Vocalisation rates of the North Atlantic right whale (*Eubalaena glacialis*)

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ABSTRACT

Vocalisation rates were measured from North Atlantic right whales (*Eubalaena glacialis*) in spring 1999-2000 in the Great South Channel and off Cape Cod, USA, and in summer 1999-2000 in the Bay of Fundy, Canada. Vocalisations were classed as either 'moans', 'low-frequency (LF) calls' or 'gunshots'. Towed hydrophone recordings (36.1 hours) were made in 21 encounters where loose aggregations of right whales were within about 1,000m. Recordings were also made using acoustic tags attached by suction cups to ten different whales (29.5 hours). Tags also recorded depth data. Moan rates (sounds per aggregation per hour) were correlated with size of whale aggregation. Individual whales produced moans at ~0-10 per hour (recorded from tags and the towed hydrophone). Small aggregations (2-10) gave higher moan rates (usually <~60 per hr) and larger aggregations (>10) higher still (~70-700 per hr) (recorded from towed hydrophone). Results from the Bay of Fundy indicate high moan rates at night. Moans were usually produced in clusters. Tag data showed that moans were usually produced when whales were within about 10m of the surface. A passive acoustic system could potentially provide supplementary information on the distribution of aggregations of right whales. This could be useful for management (1) in the long term, by aiding the prediction of right whale distribution, or (2) as a real-time tool for helping to route shipping away from concentrations of right whales. The empirical evidence presented here on vocalisation rates will assist in assessing feasibility. The clustering of moans and the tendency to produce them near the surface could hamper detection and localisation efforts. Further research is underway to investigate other important practical issues such as detectability and source levels.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; VESSEL-STRIKE; MANAGEMENT; VOCALISATION; CONSERVATION; ACOUSTICS; HABITAT; FEEDING-GROUNDS; NORTH AMERICA

INTRODUCTION

Ship strikes have been identified as a major cause of mortality in modern times for the North Atlantic right whale (*Eubalaena glacialis*). From 1970-1999, 16 of the 32 fatalities for which cause of death could be ascertained were due to vessel strikes, and a further 13 were of unknown cause (Knowlton and Kraus, 2001; Laist *et al.*, 2001). The Scientific Committee of the International Whaling Commission has made specific recommendations for reducing ship strikes following a workshop in Cape Town, South Africa (IWC, 1999). These recognise the need for surveillance systems that would give real-time information on the location of right whales in particular high-risk areas. The need for long term information on right whale distribution and its relation to other variables, such as prey abundance, is also recognised.

Passive acoustic detection has the potential to provide data on right whale locations. Vocalising whales may be detected acoustically, in poor sighting conditions, or at night, and acoustic systems may potentially be automated. The bowhead whale (*Balaena mysticetus*) migration past Point Barrow in Alaska has been monitored for over 20 years using passive acoustic methods (e.g. Clark *et al.*, 1996). In the Canary Islands, a network of hydrophones has been proposed in an effort to reduce collisions between fast ferries and cetaceans. The idea is to set up a safety corridor within which cetaceans can be detected, classified, localised and their positions notified to vessels to permit timely course alterations (Andre and Potter, 2000). The efficacy of acoustic detection systems strongly depends on the animals vocalising sufficiently frequently. This paper describes a study of the production of sounds of right whales in the western North Atlantic.

In contrast to southern right whales (*Eubalaena australis*), North Atlantic right whale sounds have not been studied extensively. Fundamental frequencies of the North Atlantic right whale are reported between about 100-400Hz (Schevill and Watkins, 1962; Caldwell and Caldwell, 1971; Thompson *et al.*, 1979); those of the southern species are principally in the range 50-500Hz (Payne and Payne, 1971; Cummings *et al.*, 1972; Clark, 1982). Vocalisations are diverse in amplitude and frequency modulations. Clark (1982) classified southern right whale vocalisations into categories such as 'up', 'down', 'high' and 'hybrid' calls based on various physical characteristics, including the 'pulsiveness' of the sounds and the character of the frequency modulations. Brief, broadband sounds lasting about 0.2 seconds are also produced, termed 'slaps' or 'gunshot slaps' (Clark, 1982; 1990). This characterisation of the southern right whale repertoire may well apply to the North Atlantic right whale, although this has not been formally demonstrated.

Little information exists on vocalisation rates of North Atlantic right whales. As far as is known, right whales do not sing (Clark, 1990), so that sequences of calls tend to be irregular and non-repetitive. ONR (1997) counted 690 North Atlantic right whale vocalisations on about 300 hours of tape from a bottom-mounted array off the coast of Florida. It is not possible to reliably estimate rates from this, *inter alia* because: (1) recordings were chosen as those 'most likely to yield vocalizations'; (2) the period of recording when whales

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were present is not known; and (3) the number of whales is not known. In a study of northern right whale vocalisations in a social context, Kraus (1991) found a high rate of vocalisations (average 12 per minute) in active groups in which a female was identified as the centre of activity.

Several researchers have studied rates from southern right whales. Clark (1983) carried out the most extensive acoustic study of southern right whales together with shore-based observations. The rates of sound production varied widely with the sound type, the activity of the whales, the sexual composition of the groups, and the sizes of the groups. A brief summary of this information, derived from Clark (1983) is given in Table 1.

METHODS

Sampling

Auditory information alone cannot distinguish between the absence of whales and the presence of silent whales. If the duration of the latter periods cannot be properly determined, rates will be biased. To ensure that periods of silence with whales present were adequately represented in this study, the presence of whales was verified by recording: (1) from towed arrays in daylight, when whales could be seen; (2) from towed arrays at night, when whales were known to be present, either on the basis of blows heard above water or (in one case) by radio-tag signals; and (3) from digital acoustic tags (DTAGs) attached to whales.

Fieldwork and equipment

Towed hydrophone recordings were made in Cape Cod Bay and in the Great South Channel in spring 1999-2000 and in the Bay of Fundy in summer 1999-2000 from *Song of the Whale*, a 14m, auxiliary powered, sailing research vessel (Fig. 1). Acoustic tag recordings were made in the Bay of Fundy in summer 1999-2000. Tags were attached by the motorboat *Hannah-T* and tracking was carried out from *Song of the Whale.*

Hydrophone arrays

The towed hydrophone array comprised two *Benthos* AQ-4 elements spaced 3m apart. Preamplifiers mounted close to the elements had 28dB gain and a high pass filter with a 3dB point at 20Hz. In 1999, recordings were made using a digital audio tape (DAT) recorder (*Sony* DAT-Pro, sample rate 48kHz) either directly to the DAT recorder or via an additional preamplifier. In either case, the low cut-off frequency was below 20Hz. In 2000, a preamplifier with a low cut-off frequency set to 47Hz was used and recordings made directly to a computer hard drive via a sound card (*Sound Blaster* Pro, sample rate 8kHz) and later archived on CD.

Recordings were analysed for those daytime occasions when the vessel was near (within approximately 500m) aggregations of right whales. In addition, in 1999, an opportunistic night-time recording was made when tracking an entangled whale carrying a VHF tag attached by a disentanglement team. The whale was estimated to be

Table 1

Summary of call and slap rates for southern right whale groups, derived from Clark (1983). The estimates of sound rates for this table were calculated as: number of sounds per group per hour × proportion of groups which were vocal.

Activity	Proportion of groups which were vocal	Recording time (hours)	No. calls of acoustic groups	No. slaps of acoustic groups	Estimate of sound rate (sounds per group per hour)	
					Calls	Slaps
Resting	10/21	11.2	28	0	1.2	0
Swimming	87/188	74.8	1,504	36	9.3	0.2
Mild activity	59/76	80	874	667	8.5	6.5
Full activity	23/23	54.9	856	136	15.6	2.5
Sexual activity	8/8	27.8	201	34	7.2	1.2
Combined	129/316	248.7	3,463	873	5.7	1.4

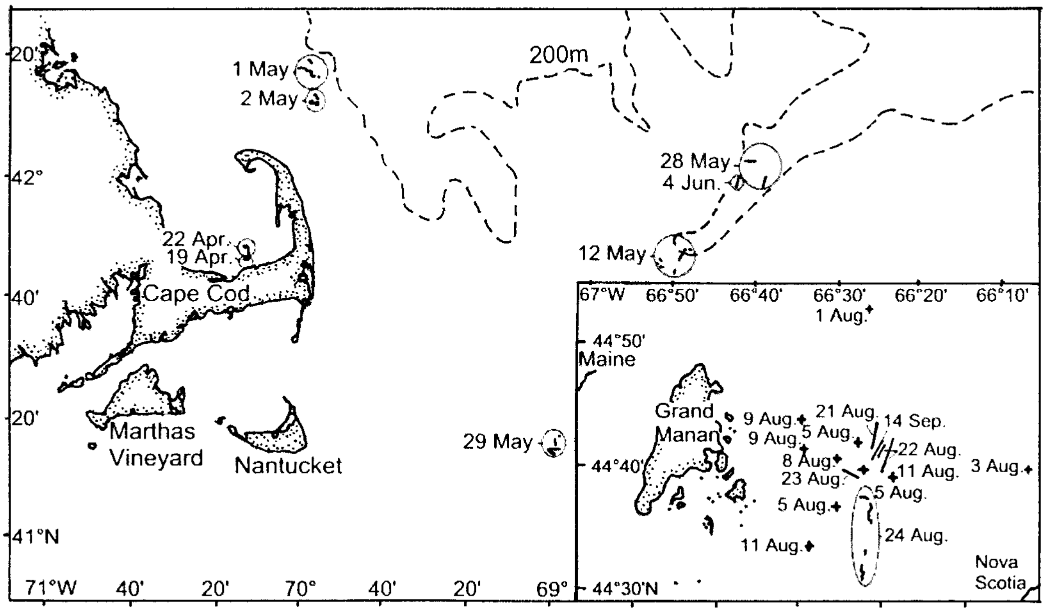

Fig. 1. Map showing dates and positions of recording locations from the towed array and DTAG off Cape Cod, USA and in the Bay of Fundy, Canada.

between 500m-1,000m away during the recording, based on the received level of the radio signal. In 2000, night-time recordings were from right whales that were followed from day into night, and from periods when blows were audible above water. As *Song of the Whale* was also carrying out photo-identification work, she moved between individuals and aggregations; consequently multiple recordings were sometimes made on the same day from different aggregations. The engine was usually idling during recordings.

The size of aggregations was estimated using the maximum of counts of animals visible at the surface at specific intervals during the recording. This is clearly somewhat imprecise, particularly for larger aggregations, because surfacings were not apparently coordinated. In order to reflect this imprecision, aggregations were somewhat arbitrarily divided into 'aggregation size' categories of 1, 2-5, 6-10 or 10+ whales. The number of individually identified animals from a recording session was not used as an estimate of aggregation size because, in larger aggregations, only a small proportion of the animals seen were subsequently identified.

Digital acoustic tags

DTAGs (Johnson and Tyack, in press) with suction cups were successfully attached to ten different individuals. DTAGs sampled at 16kHz and provided 4.7hrs of recording time each. Tags also incorporated VHF transmitters (allowing tracking of the whales at the surface) and a programmable release mechanism. Technical details and further information on other physical data recorded (depth, acceleration, magnetometric, pitch and roll data) are given in Johnson and Tyack (in press). Tags were compact (approximately 10×5×5cm) and held in place by three suction cups (one housing the hydrophone) to remove the need for skin penetration. They were attached high on the dorsal surface of the whale using a flexible 40ft pole (Moore *et al.*, 2001).

Behaviour, based on surface observations, was classified into the following categories: 'resting'; 'swimming'; 'skim feeding'; 'fluking'; and 'surface activity'. Surface activity is defined to include behaviour such as lob-tailing, flipper-slapping or head-outs. The occurrence of 'surface active groups' (Kraus and Hatch, 2001) was also noted. These are defined as 'two or more animals interacting at the surface, less than one body length apart and with frequent physical contact'.

Analysis

All recordings of sufficient quality were evaluated aurally through high-fidelity headphones (covered-ear *Sennheiser* or *Sony*). In the towed recordings, sections with high noise were omitted. Noisy sections were infrequent and quite distinct, because they were usually due to cavitation from the vessel's own propeller, when moving to stay within range of whales. Sounds were categorised by the listener and their time of occurrence entered using an event-recording computer program. The program placed the times of occurrence within a database, where they were combined with GPS positions and other information.

Since the analysis of the recordings was performed aurally, no attempt was made to use the detailed ordination and classification of the southern right whale repertoire provided by Clark (1982). The scheme used here was deliberately simple, and the call types were distinctive and classification unambiguous. Sounds were categorised as 'moans', 'gunshots' or 'LF calls' (see Fig. 2). Moans were

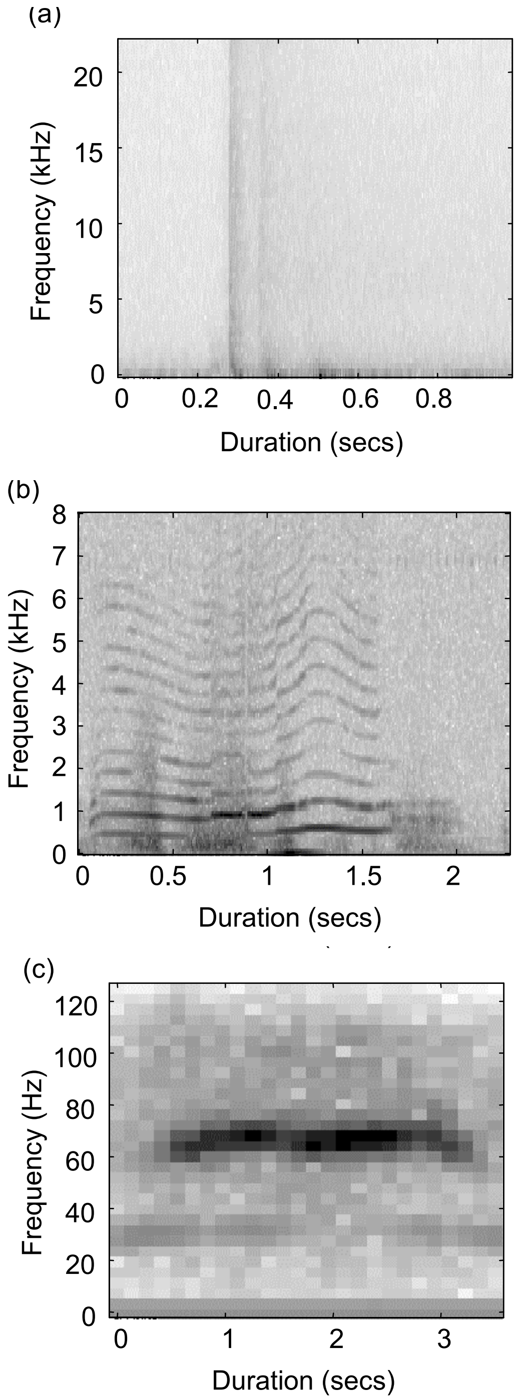

Fig. 2. Spectrograms of right whale vocalisations. (a) a gunshot; (b) a moan; (c) a low-frequency (LF) call.

broadly in the range 50-500Hz and lasted 0.4-1.5 seconds. They varied widely in amplitude and frequency modulations. Gunshots were broadband and impulsive and correspond to previously reported 'slaps' (Clark, 1982; 1983) or 'gunshot slaps' (Clark, 1990). Low-frequency (LF) calls are of constant frequency or slightly modulated, around 60-80Hz, and of variable duration (~ 0.5-10 seconds). They were only detected by DTAGs. The absence of detectable LF calls on the array recordings is probably due to their being masked by noise from the vessel's engines. In this paper, analysis focuses primarily on moans because they are the most likely candidates for passive detection.

Moans recorded by the DTAG were distinguished as 'focal' vs 'non-focal' sounds, with the former being produced by the tagged animals themselves and the latter by others. Sounds were judged to be 'focal' based on several factors including: the received level; the absence of reverberation; presence of significant high frequency harmonic components; and, in some cases, small concurrent perturbations in the pressure signal. The simpler acoustic characteristics of LF calls, however, did not allow such a distinction to be made between focal and non-focal sounds. Moreover, when brief, LF calls are not necessarily distinguishable from non-biological sounds (for example, hydrodynamic oscillations of the tag).

Recordings were made in separate 'encounters' with whales. Most encounters were with aggregations of whales found on separate days. On a few occasions, recordings were made on the same day that the vessel had left one aggregation and travelled for about an hour or more, before finding another.

For the towed array recordings, sound rates are presented as numbers of sounds per hour per aggregation. Rates are not presented as sounds per hour per individual because of the difficulty of determining the precise number of animals in an aggregation. In the tag recordings, it was possible to distinguish 'focal' moans, so sounds per hour per whale are presented in these cases. Sound rates are examined by encounter as functions of time of day of recording (local time), location (Bay of Fundy, Cape Cod Bay or Great South Channel) and aggregation size.

The mean rate (number of sounds/duration) alone is an inadequate representation in situations where the rate varies in time or tends to cluster. The intervals in recordings here were initially compared with the null model of a random (Poisson) process, where the probability of an event in any time unit is small and constant and independent between time units. In a Poisson process, the variance and mean of counts in small time intervals are equal. If the variance is found to be larger than the mean this is indicative of clustering or that the probability of an event is not constant (Cox and Lewis, 1966). In the present analysis, this comparison was made using counts over minute intervals, a period over which the probability of a vocalisation is small.

The log-survivor function (Cox and Lewis, 1966) was used to examine the intervals. The survivor function $R(x)$ is the proportion of intervals exceeding x. Intervals between events in a Poisson process are exponentially distributed, so $\log R(x)$ is a straight line, and departures from this are easily discerned. Other types of model can also be fitted to $\log R(x)$.

The Bartlett-Lewis Poisson cluster process was fitted to moan intervals (Cox and Lewis, 1966) for those encounters during which a sufficient number of moans had been made. This model gives a useful approximation when events arrive in clusters, because it allows several parameters to be estimated: the expected interval between clusters; the expected interval between events in a cluster; and the expected number of events in a cluster. Together these provide a better description of the process than would the mean rate alone. In the Bartlett-Lewis Poisson cluster process, intervals Z between clusters are exponentially distributed. Numbers of moans in a cluster are distributed as some discrete random variable S. The 'subsidiary' events within a cluster arrive after the cluster origin, with independently and identically distributed intervals Y. The separations between events in the whole process are described by the random variable X. In this study, intervals between the subsidiary events were assumed to be exponentially distributed. The model was fitted to those sequences with sufficient sounds, using the log-survivor plot and theoretical results provided by Cox and Lewis (1966).

Expected interval between clusters:

$\hat{z} = 1/\lambda$, where λ = gradient of log-survivor function for large x.

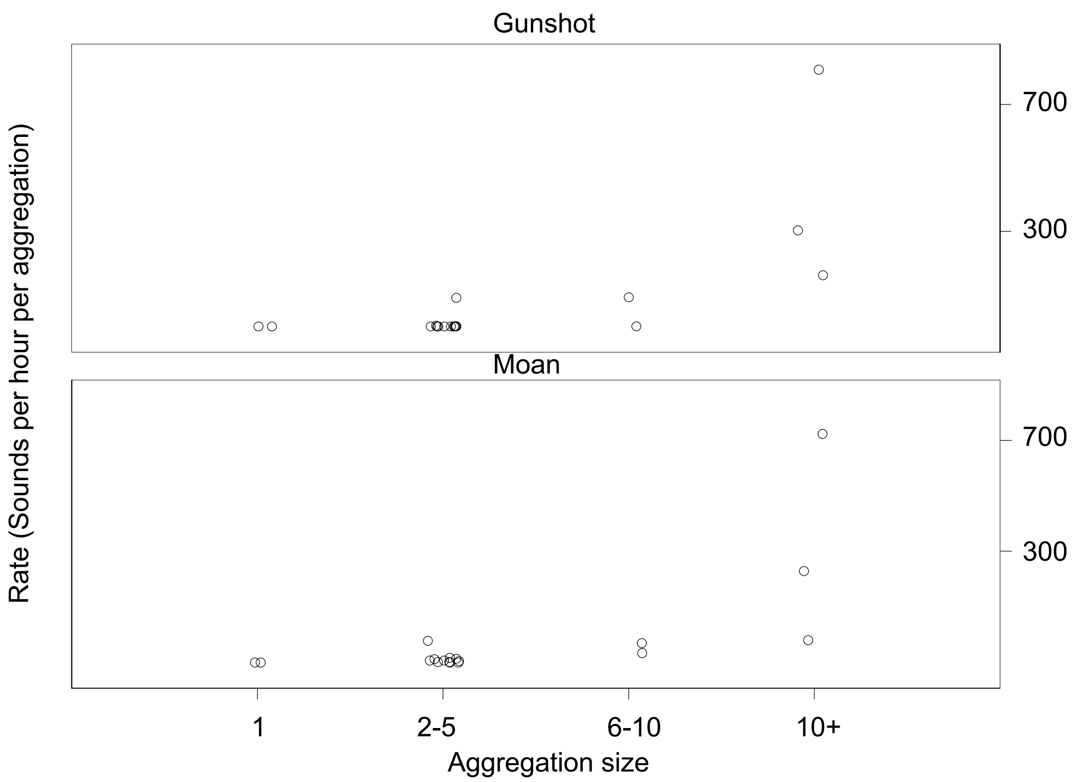

Fig. 3. Vocalisation rate (sounds per hour per aggregation) against aggregation size. Points have been jittered horizontally. The two single whales made no sounds. Rates appear to increase with aggregation size. Three night-time encounters were excluded because aggregation size was not known.

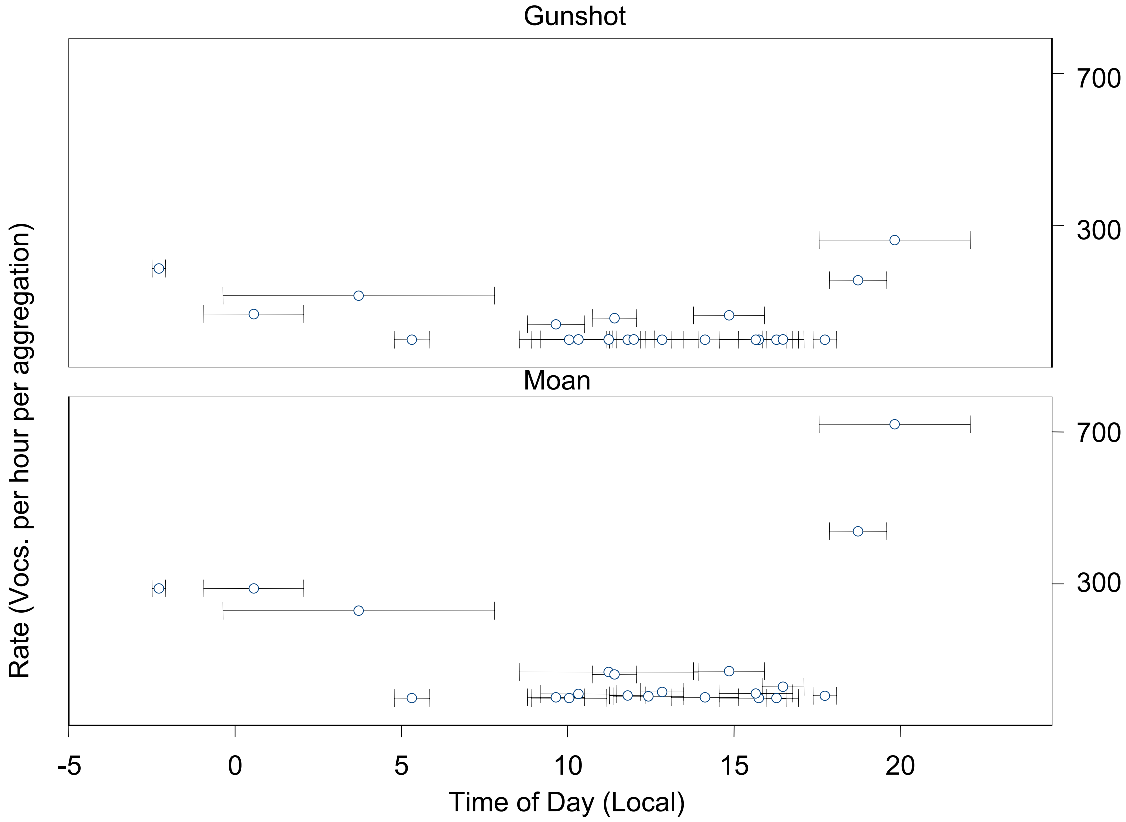

Fig. 4. Mean vocalisation rate (per hour per aggregation) of whales against time-of-day. Horizontal bars cover the period of monitoring for each encounter.

Expected cluster size:

$\hat{s} = (\hat{z}/\bar{x}) - 1$, where $\bar{x}$ = duration of recording/number of moans.

Expected interval between moans within a cluster:

$\hat{y}$ is estimated graphically from the log-survivor plot.

RESULTS

Towed hydrophone recordings

Information relating to recordings made from the towed hydrophone is shown in Table 2. A total of 36.1 hours of acoustic data of acceptable quality were collected in 21 encounters on 13 days. Rates of moans and gunshot are shown as means and variances of minute counts, which may be compared for evidence of departure from a Poisson process.

Mean vocalisation rates are shown against estimated aggregation sizes (for recordings in daylight only) in Fig. 3, and against time of day in Fig. 4. No moans were heard from solitary whales, but, as expected, rates (i.e. number of sounds per aggregation, *not* individual) increase with number of whales in the aggregation. Both moans and gunshots were more frequent at night.

As shown in Table 2, variances were usually larger than means for the minute counts, indicating that sounds were not produced as a Poisson process. This situation may arise when, within encounters, the rate varies as a function of time. However, within each encounter, the dominant external variables which affect moan rate (namely, number of animals present and time-of-day) were more-or-less constant. The cumulative counts of moans for each of the encounters where moans were heard is shown in Fig. 5. Within some encounters, a few noisy sections were removed, and the remainder of the series concatenated. The slopes are fairly constant, although there are occasional changes over the long term in the rate.

Clustering of sounds would also cause the observed variance > mean relationship. The cumulative count of moans with time is shown in Fig. 6a, for the example of encounter 19. The steps in the curve indicate a degree of clustering. The log-survivor plot using the intervals between moans from encounter 19 is shown in Fig. 6b. The curvature in the moan interval data indicates that this is not a simple Poisson process. However, for large time intervals, the curve does approach a straight line, suggesting that a Poisson

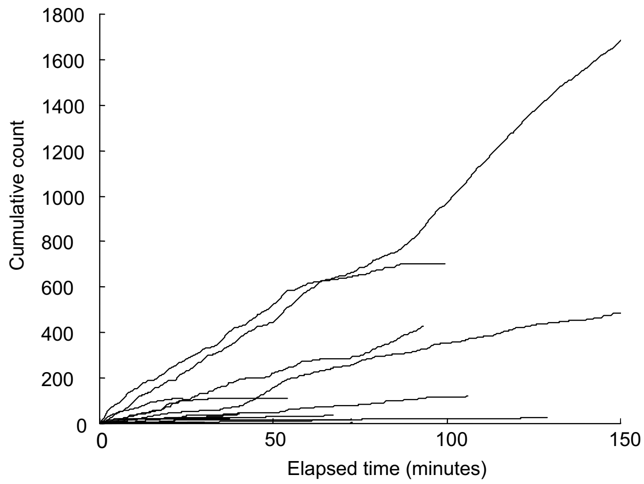

Fig. 5. The cumulative count of moans during encounters with whales. Two lengthy recordings have been truncated for this illustration.

Table 2

Sound rates (calls) of whales in 21 encounters, with auxiliary information, from towed hydrophone recordings in 1999-2000. The rates are given as the mean of the minute counts per aggregation. The variances of the minute counts are also given. The variances are usually larger than means, indicating clustering. Note encounter 14 was unusual, as the whale was entangled and being radio-tracked.

			Moans			Gunshots						
Encounter number	Date	Total monitoring time (hrs)	Total no.	Mean (count per min)	Variance (count per min)	Total no.	Mean (count per min.)	Variance (count per min.)	Location	Times (GMT)	Approx. no. whales	Behaviour
1	19 Apr. 1999	1.29	20	0.26	0.46	0	0	0	Cape Cod Bay	17:12-18:29	2-5	Skim feeding; some surface activity
2	22 Apr. 1999	2.01	21	0.18	0.44	2	0.02	0.03	Cape Cod Bay	14:11-16:27	2-5	Skim feeding; swimming
3	1 May 1999	1.95	4	0.03	0.05	0	0	0	Nr. Wildcat Knoll	18:06-20:08	2-5	Fluking
4	1 May 1999	0.58	0	0	0	0	0	0	Nr. Wildcat Knoll	20:59-21:34	1	Swimming; fluking
5	2 May 1999	0.59	0	0	0	0	0	0	Nr. Wildcat Knoll	09:47-10:51	1	Skim feeding; some fluking
6	2 May 1999	1.87	0	0	0	0	0	0	Nr. Wildcat Knoll	13:54-16:11	2-5	Fluking
7	12 May 1999	0.91	6	0.11	0.33	0	0	0	Great South Channel	16:15-17:21	2-5	Swimming; occasional fluking
8	12 May 1999	1.31	0	0	0	0	0	0	Great South Channel	19:33-21:56	2-5	Fluking; occasional distant surface activity
9	29 May 1999	1.36	116	1.40	7.94	1	0.01	0.01	Great South Channel	17:26-18:55	2-5	Fluking; occasional SAGs and other surface activity
10	29 May 1999	1.25	37	0.49	1.25	1	0.01	0.01	Great South Channel	20:50-22:06	6-10	Occasional fluking; occasional surface activity
11	24 Aug. 1999	0.97	2	0.04	0.03	38	0.68	1.51	Bay of Fundy	12:47-14:30	2-5	Fluking
12	24 Aug. 1999	0.70	42	1.03	2.23	39	0.95	1.54	Bay of Fundy	14:45-16:04	6-10	Surface activity; SAG; fluking
13	24 Aug. 1999	1.79	121	1.17	2.80	112	1.07	2.70	Bay of Fundy	17:47-19:55	>10	Fluking; much surface activity
14	14 Sep. 1999	7.48	1,676	3.82	11.39	845	1.93	3.65	Bay of Fundy	03:38-11:47	Night	-
15	28 May 2000	1.09	5	0.08	0.14	1	0.02	0.02	Great South Channel	16:22-17:37	2-5	Fluking
16	28 May 2000	2.21	25	0.20	0.33	0	0	0	Great South Channel	19:33-21:45	2-5	Fluking
17	4 Jun. 2000	0.55	7	0.10	0.16	0	0	0	Great South Channel	22:23-23:05	2-5	Fluking
18	21 Aug. 2000	4.47	3,161	12.0	31.7	1,153	4.37	13.49	Bay of Fundy	21:33-02:06	>10	Several SAGs; some fluking
19	21 Aug. 2000	1.56	434	4.8	10.9	101	1.13	1.94	Bay of Fundy	03:05-06:04	Night	-
20	22 Aug. 2000	1.71	726	7.3	39.3	261	2.61	5.05	Bay of Fundy	21:52-23:35	>10	Several SAGs
21	23 Aug. 2000	0.41	113	4.8	13.8	75	3.13	1.77	Bay of Fundy	01:30-01:55	Night	-
Total		36.06	6,516			2,629						

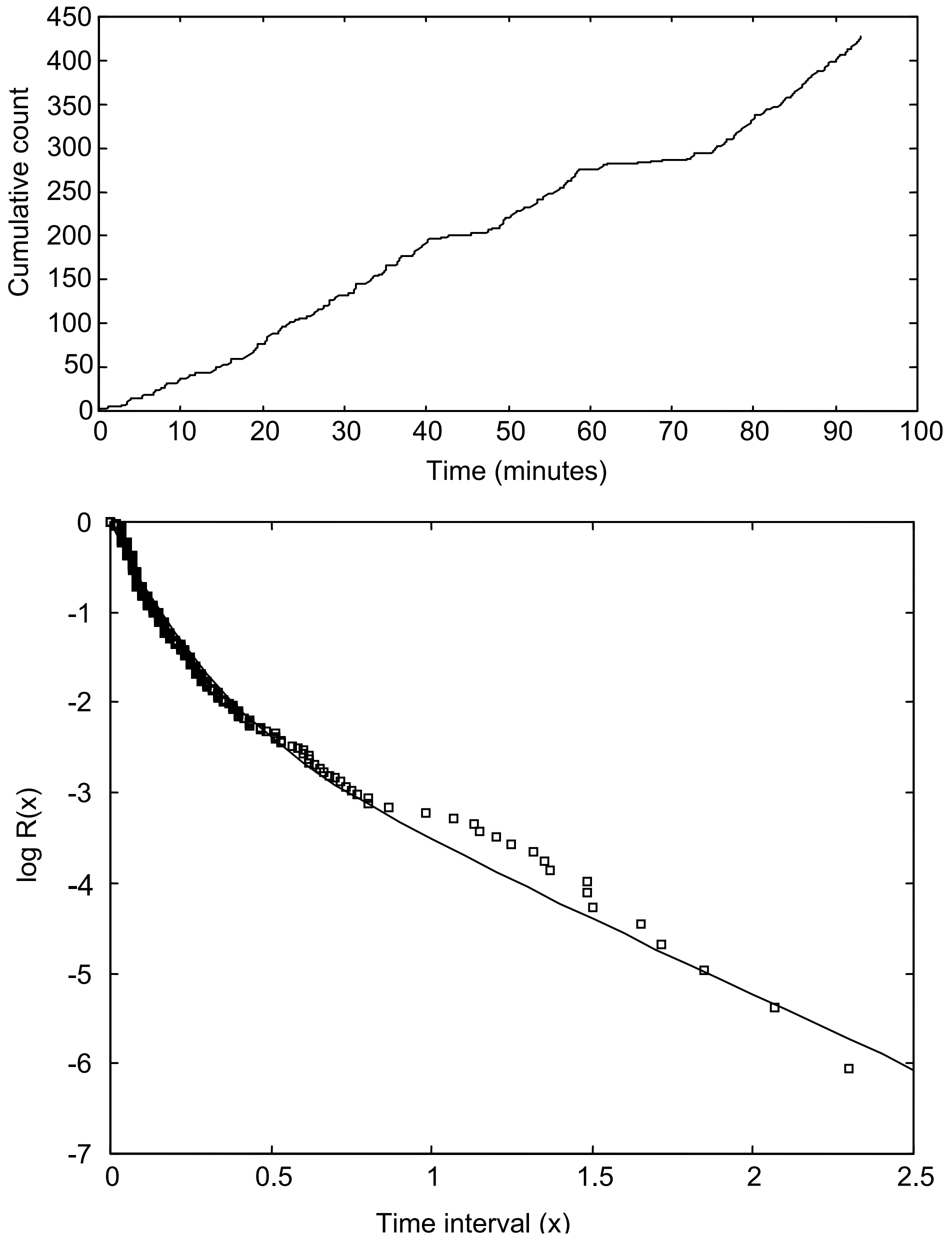

Fig. 6a. The cumulative count of moans with time through encounter 19. The steps of the line indicate some clustering is occurring. The steps have a short rise and a short tread, indicating that in this encounter moans are produced in small clusters with short intervals between clusters. Fig. 6b. The log-survivor function log $R(x)$, for the intervals between calls (x) in encounter 19, and a fitted line from a Poisson cluster process. $R(x)$ is the proportion of intervals exceeding x. Intervals from a Poisson process are exponentially distributed, so that log $R(x)$ would be a straight line. In this example, the curvature at small x indicates that clustering is occurring,

cluster process may be appropriate (the separation between clusters being exponentially distributed). A fitted curve from a Poisson cluster model is shown for the example encounter (parameter estimates: $\hat{z} = 0.6$ minutes, $\hat{y} = 1.96$ moans and $\hat{y} = 0.25$ minutes).

For each encounter containing moan intervals, observed statistics for these intervals are shown in Table 3. In addition, the longest period of silence is given: this includes the intervals between moans; the intervals between moans and any adjacent noisy sections excluded from analysis; and the intervals between the start of a recording and the first moan or the last moan and the end of a recording. Fitted values for the parameters of the Poisson cluster process are also shown for encounters with over 100 moans. A theoretical log $R(x)$ curve for a Poisson cluster process fitted reasonably for the intervals of five of the seven series. In these series, clusters are on average small (1-4 moans) and the clusters are produced at rates not very much less than the rates of moans within clusters.

Tag data

A total of 29.5 hours of acoustic and other physical data were collected from ten whales with tags attached (some further extraneous data between activation and attachment of the tags were excluded). Four of the five whales tagged in 1999 were feeding during the tag recording, and the fifth spent 2.3 hours lying at the surface. Four of five whales tagged in 2000

Table 3

Observed statistics for towed hydrophone recordings of series of moans. The table shows statistics for intervals between moans (x). The maximum period of silence (minutes) is shown, this includes intervals between moans, intervals between moans and adjacent noisy sections excluded from the recording, the interval between the start of recording and the first call, and the interval between the last call and the end of the recording. Parameter estimates from fitted Poisson cluster models are also shown for encounters with over 100 calls. $\hat{z}$ is expected interval between clusters, $\hat{s}$ is expected cluster size and $\hat{y}$ is expected interval between events in clusters. *1-2 outliers removed before fitting; + poor fit. All values are in minutes.

Encounter	*n*	Mean (x)	SD (x)	Min. (x)	Max. (x)	Max. (silence)	$\hat{z}$	$\hat{y}$	$\hat{s}$
1	20	3.42	6.10	0.05	20.21	20.21			
2	21	0.93	1.26	0.02	3.80	81.87			
3	4	0.41	0.22	0.25	0.57	56.78			
4	0	-	-	-	-	34.8			
5	0	-	-	-	-	35.4			
6	0	-	-	-	-	112.2			
7	6	5.53	7.34	0.12	5.53	15.98			
8	0	-	-	-	-	78.6			
9	116	0.33	0.96	<0.01	9.53	28.18	+	+	+
10	37	1.89	3.64	0.05	14.83	14.83			
11	2	0.87	0	0.87	0.87	30.58			
12	42	0.55	1.16	0.02	6.75	7.17			
13*	121	0.74	1.20	0.02	7.62	7.62	1.51	0.33	1.03
14*	1,676	0.24	0.43	<0.01	11.62	27.38	0.57	0.33	1.43
15	5	1.87	2.78	0.10	5.06	29.17			
16	25	5.12	6.97	0.07	28.5	8.15			
17	7	0.38	0.40	0.05	0.83	11.33			
18*	3,161	0.08	0.11	<0.01	2.78	2.78	0.21	0.17	1.54
19	434	0.20	0.31	<0.01	2.30	2.30	0.6	0.25	1.96
20	726	0.12	0.20	<0.01	2.38	5.45	0.63	0.20	4.13
21*	113	0.21	0.35	<0.01	2.90	2.90	+	+	+

were engaged primarily in feeding while the tags were attached. All four of these, however, interacted with other whales during tagging, and at least three of the tags were knocked off during contact. The fifth tagged whale in 2000 was travelling and the observation vessel had difficulty maintaining visual contact. This whale eventually joined a surface active group (SAG) and the tag was knocked off.

Information on the individual whales and vocalisation rates is shown in Table 4. LF calls were counted in the 1999 data; they are more frequent than moans. However, it was not possible to distinguish focal LF calls from non-focal LF calls. Only one gunshot was heard on the tags, in 1999.

The times of moans since the attachment of the tag to the whale are shown in Fig. 7 for the five tagged whales which

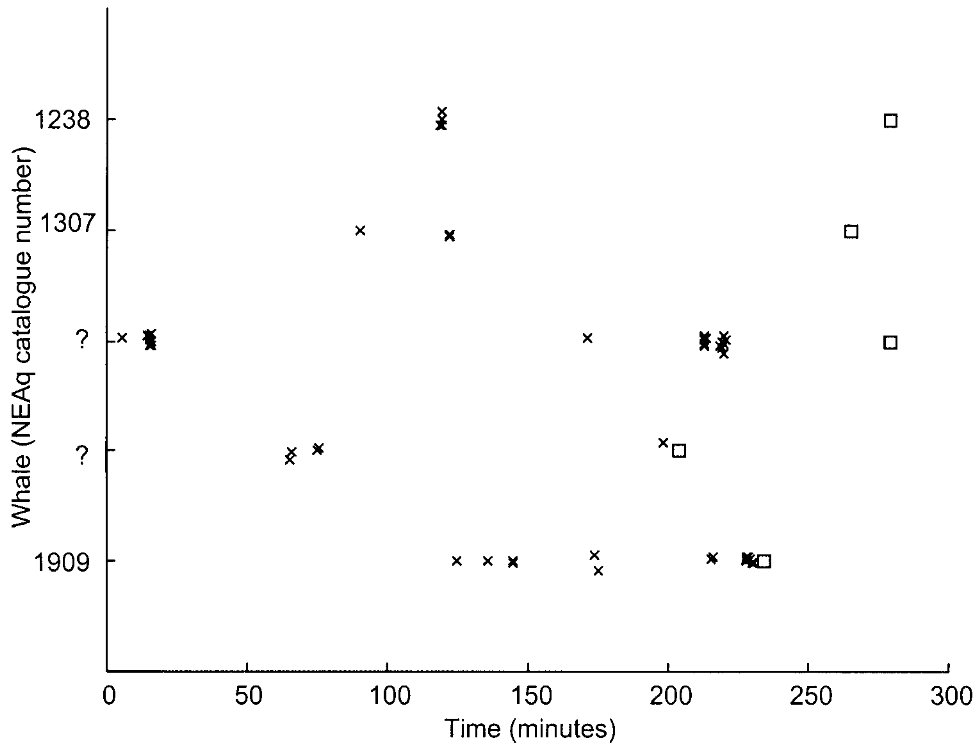

Fig. 7. Times of occurrences of moans since the start of recordings (crosses), for the five (of ten) tagged whales which vocalised in 1999-2000. Squares mark the end of the recording. Crosses have been jittered vertically.

Table 4

Summary information of individuals and vocalisation rates (per hour) recorded by the DTAGs. ID information was not available for three individuals at the time of writing. LF calls were counted in 1999 only. The predominant behaviour of each individual is given. Those individuals whose tags were dislodged during social activity are marked with an asterisk.

NEAq catalogue number	Age	Sex	Date	Time of tagging (GMT)	Recording time (hrs)	Moans No.	Moans Rate	Moans from focal whale only No.	Moans from focal whale only Rate	LF sounds No.	LF sounds Rate	Behaviour
1909	10	F	3 Aug. 1999	15:46:43	3.9	24	6.2	15	3.85	86	22.1	Foraging
2209*	7	M	5 Aug. 1999	16:35:05	0.92	1	1.1	0	0	99	107.6	Foraging
?	?	?	5 Aug. 1999	19:40:31	3.40	24	7.1	5	1.47	76	22.4	Foraging
1607*	13	M	8 Aug. 1999	13:43:23	4.06	11	2.7	0	0	129	31.8	Foraging
1307*	>17	M	11 Aug. 1999	13:54:53	4.42	19	4.3	3	0.67	85	19.2	Foraging/resting
1309*	?	M	1 Aug. 2000	18:26:47	4.5	328	72.9	0	0	-	-	Foraging
?	?	?	5 Aug. 2000	17:30:19	3.70	196	52.9	25	6.8	-	-	Travelling
2760*	?	?	9 Aug. 2000	13:29:16	1.63	20	12.2	0	0	-	-	Foraging
?*	?	?	9 Aug. 2000	18:40:20	1.03	69	66.9	0	0	-	-	Social
1238*	>19	M	11 Aug. 2000	19:38:06	1.9	88	46.3	4	2.1	-	-	Foraging

vocalised in 1999-2000. When the number of moans is sufficiently high, there is a clear tendency for clustering.

The depths at which the tagged whales in 2000 were swimming when the focal moans were recorded are shown in Fig. 8. The most important result is the depth of the tagged whale when vocalising. When producing their own sounds, tagged whales were almost exclusively in the upper 10m of the water column (1999 and 2000 data). LF calls were recorded at all depths in 1999, as shown in Fig. 9, but the majority of longer duration (> 1.5 seconds) sounds were produced near the surface.

DISCUSSION

Clark (1983) demonstrated that, for 'groups' (single animals or animals within approximately 15m of one another) of southern right whales, vocalisation rates (expressed as number of sounds per unit time divided by number of

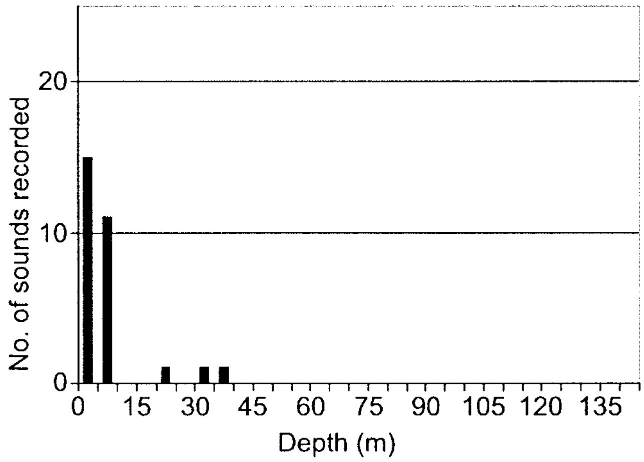

Fig. 8. The depth at which tagged whales were swimming when the focal sounds were recorded in 2000. Tagged animals rarely produced moans below 10m depth.

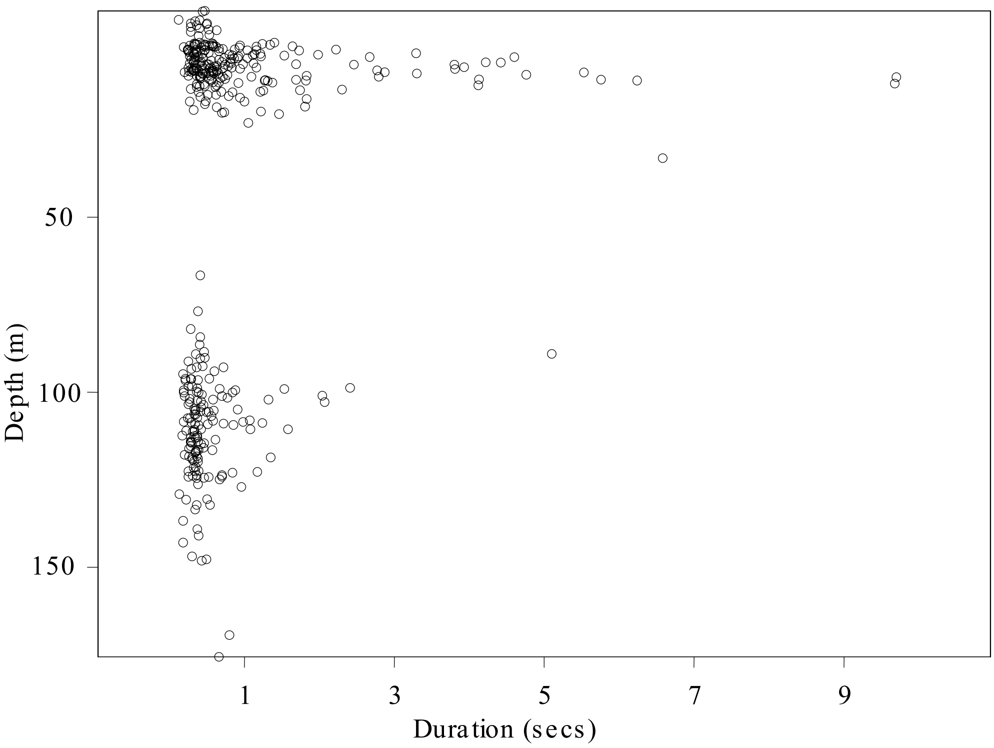

Fig. 9. The depths at which LF calls were recorded against duration of call (1999 data). There is a tendency for longer duration sounds to be made near the surface. Some sounds in this plot were excluded, because their duration could not be measured due to the noise.

animals in group) were dependent on activity state, group size and sexual composition. There is reason to expect that North Atlantic right whale vocalisations are similarly dependent on these and other factors. The present study investigated the influence of aggregation size, location, and time-of-day; but not activity states or sexual composition. Combined visual and acoustic studies of baleen whales have typically used shore-based observation to estimate aggregation size and log behaviour (Clark, 1983; Frankel *et al.*, 1995). The advantages of a shore-based platform were not available in the present study, which was carried out in the open sea from a relatively low and unstable platform and with limited personnel. Therefore, the estimation of numbers of whales was imprecise in larger aggregations; and detailed assessment of activity states was not possible.

Aggregation size

In this study, moan rates (per aggregation per hour) were correlated with the sizes of the aggregations. Two lone feeding whales did not produce moans in recordings from the towed array (Fig. 3), and tagged lone whales rarely produced focal moans (< ~ 10 per hr) (Table 4). Small aggregations (2-10) of whales gave higher moan rates (< ~ 60 per aggregation per hour), and larger aggregations (> 10) higher again (~ 70-700 per aggregation per hour) (Fig. 3). Gunshot sound rates were similarly correlated with aggregation size. It was not possible to examine rates of individuals (sounds per whale per hour) as opposed to rates of aggregations (sounds per aggregation per hour), because only rough estimates of aggregation sizes could be made.

Aggregation sizes appeared to be generally larger in the Bay of Fundy than Cape Cod Bay or the Great South Channel (Table 2). However, it is not known whether this represents a true difference. The dataset used here is fairly small (21 encounters) whilst historical survey data on aggregation size in the Bay of Fundy and the Great South Channel may be difficult to compare directly because survey methodology differed (the former area was surveyed by boat and the latter by plane).

Although the results presented here revealed increasing sound rates with aggregation size, the relationship between sound rates and aggregation size is not necessarily linear. Vocalisation rates of individuals will be dependent on *inter alia* social context and this will be related in some way to aggregation size. Kraus (1991) found a noticeably high rate of vocalisations from eight ‘surface active groups’ in which activity centred on a female. The average vocalisation rate was 12 per minute (range 4-23) and the groups contained between 2-12 individuals. Clark (1983) showed that ‘swimming’ (‘moving from one location to another at a fairly constant speed’) southern right whales often produce ‘up calls’, which may function to maintain contact between whales. Lone swimming whales had higher contact call rates than swimming groups containing two or more whales.

Diurnal variation

The towed hydrophone results from the Bay of Fundy provide evidence of diurnal changes in rates of both moans and of gunshot sounds, both being more frequent at night. These findings are broadly in agreement with other research on vocalisation rates. Payne and Payne (1971, p159) report that, for a small sample of recordings of southern right whales in Golfo San Jose, Argentina, ‘In the daytime the sounds were infrequent, about one isolated sound per half hour. The sample recorded at night shows at least one sound every minute, and occasionally clusters of up to 15 sounds per minute’. North Atlantic right whales recorded from a bottom-set coastal array in northeast Florida vocalised considerably more frequently between the hours of about 17:00 and 05:00 (Office of Naval Research, 1997). On the other hand, Cummings *et al.* (1972) recording southern right whales for 15 minutes every two hours over three days, found ‘no indication of a difference in day-time versus night-time activity in sound production’ in the Golfo San Jose, Argentina.

Two important caveats to the interpretation of diurnal changes in the present study should be noted. Firstly, the recordings at night were made in the Bay of Fundy, and there is no information on night-time rates in the Great South Channel. Secondly, it was not possible to estimate aggregation sizes in darkness. Therefore, it is not possible to determine whether or not the underlying cause of diurnal changes in sound rates in the Bay of Fundy are changes in aggregation size.

Vocalisation patterns within encounters

Within encounters, moans were not produced randomly. This departure is mainly due to a tendency to cluster, although there were also occasional changes in the mean rate. In recordings from aggregations, the occasional changes observed in moan rate within encounters may be real changes in moan rates, or possibly changes in the detection response due to unobserved external variables (for example, oceanic changes affecting sound propagation, or changes in ambient noise). Overall though, patterns of moans within encounters, most of which lasted about one or two hours, were fairly constant, hence the relatively straight gradients of the lines. The Poisson cluster model appeared to fit reasonably well to the intervals in five of the seven encounters with sufficient moans (i.e. higher moan rates). This showed that, on average in these high-rate encounters, clusters of moans were small and produced at rates not very much less than the rates of moans within clusters. For the five tagged whales which produced moans in 1999-2000, clustering became apparent when sufficient moans were made.

Most sounds were produced by tagged whales when at or near the surface. When whales are diving this will result in a tendency for moans from single individuals to occur in clusters. It seems likely that this is one of the factors contributing to the observed clustering of moans in towed array recordings from aggregations. There are many other behavioural factors, including interactions between individuals, which will also affect the temporal distribution of moans.

Detection and localisation of sounds

In addition to the rate at which an individual vocalises, the type of sound, the extent of clustering and the depth at which sounds are produced have significant implications for detection and localisation of that animal by a receiving system. Moan rates discussed here include tonal or pulsatile sounds, which are the most reliable for detection and localisation. These sounds have a typical duration of 0.4-1.5 sec and often involve frequency modulation over ~ 100Hz giving a time-bandwidth product of ≥50. Other sounds such as noisy or impulsive exhalation, gunshots, and brief grunts are poor candidates for remote detection due to limited time-bandwidth product and lack of distinction from other common aquatic sound sources.

The tendency for moans to cluster could reduce the probability of detection in a passive system. If intervals of silence are not small relative to the periods for which whales are in detection range, this will significantly reduce the effectiveness of passive detection. In towed recordings, in aggregation sizes of 1-10, no moans were detected in four encounters with recordings between one and two hours long. In encounters with moans, maximum periods of silence were mostly between ~10-40 minutes but reached as high as 82 minutes. In larger aggregations, or at night, maximum silent periods were <~10 minutes except in one case of 27 minutes. Among tagged whales, the focal whale produced no moans in five recordings, and in the five that vocalised, maximum periods of silence were between 120-150 minutes.

Moans appear to be generally produced at or near the surface. Sounds produced near the surface are often attenuated more rapidly with propagation distance than are sounds from a deep source. In summer, this is due to downwards refraction of sound brought about by the (often substantial) temperature difference between surface and deeper waters. Depending on latitude, significant refraction effects can be present from mid-summer through autumn. In winter and spring, high winds and sea states often result in mats of air bubbles near the sea surface. These mats cause extreme broadband attenuation of sound (Medwin and Clay, 1998). While none of the issues raised here indicate that remote detection will fail, they do highlight the need for care both in design of a detection system and in assessing its efficacy and costs versus benefits.

Implications for management and research

The empirical evidence presented here on vocalisation rates should assist in assessing the feasibility of using passive acoustics to detect the presence of aggregations of right whales as part of a management system. These techniques could in the future provide valuable long term information for the prediction of right whale distribution. More sophisticated systems could aid in the gathering of real-time information on right whale distribution, and supplement existing surveillance systems designed to mitigate against vessel strikes. Passive acoustic monitoring could potentially be especially valuable in bad weather, at night or in offshore areas. However, many other issues require further research, including detection rates, misclassification rates with other biogenic sounds, localisation errors and ranges.

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