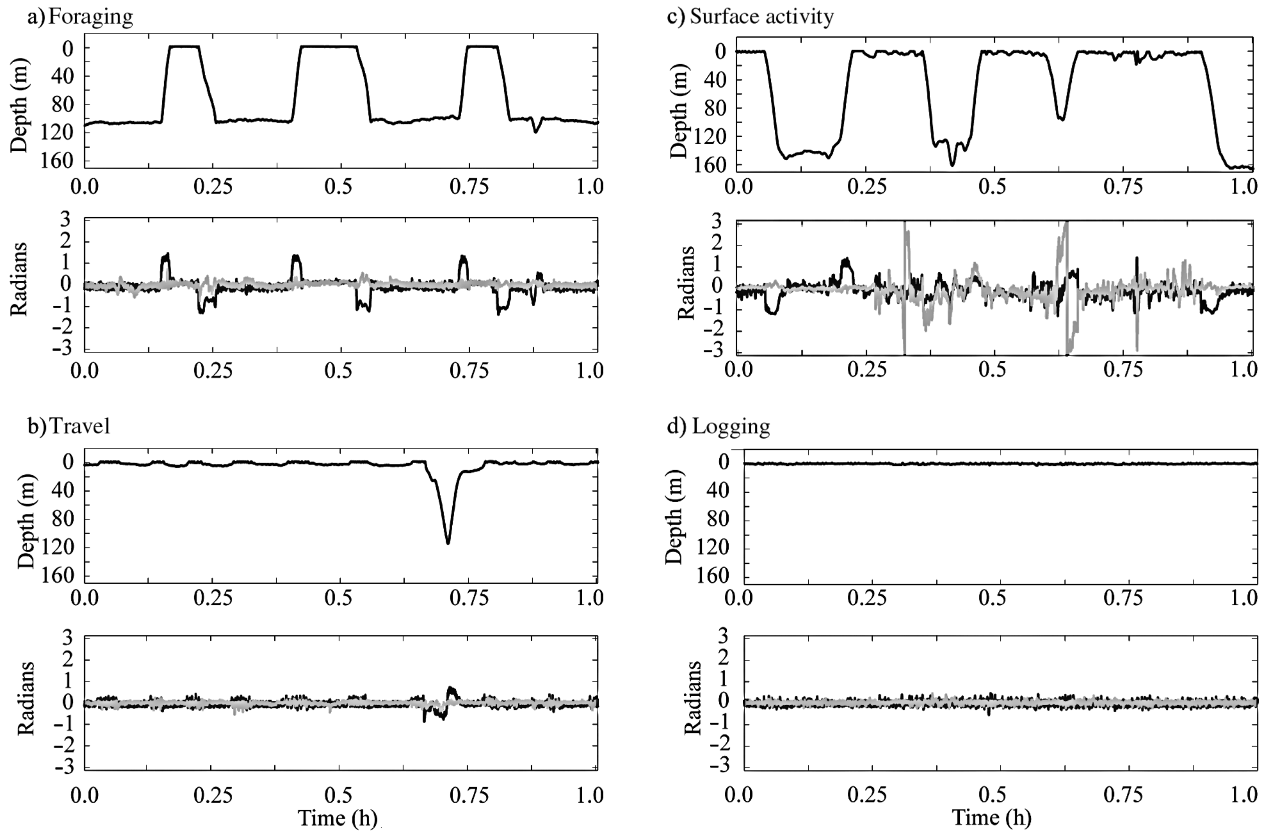


Fig. 1. *Eubalaena glacialis.* Examples of 4 behavioral states of tagged right whales: (a) foraging, (b) traveling, (c) surface activity (preceded by 1 foraging dive to show contrast in rolling behavior), and (d) logging. In each part, the top panel shows a typical dive pattern of whale depth versus time. The bottom panel shows the pitch (black) and roll (gray) of the individual whale, time aligned with the dive profile

acoustic record when the tagged whale was >5 m below the surface, presumably the sounds of nearby whales respiring. In these instances, the tagged whales were close enough to other right whales that loud calls could not be definitively assigned to the tagged whale. For periods when the tagged whale was determined to be near another whale, we calculated a separate call rate which included all calls with a high SNR ratio and so likely included calls from whales other than the tagged whale. This resulted in a description of call production of single whales during foraging, traveling, approaches joining other whales, and solitary periods of surface activity (i.e. flipper slapping) and of multiple whales during prolonged interactions between pairs or in social surface-active groups (Kraus & Hatch 2001).

## Call rates

Call rates were calculated for each whale as the total number of calls with SNR > 10 dB $h^{-1}$ of tag data. Call rates were calculated separately for periods when the whale was alone, when the whale was near other whales, and within different behavioral states. The maximum duration of tag recording with no calls from the tagged whale and the maximum duration of tag recording with no calls from any right whale were calculated for all tag records. Vocalizations of right whales often occur in bouts (Matthews et al. 2001, Parks & Tyack 2005). To objectively estimate the minimum interval separating different bouts of calling by tagged whales, the bout criterion interval (BCI) was determined using a log-survivorship analysis of inter-call intervals (Slater & Lester 1982, Martin & Bateson 1993). The BCI analysis assumes that the within- and between-bout call intervals are generated by separate random processes with different rate constants, leading to 2 distinct slopes on a log-survivorship plot of inter-call intervals (Martin & Bateson 1993). The intersection of these 2 lines is defined as the BCI. The mean and standard deviation for inter-call intervals (ICI) within bouts and inter-bout intervals (IBI) were calculated based on the BCI.

The ICI and BCI were only calculated from tag records with multiple calls attributed to the tagged whale. Using short-term tags to measure inter-call intervals effectively results in censored data because of the inconclusive interval between the last call in the recording and the end of recording. For this reason, survivorship analysis was performed to obtain robust estimates of the mean ICI of tagged whales. The Kaplan-Meier estimator of the survivorship function (Kaplan & Meier 1958, Hosmer & Lemeshow 1999) was implemented using Systat 12 statistical software.

### Call depths

The depth of the whale at the time of each vocalization was obtained from the tag pressure record. These data were limited to periods when the tagged whale was alone, allowing the call to be definitively assigned to the tagged animal. Therefore, depth analysis did not include calling behavior of whales in pairs or larger social groups at the surface. The percentage of calls produced in 10 m depth bins was compared to the percentage of time spent by the whales in the same depth bins using a Mann-Whitney *U*-test. The dive profiles of vocalizing whales were inspected, and the phase in the dive cycle in which calls were produced was noted. We distinguished the descent, bottom, ascent, and post-dive surface phases of dives based on the parameters described in Baumgartner & Mate (2003). A Mann-Whitney *U*-test was conducted to determine if whales were more likely to produce calls during particular phases of the dive cycle. The Kruskal-Wallis test was used to determine if there was a difference in the depth of call production by call type.

### Call behavior by age and sex

Sound production was compared to the age-class and sex of tagged whales. Animals were allocated to 1 of 2 age-classes: juveniles (<9 yr) and adults (≥9 yr) (Hamilton et al. 1998). Animals of unknown age-class or sex were excluded from this analysis. To take into account multiple independent observations from the same individual in the analysis (i.e. multiple calls from the same individual), a mixed model as implemented in the PROC MIXED function in SAS 9.1 (SAS Institute) was used to assess the effects of age-class, sex, and an interaction factor (age-class × sex) on calling parameters. Step-wise elimination of non-significant parameters ($p > 0.05$) was used in the analysis, and the individual caller ID was used as a random factor to account for multiple observations from specific individuals. Pair-wise comparisons by age-class and/ or sex (juvenile vs. adult; male vs. female) for call parameters with significant differences in the mixed model were made using least-square means with a Tukey-Kramer adjustment for multiple contrasts (Littell et al. 2006).

### Assessment of potential behavioral disturbance from playback experiments

The data reported here were collected opportunistically during studies that included playback of sounds to the tagged whale (Nowacek et al. 2004). Playbacks comprised variously ship noise, an alarm sound, and previously recorded right whale sounds. The calling rates between whales with and without playbacks were compared using a 2-sample *t*-test, and the call rates of the tagged whale 1 h before and 1 h after the onset of playback were compared with a paired *t*-test to determine if there was any evidence that playback experiments affected the call rates of individuals.

Table 1. *Eubalaena glacialis*. Tag data used in this analysis. Adults were defined as ≥9 yr of age. Age-class categories are — AF: adult female; AM: adult male; JF: juvenile female; JM: juvenile male; UF: unknown age-class female; UM: unknown age-class male; UU: unknown age-class and unknown sex. Number of tags: number of tagging events in each age-class category; number of individuals: number of unique individual whales tagged in each age-class category; tonal calls (tagged whale): number of upcall and variable tonal calls produced by the tagged whale while alone (excluding calls during social interactions where identity of the caller could not be definitely assigned); tonal calls (any whale): all right whale tonal calls in the acoustic recordings, including calls with signal-to-noise ratio <10 dB

| Age-class | No. of tags | No. of individuals | Data (h) | Tonal calls (tagged whale) | Tonal calls (any whale) |
|---|---|---|---|---|---|
| AF | 7 | 5 | 32.3 | 78 | 223 |
| AM | 8 | 7 | 23.6 | 133 | 776 |
| JF | 16 | 11 | 60.6 | 68 | 744 |
| JM | 8 | 7 | 33.9 | 29 | 301 |
| UF | 1 | 1 | 1.4 | 0 | 1 |
| UM | 5 | 3 | 13.2 | 6 | 432 |
| UU | 1 | 1 | 3.7 | 57 | 74 |
| Total | 46 | 35 | 168.7 | 371 | 2550 |

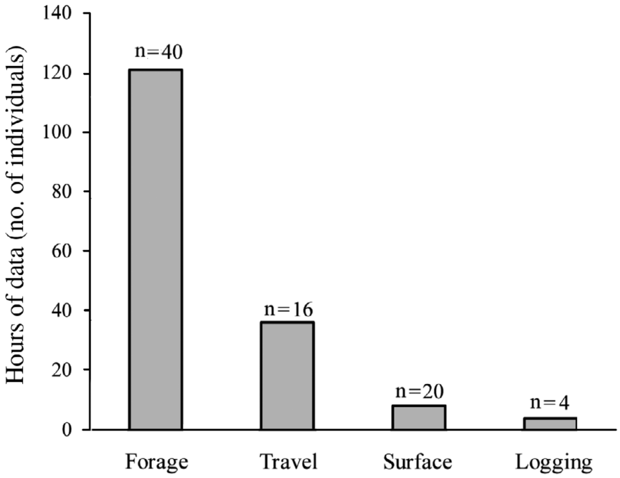


Fig. 2. *Eubalaena glacialis.* Number of tags (n) and total number of hours of data in each of the 4 behavioral states (foraging, traveling, surface activity, and logging)

## RESULTS

### Tag data

Data were collected from a total of 46 tag attachments >30 min in duration on 35 ind. of *Eubalaena glacialis* (Table 1). The acoustic recording duration analyzed on the tags ranged from 41 min to 16.5 h (mean = 3.98 h, SD = 3.3 h) for a total of 168.7 h. The exact age was known for 21 of 35 ind., and the age-class was known for 9 whales, leaving 5 whales of unknown age-class in the study. The sex was known for 33 of 35 tagged ind. The predominant behavioral state of tagged whales was foraging (40 tags, 121 h), followed by traveling (16 tags, 36 h), surface activity (20 tags, 8 h), and logging (4 tags, 4 h) (Fig. 2). Recordings of social activity were limited by the tags frequently being knocked off during close contact between 2 or more whales. Tags were attached during daylight hours, and, therefore, most data described here are from the daytime behavior of right whales between 9:00 and 22:00 h local time. Only 2 tags were attached to whales between 0:00 and 8:00 h.

### Call types

Calls produced by tagged whales while alone were detected in 18 of the 46 tag records. Calls from any right whale, including other right whales in the area, were detected in 41 of 46 tag records. Four previously described right whale sound types (Clark 1982, Parks & Tyack 2005, Parks et al. 2005) were recorded from the tagged whales: upcalls, variable tonal calls,

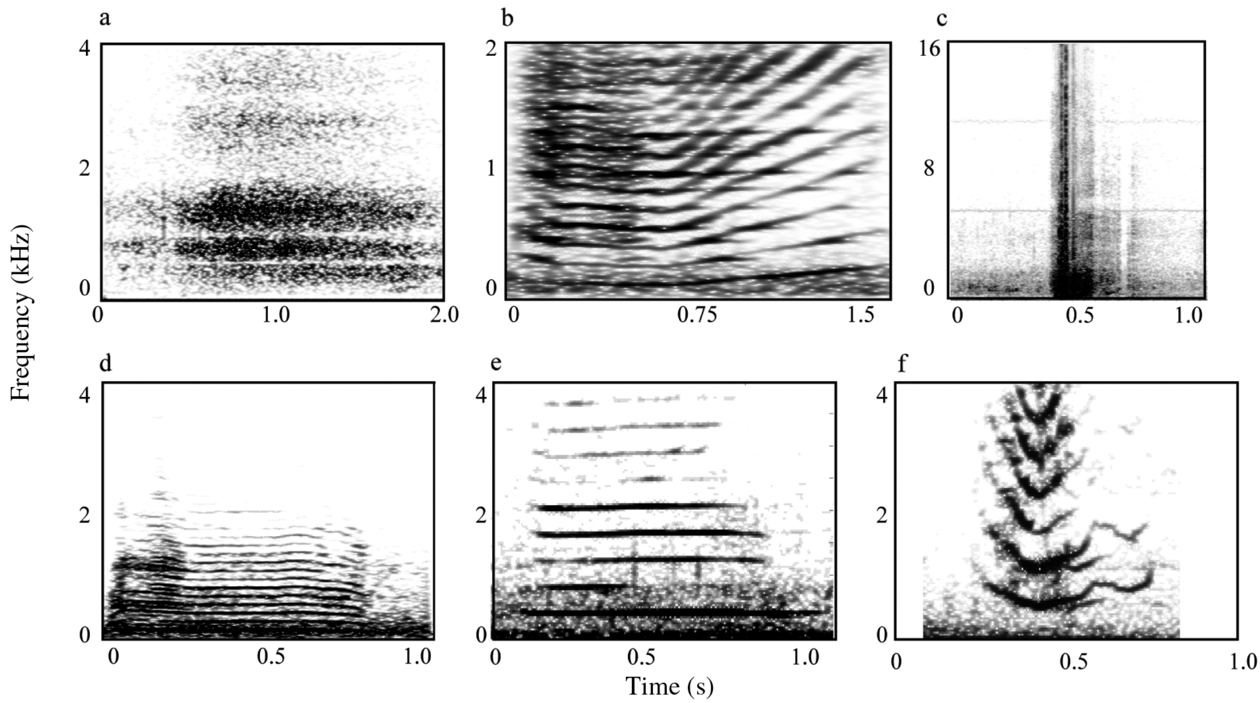


Fig. 3. *Eubalaena glacialis.* Examples of sounds recorded from tagged right whales stereotyped as (a) exhalation, (b) upcall, (c) gunshot, and variable tonal calls: (d) low-frequency tonal (F0 < 100 Hz), (e) mid-frequency tonal (100 < F0 < 300 Hz), (f) high-frequency tonal (F0 > 300 Hz). For all spectrograms, 1024 point (Fast Fourier transform, FFT), 75 % overlap, 16 kHz sampling; except the 'gunshot', 512 point FFT, 75 % overlap, 16 kHz sampling

gunshot sounds, and exhalations (Fig. 3). Exhalations were documented from most tagged whales (45 of 46) during surfacing events when the whale was alone. Exhalations were used to confirm that the whale was alone when out of visual range from the observation platform (exhalations documented when the tagged whale was >5 m below the surface indicated the presence of another whale) and were not included in the analysis of call rates or depths. Upcalls and tonal calls were produced by 15 and 14 whales, respectively, but overall, more upcalls were produced (upcalls: n = 264, tonal calls: n = 107). The gunshot sounds were only documented in 1 tag record from an adult male on 9 August 2011 (n = 189 gunshots).

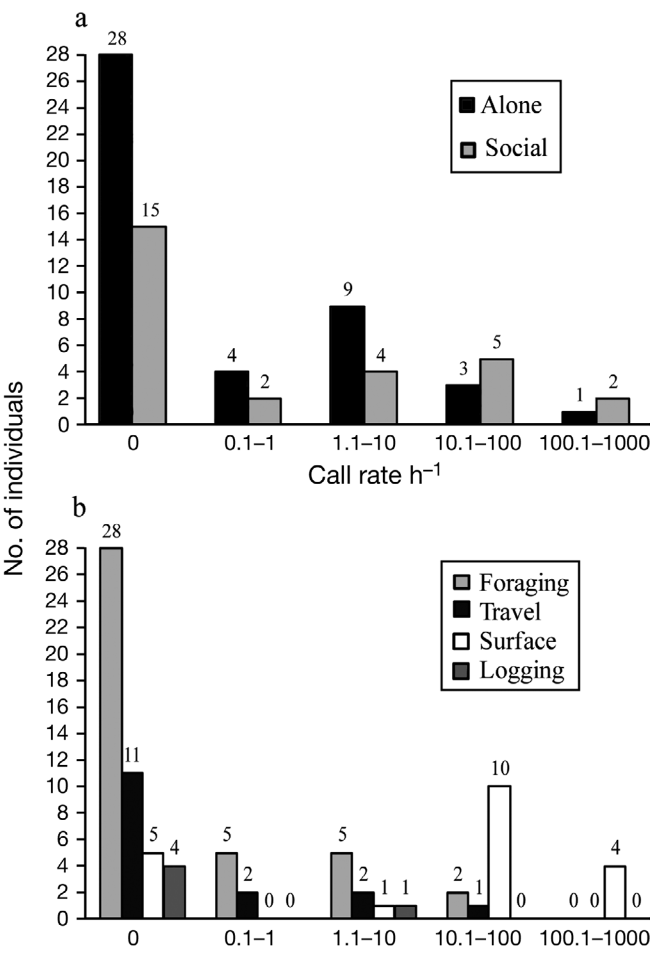


Fig. 4. *Eubalaena glacialis.* Histograms showing the number of whales with different call rates (calls $h^{-1}$) for calls with a high signal-to-noise ratio (≥10 dB): (a) when the whale was alone versus when the whale was with 1 or more other whales (social) and (b) broken down by the behavioral state of the tagged whale as foraging, traveling, surface active, or logging

## Call rates

Call rates (calls $h^{-1}$) for individual tagged whales ranged from a low of 0 calls in 14.1 h to a high of 10 calls in 3 min. The longest period of silence in each tag recording for calls from the tagged whale was between 0.35 and 14.1 h (n = 46, mean ± SD = 2.9 ± 2.8 h, median = 1.1 h, interquartile range, IQR = 0.43 to 3.4 h). The maximum duration of tag re-

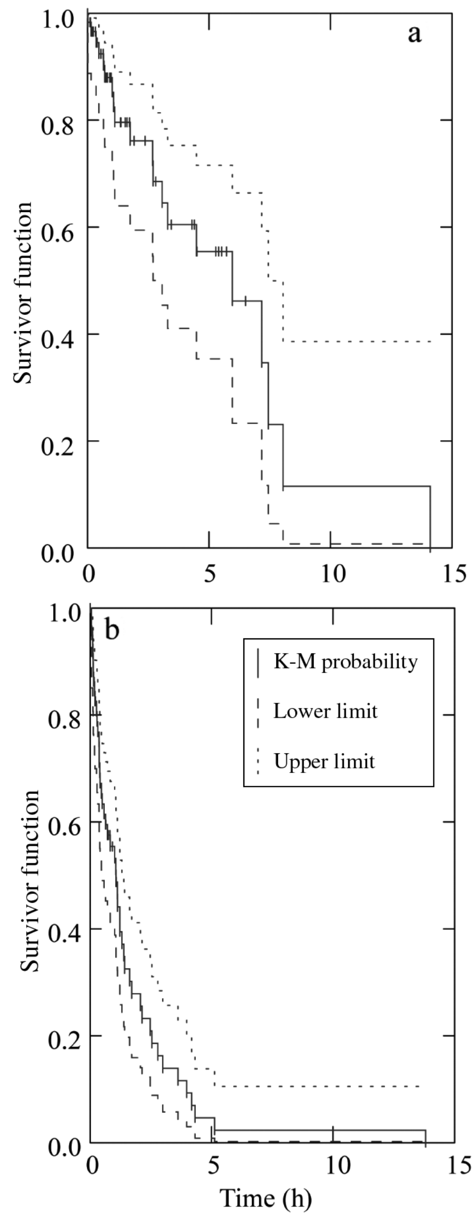


Fig. 5. *Eubalaena glacialis.* Kaplan-Meier (K-M) survival plot for the maximum inter-call interval, including completely censored tag records (i.e. tag records with no whale calls): (a) survival plot for calls from the tagged whales and (b) survival plot for calls from any right whale recorded on the tag

cording with no calls from any right whale ranged from 0.11 to 13.8 h (n = 46, mean ± SD = 1.7 ± 2.2 h, median = 0.71 h, IQR = 0.21 to 1.4 h). The overall call rates for tagged whales when alone ranged from 0 to 200 calls $h^{-1}$ (n = 46, median = 0, IQR = 0 to 1.94 calls $h^{-1}$). The overall call rate for any high signal-to-noise ratio signal on the tag with 2 or more whales present was higher, as this included periods of social interactions and ranged from 0 to 333 calls $h^{-1}$ (n = 28, median = 0, IQR = 0 to 7.69 calls $h^{-1}$) (Fig. 4a). Call rates for any high signal-to-noise ratio signal were the lowest during periods of foraging and logging, and higher during travel and social activity (Fig. 4b). The Kaplan-Meier estimator of the survivorship function predicts that the maximum inter-call interval from the tagged whales while alone would be on average 5.7 h (SE = 0.95, IQR = 3.8 to 7.6 h) (Fig. 5a). The Kaplan-Meier estimator of the survivorship function predicts that the maximum inter-call interval from any whale audible on the tag would be on average 1.7 h (SE = 0.34, IQR = 1.0 to 2.3 h) (Fig. 5b).

Calls from the tagged whale tended to occur in clusters separated by longer periods of silence (Fig. 6). The BCI, calculated from the survivor plot (Fig. 7), was 130 s, longer than a previously reported value of 90 s for calls produced in right whale surface-active groups (Parks & Tyack 2005). The means and standard deviations for intercall intervals within bouts (ICI) and between-bout intervals (IBI), calculated for all records with ≥2 calls, are given in Table 2.

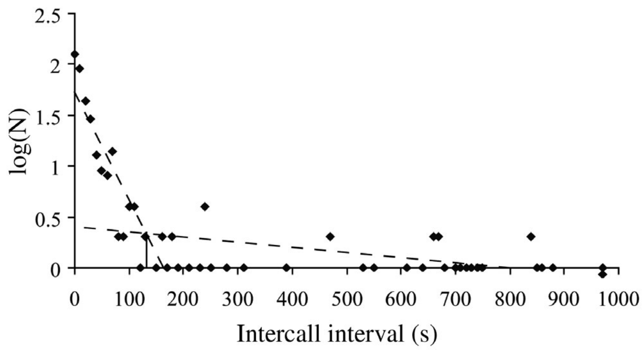


Fig. 7. *Eubalaena glacialis.* Log-survivorship plot of intervals between calls produced by all tagged whales. Dashed lines indicate the approximate slopes for the 2 parts of the curve. The solid vertical line indicates the bout criterion interval value at the intersection of the 2 slope lines

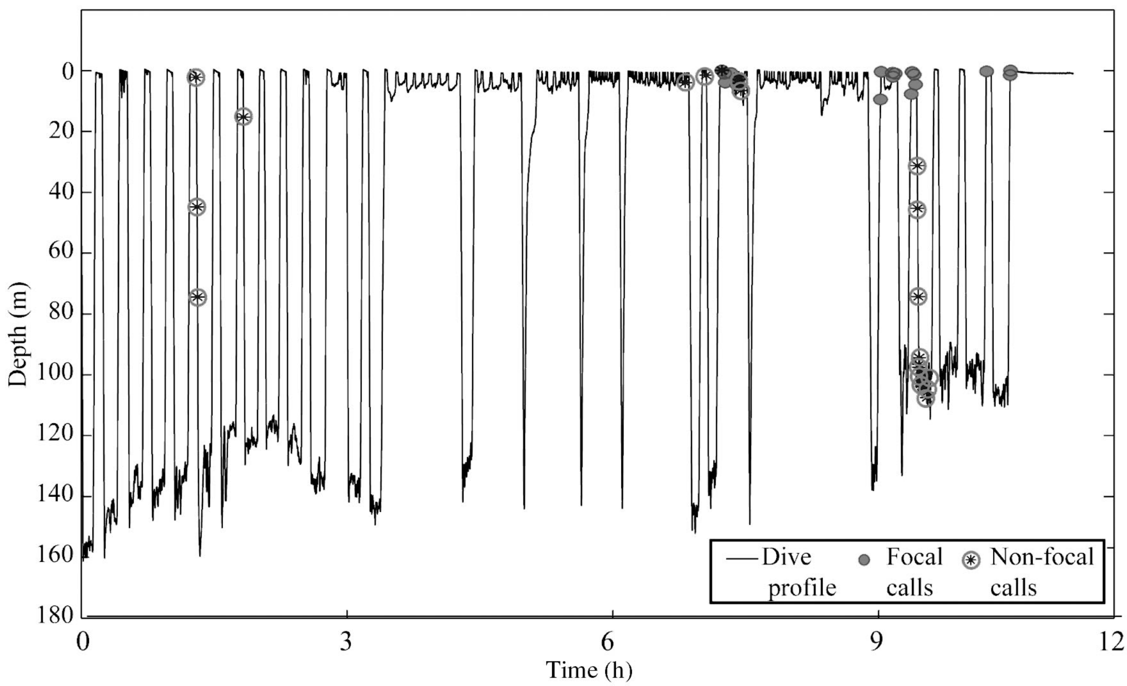


Fig. 6. *Eubalaena glacialis.* Example of bouts of calling by a whale tagged on 29 July 2005, whale ID no. 3323, a 2-yr-old male. The figure shows the dive profile for this whale over the course of 11 h. Tonal calls (including upcalls and other tonals) produced by the tagged whale are marked by solid gray circles; calls produced by other whales are marked by encircled black asterisks

Table 2. *Eubalaena glacialis*. Observed call rate values for each of the tagged whales producing a minimum of 2 calls. n: number of calls from the tagged whale; ICI: inter-call interval — time between the start of successive calls within a bout in seconds; IBI: inter-bout interval — between-bout intervals in minutes, defined by a bout criterion interval of 130 s; –: ≤2 values available. Values include censored values of the time from the last call from the tagged whale to the end of the acoustic record and do not include calls from surface-active groups

| Date | Age-class | Tag duration (h) | n | Call rate (calls $h^{-1}$) | Min. ICI (s) | Mean ICI (s) | ±SD ICI (s) | Max. IBI (min) | Mean IBI (min) | ±SD IBI (min) |
|---|---|---|---|---|---|---|---|---|---|---|
| 5 Aug 2000 | UU | 3.7 | 57 | 15.5 | 2.2 | 7.6 | 8.7 | 195.8 | 69.3 | 109.6 |
| 1 Aug 2001 | JM | 0.6 | 4 | 7.3 | 63.7 | 66.2 | 3.5 | 17 | – | – |
| 9 Aug 2001 | UM | 1.7 | 5 | 2.9 | 12.8 | 28.6 | 22.3 | 67.1 | 39.4 | 39.2 |
| 15 Aug 2001 | AF | 4.2 | 64 | 15.2 | 4 | 21.6 | 24.1 | 61.2 | 10 | 12.2 |
| 9 Aug 2002 | AM | 7.7 | 115 | 14.9 | 0.3 | 28.8 | 17.7 | 268.8 | 55.6 | 92.9 |
| 10 Aug 2002 | JF | 1.7 | 28 | 16.2 | 3.5 | 40.8 | 27.2 | 27.7 | 15.3 | 6.9 |
| 20 Aug 2002 | AM | 4.2 | 11 | 3.0 | 4 | 16.3 | 23.3 | 105.2 | – | – |
| 21 Aug 2002 | AM | 1.8 | 7 | 4.0 | 8.7 | 33.8 | 23.5 | 42.6 | 23.8 | 12.5 |
| 29 Jul 2005 | JM | 10.9 | 19 | 2.0 | 14 | 47.5 | 30 | 446.4 | 79.9 | 151.7 |
| 3 Aug 2005 | AF | 16.5 | 14 | 1.0 | 7.1 | 19.1 | 10.1 | 846 | – | – |
| 7 Aug 2005 | JF | 11.5 | 9 | 1.0 | 4.1 | 29 | 28.9 | 430.1 | 144.4 | 198.7 |
| 12 Aug 2005 | JM | 8.5 | 2 | 0.2 | 57.8 | – | – | 483 | – | – |
| 14 Aug 2005 | UF | 9.0 | 30 | 3.0 | 2.9 | 30.5 | 33.9 | 357.6 | 75.2 | 132.2 |
| 15 Aug 2005 | J | 3.0 | 3 | 1.0 | 39.4 | 75.1 | 50.5 | 162 | – | – |
| Average | | 6.1 | 26.3 | 6.2 | 16.0 | 34.2 | 23.4 | 250.8 | 57.0 | 84.0 |
| SD | | 4.7 | 32.2 | 6.3 | 21.3 | 19.2 | 12.1 | 238.6 | 41.8 | 69.8 |

### Call depths

The depth of the tagged whale when producing upcalls ranged from 0 to 109 m (n = 264, median = 2 m, IQR = 0.5 to 8 m), the depths of tonal calls ranged from 0 to 200 m (n = 107, median = 4.6 m, IQR = 2.6 to 40.5 m), and 'gunshot' sounds were produced at depths from 0 to 11 m (n = 189, median = 0 m, IQR = 0 to 0.5 m). There was a significant difference in the depth of sound production across the 3 main call types (gunshot, upcall, and tonal) (Kruskal-Wallis test: $H_{574}$ = 242, p < 0.0001). Tonal calls were produced at greater depths than upcalls (Mann-Whitney $U$ = 20 242.5, $\chi^2$ = 29.0, df = 1, p < 0.0001) and gunshot sounds (Mann-Whitney $U$ = 7502, $\chi^2$ = 171.2, df = 1, p < 0.0001). There was no significant difference between upcalls and gunshot sounds in the depth of production, but only 1 ind. produced gunshot sounds.

Tagged whales spent only 36% of their time in the top 10 m of the water column. But despite this, 77% (287 of 371) of tonal vocalizations (i.e. all calls excluding gunshots) from tagged whales were produced at depths <10 m. As a result, calls were not produced randomly throughout the dive cycle (Mann-Whitney $U$ = 176, $\chi^2$ = 5.36, df = 1, p = 0.02); most calls (260 of 371) were produced during the surface interval between dives. Calls produced at depths >10 m (84 of 371) were most often produced during the ascent phase of a dive (57 during ascent, 20 at the bottom of the dive, and 7 during the descent). Calls produced at depths >10 m had higher minimum frequencies (n = 84, median = 93 Hz, IQR = 75 to 231 Hz) than calls produced near the surface (n = 287, median = 79 Hz, IQR = 62 to 107 Hz); Kruskal-Wallis test: $H_1$ = 15 929, p = 0.002).

### Call behavior by age and sex

Differences in the depth of production, call duration, minimum frequency, and peak frequency of calls were tested against age-class and sex using a mixed model. For upcalls, the only detectable difference by age-class was in the duration of the calls (all other tests: p > 0.05), with adults tending to produce longer upcalls than juveniles (least-square mean ± standard error — adult: 1.34 ± 0.1 s; juvenile: 1.04 ± 0.1 s; df = 234, $t$ = 1.99, p = 0.048). No differences in upcalls were seen between the sexes (p ≥ 0.5). For tonal calls, there were no significant differences by age-class or sex.

### Assessment of potential behavioral disturbance from playback experiments

A total of 28 of 46 tags had at least 1 playback trial during tag attachment. Of these, 13 records had no calls from the tagged whale, and 15 had at least 1 call that could be assigned to the tagged whale. As playbacks required longer tag attachment, these tag records were on average 4.7 ± 3.4 h in duration compared to attachment durations of 1.8 ± 2.7 h for whales that did not receive playbacks. A comparison of tag records with and without playbacks showed no statistically significant difference in the average rate of calling (2-sample $t$-test: $t = -1.011$, df = 44, p = 0.318) and the number of calls (2-sample $t$-test: $t = -1.83$, df = 44, p = 0.075). A paired $t$-test comparison of the call rate 1 h before and 1 h after the commencement of playbacks also showed no significant difference (paired $t$-test: $t = -0.452$, df = 26, p = 0.655). There were 2 cases when the tagged whale produced upcalls within 5 min of a playback of previously recorded right whale sounds. These 2 cases may represent overestimates of the normal calling behavior for these individuals. No other tagged whales receiving playbacks produced calls in the 10 min following the start of the playback.

## DISCUSSION

### Tag data

Information about the individual calling behavior of right whales *Eubalaena glacialis* is needed to assess the potential for passive acoustic detection as a tool for locating and protecting the endangered North Atlantic right whale (Clark et al. 2007). Passive acoustic monitoring can be used both to locate biologically important regions and times of the year (e.g. breeding grounds during the breeding season) and to provide more immediate protection in the form of real-time warning systems for mariners traversing areas with right whales (Van Parijs et al. 2009). The present study used an acoustic recorder attached to whales to track the sound production of individual whales through time in the Bay of Fundy, Canada. This data set contains most of the recordings from known individual North Atlantic right whales currently available. The use of tag data reduces uncertainty of which animal is vocalizing and results in high-quality recordings suitable for parameter extraction. Our objective was to describe the variability of sound production by individual whales as an aid to designing, and interpreting data from, passive acoustic monitoring systems. These results also deepen our understanding of how acoustic communication in right whales relates to the behavioral state and age and sex of individual animals.

### Call types

All 3 major call types described for North Atlantic right whales (stereotyped upcalls, variable tonal calls, and gunshot sounds (Parks & Tyack 2005) were recorded from tagged whales. Whales of all ages and both sexes produced upcalls and variable tonal calls, but gunshot sounds were only documented from 1 individual, an adult male. There were no clear differences in the rates or parameters of tonal call types produced by either sex, but this may be biased by the exclusion of vocalizations during social interactions and surface-active groups when calls could not be assigned with confidence to tagged individuals. Previous studies have indicated that females produce the majority of tonal calls in surface-active groups (Kraus & Hatch 2001, Parks & Tyack 2005). The current study shows that both age-classes and sexes produce upcalls. This call type is commonly used for passive acoustic detection of this species (Clark et al. 2007, Mellinger et al. 2007b), and our results support using this call type as the most appropriate for detecting any right whale in an area. Lumping of all right whale tonal calls, stereotyped upcalls, and variable tonal calls leads to higher call rates because of the inclusion of the frequent tonal calls produced by surface-active groups (Parks & Tyack 2005). Therefore, inclusion of tonal calls and gunshot sounds in detectors are likely to increase the probability of detection of right whales in habitats where these behaviors are common. These call types may be particularly advantageous when trying to locate right whales outside of their known habitat areas.

### Call rates

The call rate of individual right whales in the present study was highly variable. The behavioral state of whales strongly affected call rates, with low rates typical during periods of foraging, traveling, or logging as compared to surface activity. Overall, call rates were low for most individuals, reflecting the greater allocation of time to less vocal behaviors: foraging was the predominant behavior of tagged whales. One caveat is that most of the tag records described here contained only daytime data. Previous studies have shown a marked increase in calling activity of right whales during the night (Matthews et al. 2001, Munger et al. 2008). For whales that did produce vocalizations, sounds were produced in bouts of several calls, separated by relatively long periods of silence. To be conservative, an acoustic sampling window for passive acoustic detection of a single right whale in the Bay of Fundy may need to be greater than the maximum between-bout interval, which averaged approximately 2 h for whales that produced any vocalizations, with a broad range from 4 min to >14 h. However, shorter detection windows may be possible for areas where multiple right whales are likely to be present. There were few tags in which sounds from other right whales in the area were not recorded, and call rates were higher during periods of social interactions. Inclusion of gunshot sounds and variable tonal calls may improve the probability of detection in the Bay of Fundy where these sounds are common (Van Parijs et al. 2009).

### Call depths

The majority of calls recorded from tagged whales were produced either at the surface or in the last 10 m of ascents from dives, with few calls produced during descents or at the bottom of dives. The few calls produced at deeper depths were generally higher in frequency than those produced at shallow depths, which is similar to the results reported by Ridgway et al. (2001) for beluga whales, but contrary to those reported by Jensen et al. (2011). It is unclear whether the observed trend for sound production near the surface is a result of biophysical limitations in the call production mechanism (Ridgway et al. 2001, Thode et al. 2002), or a behavioral tendency not to call while feeding at depth. Whatever the reason, the preponderance of call production near the surface may have implications for the detection range of right whale calls. Propagation of sound underwater is affected by the depths of signal production and reception, and by the physical environment. Given the low frequency (~100 Hz) of right whale upcalls, propagation of signals from shallow sources will be influenced by the Lloyd mirror effect, in which reflection of the signal from the sea surface can lead to constructive and destructive interference of the propagating sound (Medwin & Clay 1998).

Environmental characteristics will also strongly influence sound propagation. The Bay of Fundy can be considered a shallow-water (~200 m) environment for the low-frequency signals (wavelength of approximately 15 m) produced by right whales. In summer months, a near-surface thermocline forms in the water column, leading to a weakly downward-refracting sound speed profile (sound speed variation throughout the water column has been measured at <15 m s$^{-1}$ (Desharnais et al. 2004, 2006). Additional environmental factors affecting sound propagation include wind and waves that generate bubble clouds in near-surface waters (Medwin & Clay 1998). A theoretical model of right whale call detection in the Bay of Fundy, based on a 10 m source depth, predicted that direct path propagation of right whale signals to bottom-mounted recorders would be limited beyond 5 to 8 km (Chapman 2004).

### Differences by age and sex

Few differences in calling behavior by age-class and sex were detected in this analysis. This is likely a result of inter-individual variability being greater than variability between age-class or sex for some parameters, as well as the limited sample size of calling animals when divided into age/sex-classes. The only notable difference between age-classes was a longer duration of upcalls in adults versus juveniles. This may be a factor of individual size, and more detailed studies of individual distinctiveness of calls may be useful for passive acoustic monitoring.

### Sources of bias

Most tagged whales were tracked by a vessel (usually within 1 km of the whale), and about half of the tagged whales were subjected to playback experiments of conspecific calls, alerting stimuli, or vessel noise (Nowacek et al. 2004). The tagging, vessel follows, and playbacks all have the potential to modify the behavior of whales, possibly leading to bias in the measurements reported here. While it is difficult to assess the disturbance caused by tagging, no clear differences in call types, rates, or depths were seen between whales that did or did not receive playbacks. There were 2 cases where tagged whales called during or immediately after receiving playbacks of natural whale calls, possibly in answer to the playback signals, but this represents a small bias in the statistics, given the large sample size.

Many studies have investigated human-caused disruption of normal behavior in animals (Frid & Dill 2002). One prediction for a disturbance reaction from right whales would be a reduction in the overall call rate of an individual, resulting in the call rates described here being a low estimate of the true calling behavior of individual right whales. However, while there is potential for the data collection process to influence the behavior of the whales, the normal habitat of the North Atlantic right whale regularly includes numerous sources of disturbance from vessels and other human sound-generating activities (Clark et al. 2007). The areas with the highest levels of human activity are the areas of primary concern for passive acoustic detection, so the calling activity described here may reflect fairly 'typical' scenarios in the lives of right whales. Another concern is that these data were collected exclusively in the Bay of Fundy, and so may not be representative of the calling behavior of right whales in other areas. However, the Bay of Fundy is a region with high levels of commercial shipping, and therefore an important habitat area for protection of right whales from ship strikes. If passive acoustic monitoring is to be used to guide potential sources of disturbance, such as large vessels, away from right whales, it is critical to document call rates in the presence of such disturbances.

**Implications for passive acoustic monitoring and conservation**

The present study indicates that there is wide variability in the calling behavior of individual right whales. For whales that did produce calls, these were typically produced in bouts separated by long periods of silence, as has been described in previous studies (Matthews et al. 2001, Parks & Tyack 2005). The results of the Kaplan-Meier survivorship analysis indicate that a 1 h listening period would allow detection of the presence of right whales about 40% of the time during the daylight hours and summer months in the Bay of Fundy. A 4 h listening period is required for 90% detection of right whale presence in this area.

As described by Matthews et al. (2001), most calls were produced near the surface, although some calls were produced down to 200 m in depth. The predominance of shallow calls may lead to shorter than expected detection ranges due to increased attenuation of sounds propagating near the surface in some conditions. There were few differences in upcall or tonal call production by age- and sex-class, suggesting that the upcall, commonly used to detect right whales acoustically, potentially allows for the detection of all individuals in the population. Further research on the vocal behavior of individual whales at different times of the year, in different habitats, and in different behavioral contexts, including disturbance, are necessary to improve our understanding of the sound production behavior and the possibilities for acoustic detection of this species.

*Acknowledgements.* Numerous field teams and funding agencies contributed to the collection of these data over the years. We thank the field teams from the Woods Hole Oceanographic Institution, the International Fund for Animal Welfare, the North Atlantic Right Whale Consortium, and the New England Aquarium for assistance with data collection and analysis. Thanks to M. Weinrich, C. Hotchkin, and 3 anonymous reviewers for their insightful comments and suggestions, and to A. McGregor for her assistance in data processing. Funding for this work was provided by the Office of Naval Research (Grant No. N00014-99-10831), the National Marine Fisheries Service of the US National Oceanic and Atmospheric Administration (Contract Nos. NA87RJ0445 and NA04NMF4720405), the Massachusetts Environmental Trust, the International Fund for Animal Welfare, the National Ocean Partnership Program (NOPP), and a Cecil and Ida Green technology award. This work was conducted under a NOAA Fisheries permit to conduct scientific research (No. 1014) issued to Dr. Scott Kraus, and Canadian Department of Fisheries and Oceans Permits 2000-489, 2001-559, 2002-568, and MAR-SA-2005-003.

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*Editorial responsibility: Sascha Hooker, St. Andrews, UK*

*Submitted: February 5, 2009; Accepted: July 12, 2011*
*Proofs received from author(s): August 18, 2011*