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# Passive acoustic monitoring predicts daily variation in North Atlantic right whale presence and relative abundance in Roseway Basin, Canada

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## Abstract

North Atlantic right whale monitoring in Roseway Basin, Canada, is primarily based on short-term (<14 d) visual surveys conducted during August–September. Variability in survey effort has been the biggest limiting factor to studying changes in the population's occurrence and habitat use. Such efforts could be enhanced considerably using passive acoustic monitoring (PAM). We sought to determine if variation in whale presence, relative abundance, demography, and/or behavior (estimated through visual surveys) could be explained by variation in three right whale call types in this habitat. A generalized linear model was fit to 23 d of concurrent PAM and visual monitoring during four summers within the Roseway Basin Right Whale Critical Habitat boundaries. The model revealed significant positive relationships between relative abundance, call counts and presence of surface-active group behavior. PAM can refine daily right whale presence estimates. While visual observations ($n$ = 23 d) implied a 40% decline in right whale presence during 2014–2015 relative to 2004–2005, PAM data ($n$ = 211 d) showed right whales were present between 71%–85% of survey days throughout all years analyzed. We demonstrate that PAM is a useful tool to extend

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periods of right whale monitoring, especially in areas where visual monitoring efforts may be limited.

Key words: right whale, acoustic-visual monitoring, call counts, abundance, upcall, gunshot, moan, surface-active group.

Monitoring rare and migratory baleen whales is challenging yet essential for ecological studies and conservation interests. Information used to assess population status and to develop management strategies for baleen whales is conventionally derived from airborne and vessel visual-count surveys (*e.g.*, Buckland *et al.* 2001, Khan *et al.* 2009, Waring *et al.* 2016). For example, the ship rerouting zones around North Atlantic right whale (*Eubalaena glacialis*; hereafter right whale) critical habitats, such as the Grand Manan Basin and Roseway Basin (and its associated vessel Area to be Avoided, ATBA; IMO 2008) in Canadian waters were defined using sightings data (Brown *et al.* 2009). However, visual surveys and associated photo identification (ID) data tend to have limited spatial and temporal coverage mainly due to costs, weather, and daylight. Passive acoustic monitoring (PAM) offers an alternative method for collecting information on whale occurrence and is widely used to monitor whale presence (Mellinger *et al.* 2007, Van Parijs *et al.* 2009, Van Opzeeland *et al.* 2013), but does come with its own challenges and limitations. It may be desirable to draw inferences on seasonal and annual variation of whale presence and abundance from PAM data, yet this may be challenging to do as PAM data are often collected in absence of visual monitoring data that can provide a degree of ground-truthing (Mellinger *et al.* 2007, Van Parijs *et al.* 2009, Parks *et al.* 2011, Morano *et al.* 2012). Additional challenges due to variation in whale behavior and local environmental conditions, that affect sound propagation, need to be considered when interpreting acoustic data.

The endangered right whale is one of many whale species that, until recently, has been studied predominantly using visual survey efforts (CETAP 1982, Pettis and Hamilton 2016, Waring *et al.* 2016). The known right whale range includes the eastern seaboard of North America from at least Florida to Newfoundland and occasionally as far north as Greenland (Knowlton *et al.* 1992) and Norway (Jacobsen *et al.* 2004). The population was recently estimated at ~458 individuals (Pace *et al.* 2017). The whales typically migrate in a relatively dispersed manner (Firestone *et al.* 2008) and tend to aggregate in a few known or suspected breeding, feeding, and calving habitats separated by 100–1,000 km (CETAP 1982, Winn *et al.* 1986, Cole *et al.* 2013). Such movement patterns challenge the efficacy of surveys and considerable knowledge gaps in the ecology and distribution of these whales remain (Weinrich *et al.* 2000, IWC 2001, Kraus and Hatch 2001). These knowledge gaps present a conservation challenge as right whales are at risk from vessel strikes and fishing gear entanglements throughout their migratory range (Kraus 1990, Knowlton and Kraus 2001, Kraus *et al.* 2005, Ward-Geiger *et al.* 2005).

Most right whale observations in Canadian continental shelf waters occur in summer through autumn (June–December; CETAP 1982, Winn *et al.* 1986, Brown *et al.* 2007, Mellinger *et al.* 2007), though monitoring in Canadian waters has been inconsistent from year-to-year (with the exception of annual surveys in the lower Bay of Fundy), as well as spatially and temporally limited. The distribution of right whales throughout most of their suspected Canadian range remains largely unknown. Visual surveys in the Roseway Basin Critical Habitat and ATBA have occurred with <14 d of survey effort per year and some years with no effort (Kenney 2001, Vanderlaan *et al.* 2008, Davies *et al.* 2015*a*, Pettis and Hamilton 2016). The consequences of disparate monitoring in Canadian waters have become readily apparent. Since 2010, right whale distribution appears to have changed as compared to previous documentation, with fewer whale detections per unit effort in spring and summer in the Gulf of Maine and Bay of Fundy, and on winter calving grounds off Florida, and increased sightings during summers in other areas such as the Gulf of St. Lawrence (Pettis and Hamilton 2015, 2016; Pettis *et al.* 2017; Davis *et al.* 2017). These changes in right whale distribution have increased interest in using PAM to expand temporal monitoring of known and potential right whale habitats. Population monitoring could be considerably advanced by PAM if inferences can be reasonably made about whale occurrence and abundance using acoustic indices, such as call presence and call counts.

PAM has proven to be a valuable tool for right whale research and management (*e.g.*, Laurinolli *et al.* 2003, Vanderlaan *et al.* 2003, Clark *et al.* 2010, Morano *et al.* 2012, Davis *et al.* 2017, DFO 2018). Right whales produce a variety of sounds, of which three characteristic sounds were used in this study, postulated to have different communication functions: a tonal upsweep or "upcall" that is considered a contact call produced by both sexes and all ages (Parks and Tyack 2005), a broadband "gunshot" sound produced ostensibly by males and considered a reproductive warning to other males (Parks and Tyack 2005, Parks *et al.* 2011, Matthews *et al.* 2014), and tonal "moans" thought to be produced predominantly by females (Matthews *et al.* 2001, Parks and Tyack 2005). While upcalls are typically used as indicators of right whale presence, it is possible that gunshots may be better indicators of presence in Canadian habitats. Gunshots are produced frequently in Roseway Basin, a male-dominated habitat, and predominately by lone males or males in association with male displays and (or) surface-active groups (SAGs; Brown 1994; Parks *et al.* 2011, 2012; Matthews *et al.* 2014; Bort *et al.* 2015). SAGs are defined as two or more whales "interacting" at the surface with frequent physical contact (Kraus and Hatch 2001). This leads to the question of how presence and number of each call type, or combinations thereof, might relate to variability in local whale distribution and abundance (Van Parijs *et al.* 2009).

### *Goals*

Concurrent visual monitoring and single-hydrophone PAM for right whales occurred during their presumed maximum occupancy period (August–September; Brown *et al.* 2007, Pettis and Hamilton 2015) in

Roseway Basin in 2004, 2005, 2014, and 2015. These data provided the opportunity to assess the ability of PAM to supplement long-term right whale monitoring efforts. Our primary goal was to determine how variation in acoustic indices of right whale presence (through the detections of right whale upcall, gunshots, and moans) may be related to visually estimated right whale presence, relative abundance, demographics, and behavior at daily and interannual time scales in the Basin. The results are instrumental in determining (1) what inferences might be reasonably made about right whale presence and relative abundance based on single hydrophone PAM data, and (2) how whale habitat occupancy and abundance might be appropriately interpreted at larger spatial and longer temporal monitoring scales through PAM.

## Methods

### *Visual Monitoring*

Right whale visual surveys (detailed in Brown *et al.* 2007) were conducted from a vessel in the Roseway Basin Critical Habitat and ATBA (nominally 42°57′N, 65°12′W, 4,030 km$^2$; Fig. 1) for a total of 23 d among 4 yr during August–September when bottom-mounted archival PAM systems were also present in the Basin. The 23 d were distributed among two pairs of consecutive years separated by a decade (Fig. 2). The visual surveys were conducted during daylight

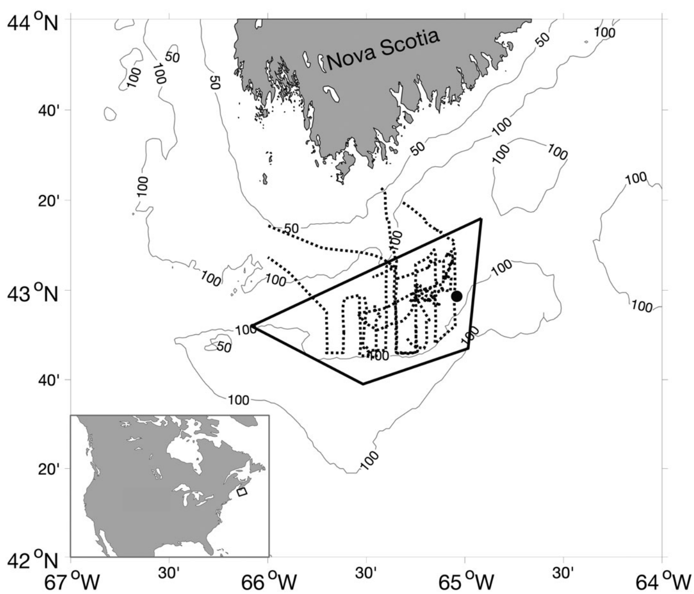


*Figure 1.* Bathymetric chart showing the 2014 visual survey track-lines (dotted) in the Roseway Basin Area To Be Avoided (ATBA; polygon) and locations of bottom mounted PAM systems (solid circle). Similar figures for each survey day of each year are provided in Fig. S1A–E.

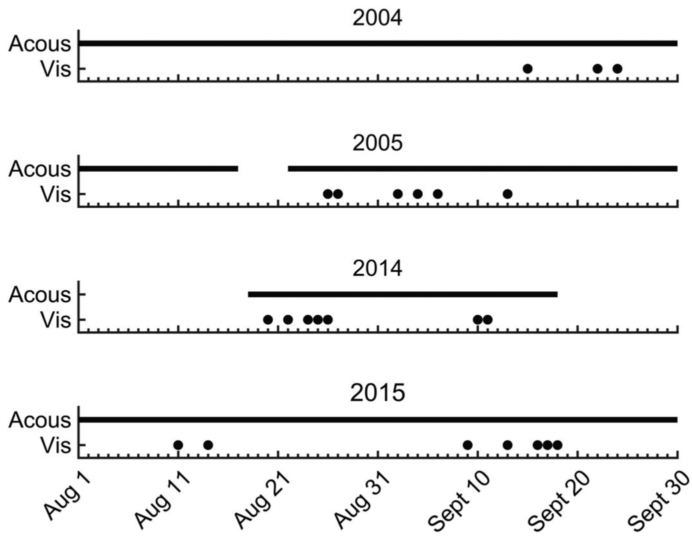


*Figure 2.* Time series illustrating near continuous passive acoustic (Acous; horizontal bars) and 23 d of concurrent discontinuous visual (Vis; solid circles) monitoring days in the Roseway Basin ATBA during the August–September period of each year.

(up to 15 h between morning and evening nautical twilight for the August–September period; weather permitting).

Visual survey records included 1 min interval GPS coordinates, Beaufort-scale sea state, visibility (nominal 5 nmi), on-track survey effort, and species identification of marine mammals sighted. When one or more right whales were sighted the vessel slowed, broke track-line, and identification (ID) information was collected, all while remaining on-effort. At the same time, whale behavior, (*e.g.*, presence of SAGs) and group composition (number, sex, mother-calf pair, *etc.*) were recorded and intermittent biopsy samples collected. The track-line survey was resumed once sampling activities were completed. All whales used in our analyses are based on IDed whales (adults only; including SAGs) where IDs and sex (if known) were provided through the North Atlantic Right Whale Consortium Catalogue (Hamilton *et al.* 2007).

Only sightings and effort within the Roseway Basin ATBA were included in our analyses because the probability of observing a right whale is highest within the ATBA (Vanderlaan *et al.* 2011). Further, the majority of visual survey effort among the 23 d was expended within this area (Fig. 1, S1A–E). Weather limitations resulted in an average ~8 h/d of survey effort (range ~2.1–13.6 h/d, Table 1). We assumed that for each of the 23 d, the spatial distribution of effort provided a representative subsample of the right whale population in the Basin because surveys covered on average 56% (~2,259 km$^2$) of the ATBA each day (Appendix S1, Fig. S1A–E). In this study, a relative measure of daily right whale abundance was estimated by the ratio of the number of IDed whales sighted and number of on-effort survey hours.

*Table 1.* Information for day (D) and month (Mo) of year (Yr) summarizing daily right whale visual survey effort (h/d), total (ID), male (M) and female (F) number of identified whales counted, and total (IPUE), male (MPUE) and female (FPUE) number of identified whales per unit effort, presence/absence (Y/N) of surface-active groups (SAG), and number of upcalls, gunshots, moans and total calls concurrently recorded over 23 d (15 h/d) within the Roseway Basin ATBA in each of 2004, 2005, 2014, and 2015

| Yr (d) | Mo | D | Visual effort (h) | ID | IPUE | M | MPUE | F | FPUE | SAG | Upcalls | Gunshots | Moans | Total calls |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2004 (3) | 9 | 15 | 10.2 | 40 | 3.9 | 32 | 3.1 | 5 | 0.5 | Y | 150 | 154 | 84 | 388 |
| | 9 | 22 | 9.9 | 23 | 2.3 | 19 | 1.9 | 3 | 0.3 | Y | 26 | 85 | 10 | 121 |
| | 9 | 24 | 9.7 | 15 | 1.5 | 10 | 1.0 | 4 | 0.4 | Y | 104 | 67 | 4 | 175 |
| 2005 (6) | 8 | 26 | 6.8 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| | 8 | 27 | 11.1 | 5 | 0.5 | 4 | 0.4 | 1 | 0.1 | N | 3 | 0 | 0 | 3 |
| | 9 | 2 | 8.0 | 2 | 0.3 | 0 | 0.0 | 2 | 0.3 | N | 60 | 1 | 4 | 65 |
| | 9 | 4 | 10.3 | 3 | 0.3 | 1 | 0.1 | 2 | 0.2 | N | 34 | 12 | 0 | 46 |
| | 9 | 6 | 9.8 | 3 | 0.3 | 3 | 0.3 | 0 | 0.0 | N | 34 | 12 | 0 | 46 |
| | 9 | 13 | 6.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 14 | 0 | 0 | 14 |
| 2014 (7) | 8 | 20 | 10.7 | 24 | 2.3 | 11 | 1.0 | 9 | 0.8 | Y | 189 | 25 | 1 | 215 |
| | 8 | 22 | 5.6 | 2 | 0.4 | 0 | 0.0 | 2 | 0.4 | N | 3 | 34 | 0 | 37 |
| | 8 | 24 | 7.9 | 4 | 0.5 | 1 | 0.1 | 3 | 0.4 | N | 25 | 2 | 0 | 27 |
| | 8 | 25 | 13.6 | 10 | 0.7 | 7 | 0.5 | 0 | 0.0 | N | 57 | 24 | 0 | 81 |
| | 8 | 26 | 8.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| | 9 | 10 | 3.7 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 41 | 0 | 8 | 49 |
| | 9 | 11 | 7.9 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| 2015 (7) | 8 | 11 | 9.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| | 8 | 14 | 2.1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| | 9 | 9 | 7.6 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |
| | 9 | 13 | 10.0 | 9 | 0.9 | 6 | 0.6 | 2 | 0.2 | N | 345 | 44 | 121 | 510 |
| | 9 | 16 | 9.9 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 9 | 1 | 0 | 10 |
| | 9 | 17 | 12.0 | 3 | 0.3 | 1 | 0.1 | 1 | 0.1 | N | 0 | 0 | 0 | 0 |
| | 9 | 18 | 2.9 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | N | 0 | 0 | 0 | 0 |

*(Continues)*

*Table 1.* Continued

| Yr (d) | Mo | D | Visual effort (h) | ID | IPUE | M | MPUE | F | FPUE | SAG | Upcalls | Gunshots | Moans | Total calls |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Maximum | 13.6 | 40 | 3.9 | 32 | 3.1 | 9 | 0.8 | | 345 | 154 | 121 | 510 |
| | | Minimum | 2.1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | | 0 | 0 | 0 | 0 |
| | | Mean | 8.4 | 6.2 | 0.6 | 4.1 | 0.4 | 1.5 | 0.2 | | 47.6 | 20 | 10.1 | 77.7 |
| | | Median | 9.0 | 2.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | | 14 | 1 | 0 | 27 |
| | | Total | 192.4 | 143 | 14.2 | 95 | 9.1 | 34 | 3.7 | | 1,094 | 461 | 232 | 1,787 |

*Note*: ID may be greater than M+F as the sex of some ID remain unknown.

Repeat sightings of an IDed whale within a survey day and any unidentified whales were excluded from the analyses to avoid inflated estimates of the number of whales occupying the Basin. Thus, daily relative abundance indices per unit effort (PUE, per hour) were used to estimate the total number of IDed whales (IPUE), IDed males (MPUE), and IDed females (FPUE).

The presence of SAG behavior on each survey day was also considered in the analyses, referred to as "SAG days." The size and demographic composition of a SAG can be fluid as individuals leave and join the group through time (Parks *et al.* 2007), whereas each vessel survey provided only single realizations in time and space of the distribution and composition of SAGs in the habitat. Therefore, SAG presence on a survey day can only be interpreted as a day with a higher probability of more SAG (of any size or composition) occurring within the habitat. Each IDed whale in the SAG was recorded and used in the analyses.

### *Acoustic Monitoring*

Bottom-mounted archival PAM systems were deployed at depths of 140 to 165 m inside the Roseway Basin ATBA, each within 15 km of one another (Fig. 1, Table 2). Pacific Marine Environmental Laboratory (PMEL) pop-up systems (hereafter "pop-up"; Fox *et al.* 2001) were deployed and recorded continuously for 61 d in 2004 and 59 d in 2005 (details in Table 2 and Mellinger *et al.* 2007) with no data for 18–19 August 2005 due to battery replacement. Autonomous multichannel acoustic recorders (AMAR; JASCO Applied Sciences) were deployed in the Basin and recorded data for 30 d in 2014 and 61 d in 2015 (Table 2). The 2014 data had the lowest duty cycle of 8.5 out of 10 min. For the acoustic analyses, the data collected in the other years were down-sampled to match the duty cycle used in 2014 to provide a constant 85% temporal coverage for all years (*e.g.*, for the 2015 recordings, 12.75 min of every 15 min recordings were analyzed). There was a total of 211 d of acoustic records over the 4 yr.

From the 211 d of acoustic records, we isolated 23 d of a daily 15 h period ($d_{15}$; 0530–2030 local Atlantic Time) concurrent with the 23 visuals survey days. This daily period was chosen to liberally encompass daytime between morning and evening nautical twilight during which visual monitoring was conducted. We did not attempt to precisely match the time spans of visual and acoustic effort on any particular day; instead, we assumed that right whales sighted within the ATBA were also available to be recorded by the PAM system; similar to the protocol of Clark *et al.* (2010). This is a good assumption as right whale tonal and broadband sounds can travel up to 30 km in some basin habitats (Laurinolli *et al.* 2003), right whales are mobile, moving as much as 80 km during a 24 h day (Baumgartner and Mate 2005), and the bathymetric feature near the location of the deployed acoustic moorings (the southeastern slope of Roseway Basin,) is known to be an area where the right whale's preferred food source (copepod zooplankton) is concentrated by the oceanographic conditions (Davies *et al.* 2013, 2014). If the

*Table 2.* Deployment details for four bottom-mounted PAM systems deployed in the Roseway Basin Area to be Avoided during 2004, 2005, 2014, and 2015 detailing instrument, sampling rate, duty cycle, deployment period, bottom depth, and geolocation. The Pop-up recorders (Fox *et al.* 2001) were fitted with ITC 1032 hydrophones with nominal sensitivity of −192 dB re 1V/μmPa (Stafford *et al.* 1999). The AMAR recorders were fitted with Geospectrum M8E-V35 hydrophones with a nominal sensitivity of −165 dBV/μPa (±dB within the recording bandwidths)

| Instrument | Recording bandwidth (Hz) | Sampling rate (kHz) | Recording duration (min) | Duty cycle | Deployment period | Depth (m) | Location |
|---|---|---|---|---|---|---|---|
| Pop-up | 30–840 | 2 | None | None | 2 Jul 2004–17 Aug 2005 | 140 | 42°58′00″N 65°03′24″W |
| Pop-up | 30–840 | 2 | None | None | 19 Aug 2005–30 Jun 2006 | 140 | 42°58′00″N 65°03′24″W |
| AMAR | 10–30,000 | 64 | 8.5 | 10 min | 18 Aug 2014–16 Sep 2014 | 140 | 42°58′38″N 65°02′27″W |
| AMAR | 10–3,750 | 8 | 14 | 15 min | 30 Jun 2015–26 Nov 2015 | 165 | 42°56′53″N 65°13′31″W |

vessel observers sighted right whales anywhere within the ATBA, the hydrophone was likely to record that whale if it was producing sounds. In contrast, considering the extent of tonal and broadband right whale vocalizations propagation and the size of the ATBA is ~4,030 $km^2$, whales outside are likely not heard until they are within the ATBA. The entirety of each 15 h period of PAM in each of the 23 d was visually and aurally examined by the lead author using Raven Pro 1.4 software (1.95 Hz frequency resolution using 0.25 s of data (zero padded) for each FFT with 0.125 s advance (Hann Window), no analysis was performed above 1 kHz; Bioacoustics Research Program 2011). All upcalls, gunshots, and moans (Matthews *et al.* 2001, Parks 2003, Vanderlaan *et al.* 2003, Waite *et al.* 2003; see Appendix S2) were classified and annotated. Daily call presence or absence (1, 0) and call counts (number detected) were derived for each call type.

Because we were limited to a relatively small sample size of 23 d of concurrent visual and acoustic monitoring, compared to 211 d of near-continuous PAM among all four years (Fig. 2), we analyzed the full acoustic record to assess how the more complete acoustic data set could expand on right whale occurrence and relative abundance information obtained by visual surveys. For the purposes of this analysis only the upcall was used because it is the most well characterized indicator of right whale presence (*e.g.*, Van Parijs *et al.* 2009). Each of the annual (*y*) series of the full acoustic record (66, 59, 30, and 61 $d_{24}$, respectively) were processed using the low-frequency detection and classification system (LFDCS, Baumgartner and Mussoline 2011) to direct the analyst to upcalls for classification and validation (Appendix S3). Daily PAM indices over the same period (18 August–16 September) among years (Fig. 2) included the number of upcalls $d_{24}^{-1}$ and daily ($d_{24}$) call presence (0,1). To avoid confusion, we refer to "daily" as $d_{24}$ for the 24 h day acoustic record and $d_{15}$ for the 23 intertwilight days used in the concurrent visual and acoustic analysis.

## *Statistical Analysis*

A generalized linear model (GLM) was used to assess how the variation of daily IDed whales explained the variation of the effects of year, presence of SAGs, call counts, and call type (Eq. 1). The whale sightings data were over-dispersed (ratio of variance and mean of the response variation = 16.8 > 1) and thus were modeled with a negative binomial error distribution and a logarithmic link function. The response variable was ID, the number of identified whales, and predictor variables were year, SAG, and call count (detected in 15 h acoustic effort). Sex variables (MPUE and FPUE) covaried with IPUE and were not explicitly tested in the model. Furthermore, the effect of call type could not be tested directly in this model due to data limitations since there were three call count values (one for each call type) per ID. The data were reformatted for the model to allow an interaction effect between call type and call counts to be included, essentially testing if call counts varied among call types (equivalent to an ANCOVA). No other interaction terms were tested, as to limit the number of degrees of freedom. The natural log of daily visual survey effort was included as an offset. The model implemented in R using the glm.nb() function from the MASS library with the full model taking the form:

$$\begin{aligned} \text{ID} \sim \text{Intercept} + \text{Year} + \text{SAG} + \text{call count} + \text{call type} : \text{call counts} \\ + \text{Offset} = \ln(\text{Visual Effort}) \end{aligned} \tag{1}$$

A backwards, AIC-based stepwise model comparison starting with Equation 1 was performed to select the most parsimonious variable combination and tested with an analysis of deviance (based on likelihood ratio test) using the anova() function for glm.nb() in R. Parameter estimates for the covariates and each level of the factors were calculated for the selected model, along with their associated standard errors, $z$-value and $P$-values. Wald chi-squared tests were used to test each individual predictor against the 2-sided alternative hypothesis that their effects on the model were equal to zero, given that all other predictors were in the model, with a significance level of 5%. The model assumes independence of the response variable, accommodation of over-dispersion, and normality of the residuals. Due to the small sample size, assumption conformity was assessed qualitatively and visually (Cameron and Trivedi 1998).

Kruskal-Wallis (K-W) tests were used to assess interannual variation among annual estimates of right whale presence (0,1) and relative abundance (indices of visual surveys; IPUE, and PAM; call counts of each call type). Spearman's rank correlation were calculated to measure the direction and strength of the association between IPUE and each different call types. The demographic and behavioral composition of right whales in Roseway Basin relative to the total number of IDed whales and associated numbers of each sex during visual survey days from 1987 to 2015 were analyzed using a simple linear regression and $t$-test. Analyses were completed using Matlab R2015-b (Mathworks Inc. 2015), R statistical environment (R Development Core Team 2015).

## Results

### *Visual and Acoustic Comparison*

A total of 143 IDed whales were sighted over 13 of the 23 visual survey days across years (3 to 7 $d_{15}$ each year) resulting in the various PUE indices being skewed toward zero (Table 1). The overall annual survey effort (median 9 h/d) resulted in IPUE ranging from 0 to 4 whales/h (median 0.3) with 19 of 23 d with <1 whale/h. A total of 1,787 right whale calls were detected and verified over 15 of the 23 $d_{15}$ monitoring period, of which 61% were upcalls, 26% were gunshots and 13% were moans (Table 1). The various estimates derived from the two independent and concurrent monitoring methods detected whales on 16 of the 23 survey days. Right whales were detected visually on 13 of 23 (57%) d, and acoustically on 12 of the same days plus an additional 3 (65%) of the 23 d (Table 1).

The model revealed significant positive relationships between relative abundance and both call counts and presence of SAG behavior, while the year factor and the call count × call type interaction showed no significant effect and were sequentially removed in the AIC model selection (Table 3; likelihood ratio tests of negative binomial models = 12.011, df = 7, $P = 0.1$). Call counts had a marginally positive influence on the response variable (parameter estimates ± SE = 0.006 ± 0.002, Table 4). In other words, for an increase of one IDed whale in the habitat, the log change in the expected call counts is 0.006, given the other predictor variables in the model are held constant. SAG presence had a much larger positive influence on ID than SAG absence (parameter estimates ± SE = 2.059 ± 0.243), and much larger in comparison to the effect of call count, given that all other parameters were kept constant in the model. Model assumptions were met; whale sightings were independent observations, the negative-binomial error distribution of the selected model accounted for the over-dispersion of the whale sightings data as evidenced by a residual deviance less than −2 × log likelihood (residual deviance = 90.292, df = 66, −2 × log-likelihood = 293.011; Crawley 2007), and a single error term describes the negative binomial error structure as can be observed from the typical negative binomial J-shape on the normal QQ plot of the selected model (Appendix S5, Fig. S2). The residuals plotted against the fitted values of the selected model show that the residual values near zero on the *x*-axis are negative, which is caused by zero-inflation of the response and predictor variables implemented in the model (Appendix S5, Fig. S2).

*Table 3.* Results of performed AIC-based stepwise model comparisons to select the most parsimonious variable combination for the negative binomial Generalized Linear Model. The response variable of the full model was ID, the number of identified whales detected in the survey day, and predictor effects were years (Yr; 2004, 2005, 2014, 2015), presence of SAGs (1, 0), and call counts (Continuous; detected in 15hr acoustic effort). An interaction effect between call type (upcall, gunshot, moan) and call counts was included. Because the daily visual survey effort varied, its natural log was included as an offset in the model. AIC and deviance changes are presented with every omitted nonsignificant term

| Model | AIC | Deviance |
|---|---|---|
| ID ~ year + SAG + Call Count * Call Type + offset[log(Visual Effort)] | 301.00 | 96.341 |
| ID ~ year + SAG + Call Count + Call Type + offset[log(Visual Effort)] | 300.68 | 93.076 |
| ID ~ year + SAG + Call Count + offset[log (Visual Effort)] | 299.76 | 90.354 |
| ID ~ SAG + Call Count + offset[log(Visual Effort)] | 299.01 | 90.292 |

*Table 4.* Parameter estimates (scaled to the log link function) of the most parsimonious negative binomial Generalized Linear Model (Table 3). The response variable was ID, the number of identified whales detected in the survey day and predictor effects were presence of SAGs (1, 0), and call counts (Continuous; detected in 15 h acoustic effort). Because the daily visual survey effort varied, its natural log was included as an offset in the model. Model form was ID ~ SAG + call count + offset[log(visual effort)]

| Parameter | Estimates | SE | *z* | *p* |
|---|---|---|---|---|
| (Intercept) | −1.558 | 0.135 | −11.472 | <0.001 |
| [SAG = 1] | 2.059 | 0.243 | 8.461 | <0.001 |
| Call counts | 0.006 | 0.002 | 3.423 | <0.001 |
| Null deviance: 236.458 on 68 df | | | | |
| Residual deviance: 90.292 on 66 df | | | | |
| Theta: 2.62 | | | | |
| SE: 1.25 | | | | |
| 2 × log-likelihood: −293.011 | | | | |

## *Annual Variation*

Acoustic monitoring over 211 $d_{24}$ showed that right whale presence was relatively high in Roseway Basin during August–September of all 4 yr (Fig. 3, 4b). Right whale upcalls were present on 97%, 81%, 71% and 85% of days ($d_{24}$) in 2004, 2005, 2014, and 2015, respectively (Fig. 3). Average

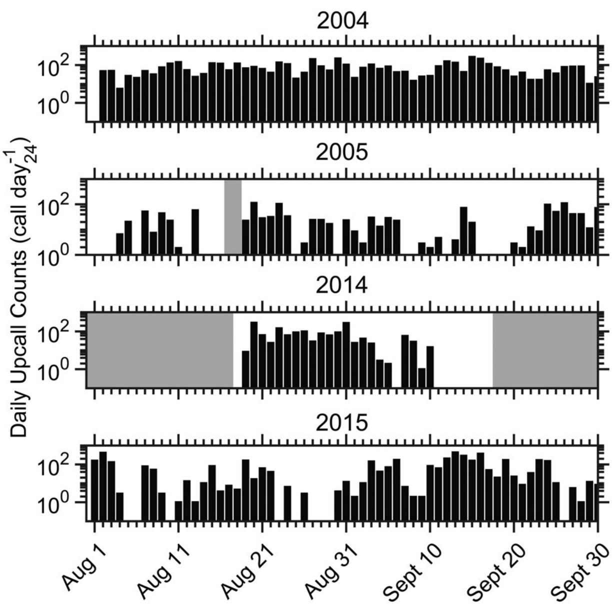


*Figure 3.* Time series depicting inter- and intra-annual variability in validated (low-frequency detection and classification system, LFDCS; Baumgartner and Mussoline 2011) right whale daily upcall counts spanning the August–September period of 2004, 2005, 2014, and 2015.

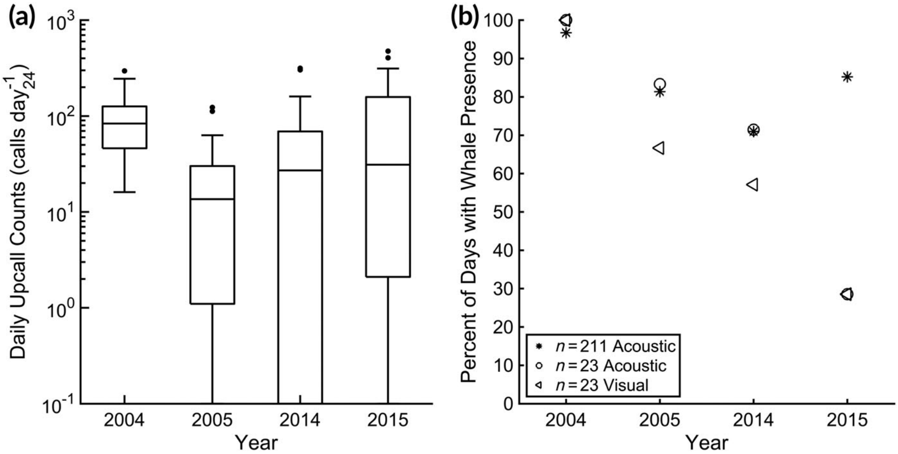


*Figure 4.* (a) Boxplots depicting interannual variation in daily upcall counts recorded 19 August through 17 September 2004, 2005, 2014, and 2015 ($n$ = 211) in Roseway Basin where the lines indicate the 1st, 2nd (median) and 3rd quartiles and whiskers the maximum excluding outliers (solid circle, 3/2 times the upper quartile; included in the analyses), (b) estimates of daily right whale presence derived from data of three monitoring methods; the full acoustic record ($n$ = 211 d), and the concurrent acoustic and visual surveys ($n$ = 23 d).

daily upcall counts were significantly higher in 2004 than in other years (K-W; $\chi^2$ = 23.2, $P$ < 0.001; Fig. 4a). In contrast, a declining trend among survey years was apparent in several of the acoustic and visual indices collected during the 23 d of concurrent monitoring (2004 > 2005 > 2014 > 2015, Fig. 4b). The annual percentage of survey days when IDed whales were visually observed declined sequentially in each year from 100% to 66%, 57%, and 29%, respectively. Similarly, the annual percentage of the 23 $d_{15}$ containing any calls generally decreased each year from 100% to 86%, 71%, and 29%, respectively. This apparent trend is likely an artifact of low sample size (Fig. 4b). Daily counts of gunshots and moans were each higher in 2004 than other years (K-W; $\chi^2$ > 8.33, $P$ < 0.03), whereas we failed to find differences in upcall counts among years.

### *Variation in Right Whale Acoustic Presence by Call Type*

The three right whale call types each provided different estimates of acoustic presence at daily and hourly scales, over the 23 $d_{15}$ analyzed. The distribution of daily call counts by type (highly skewed toward zero) were different (K-W, $P$ = 0.022) with medians of 14, 1, and 0 calls/$d_{15}$ for upcalls, gunshots, and moans, respectively over all years (Table 1). Upcalls were detected on 65% of survey days, gunshots on 53% and moans on 30%, suggesting upcalls are the best indicator of whale presence, followed by gunshots. All three call types were positively correlated with IPUE, and the correlation with gunshots was at least 13% higher than upcalls or moans (Spearman's rank correlation, gunshots *rho* = 0.86; upcalls *rho* = 0.73; moans *rho* = 0.58, $P$ < 0.005). Over all hours manually

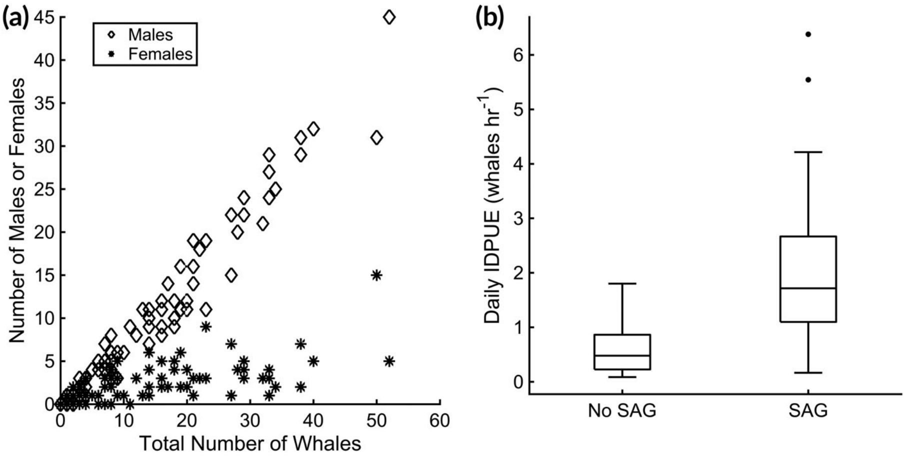


*Figure 5.* (a) Number of female (asterisk) and male (diamond) right whales sighted in Roseway Basin during all survey days over the period 1987 through 2015 and (b) boxplots depicting daily IPUE whales when surface-active groups (SAG) were observed compared to not observed in Roseway Basin during all survey days over the period 1987 through 2015.

validated in the Basin across years (345 h), right whales were acoustically present during 72 h. Ninety percent of these 72 h contained upcalls, whereas 57% contained gunshots, most of which (75%) also contained upcalls, and 27% contained moans (Table S1). Moans were never recorded in the absence of upcalls. We failed to find a difference in the gunshot to upcall ratio between SAG days and non-SAG days (K-W, $P$ = 0.05) suggesting that the call-count ratio did not change when SAGs were present in the habitat.

### *Variation in Demographics and Behavior*

High whale densities in Roseway Basin cooccurred with SAG behavior and increasing densities of male whales (Table 1). SAG behavior was observed on three of 3 d in 2004 and one of 7 d in 2014 for which the number of SAGs observed ranged from 1/d to 6/d between the 2 yr, and the number of IDed whales in each SAG ranged between 2 and 19. No SAG behavior was observed in 2005 and 2015. Although MPUE and FPUE were rank correlated ($rho$ = 0.54, $P$ = 0.007) there were typically more males than females per unit effort across all years by a factor of ~2.5 (Table 1).

SAGs usually occurred when IPUE was high, but the sample size was too small to be conclusive, so to further study the correlation between IPUE and SAGs we examined the entire time series of intermittent monitoring data (1987–2015). To address this, we examined the demographic and behavioral composition of right whales in the habitat relative to the total number of IDed whales and numbers of each sex during all visual survey days from 1987 to 2015 (Fig. 5). Most of the daily variation in ID was driven by number of males and not females (slope = 0.72 and 0.12

respectively, Fig. 5a). Further, the daily number of ID whales was higher when SAGs were observed compared to not observed (*t*-test, $P < 0.001$; Fig. 5b). This suggests that males dominate the habitat and that SAGs are more likely to occur when whale densities are high.

## Discussion

Our primary goal was to determine how acoustic indices of the right whale occurrence in Roseway Basin are related to visual survey indices of right whale presence, relative abundance, demographics and behavior at daily and interannual time scales and what inferences might be made about whale presence and relative abundance from PAM. This is one of few studies that have investigated the relationship between right whale relative abundance indices derived from visual and acoustic monitoring at a known habitat scale (see also Clark *et al.* 2010, Matthews *et al.* 2014). The model demonstrates the existence of a positive relationship between call counts and relative abundance in Roseway Basin during the August–September period. The presence of SAG behavior occurred on survey days with increased call counts. Variation among years and among different call types likely had no effect on this relationship. The results demonstrated that acoustic presence was high and persistent in all four years – higher than indicated by visual presence. The acoustic data were also temporally extended well beyond that which could be inferred from limited visual monitoring. Overall, our study demonstrates that useful information about right whale relative abundance and habitat use can be derived from PAM in Roseway Basin and may have applications in other areas where visual monitoring is limited. A few caveats to note; the relationships between visual and acoustic monitoring estimates have large confidence limits and should be interpreted with a degree of caution. Only relative abundance is addressed in this study, as opposed to absolute whale abundance, which would require a confident understanding of the changes in visual detection probabilities. Further, the acoustic data was collected from two different recording systems which could have caused differences in acoustic detections.

The GLM showed no evidence that call type had an effect on right whale abundance, implying that gunshots, upcalls or moans can equally well be used to predict relative whale abundance in Roseway Basin. However, there was a relatively stronger correlation between gunshots and IPUE than other call types, which suggests that gunshots may be the best choice for this application. We hypothesize that the cumulative effect of increasing number of animals present, the number and size of aggregations (through SAG behavior) and the number of males contribute to a relatively stronger correlation between gunshots and IPUE compared to other call types. This is based on the fact that gunshot production increases with SAG-size (Matthews *et al.* 2001), that gunshots are possibly produced solely by males (Van Parijs *et al.* 2009, Parks and Tyack 2005, Parks *et al.* 2011), and that the variation in abundance in Roseway Basin is primarily driven by variation in the male demographic (Fig. 5). While gunshots may be best for estimating relative abundance in Roseway Basin, upcalls are adequate for estimating presence. Both upcalls and gunshots were good indicators of right whale presence in Roseway Basin, whereas moans were not. Since the detection of certain calls may be influenced by the propagation properties of different call types and the production of calls may vary among the behavior and habitat of the whale (Van Parijs *et al.* 2009), using upcalls for estimating right whale presence facilitates comparison across a range of habitats and conditions (*e.g.*, Davis *et al.* 2017). Therefore, deciding what call type to use when comparing relative abundance and call counts is indeed important and may vary differently in habitats other than Roseway Basin.

We considered alternate reasons to explain why the presence of SAGs had an effect on how many animals were sighted in the Roseway Basin habitat. This may occur because the animals have more opportunity to engage in social behavior when high densities of animals are present in the habitat. Density estimates derived from visual surveys may also be biased by the presence of animals aggregated in SAGs that are more likely to be visually detected than lone individuals dispersed across the habitat, though the densities may be the same in both cases. The latter explanation seems less likely because the survey teams appeared capable of effectively monitoring the whales across a range of SAG-sizes within and among days when SAG-size was highly variable. For example, on 20 Sep 2014, 24 IDed whales were sighted among 27 separate sightings along the survey track, including SAGs all in group sizes of one (others not identified) to 3 IDed whales. In contrast, on 22 September 2004, 23 IDed whales were sighted among 10 separate sightings along the survey track, wherein 18 IDed whales were associated with a sole SAG; all other sightings observed along the track were either one or to two IDed whales.

The variable nature of right whale occupancy in Roseway Basin and the small sample size restrictions of visual survey effort, together, make statistical evaluation of right whale intra- and interannual habitat occupancy patterns uncertain in this habitat. In this study, small sample sizes from visual surveys resulted in an apparently spurious decline in occupancy in late summer that was not apparent when the long-term acoustic data sets were compared. Given the high intra-annual variation in both the acoustic and visual estimates, it is reasonable to ask at what confidence level a sample size of 3–7 d of visual survey effort per year (typical range for Roseway Basin surveys) can yield robust annual estimates of whale presence and relative abundance measured either visually or acoustically. Using a simple statistical approach (Appendix S4) we demonstrate that the annual estimates of right whale acoustic presence derived from small sample sizes are highly uncertain (falling within 42% of the "true" mean), and persistent monitoring over at least several weeks (>21 survey days over the August–September period) would be required to detect the "true"' interannual variation in summertime occurrence with reasonable confidence. Presumably this result would similarly apply to visual survey data, which are comparably distributed and have similar high intra-annual variation as seen among the acoustic records. This finding has implications not only for interpreting historical occupancy trends and variations that are based solely on the limited visual surveys, it also argues well for the wealth of seasonal occupancy information provided using PAM that is far less temporally limited.

Over the past three decades, several inferences have been drawn about interannual variation in right whale occupancy of Roseway Basin based on sparse visual surveys and the inferences (*e.g.*, abandonments, propensities of males, habitat fidelity, extrahabitat transitions) have perpetuated in the literature despite the sparse nature of the data (Hamilton *et al.* 2007, Batten and Burkill 2010, Patrician and Kenney 2010, Van der Hoop *et al.* 2012, Brillant *et al.* 2015, Davies *et al.* 2015*b*). Although Roseway Basin is monitored as one of the right whale Critical Habitats, along with others such as Grand Manan Basin, the efforts spent in Roseway is far more limited than Grand Manan. However, there remain the above inferences of reduced habitat occupancy since 2010 (Pettis and Hamilton 2016) and the apparent abandonment in several years prior to, *e.g.*, 1993, 1994, 1996–1999 (Brown *et al.* 2001). Our analyses indicate there is no strong evidence of substantial changes in the occupancy of Roseway Basin in 2014 or 2015 in spite of low visual sightings, leaving us also skeptical of "abandonment" in the earlier years when visual survey effort was anomalously low. The only solution is an increased sampling frequency, and the most logistically feasible and economically viable option available to achieve that is PAM.

*Implications for Monitoring*

For conservation management purposes, right whale monitoring priorities have been to determine (1) when and where the whales are present in relatively well-known habitats, (2) estimate the number of animals, and (3) collect photographic and biopsy data used for individual identification and population health monitoring purposes (Clark *et al.* 2010). Here, we have demonstrated that daily upcall and gunshot counts were reasonable indicators of whale presence and relative abundance at daily, seasonal, interannual, and habitat scales in Roseway Basin. The results demonstrate that the use of a single hydrophone can be beneficial, with a quantified degree of uncertainty, to address the first two priorities in the absence of visual surveys in the Basin and, perhaps most importantly, to extend right whale monitoring beyond the temporal limitations of visual surveys. This could be instrumental in providing the additional needed knowledge to address management and conservation issues that have been of particular interest since 2010 when shifts in summertime right whale habitat use has been noted based on visual surveys and acoustic monitoring (KTAD, personal observation; Pettis and Hamilton 2015, Pettis et al. 2017, Davis *et al.* 2017).

In addition, the kinds of analyses and ensuing results we have presented above can also be of considerable value in planning and executing near real-time monitoring efforts using fixed and mobile PAM systems (*e.g.*, Baumgartner *et al.* 2013) that in themselves can be further used to optimize visual survey effort. In particular, upcalls have been widely used in PAM studies across several habitats using archival and near real-time data (Mellinger *et al.* 2007, Parks *et al.* 2009, Clark *et al.* 2010, Baumgartner and Mussoline 2011, Davis *et al.* 2017). Thus, it may be optimal to use upcalls to estimate relative abundance in some situations or habitats and potentially gunshots in others. If detecting right whale presence is the primary goal—for example across habitats throughout the right whale migratory range—the consensus appears to be that upcall assessment is the preferred and most efficiently detected call type to use (*e.g.*, Van Parijs *et al.* 2009; Parks *et al.* 2011, 2012; Davis *et al.* 2017). However, to derive additional information from PAM data, such as habitat-specific whale abundance indices, demographics and behavior, it is important to further develop software that effectively and efficiently detects other call types such as the gunshot (Parks *et al.* 2011, 2012) that could be essential in relation to SAG activity (Parks *et al.* 2007) and may be of use in searching for, and diagnosing, the function(s) of other potential habitats in Canadian waters.

In light of the endangered status of the right whale and the recent elevated concerns arising from high mortalities observed in Canadian waters in the summer of 2017 (at least 16 mortalities in Canadian waters between 2015 and 2017; Daoust *et al.* 2017) monitoring the species' behavioral and demographic variability in different habitats is critical in understanding the changes in their population. Such population monitoring could be considerably advanced through persistent PAM if inferences can be reasonably made about whale occurrence and relative whale abundance. By demonstrating the existence of a relationship from which such inferences could be made, the current research is a necessary stepping-stone to further optimize limited monitoring resources as well as conservation initiatives among known and unknown right whale habitats.

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## Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12602/suppinfo.

*Figures S1A–E.* Bathymetric charts showing each daily visual survey-day track-lines (dotted) in the Roseway Basin Area To Be Avoided (ATBA; polygon) and locations of IPUE whales (solid symbol) in 2004 (I–III), 2005 (IV–IX), 2014 (X–XVI) and 2015 (XVII–XXIII). XXIV Area of the Roseway ATBA covered by visual survey effort with mean (dashed line) and median (dotted line).

*Figure S2.* Residuals against fitted values from the model (left) and normal QQ plot (right) the minimal adequate GLM used in the analysis.

*Appendix S1.* The spatial distribution of effort within Roseway Basin ATBA.

*Appendix S2.* Classification of three right whale vocalizations; upcalls, moans, and gunshots.

*Table S1.* Pairwise comparison matrix of number of hours (15/d) during which combinations of upcalls, gunshots and moans and total calls per type recorded where calls were detected for a total of 72 h over the 23 d of monitoring.

*Appendix S3.* A brief description of the low-frequency detection and classification system (LFDCS).

*Appendix S4.* The annual estimates of right whale acoustic presence statistically derived from small sample sizes.

*Appendix S5.* Assessment of model assumption; independence of the response variable, accommodation of over-dispersion, and normality of the residuals.