



Singing through winter nights: Seasonal and diel occurrence of humpback whale (*Megaptera novaeangliae*) calls in and around the Gully MPA, offshore eastern Canada

KATIE KOWARSKI,¹ JASCO Applied Sciences Ltd., 202-32 Troop Avenue, Dartmouth, Nova Scotia B3B 1Z1, Canada; CLAIR EVERS, HILARY MOORS-MURPHY, Fisheries and Oceans Canada, 1 Challenger Drive, Dartmouth, Nova Scotia B2Y 4A2, Canada; BRUCE MARTIN, SAMUEL L. DENES, JASCO Applied Sciences Ltd., 202-32 Troop Avenue, Dartmouth, Nova Scotia B3B 1Z1, Canada.

ABSTRACT

Humpback whale use of areas off eastern Canada is poorly understood, a knowledge gap that could impact future conservation efforts. We describe the acoustic occurrence of humpback whales in and around the Gully Marine Protected Area (MPA), an eastern Scotian Shelf submarine canyon. Near-continuous acoustic recordings sampling at 16 kHz were collected from the MPA and nearby slope areas from October 2012 to September 2014 using near-bottom recorders. In an offshore region where humpbacks were thought to be rare, we observed calls from October to June with a peak in song and nonsong calls in December and January. This suggests that some individuals occur in Canadian waters in winter and the Gully region may be a North Atlantic humpback whale migratory corridor. Calls were predominantly songs indicating potential mating activities. Song and nonsong calls occurred more at sunset and during hours of darkness than during daylight. This study improves our understanding of the seasonal occurrence of humpback whales on the Scotian Slope and, more specifically, their use of an offshore protected area.

Key words: marine protected areas, humpback whales, *Megaptera novaeangliae*, acoustics, diel patterns, migration, song, stationary passive acoustics.

The Gully is a large, deep-water, submarine canyon located on the continental shelf break off Nova Scotia, Canada. It was designated a marine protected area (MPA) in 2004 to protect its ecological and biological diversity (DFO 2008). Many cetacean species, including those considered rare and endangered such as the northern bottlenose whale (*Hyperoodon ampullatus*) and the blue whale (*Balaenoptera musculus*), are known to frequent the Gully (Whitehead 2013, DFO 2016). Assessing the year-round presence and activity of cetaceans in the MPA has been identified as a high priority indicator to monitor for protecting the health and integrity of the Gully ecosystem (DFO 2010). Humpback whales (*Megaptera novaeangliae*) are known to occur within the Gully and adjacent areas (Hooker *et al.* 1999, Whitehead 2013), but

¹Corresponding author (e-mail: katie.kowarski@jasco.com).

relatively little is known about their year-round use of this offshore region due to limited survey effort in fall, winter, and spring. Our lack of understanding of the seasonal occurrence of a species suspected to be so ecologically important (Roman *et al.* 2014), limits the ability of policymakers to apply appropriate and effective conservation measures for humpback whales, and for protecting the Gully ecosystem.

Most mysticete whales, including humpbacks, undertake large-scale seasonal migrations between productive high-latitude waters in summer to feed and warm low-latitude waters in winter to mate and give birth (Kellogg 1929; Mackintosh 1942, 1966; Norris 1967). North Atlantic humpback whales occur at several coastal summer feeding grounds ranging from the northeast United States to the Arctic including the Gulf of Maine, Atlantic Canada, West Greenland, Iceland, and Norway (Katona and Beard 1990, Smith *et al.* 1999). There is evidence that summer feeding grounds also exist offshore, but none have been described to date (Reeves *et al.* 2004). From January to early April humpback whales overwinter on breeding grounds in the West Indies and Cape Verde Islands (Whitehead and Moore 1982, Martin *et al.* 1984, Palsbøll *et al.* 1997, Jann *et al.* 2003). Outside of coastal feeding and breeding grounds, North Atlantic humpback whale movements remain poorly understood.

In the Gully MPA, cetacean visual surveys have been carried out since the late 1980s by researchers from the Whitehead lab of Dalhousie University, but have been limited to summer months (*e.g.*, Whitehead 2013). During these surveys humpback whales were sighted more in late summer (August and September) than early summer (June and July) (Gowans and Whitehead 1995, Hooker *et al.* 1999, Whitehead 2013). From 1988 to 2011, humpback whales were sighted in the Gully on 46 occasions with a sighting rate decrease of 15% per year, a trend potentially related to changes in prey abundance (Whitehead 2013). Summer surveys have also been carried out in the nearby smaller Shortland and Haldimand canyons, but no humpbacks were sighted (Whitehead 2013). Sightings obtained from the Canadian Department of Fisheries and Oceans (DFO) cetacean sightings database, which includes a compilation of records from research groups, fisheries observers, fisheries officers, marine mammal observers from oil and gas platforms, whale watching tour operators, and other organizations between 1975 and 2015 indicate that humpback whales occur in Eastern Canadian waters on the continental shelf and along the shelf break throughout the year (Fig. 1). Winter humpback whale sightings are notably sparse, but it is not known if this is due to fewer whales or lack of effort during a season when poor weather and high sea states limit maritime activities.

Humpback whales produce a range of acoustic signals, thus, passive acoustic monitoring (PAM) offers a method to observe their occurrence in the Gully area year-round, removing the seasonal bias inherent in relying on visual sighting methods. While overwintering on breeding grounds, songs are produced (Payne and McVay 1971). Humpback songs have been recorded and studied worldwide (*e.g.*, Cerchio and Dahlheim 2001, Cerchio *et al.* 2001, Arraut and Vielliard 2004, Au *et al.* 2006, Garland *et al.* 2011). Songs are sung by males (Payne and McVay 1971, Winn and Winn 1978) to attract females and/or establish dominance over competitors *via* male-male competition (Winn and Winn 1978, Tyack 1981, Darling and Bérubé 2001, Smith *et al.* 2008, Darling *et al.* 2012, Herman *et al.* 2013).

In addition to singing, humpback whales produce a variety of calls that have been linked to social and feeding behaviors (Silber 1986, Dunlop *et al.* 2007, Stimpert *et al.* 2007). Stimpert *et al.* (2011) described the occurrence of nonsong calls produced by humpbacks in the Stellwagon Bank National Marine Sanctuary (SBNMS) including “wops” and “grunts.” Zoidis *et al.* (2008) observed nonsong calls to be

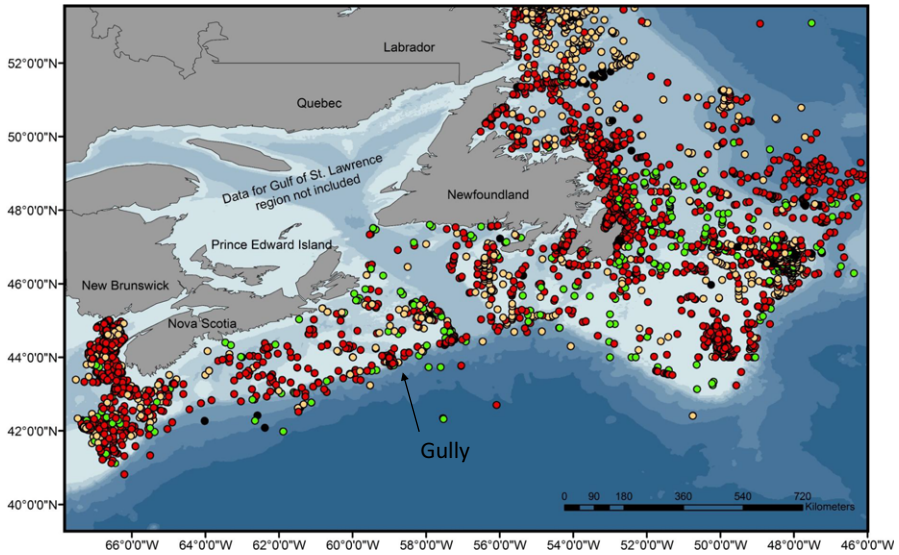


Figure 1. Humpback whale sightings in the fall (yellow; $n = 3,342$), spring (green; $n = 412$), summer (red; $n = 8,437$), and winter (black; $n = 57$) obtained from Fisheries and Oceans cetacean sightings database. Sightings were reported from research groups, oil and gas marine mammal observers, fisheries observers, fisheries officers, and whaling records from 1975 to 2015. Effort is not accounted for in this figure.

typical of humpback calves off Hawaii where grunts were predominant in groups with calves, especially mother-calf pairs. Dunlop *et al.* (2008) found that migrating humpback whales in Australia produce different calls depending on the social group. “Blows” and “cries” were associated with competitive groups, “snorts” and wops seemed to function for within and between group communication, and grunts and “barks” were produced when groups came together (Dunlop *et al.* 2008).

Autonomous acoustic recorders were used to collect acoustic data from the Eastern Scotian Slope region near-continuously over 2 yr (2012–2014). We provide the first description of the seasonal occurrence of humpback whale song and nonsong acoustic signals, and any diel patterns observed in these call types, on the Scotian Slope, where movements of this species have been largely undescribed. By understanding how humpback whales use the Gully MPA and nearby areas, we can better inform future conservation measures for the species and protected area. In doing so, we present a method to examine large acoustic data sets for the presence of humpback whale acoustic signals.

METHODS

Data Collection

Acoustic recordings were collected near-continuously from October 2012 to September 2014 from three stations along the edge of the Scotian Shelf: “MidGul” in the central deep waters of the Gully MPA; “GulSho” on the slope area between the

Gully and Shortland canyons; and “ShoHald” on the slope between Shortland and Haldimand canyons (Fig. 2). MidGul was located 26 km from GulSho and 73 km from ShoHald. GulSho and ShoHald were 50 km apart. The recorders were deployed approximately every 6 mo resulting in four recording periods: 2012–2013 overwinter, 2013 summer, 2013–2014 overwinter, and 2014 summer (Table 1). Data were collected using autonomous multichannel acoustic recorders (AMAR; JASCO Applied Sciences) suspended 55 m off the seafloor by moorings that sat at depths of 1,400–1,900 m (Fig. 3). The sampling rate of the duty-cycled recorders was 16 kHz for 13 of every 15 min for the 2012–2013 overwinter and 2013 summer recordings, and 18 of every 20 min for the 2013–2014 overwinter and 2014 summer recordings. The recorders had a spectral noise floor of 25 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ over the 10–7,500 Hz frequency band and a broadband dynamic range of 104 dB re 1 μPa . About 265 d of data (~0.5 TB) were produced by each recorder per year yielding over 1,688 d (~6.4 TB) of data.

Automated Detectors

To analyze such a large data set an efficient protocol was essential. The primary analysis unit was the presence of song and nonsong humpback whale calls per hour as determined by experienced analysts. Automated detector results were used to guide manual analysis efforts. Our JAVA (version 1.7; Oracle, Redwood Shores, CA) based PAMlab (JASCO Applied Sciences) contour detector identified calls based on energy in the time-frequency domain as described in Delarue *et al.* (2014), Martin *et al.*

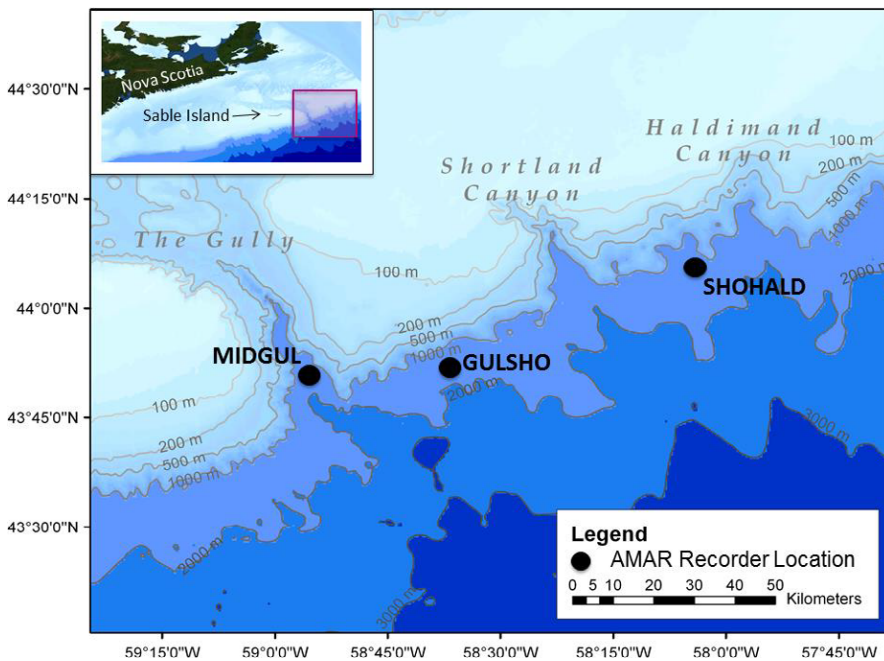


Figure 2. Bathymetric map displaying the MidGul, GulSho, and ShoHald stations on the Scotian Slope offshore Nova Scotia, Canada.

Table 1. Deployment and retrieval dates, location, and depth for the three recording stations during the four recording periods.

Station	Recording period	Deployed	Retrieved	Latitude (N)	Longitude (W)	Depth (m)
MidGul	2012–2013 overwinter	12 Oct 2012	10 Apr 2013	43°49'44.4288"	58°55'10.2000"	1,780
	2013 summer	4 May 2013	26 Sep 2013	43°51'43.9200"	58°54'35.8920"	1,580
	2013–2014 overwinter	15 Nov 2013	6 Apr 2014	43°51'44.0939"	58°54'35.9028"	1,525
	2014 summer	7 May 2014	26 Sep 2014	43°51'50.6941"	58°54'29.7108"	1,614
GulSho	2012–2013 overwinter	12 Oct 2012	10 Apr 2013	43°52'4.5120"	58°35'44.5200"	1,516
	2013 summer	4 May 2013	26 Sep 2013	43°51'49.5360"	58°35'17.4480"	1,583
	2013–2014 overwinter	15 Nov 2013	6 Apr 2014	43°51'41.8741"	58°35'16.4339"	1,530
	2014 summer	8 May 2014	26 Sep 2014	43°51'49.2228"	58°21'17.3268"	1,573
ShoHald	2012–2013 overwinter	12 Oct 2012	10 Apr 2013	44°5'19.1040"	58°3'55.2168"	1,700
	2013 summer	4 May 2013	26 Sep 2013	44°5'51.7920"	58°3'22.8960"	1,545
	2013–2014 overwinter	15 Nov 2013	7 Apr 2014	44°5'50.7120"	58°3'22.7268"	1,550
	2014 summer	8 May 2014	26 Sep 2014	44°9'47.4300"	58°6'15.1920"	1,559

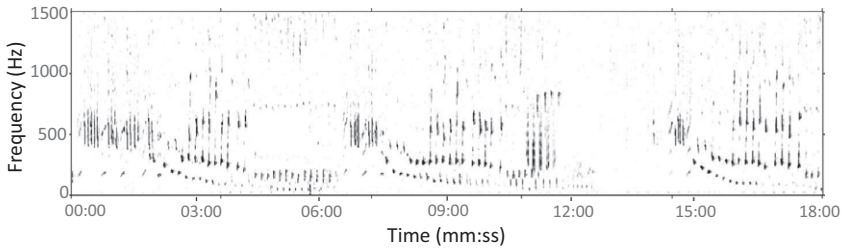


Figure 3. Spectrogram of 18 min of three humpback whale songs recorded on the Scotian Slope at station ShoHald on 5 January 2014 UTC (2 Hz resolution, 0.128 s time window, 0.032 s time step, Hamming window).

(2014), and Frouin-Mouy *et al.* (2017). The algorithm was applied to spectrograms with a 2 Hz frequency resolution created with 0.2 s long time windows overlapped by 0.15 s. The spectrograms were converted to binary spectrograms with a value of 1 when the time-frequency bins exceeded the 30 s median level by a factor of 4 (6 dB). The detected time frequency cells (1's) were joined to their nearest neighbors that were also 1 to create contours that were then interpreted with a contour-following algorithm.

An array of parameters was used to classify a contour as a humpback whale call. Table 2 provides examples of the frequency, duration, and sweep rate (where appropriate) used for the contour classifiers for each humpback whale call described by

Zoidis *et al.* (2008) and Stimpert *et al.* (2011). These calls can be produced during both song and nonsong acoustic behavior. The calls described in Table 2 represent a sample of the detectors run on the present data set. Detectors were designed to broadly detect all signals occurring within humpback whale call frequency range from 40 Hz to 5,000 Hz be they short and impulsive, or long and tonal. In this manner, we sacrificed the precision of the detector by allowing many other sounds to be detected, but increased the probability of capturing all humpback acoustic signals that were then validated through manual analysis. While the contour-based detectors were for discrete calls, the resulting detections were lumped together, as discrete call unit analysis was not a goal of this study.

Manual Validation of Call Presence

Manual validation of automated detectors occurred in two phases. The first phase entailed preliminary analysis of a subset of the data that was distributed across stations, time of year, and quantity of automated detections per file. This included recordings lacking detections and allowed us to determine detector performance and to define parameters for the second phase of analysis. During phase two of manual validation, all remaining recordings with humpback whale detections that fell within the guidelines determined in phase one were analyzed.

During manual validation, recordings were visually and aurally analyzed to verify the presence/absence of humpback whale calls using PAMlab acoustic analysis software (JASCO Applied Sciences). Humpback whale calls within each 13 or 18 min file were classified as either song or nonsong. A song was characterized by a series of discrete calls (units) that formed repeating phrases, creating themes that occurred in sequence as described by Payne and McVay (1971) (Fig. 3). A call was defined as song if there were at least three themes present that were then repeated at least once, as described by Frumhoff (1983). Humpback call units that did not conform to such criteria were characterized as nonsong calls (Fig. 4).

Statistical Analysis and Propagation Modeling

Previous studies have used the number of detections or detection rate as a primary unit in analysis of whale call patterns (*e.g.*, Wiggins *et al.* 2005, Munger *et al.* 2008). While such analysis can be useful, it tends to make comparison and replication across studies challenging as results are based on different automated detectors. Even the same detector software can produce different results if the parameters are changed or

Table 2. Examples of parameters used to classify detector contours as humpback whale calls.

Call	Frequency range (Hz)	Duration range (s)	Sweep rate (Hz/s)
Grunt	50–130	0.3–0.9	—
Low-frequency downsweep	20–200	0.8–2.5	–20 to –40
Low-frequency upsweep (wop)	20–200	0.8–2.5	4 to 40
Low-frequency moan	50–200	1.0–5.0	—
Mid-frequency drop	100–400	0.8–2.5	—
High-frequency cry	300–900	2.0–8.0	—
Purr	50–500	0.4–2.0	—

the background noise differs between studies or locations. To avoid such ambiguity, the present study transferred the manually verified detection results into hourly presence/absence data, a more robust and reliable measure that can easily be replicated. We refer to hours with humpback whale calls present as *call hours* unless referring to a specific call type when *song hour* or *nonsong hour* is used.

The mean call hours per day were compared between the two call types (song and nonsong) and across the three recording stations using nonparametric Kruskal-Wallis tests (Zar 1999, Vu *et al.* 2012), as the data did not meet the assumption of normality required for parametric tests. Only days in which humpback whale calls occurred were included in the analysis.

This method is biased if multiple recorders simultaneously detect the same acoustically active whale. To address this bias, we modeled the expected detection range for humpback whales in the recording area to estimate the overlap area. Modeling was performed for the Gully (MidGul) and one of the noncanyon sites (GulSho). Given the similarities in the topography and oceanographic conditions around GulSho and ShoHald, propagation results are assumed to be very similar between the two. The modeled signal was considered detectable if the signal-to-noise ratio (SNR),

$$\text{SNR}_{n,f} = \text{SPL}_{\text{source},f} - \text{NSPL}_{n,f} - \text{PL}_f,$$

exceeded 6 dB, which was the automated detector threshold. $\text{SPL}_{\text{source},f}$ is the frequency dependent source sound pressure level, $\text{NSPL}_{n,f}$ is the frequency dependent noise sound pressure level, and PL_f is the frequency dependent propagation loss from the whale to receiver points all around it. The source sound pressure level (SPL) was estimated from peer-reviewed humpback whale source levels assuming the energy was distributed equally across each 1/3-octave frequency band (20–1,800 Hz) in the calls (Au *et al.* 2006). The source levels reported by Au *et al.* (2006) varied from 151 to 173 dB re 1 μPa . The source level used for the model was the geometric midpoint of 162 dB re 1 μPa . This SPL was evenly divided between the 1/3-octave bands of 20–1,800 Hz at a level of 146.6 dB, which puts relatively more energy in the lowest

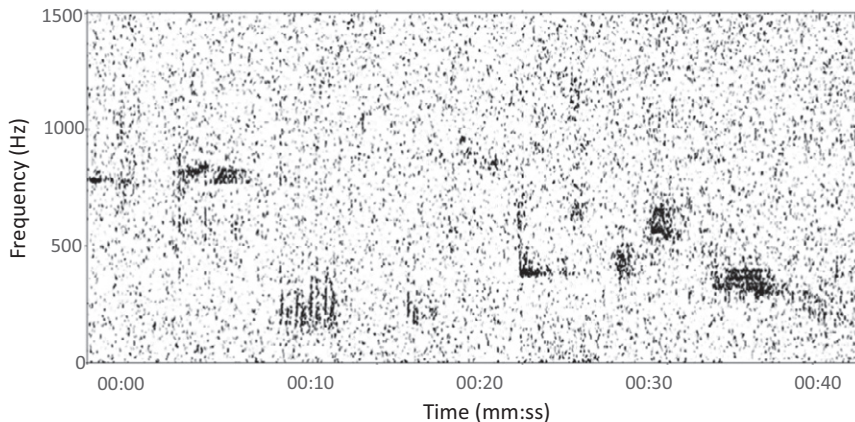


Figure 4. Spectrogram of 40 s of humpback whale nonsong calls recorded on the Scotian Slope at station ShoHald on 8 April 2013 (2 Hz resolution, 0.128 s time window, 0.032 s time step, Hamming window).

frequency bands that travel the furthest in the deep waters off the shelf. As a result, the predicted detection ranges should be conservative (*i.e.*, long). To account for different levels of ambient noise, five different noise sound pressure levels were used ($n = 5$). These levels are the 5, 25, 50, 75, and 95 percentiles of the cumulative distribution functions for the 1 min 1/3-octave band SPLs. Different percentile levels were calculated for the summer and winter periods. JASCO's Marine Operations Noise Model (MacGillivray 2006), a parabolic equation model, was used to estimate propagation loss at 1/3-octave band center frequencies along 36 equally spaced radials around the recorder locations, assuming the whale was calling at 50 m depth. Seasonally dependent sound velocity profiles were obtained from the World Ocean Atlas (Boyer *et al.* 2013). Bathymetry profiles along each azimuth were obtained from TOPO15+ (Smith and Sandwell 1997, Becker *et al.* 2009). Propagation was modeled up to 100 km from the recorder locations providing seasonally dependent propagation losses. The modeled sound level at the recording location of the seabed were used to estimate the detection range.

Diel patterns were analyzed using all days at the three stations where calls occurred for song and nonsong calls. Each day, every call hour was assigned to one of the following four light periods: dawn (the period from when the sun was below the horizon by 12° to sunrise), light (the period from sunrise to sunset), dusk (the period from sunset to when the sun was 12° below the horizon), and dark (the period when the sun was $<12^\circ$ below the horizon). Sunset, sunrise, and twilight (nautical dusk and dawn) times were determined using Reda and Andreas (2004). To normalize call occurrence and account for the variability in the diel time frames over the course of the 2 yr, call hours for each light period were divided by the number of hours in the light period to provide the mean call hours for each diel light period. To account for the variation in total number of call hours each day, the data were transformed by subtracting the mean call hours over each 24 h day from the mean call hours over each light period for that day. The null hypothesis that the mean adjusted call hours were constant across diel light periods was tested using nonparametric Kruskal-Wallis tests (Zar 1999). Finally, a Tukey-Kramer multiple comparison test was used to determine if the mean-adjusted hours with humpback whale calls differed significantly for any of the diel light periods within and between the two call types (Wiggins *et al.* 2005, Munger *et al.* 2008).

RESULTS

Detector Performance

Of the 163,313 acoustic files recorded from the three sites over the 2 yr period, there were 39,177 (24%) files with automated humpback whale call detections. Preliminary manual analysis of 13,378 sound files (7,512 files with automated humpback whale call detections and 5,866 files without) revealed that the automated detector performed well, identifying 90% of files containing calls. However, the wide variety of humpback whale calls can overlap in duration and frequency with other sounds, making automatically detecting all humpback calls while avoiding misidentifying nonhumpback calls challenging. Approximately 84% of files with 10 detections or less were falsely triggered by other sounds, such as sei whale (*Balaenoptera borealis*) calls. All detections in June through September were falsely triggered by vessel noise, seismic survey noise, sei whale calls, and blue whale arch calls except for 6

June 2013 when humpback calls were recorded at MidGul. To increase the efficiency of the remaining manual analysis, only files with more than 10 detections were analyzed. In June through September, analysis was further limited to only one file per detection event, where a detection event was defined as one or more consecutive files with detections. In total, 4,484 h of recordings (~12% of all sound files) were analyzed manually for humpback whale call presence/absence: 2,133 h at MidGul, 1,099 h at GulSho, and 1,252 h at ShoHald.

Detectability

Humpback whale calls were observed on 359 of the 1,835 recording days resulting in 1,855 call hours across the three stations (Fig. 5). Specific call hours rarely overlapped between stations with 67.2% of call hours only occurring at a single site. The distance between recording stations was 26 km from MidGul to GulSho and 73 km from MidGul to ShoHald. Propagation modeling estimated that the maximum detection range of humpback calls was 75 km in winter, and 100 km in summer. During 75% of the study period the detection range was <16 km in winter and <60 km in summer (Table 3, Fig. 6).

Songs

Songs were observed on 212 of the 1,835 recording days resulting in 1,086 song hours across the three stations (Fig. 5). While slightly more song hours occurred at MidGul (mean \pm SD: 0.64 ± 0.64 call hours/d, $n = 86$) than either GulSho (0.50 ± 0.52 , $n = 77$) or ShoHald (0.46 ± 0.49 , $n = 70$), the mean song hours per day was not significantly different between any of the stations (Fig. 7; Kruskal-Wallis test; $\chi^2 = 3.97$, $df = 2$, $P = 0.14$). Most song hours (88%) occurred in December and January

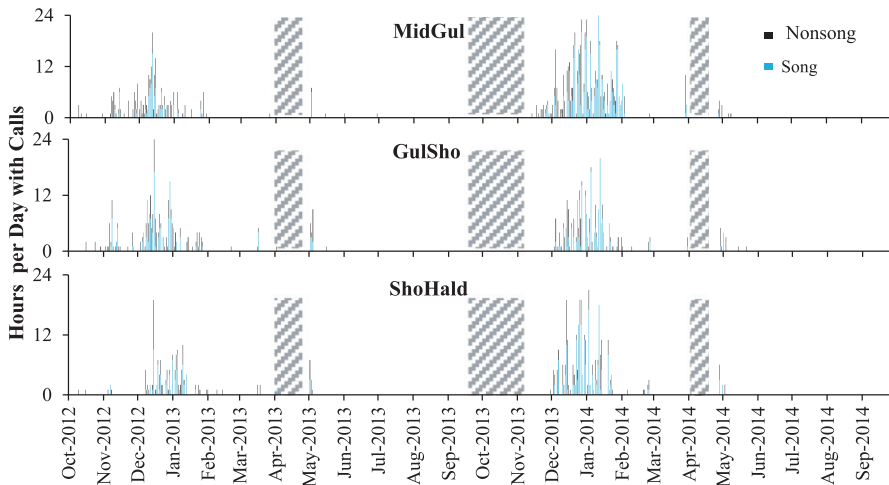


Figure 5. Plots of the number of hours per day in which humpback whale song and nonsong calls occurred for the MidGul, GulSho, and ShoHald stations on the Scotian Slope from October 2012 to September 2014, where the hashed gray areas indicate time frames when recording did not take place.

Table 3. Modeled maximum range of detection for humpback whales in winter and summer for 5, 25, 50, 75, and 95 noise percentiles over all radials and all 1/3-octave bands in 20–1,800 Hz at MidGul and GulSho.

Station	Cumulative distribution function percentiles	Maximum range (km)	
		Winter	Summer
MidGul	5	75	100
	25	16	53
	50	5	23
	75	2	14
	95	1	4
GulSho	5	73	100
	25	15	59
	50	4	28
	75	2	12
	95	1	3

for both years, though songs were also observed in March, April, May, and November (Fig. 5). After a peak in daily song hours in late December to mid-January, song occurrence became sparse from February through early May. Both recording years lacked data for much of April due to a recording gap between retrievals and deployments (Table 1). Humpback whale songs were not detected from June to October, but resumed in November (MidGul 2012 and 2013 and GulSho 2012) to early December (ShoHald 2012 and 2013 and GulSho 2013) (Fig. 5).

The null hypothesis that the mean hours with humpback whale songs did not differ between the four light periods was rejected (Fig. 8; Kruskal-Wallis; $\chi^2 = 100.48$, $df = 3$, $P < 0.001$). The adjusted average song hours were highest during dark (0.13 ± 0.35 ; $n = 233$) and lowest during light (-0.17 ± 0.41 ; $n = 233$) with dawn and dusk values intermediate at -0.11 ± 0.75 ($n = 233$) and 0.09 ± 1.03 ($n = 233$), respectively. The results of the Tukey-Kramer multiple comparisons test show that the mean adjusted song hours at dawn were significantly lower than the dusk ($t = 3.11$, $P = 0.01$) and dark ($t = 3.71$, $P = 0.001$) periods. Similarly, the mean adjusted song hours during light was significantly lower than both the dusk ($t = 4.00$, $P < 0.001$) and dark ($t = 4.59$, $P < 0.001$) periods. The mean adjusted song hours at dusk did not differ significantly from dark (Fig. 8; $t = 0.59$, $P = 0.93$) and song hours at dawn did not differ from light ($t = -0.88$, $P = 0.81$).

Nonsongs

Humpback whale nonsong calls were recorded in every month that contained songs as well as sporadically through October and once on 7 June 2013 at MidGul (Fig. 5). Like songs, nonsong calls peaked in December and January with 76% of nonsong call hours occurring during this period for both years (Fig. 5). Nonsong calls were observed on almost 90 more days than songs (302 of the 1,835 recording days) across the three stations, but had 317 less call hours (769 nonsong call hours). Humpback whale nonsong calls occurred during significantly less call hours per day than songs (Kruskal-Wallis test; $\chi^2 = 48.40$, $df = 1$, $P < 0.001$, Fig. 5, Fig. 7). Mean nonsong hours per day at MidGul (0.18 ± 0.18 , $n = 128$), GulSho (0.15 ± 0.14 ,

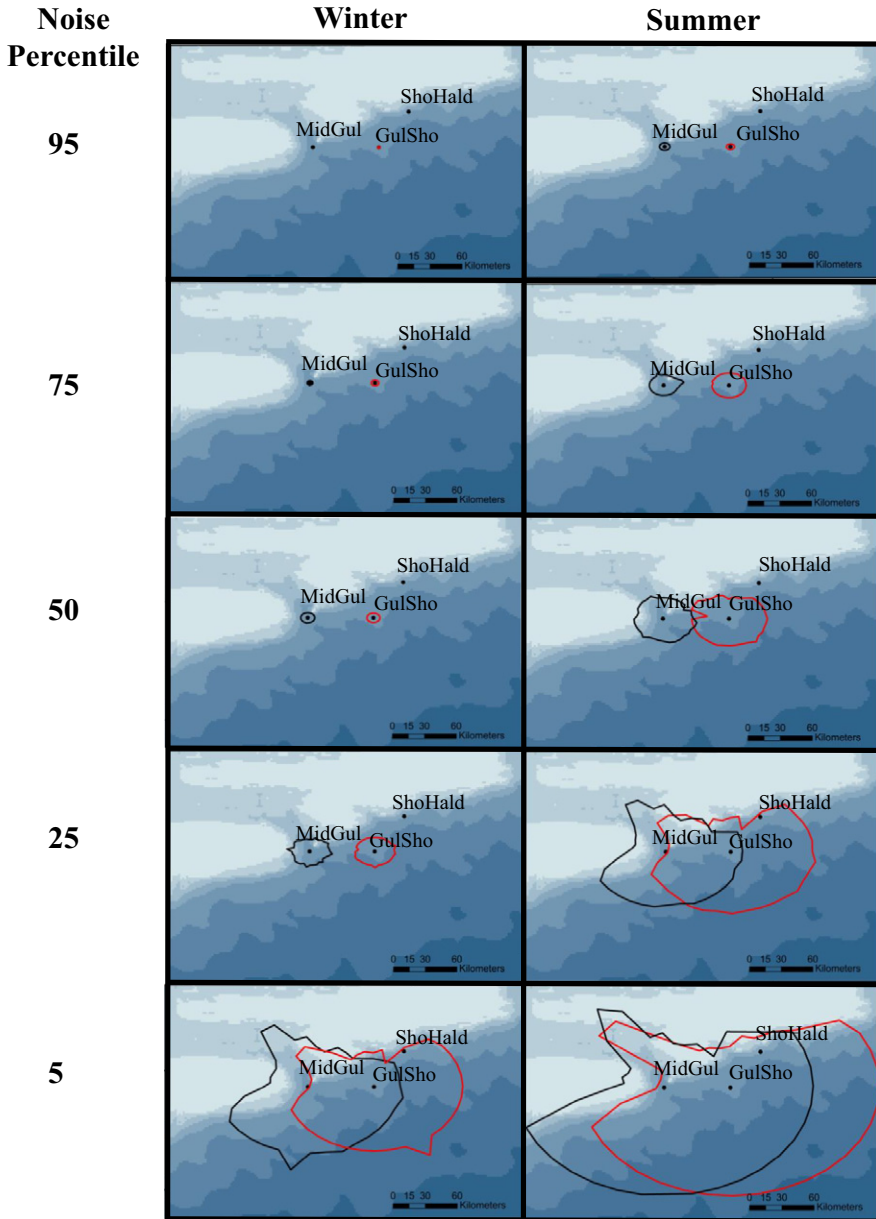


Figure 6. Polar plot of maximum detection range for humpback whale calls (SL = 162 dB re 1 μ Pa) in summer and winter for different noise percentiles at MidGul (black) and GulSho (red).

$n = 110$), and ShoHald (0.14 ± 0.17 , $n = 86$) were found to be different using a Kruskal-Wallis test ($\chi^2 = 8.35$, $df = 2$, $P = 0.02$). Further Tukey-Kramer pairwise comparisons, however, found no difference between MidGul and GulSho ($t = 1.55$,

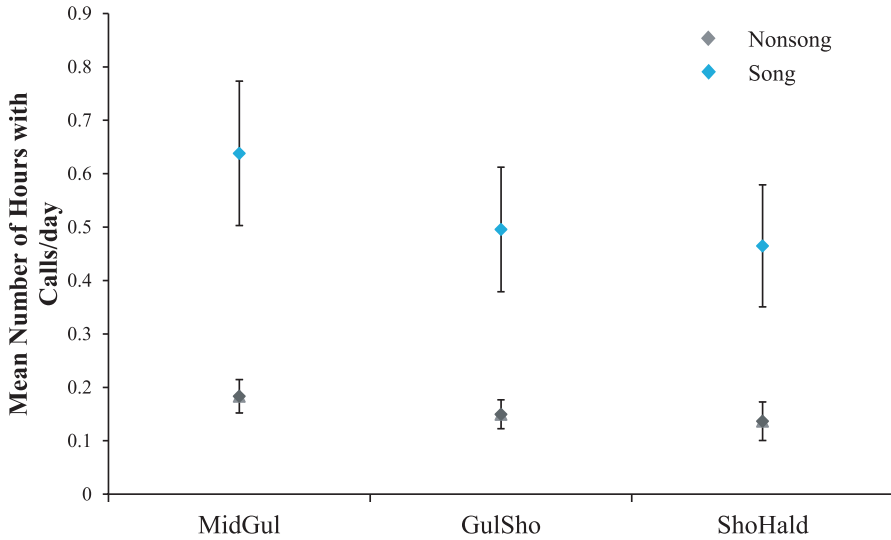


Figure 7. Mean hours with humpback whale song and nonsong calls per day with 95% confidence intervals for the MidGul (song: SD = ± 0.64 , $n = 86$; nonsong: SD = ± 0.18 , $n = 128$), GulSho (song: SD = ± 0.52 , $n = 77$; nonsong: SD = ± 0.14 , $n = 110$), and ShoHald (song: SD = ± 0.49 , $n = 70$; nonsong: SD = ± 0.17 , $n = 86$) recording stations from October 2012 to October 2014 on the Scotian Shelf.

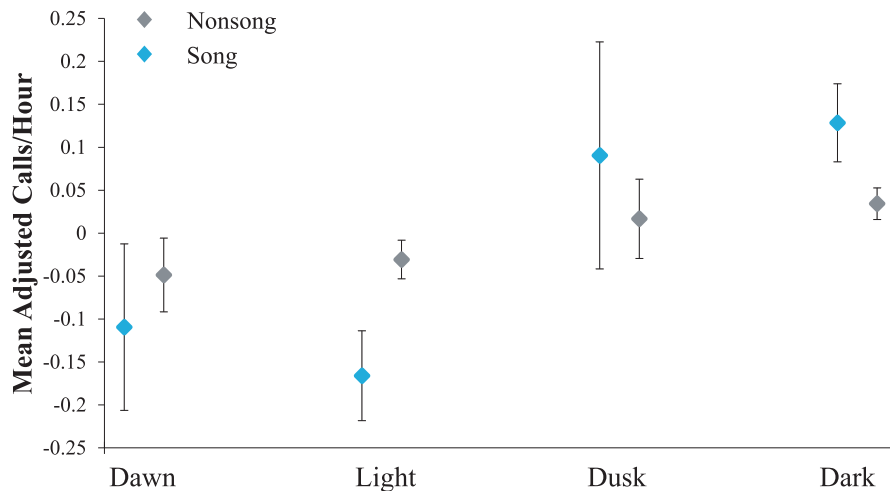


Figure 8. Adjusted-mean hours with humpback whale song and nonsong calls with 95% confidence intervals in four light periods: dawn (song: SD = ± 0.75 , $n = 233$; nonsong: SD = ± 0.39 , $n = 324$), light (song: SD = ± 0.41 , $n = 233$; nonsong: SD = ± 0.21 , $n = 324$), dusk (song: SD = ± 1.03 , $n = 233$; nonsong: SD = ± 0.42 , $n = 324$), and dark (song: SD = ± 0.35 , $n = 233$; nonsong: SD = ± 0.17 , $n = 324$). Light period times were obtained from Reda and Andreas (2004).

$P = 0.27$), MidGul and ShoHald ($t = -2.01$, $P = 0.11$), or GulSho and ShoHald ($t = -0.54$, $P = 0.85$).

A Kruskal-Wallis test revealed that nonsong calls differ between the four light periods, though not to the extent of songs (Fig. 8, $\chi^2 = 161.77$, $df = 3$, $P < 0.001$). The adjusted average nonsong hours during dawn, light, dusk, and dark were -0.05 ± 0.39 ($n = 324$), -0.03 ± 0.21 ($n = 324$), 0.02 ± 0.42 ($n = 324$), and 0.03 ± 0.17 ($n = 324$), respectively (Fig. 8). The Tukey-Kramer multiple comparisons test showed that the mean adjusted nonsong hours at dawn was lower than during dusk ($t = 2.61$, $P = 0.04$) and dark ($t = 3.31$, $P = 0.01$) periods. Similarly, mean adjusted nonsong hours during light was lower than dark ($t = 2.60$, $P = 0.05$). Light nonsong hours did not differ from dawn ($t = 0.72$, $P = 0.89$) or dusk ($t = 1.90$, $P = 0.23$) periods and dark did not differ from dusk ($t = 0.70$, $P = 0.90$). In comparing diel trends between song and nonsong calls, there was no difference in mean adjusted call hours at dawn ($t = -1.39$, $P = 0.86$) or dusk ($t = 1.68$, $P = 0.70$).

DISCUSSION

Humpback whale song and nonsong calls were detected in and around the Gully deep-water submarine canyon. Calls were produced by animals located on the slope and off the shelf as modeling results indicate that animals calling on the shelf would go undetected due to bathymetric effects of sound propagation in the region. Both song and nonsong calls were detected predominantly in the winter months. During this time frame, the area over which recorders could detect humpback whales was found to be similar across recording sites, allowing us to confidently compare results between stations. Song and nonsong call occurrence did not differ between stations, suggesting that the whales use the region homogeneously. Modeling results indicate that in extremely quiet conditions, homogeneous use of sites could be explained by calls being detected simultaneously on multiple stations. However, given that the detection range is limited to less than the distance between recorders in more than 75% of noise conditions in winter (when most calls occurred), and that for most call hours (67.2%) the calls only occurred at one site rather than at two or three sites during the same hour, this is not expected to greatly influence results. Thus, the homogeneous use of the region is likely a real pattern and not an artifact of multiple systems picking up calls.

The peak in humpback whale nonsong and song calls in December and January observed here is preceded by a peak in songs during October to December described in a known feeding ground off Massachusetts, the SBNMS (Vu *et al.* 2012, Stanistreet *et al.* 2013). As winter approaches and productivity in inshore feeding grounds declines, some humpback whales may move from areas such as the SBNMS, Atlantic Canada, and/or West Greenland to offshore regions that maintain productivity throughout the year, such as the Gully MPA (Rutherford and Breeze 2002). The whales presumably then continue their journey south to their breeding areas in the West Indies, where they are known to begin arriving in early January, with densities peaking in mid-February (Whitehead and Moore 1982), a pattern consistent with the decrease of calls in the Gully in mid-January observed here. If mean migration speeds collected by Garrigue *et al.* (2015) are accurate, the migration time from the Gully to the West Indies is approximately 30 d.

Humpback whale calls in the Gully region were predominantly songs, indicating the presence of males (Payne and McVay 1971, Winn and Winn 1978). Humpbacks

have similarly been observed singing outside of known breeding grounds elsewhere in the North Atlantic (Mattila *et al.* 1987, Clapham and Mattila 1990, Charif *et al.* 2001, Clark and Clapham 2004, Clark and Gagnon 2004, Vu *et al.* 2012, Stanistreet *et al.* 2013, Magnúsdóttir *et al.* 2015), the North Pacific (Baker *et al.* 1985, McSweeney *et al.* 1989, Norris *et al.* 1999), New Zealand (Helweg *et al.* 1998), Australia (Cato 1991, Dunlop *et al.* 2007, Noad and Cato 2007), and Antarctica (Garland *et al.* 2013). Several explanations have been proposed to singing outside of breeding grounds. One explanation is that males practice songs during migration to increase their mating success once on the breeding grounds (Clark and Clapham 2004). Singing on feeding grounds may provide important opportunities for cultural transmission of behavior (Garland *et al.* 2013). Immature males may benefit from singing through social learning resulting in greater mating success as adults (Herman *et al.* 2013). Alternatively, males sing during migration for the same purpose as on the breeding grounds, to mate (Stimpert *et al.* 2012). Clark and Clapham (2004) concluded that the breeding season should not be considered constrained to only low-latitude areas, and suggests that singing in high-latitude areas may present opportunities for males to advertise to females before reaching the breeding grounds where competition is comparatively higher. One proximate explanation for whales singing outside of breeding grounds is that the behavior is driven by the onset of associated hormones in the spring (Cato *et al.* 2001, Stafford *et al.* 2008), a documented process in some oscine birds (Vergauwen *et al.* 2014). Further research on the timing and manner in which male humpbacks begin singing may shed light on the driving forces.

The majority of humpback whale song and nonsong call detections ceased by February; however, calls continued sporadically through March. This finding indicates that some individuals either migrate south very late in the season, return from the south early in the season, or alternatively, do not migrate south, but remain north for the entirety of the winter. Segregated migrations of humpback whales have been reported with age, sex, and reproductive status impacting the timing of migrations (Craig *et al.* 2003, Stevick *et al.* 2003). Humpback occurrence in northern waters in the winter has been reported in the Gulf of Maine, Alaska, and Iceland (Straley 1990, Clapham *et al.* 1993, Vu *et al.* 2012, Stanistreet *et al.* 2013, Magnúsdóttir *et al.* 2015). Brown *et al.* (1995) observed a skewed male to female ratio in the West Indies indicating that some female humpbacks do not migrate south in the winter, a finding also made in Hawaii by Craig and Herman (1997). It has been proposed that for some individuals the trip to the low latitudes is not sufficiently beneficial to justify the energy costs of migration (Stevick *et al.* 2003). Such could be true for reproductively immature whales (Clapham *et al.* 1993), resting females that wait one or more years between pregnancies (Straley 1990), whales that do not gain sufficient calories in the summer months to sustain them through the demands of migration, mating, and calving (Straley 1990), or females that become pregnant on route to breeding grounds so they return to, or remain in, high latitudes (Craig and Herman 1997).

Moors-Murphy (2014) summarized how the unique oceanographic features of areas, such as the Gully submarine canyon, allow for mechanisms that cause aggregations and/or concentrations of baleen whale prey. Even in the winter, a gyre over the Gully is thought to retain prey that may include krill most common off Nova Scotia: *Meganyctiphanes norvegica*, *Thysanoessa raschii*, and *T. inermis* (Rutherford and Breeze 2002, Sameoto *et al.* 2002, Han and Loder 2003). The Gully therefore may provide alternative habitat for individual humpbacks in the eastern Scotian Shelf area at a time when feeding grounds have become unproductive and/or ice-covered and low-

latitude breeding grounds lack sufficient fitness benefits. Based on the small number of call detections in February–March, overwintering in the Gully is either rare, or those individuals in the area are not regularly acoustically active.

A lack of acoustic recordings collected in the month of April makes it difficult to discern how humpback whales use the Gully region in the spring. However, a small peak in humpback whale calls (both song and nonsong) at the end of March and beginning of May provides some evidence of what may be whales returning from the breeding grounds. A spring migration from the West Indies to the Scotian Slope was observed during a satellite tag study (Kennedy *et al.* 2013). Kennedy *et al.* (2013) described the occurrence of one male and one mother-calf pair occurring on the Scotian Slope in the spring of 2009 and 2012, respectively, after departing the West Indies in early April. Continuous acoustic recordings in the Gully throughout the spring season is required to determine whether the area is utilized by humpback whales at this time.

Humpback whale calls in and around the Gully MPA were absent throughout the summer and early fall. This is a timeframe when nonsong calls would be expected, and the lack of such calls suggests that animals were absent, rare, not acoustically active, or calling at undetectable source levels (Silber 1986, Dunlop *et al.* 2007, Stimpert *et al.* 2007). Modeling results indicate that calls can be detected at a greater range in the summer than in the winter, providing evidence that the absence of humpback whale calls in the summer is not related to other factors such as the masking effects of anthropogenic and biological noise. Visual summer surveys previously conducted in the Gully region similarly found humpback sightings to be rare, predominantly occurring late in the season (Hooker *et al.* 1999). Such is expected, as in the summer humpback whales are known to reside at their highly productive coastal feeding grounds including the Gulf of Maine, Atlantic Canada, West Greenland, Iceland, and Norway (Mattila *et al.* 1987, Katona and Beard 1990, Smith *et al.* 1999, Clark and Clapham 2004, Vu *et al.* 2012).

Humpback whale nonsong calls having fewer call hours than songs is expected as singing bouts can last for many consecutive hours (Garland *et al.* 2013), a characteristic yet to be reported of nonsong calls. Nonsong calls were less limited temporally than songs, occurring both earlier in the fall and later in the spring, indicating that this call type may not be as seasonally limited as songs. While an increase in singing in the winter is expected in humpbacks, a similar phenomenon in the relatively understudied nonsong calls has not been reported. A detailed description of nonsong calls was beyond the scope of the current study. It is unclear whether these nonsong calls are typical of those described in the literature (Dunlop *et al.* 2008, Zoidis *et al.* 2008, Stimpert *et al.* 2012), or if they represent a transitional call type from the summer nonsong calls to the winter songs of the breeding grounds. For example, a single theme unrepeated would not be defined as song by the classic definition (Payne and McVay 1971, Frumhoff 1983) and would therefore be defined here as nonsong. However, such patterning may represent a call type neither typical of social calls nor of songs, but rather something in-between. More detailed analysis in the future could be revealing.

Humpback whales in and around the Gully MPA produce both song and nonsong calls more at night than during the day. One explanation proposed for similar behavior in blue and fin whales (*Balaenoptera physalus*) is that they lunge feed on krill at depth during the day when prey form aggregations, and are left to call at night when prey are more dispersed at the surface and lunge feeding is less efficient (Brinton 1967, Lampert 1989, Croll *et al.* 1998, Stafford *et al.* 2005, Wiggins *et al.* 2005).

However, Stimpert *et al.* (2012) found that humpback foraging and singing behaviors were not mutually exclusive on an Antarctic feeding ground. Furthermore, Au *et al.* (2000) also observed humpbacks singing more at night than in the day on the breeding grounds of Hawaii during a time when the animals were fasting; therefore, their behavior was not driven by foraging activities. Au *et al.* (2000) proposed that the increased singing at night in Hawaii indicates a switch to acoustic sexual advertisement as a primary mating strategy rather than physical competition, which requires visual cues and therefore daylight to be sufficiently beneficial. In the Gully MPA region, the diel call patterns of humpbacks may be related to foraging and social behaviors, including mating strategies. Whales may call less during the day because they spend more time feeding at depth and/or engage in physical social interactions and competition for mates. Conversely, they produce social nonsong calls and songs more at night because their prey is too dispersed in the water column for optimum feeding, while acoustic signaling is the optimal form of socialization, and singing the optimum mating strategy during a time when visual cues are ineffective. If such is true, it would indicate that the nonsong calls observed here are not related to foraging behavior. However, Stimpert *et al.* (2007) described a specific nonsong call produced by humpbacks during nighttime foraging. An investigation into summer diel calling behavior would be telling to determine if the patterns observed here are seasonal, only occurring in winter, or if diel patterns also occur in the summer months.

PAM on the Scotian Slope has allowed us to collect a large amount of data at relatively low cost and effort from a remote offshore MPA. However, PAM has its limitations. Animal behavior can be inferred, but not confirmed using PAM alone. Mooring noise, vessel traffic, seismic survey activities, and even other marine mammal calls can mask humpback whale calls. Modeling results confirm that the detectability of animals varies depending on regional noise conditions, topography, and time of year. Noncalling whales go undetected. Therefore, these results are biased towards acoustically active whales that call in regions conducive to sound propagation during low noise periods, and represent the minimum occurrence of humpback whales in and around the Gully MPA.

Conclusion

This study has found evidence that North Atlantic humpback whales use the Gully MPA and the surrounding waters for migration, and potentially mating and feeding purposes in the winter. It is clear that North Atlantic humpback whales use this region during the winter likely as a migratory corridor and/or potentially as overwintering grounds for some individuals. Songs occur throughout the migration, suggesting that humpback males practice singing before the mating season or, alternatively, engage in breeding behavior in route south. While the foraging behavior of humpback whales in the Gully remains unknown, the diel patterns of calls may suggest that whales are foraging by day and mating at night. The results did not differ between the Gully submarine canyon recorder and the two intercanion stations, indicating that the entire slope region is utilized by this species annually. This should be taken into account when considering the impacts of anthropogenic activities in the area on humpback whales. While dedicated cetacean studies have been conducted in the Gully area for over two decades, it was not until long-term PAM was employed that the importance of this region to humpback whales has become apparent. In the future, expanded year-round continuous acoustic monitoring efforts both inshore and

offshore Nova Scotia, and other areas of eastern Canada will allow for (1) a more complete understanding of humpback whale and all other acoustically active marine mammal seasonal movements and (2) the identification of areas of important habitat for populations that require protection.

ACKNOWLEDGMENTS

This research was supported by DFO Strategic Program for Ecosystem Research and Advice funds and through contributions from JASCO Applied Sciences. We would like to thank Jay Barthelette and the Program Coordination and Support Division of DFO, Andrew Cogswell and other DFO staff, and the CCGS *Hudson* crew for their help with instrument deployments and retrievals. We thank all additional acoustic analysts who contributed to this work including Julien Delarue, Emma Marotte, Galaxina Renaud, and Carmen Lawrence. We also thank Briand Gaudet for compiling nautical twilight times.

LITERATURE CITED

- Arraut, E. M., and J. M. Vielliard. 2004. The song of the Brazilian population of humpback whale *Megaptera novaeangliae*, in the year 2000: Individual song variations and possible implications. *Anais da Academia Brasileira de Ciencias* 76:373–380.
- Au, W. W. L., J. Mobley, W. C. Burgess, M. O. Lammers and P. E. Nachtigall. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science* 16:530–544.
- Au, W. W. L., A. A. Pack, M. O. Lammers, L. M. Herman, M. H. Deakos and K. Andrews. 2006. Acoustic properties of humpback whale songs. *Journal of the Acoustical Society of America* 120:1103–1110.
- Baker, C. S., L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley and J. H. Straley. 1985. Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Marine Mammal Science* 1:304–323.
- Becker, J. J., D. T. Sandwell, W. H. F. Smith, *et al.* 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy* 32:355–371.
- Boyer, T. P., J. I. Antonov, O. K. Baranova, *et al.* 2013. Environment data from CTD casts, profiling floats, and ocean station data. NOAA Atlas NESDIS 72, Silver Spring, MD.
- Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California Current. *Limnology and Oceanography* 12:451–483.
- Brown, M. R., P. J. Corkeron, P. T. Hale, K. W. Schultz and M. Bryden. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society B: Biological Sciences* 259:229–234.
- Cato, D. H. 1991. Songs of humpback whales: The Australian perspective. *Defence Science and Technology Organisation, Canberra, Australia*. 15 pp.
- Cato, D. H., R. Paterson and P. Paterson. 2001. Vocalisation rates of migrating humpback whales over 14 years. *Memoirs-Queensland Museum* 47:481–490.
- Cerchio, S., and M. Dahlheim. 2001. Variation in feeding vocalizations of humpback whales (*Megaptera novaeangliae*) from Southeast Alaska. *Bioacoustics* 11:277–295.
- Cerchio, S., J. K. Jacobsen and T. F. Norris. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: Synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour* 62:313–329.
- Charif, R. A., P. J. Clapham and C. W. Clark. 2001. Acoustic detections of singing humpback whales in deep waters off the British Isles. *Marine Mammal Science* 17:751–768.

- Clapham, P., and D. K. Mattila. 1990. Humpback whale songs as indicators of migration routes. *Marine Mammal Science* 6:155–160.
- Clapham, P. J., L. S. Baraff, C. A. Carlson, *et al.* 1993. Seasonal occurrence and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine. *Canadian Journal of Zoology* 71:440–443.
- Clark, C. W., and P. J. Clapham. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proceedings of the Royal Society of London B: Biological Sciences* 271:1051–1058.
- Clark, C., and G. Gagnon. 2004. Low-frequency vocal behaviors of baleen whales in the North Atlantic: Insights from integrated undersea surveillance system detections, locations, and tracking from 1992 to 1996. *U.S. Navy Journal of Underwater Acoustics* 52:609–640.
- Craig, A. S., and L. M. Herman. 1997. Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology* 75:1923–1933.
- Craig, A. S., L. M. Herman, C. M. Gabriele and A. A. Pack. 2003. Migratory timing of humpback whales (*Megaptera novaeangliae*) in the Central North Pacific varies with age, sex and reproductive status. *Behaviour* 140:981–1001.
- Croll, D. A., B. R. Tershy, R. P. Hewitt, *et al.* 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep Sea Research Part II: Topical Studies in Oceanography* 45:1353–1371.
- Darling, J. D., and M. Bérubé. 2001. Interactions of singing humpback whales with other males. *Marine Mammal Science* 17:570–584.
- Darling, J. D., M. E. Jones and C. P. Nicklin. 2012. Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song (L). *Journal of the Acoustical Society of America* 132:2955–2958.
- Delarue, J., J. MacDonnell, B. Martin, X. Mouy and D. H. Hannay. 2014. Northeastern Chukchi Sea Joint Acoustic Monitoring Program 2012–2013. Technical report for ConocoPhillips Company, Shell Exploration & Production Company, and Statoil USA E&P, Inc. by JASCO Applied Sciences. vi + 104 pp.
- DFO (Department of Fisheries and Oceans). 2008. The Gully Marine Protected Area Management Plan. Oceans and Habitat Branch, Fisheries and Oceans Canada, Dartmouth, Canada. 80 pp. Available at <http://www.dfo-mpo.gc.ca/Library/333121.pdf>.
- DFO (Department of Fisheries and Oceans). 2010. Gully marine protected area monitoring Indicators, protocols and strategies. Canadian Science Advisory Secretariat Science Advisory Report 2010/066. 17 pp. Available at <http://waves-vagues.dfo-mpo.gc.ca/Library/342413.pdf>.
- DFO (Department of Fisheries and Oceans). 2016. Recovery strategy for the northern bottlenose whale, (*Hyperoodon ampullatus*), Scotian Shelf population, in Atlantic Canadian waters [Final]. vii + 70 pp. Available at http://www.registrelep-sararegistry.gc.ca/document/doc1863f/ind_e.cfm.
- Dunlop, R. A., M. J. Noad, D. H. Cato and D. Stokes. 2007. The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*). *Journal of the Acoustical Society of America* 122:2893–2905.
- Dunlop, R. A., D. H. Cato and M. J. Noad. 2008. Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 24:613–629.
- Frouin-Mouy, H., K. Kowarski, B. Martin and K. Bröker. 2017. Seasonal trends in acoustic detection of marine mammals in Baffin Bay and Melville Bay, northwest Greenland. *Arctic* 70:59–76.
- Frumhoff, P. 1983. Aberrant songs of humpback whales (*Megaptera novaeangliae*): Clues to the structure of humpback songs. Pages 81–127 in R. Payne, ed. *Communication and behavior of whales*. AAAS Selected Symposia Series. Westview Press, Boulder, CO.

- Garland, E. C., A. W. Goldizen, M. L. Rekdahl, *et al.* 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology* 21:687–691.
- Garland, E. C., J. Gedamke, M. L. Rekdahl, M. J. Noad, C. Garrigue and N. Gales. 2013. Humpback whale song on the southern ocean feeding grounds: Implications for cultural transmission. *PLOS ONE* 8:e79422.
- Garrigue, C., P. J. Clapham, Y. Geyer, A. S. Kennedy and A. N. Zerbini. 2015. Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *Royal Society Open Science* 2:150489.
- Gowans, S., and H. Whitehead. 1995. Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Canadian Journal of Zoology* 73:1599–1608.
- Han, G., and J. W. Loder. 2003. Three-dimensional seasonal-mean circulation and hydrography on the eastern Scotian Shelf. *Journal of Geophysical Research: Oceans* 108:3136.
- Helweg, D. A., D. H. Cat, P. F. Jenkins, C. Garrigue and R. D. McCauley. 1998. Geographic variation in South Pacific humpback whale songs. *Behaviour* 135:1–27.
- Herman, L. M., A. A. Pack, S. S. Spitz, E. Y. Herman, K. Rose, S. Hakala and M. H. Deakos. 2013. Humpback whale song: Who sings? *Behavioral Ecology and Sociobiology* 67:1653–1663.
- Hooker, S. K., H. Whitehead and S. Gowans. 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology* 13:592–602.
- Jann, B., J. Allen, M. Carrillo, *et al.* 2003. Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *Journal of Cetacean Research and Management* 5:125–130.
- Katona, S. K., and J. A. Beard. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Report of the International Whaling Commission (Special Issue 12):295–306.
- Kellogg, R. 1929. What is known of the migrations of some of the whalebone whales. Annual Report of the Board of Regents of the Smithsonian Institution. Pp. 467–494.
- Kennedy, A. S., A. N. Zerbini, O. Vásquez, N. Gandillon, P. J. Clapham and O. Adam. 2013. Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. *Canadian Journal of Zoology* 92:9–18.
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3:21–27.
- MacGillivray, A. O. 2006. Acoustic modelling study of seismic airgun noise in Queen Charlotte Basin. M.Sc. thesis, University of Victoria, Victoria, Canada. 98 pp.
- Mackintosh, N. A. 1942. The southern stocks of whalebone whales. *Discovery Reports XXII*:197–300.
- Mackintosh, N. 1966. The distribution of southern blue and fin whales. Pages 125–144 in K. S. Norris, ed. *Whales, dolphins, and porpoises*. University of California Press, Berkeley, CA.
- Magnúsdóttir, E. E., P. J. Miller, R. Lim, M. H. Rasmussen, M. O. Lammers and J. Svavarsson. 2015. Humpback whale (*Megaptera novaeangliae*) song unit and phrase repertoire progression on a subarctic feeding ground. *Journal of the Acoustical Society of America* 138:3362–3374.
- Martin, A., S. Katona, D. Matilla, D. Hembree and T. Waters. 1984. Migration of humpback whales between the Caribbean and Iceland. *Journal of Mammalogy*:330–333.
- Martin, B., K. Kowarski, X. Mouy and H. Moors-Murphy. 2014. Recording and identification of marine mammal vocalizations on the Scotian shelf and slope. *IEEE Oceans-St. John's*, 2014. 6 pp.
- Mattila, D. K., L. N. Guinee and C. A. Mayo. 1987. Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy* 68:880–883.

- McSweeney, D., K. Chu, W. Dolphin and L. Guinee. 1989. North Pacific humpback whale songs: A comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. *Marine Mammal Science* 5:139–148.
- Moors-Murphy, H. B. 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. *Deep Sea Research Part II: Topical Studies in Oceanography* 104:6–19.
- Munger, L. M., S. M. Wiggins, S. E. Moore and J. A. Hildebrand. 2008. North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long term acoustic recordings in the southeastern Bering Sea, 2000–2006. *Marine Mammal Science* 24:795–814.
- Noad, M. J., and D. H. Cato. 2007. Swimming speeds of singing and non-singing humpback whales during migration. *Marine Mammal Science* 23:481–495.
- Norris, K. S. 1967. Some observations on the migration and orientation of marine mammals. Pages 101–125 in R. H. Storm, ed. *Animal Orientation and Navigation*. Oregon State University Press, Eugene, OR.
- Norris, T. F., M. Mc Donald and J. Barlow. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *Journal of the Acoustical Society of America* 106:506–514.
- Palsbøll, P. J., J. Allen, M. Berube, *et al.* 1997. Genetic tagging of humpback whales. *Nature* 388:767–769.
- Payne, R. S., and S. McVay. 1971. Songs of humpback whales. *Science* 173:585–597.
- Reda, I., and A. Andreas. 2004. Solar position algorithm for solar radiation applications. National Renewable Energy Laboratory, Technical Report NREL/TP-560-34302. Pp. 577–589.
- Reeves, R. R., T. D. Smith, E. A. Josephson, P. J. Clapham and G. Woolmer. 2004. Historical observations of humpback and blue whales in the North Atlantic Ocean: Clues to migratory routes and possibly additional feeding grounds. *Marine Mammal Science* 20:774–786.
- Roman, J., J. A. Estes, L. Morissette, *et al.* 2014. Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment* 12:377–385.
- Rutherford, R., and H. Breeze. 2002. The Gully ecosystem. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2615. vi + 28 pp.
- Sameoto, D., M. Kennedy and N. Cochrane. 2002. Seasonal abundance, vertical and geographic distribution of mesozooplankton, macrozooplankton and micronekton in the Gully and western Scotian Shelf, 1999–2000. Canadian Technical Report of Fisheries and Aquatic Sciences 2427. v + 37 pp.
- Silber, G. K. 1986. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 64:2075–2080.
- Smith, W. H., and D. T. Sandwell. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. *Science* 277:1956–1962.
- Smith, T., J. Allen, P. Clapham, *et al.* 1999. An ocean basin wide mark recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). *Marine Mammal Science* 15:1–32.
- Smith, J. N., A. W. Goldizen, R. A. Dunlop and M. J. Noad. 2008. Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. *Animal Behaviour* 76:467–477.
- Stafford, K. M., S. E. Moore and C. G. Fox. 2005. Diel variation in blue whale calls recorded in the eastern tropical Pacific. *Animal Behaviour* 69:951–958.
- Stafford, K. M., S. E. Moore, K. L. Laidre and M. Heide-Jørgensen. 2008. Bowhead whale springtime song off West Greenland. *Journal of the Acoustical Society of America* 124:3315–3323.

- Stanistreet, J. E., D. Risch and S. M. Van Parijs. 2013. Passive acoustic tracking of singing humpback whales (*Megaptera novaeangliae*) on a Northwest Atlantic feeding ground. PLOS ONE 8:e61263.
- Stevick, P. T., J. Allen, M. Bérubé, et al. 2003. Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). Journal of Zoology 259:231–237.
- Stimpert, A. K., D. N. Wiley, W. W. L. Au, M. P. Johnson and R. Arsenault. 2007. 'Megapclicks': Acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). Biology Letters 3:467–470.
- Stimpert, A. K., W. W. Au, S. E. Parks, T. Hurst and D. N. Wiley. 2011. Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. Journal of the Acoustical Society of America 129:476–482.
- Stimpert, A., L. Peavey, A. Friedlaender and D. Nowacek. 2012. Humpback whale song and foraging behavior on an Antarctic feeding ground. PLOS ONE 7:e51214.
- Straley, J. M. 1990. Fall and winter occurrence of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Report of the International Whaling Commission Special:319–323.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology 8:105–116.
- Vergauwen, J., T. G. Groothuis, M. Eens and W. Müller. 2014. Testosterone influences song behaviour and social dominance – But independent of prenatal yolk testosterone exposure. General and Comparative Endocrinology 195:80–87.
- Vu, E. T., D. Risch, C. W. Clark, et al. 2012. Humpback whale (*Megaptera novaeangliae*) song occurs extensively on feeding grounds in the western North Atlantic Ocean. Aquatic Biology 14:175–183.
- Whitehead, H. 2013. Trends in cetacean abundance in the Gully submarine canyon, 1988–2011, highlight a 21% per year increase in Sowerby's beaked whales (*Mesoplodon bidens*). Canadian Journal of Zoology 91:141–148.
- Whitehead, H., and M. J. Moore. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology 60:2203–2211.
- Wiggins, S. M., E. M. Oleson, M. A. McDonald and J. A. Hildebrand. 2005. Blue whale (*Balaenoptera musculus*) diel call patterns offshore of Southern California. Aquatic Mammals 31:161–168.
- Winn, H. E., and L. K. Winn. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. Marine Biology 47:97–114.
- Zar, J. H. 1999. Biostatistical analysis. Pearson Education, Delhi, India.
- Zoidis, A. M., M. A. Smultea, A. S. Frankel, et al. 2008. Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. Journal of the Acoustical Society of America 123:1737–1746.

Received: 23 September 2016

Accepted: 3 August 2017