Research

Temporal variation in the vocal behaviour of southern right whales in the Auckland Islands, New Zealand

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Autonomous recorders are frequently used for examining vocal behaviour of animals, and are particularly effective in remote habitats. Southern right whales are known to have an extensive acoustic repertoire. A recorder was moored at the isolated sub-Antarctic Auckland Islands for a year to examine whether the acoustic behaviour of southern right whales differed seasonally and throughout the day at their main calving ground in New Zealand. Recordings were made in each month except June, and vocalizations were audible in all months with recordings except January. A total of 35 487 calls were detected, of which *upcalls* were the most common (11 623). Call rate peaked in August (288 ± 5.9 [s.e.] calls/hour) and July (194 ± 8.3). Vocal behaviour varied diurnally with highest call rates detected at dusk and night, consistent with the concept that *upcalls* function primarily as contact calls. Zero-inflated model results confirmed that seasonal variation was the most important factor for explaining differences in vocal behaviour. An automated detector designed to expedite the analysis process for North Atlantic right whales correctly identified 80% of *upcalls*, although false detections were frequent, particularly when call rates were low. This study is the first to attempt year-round monitoring of southern right whale presence in New Zealand.

1. Background

Animals vary their behaviour in response to a wide range of factors, including changes in light levels [1], availability of prey

[2], predation pressure [3,4] and weather conditions [5,6]. Similarly, vocal behaviour of many animals changes temporally. For example, terrestrial species, such as wolves (Canis lupus [7]) and many temperate and tropical bird species [8], exhibit diurnal variation in vocal activity with higher call rates during the late evening and dawn. The drivers of temporal variation in vocal behaviour can be difficult to determine, but may relate to optimal ambient noise and propagation conditions [9], energy reserves [10], predation risk [11] or sociality [8,12]. The calling activity of frogs [13] and some insects [14,15] is correlated with precipitation and temperature.

Marine mammals in general, and cetaceans in particular, are highly vocal, relying on sound for communication [16], navigation [17] and feeding [18]. Consequently, the occurrence of species-specific vocalizations can reveal information about a species' presence. For example, in the Gulf of Alaska, echolocation clicks made by sperm whales (Physeter macrocephalus) are detected more often in summer than in winter, consistent with known seasonal migration of reproductive males from productive high latitudes in summer, to the lower latitudes favoured by breeding females in winter [19]. Vocalization types and rates can change over short timescales (hours/days) or longer monthly or seasonal timescales revealing details of a species' behaviour. Blue whales (Balaenoptera musculus) from the eastern tropical Pacific show higher vocalization rates between February and June–thought to be associated with their foraging behaviour which is also highly seasonal [20]. Diel changes in acoustic behaviour have been observed in both mysticetes [21,22] and odontocetes [23,24]. For example, sound pressure levels of vocalizations of wintering humpback whales (Megaptera novaeangliae) off Maui increase at sunset, remain relatively high through the night and progressively decrease from sunrise [25]. Vocal behaviour can also be used to infer the level and type of activity that an animal is engaged in. Elevated echolocation rates and buzzes (associated with feeding) indicate that foraging at night is the norm for several odontocete species, including harbour porpoise (Phocoena phocoena [26]), finless porpoise (Neophocoena asiaorientalis [24]) and Risso's dolphin (Grampus griseus [23]).

Passive acoustic monitoring (PAM) has become an increasingly important research tool, particularly for documenting a species' presence [19,21] and how vocal behaviour changes with time [20]. For example, autonomous recording systems used to detect species-specific calls and monitor temporal variation in vocal behaviour have been fundamental to the establishment of protection measures for North Atlantic right whales (NARWs, Eubalaena glacialis) in and around shipping lanes [27]. Typically, passive acoustic detection and localization of right whales uses upcalls [28,29] which are the most common call type [30–32], and are produced by both males and females [33,34]. PAM is increasingly used to monitor right whales, particularly in remote regions or those with inhospitable weather conditions [35–37]. Consequently, automated detection systems [28] have been developed to facilitate processing the large quantities of data produced by PAM.

Southern right whales (SRWs, Eubalaena australis) have a circumpolar distribution in the Southern Hemisphere, with major breeding populations in South Africa, Argentina, Brazil, Australia and New Zealand. SRWs were hunted to the brink of extinction in New Zealand [38], but since the cessation of whaling the population has grown at an estimated 7% resulting in a recent abundance estimate of 2169 (95%: 1836–2563) [39]. For other SRW populations mainland calving grounds mean that they are easily observable. SRWs in New Zealand only calve in the remote sub-Antarctic Auckland Islands, so we know very little about distribution and behaviour through the year. Most knowledge of the behaviour of SRWs in New Zealand comes from visual surveys and observations at the sub-Antarctic Auckland Islands [40–43]. Right whales are the only cetacean species known to be regularly present in Auckland Island's waters [44] and arrive there each winter to calve from offshore feeding grounds [40]. Non-breeding whales are also present, potentially due to social factors [43]. Practical constraints restrict the duration of research expeditions to these remote islands; beyond a wintertime window of up to eight weeks [41] little is known about how or when right whales use this habitat. The vocal repertoire of SRWs at the Auckland Islands has received attention recently [45], but we do not know how long SRWs are present in this habitat or how their vocal behaviour varies over time. Given the limitations of the remote location and inclement weather conditions in the sub-Antarctic, autonomous acoustic recorders [46] present a robust tool for understanding the seasonal and diurnal calling behaviour of SRW.

This research addressed three specific questions: (1) what is the seasonal variation in the presence of whales at the Auckland Islands as revealed by autonomous acoustic recorders, (2) how do call rates and types vary temporally, both seasonally and diurnally and (3) how effectively does an automated upcall detector developed for North Atlantic right whales [29] perform for this population of whales?
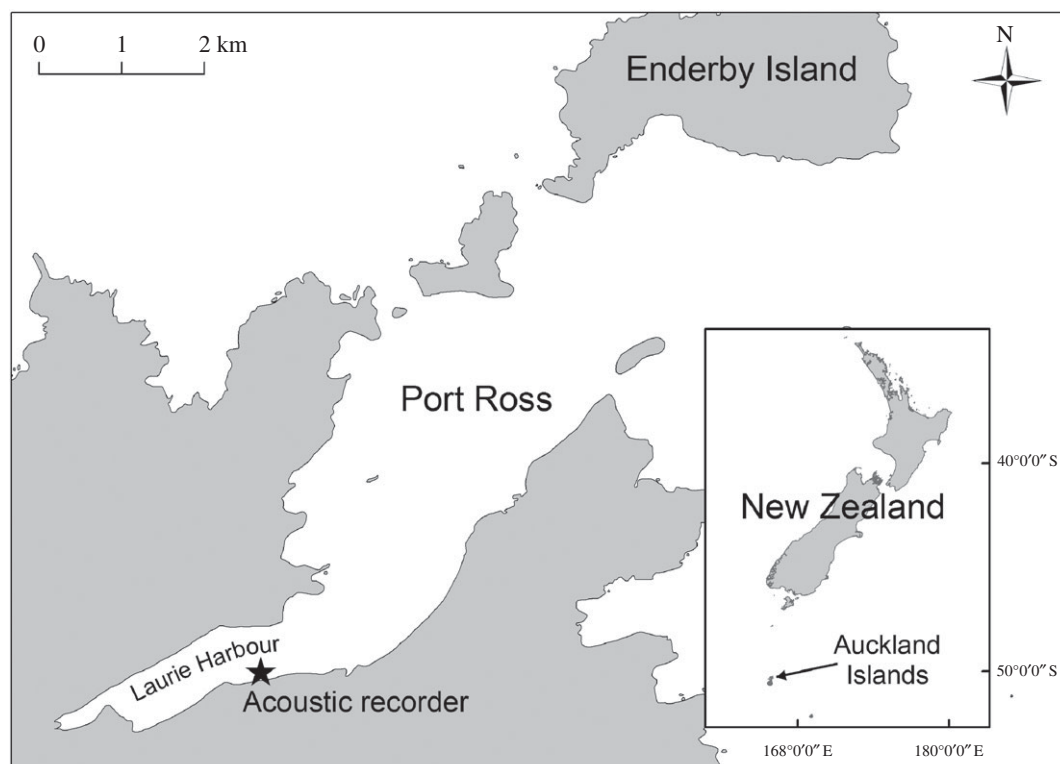
Figure 1. Location of the DSG-Ocean recorder for southern right whale vocalizations in Laurie Harbour, Port Ross, sub-Antarctic Auckland Islands.

2. Methods

2.1. Data collection

Recordings were made using a DSG-Ocean autonomous recorder (Loggerhead Instruments, USA, www.loggerhead.com) moored in Laurie Harbour in Port Ross, a large, sheltered harbour at the northern end of the Auckland Islands (figure 1), where SRWs occur at highest densities [42]. The deployment location, in the upper reaches of Port Ross (50°33.4′ S, 166°12.3′ E) was chosen for its physical characteristics: shallow depth (16–20 m), flat and sandy seabed, shelter from prevailing swells and minimal risk of fouling due to vessels anchoring.

The DSG-Ocean is a digital recorder with a single HTI-96-MIN hydrophone (sensitivity: −185.6 dBV/μPa, frequency response: 20 Hz–50 kHz ± 3 dB) and programmable sampling rate and recording schedule. DSG-Ocean recorders have been used extensively for acoustic studies on fish [47–49] and are increasingly used for marine mammal research [50].

A compromise between sampling rate and recording schedule was required to maximize data quantity, given limited battery power, over an extended deployment period. A trial deployment was made between 22 July and 1 August 2011 to verify that the recorder worked and assess the practicality of the mooring system. During the test period, the DSG-Ocean recorded at a default sampling rate of 50 kHz, recording for 2.5 min every 30 min. The first long-term deployment was from 6 August 2011 to 27 July 2012. The recorder was set to a sampling rate of 4 kHz (covering the vocalization range of this species), recording for 3.75 min every 30 min (i.e. a 12.5% duty cycle).

The mooring system was designed without surface buoys or trailing lines to minimize entanglement risk. The recorder was attached via a 1 m length of 5 mm nylon line (designed to break in the event of an entanglement) to an approximate 50 kg steel mooring weight on the seabed. A second mooring weight was connected to the first via 40 m of negatively buoyant 16 mm nylon rope. The weights were deployed so the rope stretched taut along the seabed. A flotation collar attached to the top of the PVC housing of the recorder ensured that it remained upright during deployment. The recorder was retrieved by snagging the line between the two moorings with a grapnel and winching it on board.
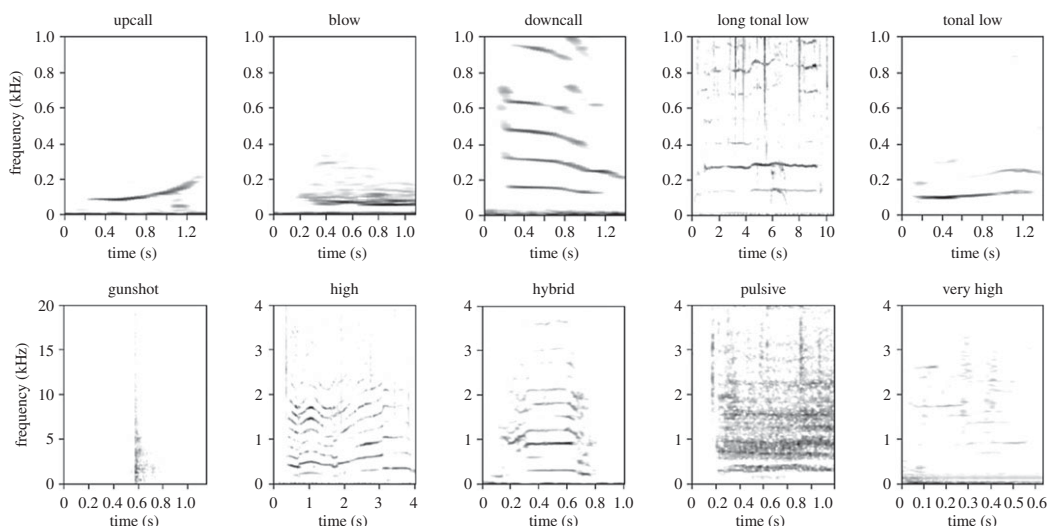
Figure 2. Spectrograms of 10 vocalization types assigned to southern right whales at the Auckland Islands. N.B.: time and frequency scales differ for some spectrograms. Long tonal low calls are a minor component of the vocal repertoire and have been included here for completeness, although they did not feature in the recordings analysed in this manuscript.

2.2. Manual vocalization detection

Acoustic data were first analysed manually using RAVEN PRO v. 1.5 (Bioacoustics Research Program, Cornell University, www.birds.cornell.edu). All SRW vocalizations in each of the recordings were highlighted and counted regardless of signal-to-noise ratio. Each vocalization was assigned to one of nine types (*upcall*, *downcall*, *gunshot*, *high*, *pulsive*, *tonal low*, *very high*, *hybrid* or *blow*; figure 2) based on a previously determined quantitative classification system described in a concurrent study of this population [45].

2.3. Automated vocalization detection

All acoustic recordings were also examined using an automated detector [29] in the eXtensible BioAcoustic Tool (XBAT [51]) written in MATLAB (The Mathworks Inc., MA, USA). The automated call detection algorithm is specifically designed to detect *upcall* vocalizations produced by NARWs [31]. The XBAT detector was set at a correlation threshold of 0.4, a value typically used for detections of NARW calls. Acoustic similarity between a call template and possible *upcall* events was assessed using a Generalized Likelihood Ratio Test based scheme, and all events exceeding this threshold were logged.

2.4. Verification of detector results

Manual and automated detections were compared in order to test the effectiveness and sensitivity of the algorithm for detecting SRW *upcalls*. We randomly selected 10% ($n = 1443$) of the total number of recordings for verification analysis which included representation of each month. Each recording was reviewed in XBAT using the *event palette* to display all detection events logged by the detector. The detection events were then annotated as either true or false *upcall* detections based on the manual classification.

Two measures of detector performance were applied [52]. The first (Positive Predictive Value; PPV) represents the percentage of the *upcalls* logged by the detector that were judged by the human analyst to have been correctly assigned, and the converse accounted for false positives. The second measure (True Positive Rate, TPR) is the percentage of *upcalls* detected by the analyst also logged by the detector, and the converse enabled estimation of false negatives.

Deviation of the automated detections from the number of manually detected *upcalls* was examined using regression. In this context, the slope of the fitted line indicated bias (1 : 1 = zero bias), while the fit of the line indicated the consistency of assignment.

2.5. Statistical analyses

Acoustic recordings were examined for any seasonal or diel patterns in vocalizations. Data on the timing of sunrise, sunset, transit time and nautical dusk/dawn at Port Ross were obtained from Land Information New Zealand (LINZ, www.linz.govt.nz). Transit was defined as the maximum altitude of the sun relative to the horizon. Nautical twilight was defined as the period between nautical dawn (or dusk), when the sun is 12° below the horizon, and sunrise (or sunset). Each acoustic recording was assigned to one of five diel periods: dawn (nautical dawn to sunrise), morning (sunrise to transit), afternoon (transit to nautical dusk), dusk (sunset to nautical dusk) and night (nautical dusk to nautical dawn). The duration of each diel period varied between season, with longer daylight hours in summer (mid-summer: dawn ≈2 h, day ≈14 h, dusk ≈2 h, night ≈6 h) than winter (mid-winter: dawn ≈1.5 h, day ≈8 h, dusk ≈1.5 h, night ≈13 h). Recordings were also classified by season; December to February was defined as Summer, March to May as Spring, June to August as Winter and September to November as Autumn.

All statistical analyses were carried out in R v. 3.0.2 (R Development Core Team 2004, www.R-project.org). To assess seasonal and diel variation in vocal behaviour, hourly calling rates (all calls) and hourly *upcall* rates were calculated from the manual call appraisal. Diel patterns were examined by comparing rates during hour-long time bins based on local time (e.g. 00.00–01.00, 01.00–02.00) and diel periods (dawn, morning, afternoon, dusk, night). Call rates were adjusted to correct for the variation observed during the year in terms of total number of calls detected each day, i.e. to remove any influence of times with very high call rates. The corrections were calculated by subtracting the overall calling rate (calls/h^{-1}) for each day from the hourly calling rate within a particular period (e.g. hour or diel period) [53–55]. This correction resulted in a mean adjusted call rate, where positive values indicate an above average (and negative a below average) rate during a particular time period allowing for seasonal variation in the total number of calls detected. A Zero Inflated Model (ZIM) with a negative binomial distribution was used to evaluate whether particular seasons and/or diel periods were important for explaining differences in right whale call presence and call rate. A ZIM is a two component mixture model [56] and was used in preference to a Generalized Linear Model (GLM) because it accounted for the false zeros which may have been present due to whales being absent from the study area [57]. The two components are a binomial GLM which models the probability of obtaining a false zero, and a negative binomial GLM which models the count data [57]. A log-likelihood ratio test [58] was used to determine whether a poisson or negative binomial distribution best fitted the count data.

3. Results

The acoustic recorder was deployed at the Auckland Islands for 347 days from 22 July 2011 during which there were a total of 302 recording days (80.5% of deployment days), resulting in 892 h of acoustic data. No recordings were made after 24 May 2012 when the batteries ran out.[1] The recorder was out of the water from 2 to 5 August 2011 inclusive. A total of 35 487 right whale calls were manually detected during the deployment period.

3.1. Seasonal variation

Right whale vocalizations were detected in all months with recordings except for January. Vocalization rates varied dramatically during the deployment period (figure 3) and showed a strong seasonal trend. Vocalization rates were highest in the austral winter (219 ± 4.9 calls h^{-1} ±s.e.) and lowest during the summer (0.2 ± 0.06). A similar seasonal pattern was evident when *upcalls* were examined separately (figure 3).

The months with the highest call rates were August (288 ± 5.9 calls h^{-1}) and July (194 ± 8.3). Mean vocalization rates remained relatively high in September (91 ± 3.6) before declining through October (27 ± 7.2) and November (6 ± 0.7). No calls were observed in January and although calls were detected in December, February, March and April, the mean rate was very low (less than 1 call h^{-1}). The vocalization rate increased sharply in May (41 ± 2.9).

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[1]There were two minor gaps in data due to software bugs. Recordings were skipped between 01.30 and 03.00 on 25 September 2011 due to daylight saving, and the entire day on 1 March 2012 due to a leap year.
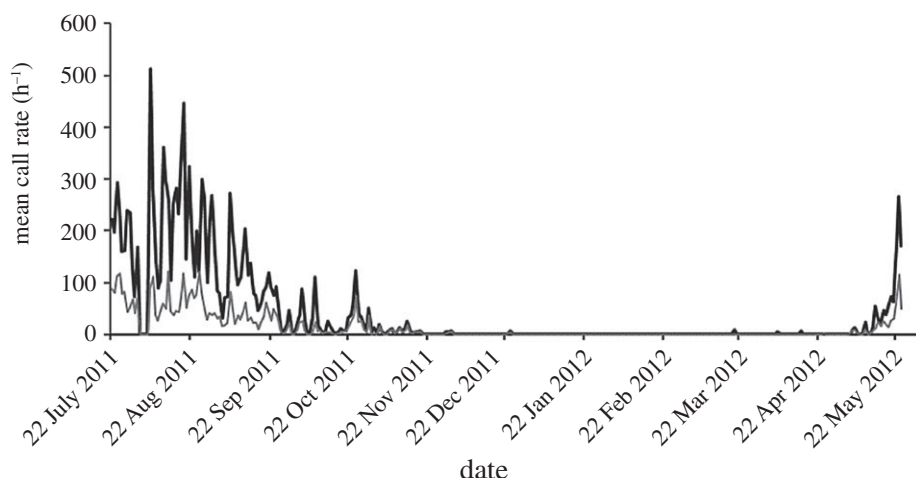
Figure 3. Mean number of all calls (black) and *upcalls* (grey) per day for southern right whales at the Auckland Islands. N.B.: no data were collected from 2 to 5 August 2011 (inclusive).
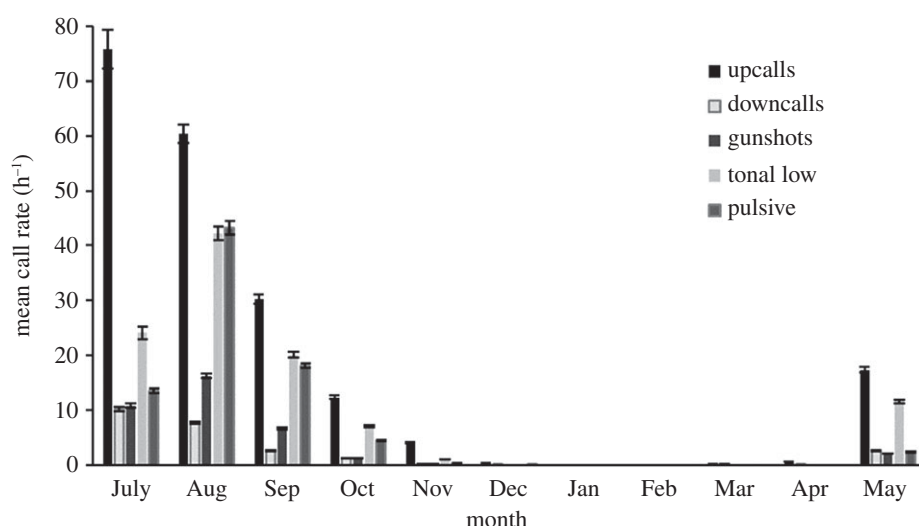

Figure 4. Mean call rate (calls h^{-1} ± s.e.) for the five most common call types (*upcall, downcall, gunshot, tonal low* and *pulsive*) in each month for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

Upcalls were evident in all months that vocalizations were detected and *upcall* rate followed a broadly similar trend to all vocalizations (figure 3). *Upcalls* were the most prevalent of the vocalization types, 11 623 (33%) of all of the calls detected. These vocalizations typically accounted for a smaller proportion of calls, 30–40%, between July and October when the overall call rate was high, and rose to 93% in April and 100% in February when vocalization rates were low. Mean *upcall* vocalization rates were highest in July (76 ± 4.1 calls h^{-1}) and August (60 ± 2.2).

Other vocalization types (*downcall, gunshot, high, hybrid, very high* and *blow*; [45]) were recorded much less frequently than *upcalls,* and in some months not at all (particularly during summer). Collectively, however, these vocalization types accounted for 67% of the total calls observed. *Hybrid, high* and *gunshot* vocalizations exhibited similar patterns of seasonal presence and were completely absent between December and April. *Very high* calls were only detected during a four-month period between July and October and at very low levels (less than 1 call h^{-1}). Seasonal patterns in vocal behaviour of SRWs for the five most abundant call types (*upcall, tonal low, pulsive, downcall* and *gunshot*) showed that call rate for each call type was highest during winter months and lowest during summer months (figure 4). The proportion of the five most abundant call types, however, varied little over the year; *upcall* rates were highest, then *tonal* and *pulsive* calls, and *gunshots* and *downcalls* were always the lowest (figure 4).
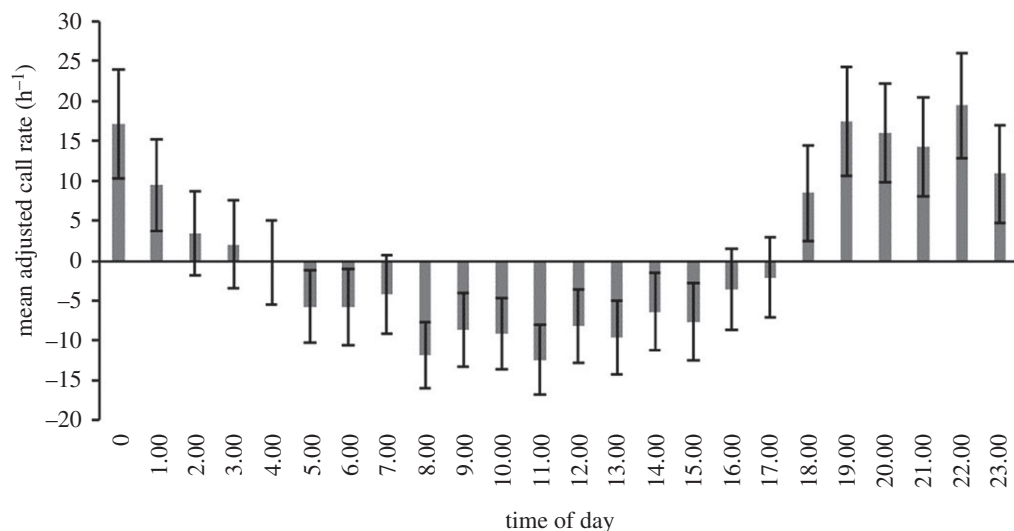
Figure 5. Mean adjusted hourly vocalization rate (calls h^{-1} ± s.e.) for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. Rates are adjusted to compensate for variation in call rate throughout the year. Positive values indicate an above average rate and negative values indicate a below average rate.

Figure 6. Mean adjusted call rate (calls h^{-1} ± s.e.) per diel period for southern right whales recorded at the Auckland Islands between July 2011 and May 2012. Rates are adjusted to compensate for variation in call rate throughout the year. Positive values indicate an above average rate and negative values indicate a below average rate.
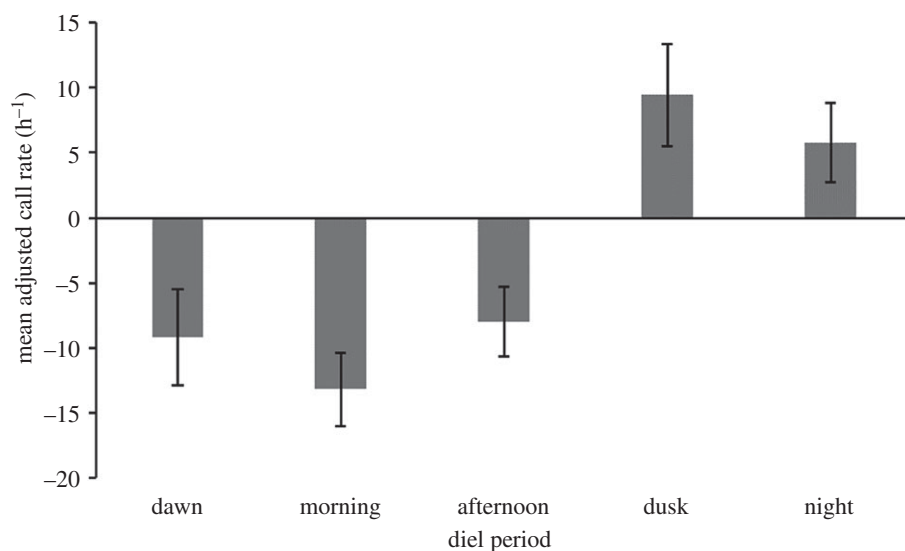
3.2. Diel variation

While vocalizations were recorded during all hours of the day and night a strong diurnal pattern was evident (figures 5 and 6). Mean vocalization rate increased during the evening and remained high throughout the night. Mean adjusted call rates exhibited a similar diel pattern to mean call rates and accounted for the fact that call rates were higher during winter months (figure 6). The same diel pattern was evident with higher call rates at dusk and night when *upcall* rate was examined separately.

Diel patterns in call rate for the five most abundant call types (*upcall*, *tonal low*, *pulsive downcall* and *gunshot*) varied throughout the day with highest rates at dusk and during the night (figure 7). There was no time of day when particular call types predominated; calls were used in broadly similar proportions within each diel period (figure 7).
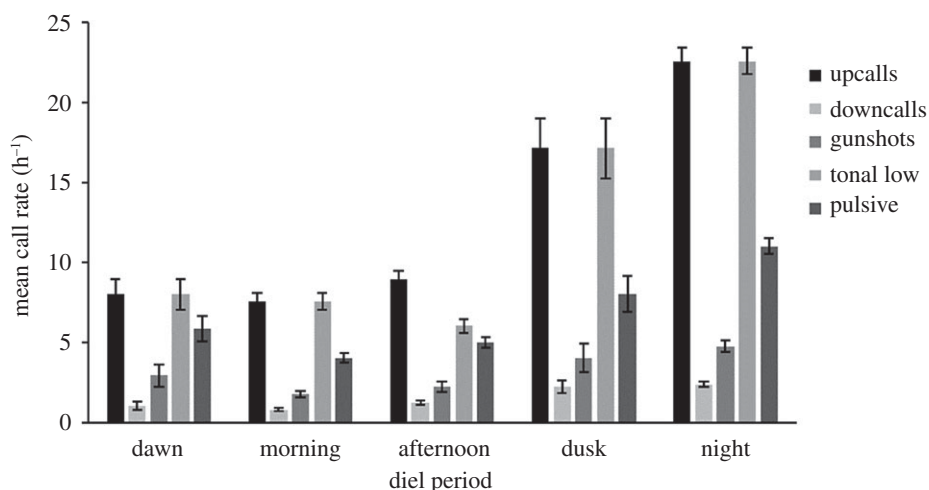
Figure 7. Mean call rate (calls h^{-1} ± s.e.) for the five most common call types (*upcall, tonal low, pulsive downcall* and *gunshot*) in each diel period for southern right whales recorded at the Auckland Islands between July 2011 and May 2012.

3.3. Modelling of effects on call presence and rate

A log-likelihood ratio test revealed that a negative binomial model best fitted the count data. The ZIM results revealed a strong effect of season on the presence and acoustic behaviour of whales, and a lesser effect of diel period (table 1). The ZIM coefficients showed that false zeros were most likely to occur in summer, suggesting whales were more likely to be absent from the study area. The count model coefficients suggest that call rate was significantly higher in winter, when whales were more likely to be present. The count data also show that call rates were higher during dusk and night-time periods and lower in the morning.

3.4. Effectiveness of automated detector

The automated detector designed to identify NARW *upcalls* [29] worked well for detecting SRW *upcalls* at the Auckland Islands. There was a positive relationship between the manually observed and automatically detected *upcalls*, although the automated detector picked out slightly more calls than the human analyst (figure 8 and table 2). The TPR (sensitivity) of the detector was high; 80.4% (s.e. ± 1.7) of manually categorized *upcalls* were identified by the detector. Thus, the rate of missed calls was around 20%. The mean PPV of the detector was, however, relatively low with only 40.4% (s.e. ± 1.9) of detected *upcalls* correctly identified. Mean PPV was higher (47–67%) when monthly vocalization rates were high, but dropped between October and April to a mean of 16% when vocal activity was minimal. Therefore, many false detections were made by the automated system, particularly when call rate was low. A large proportion of the false detections, however, were other right whale call types (e.g. part of a *hybrid* call). These were classified as false detections here because they were not strictly *upcalls*.

4. Discussion

4.1. Seasonal variation

This study found that SRWs are present more often and for far longer periods than previously observed at the Auckland Islands [41]. Call rates indicate that right whales are vocally active (and therefore routinely present) between May and November. Except for January, vocalizations were detected in every month of the year, indicating at least occasional presence in these months. Previously, SRWs were thought to be present at the Auckland Islands from early May to the end of September [41]. Long-term acoustic studies regularly find that marine mammals are present far more frequently than observed visually [37,59]. Peak vocalization rates (July–August) occurred in the same months as previous visual observations of peak abundance [41]. If SRWs are only passing through or using the outer part of the harbour it is possible that they would not be detected due to the location of the

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Table 1. Results of the zero-inflated model examining seasonal and diel differences in *all call* and *upcall* presence and rate for right whales recorded at the Auckland Islands. The reference level for diel period is afternoon and the reference level for season is autumn. Significant results are in italics.

| variable	all calls				upcalls only			
	estimate	s.e.	z-value	Pr(>|z|)	estimate	s.e.	z-value	Pr(>|z|)
count model coefficients								
season spring	0.05	0.05	0.92	0.36	0.08	0.06	1.43	0.15
season summer	−0.54	0.28	−1.91	0.06	−0.19	0.27	−0.69	0.49
season winter	0.64	0.05	12.69	$<2.00 \times 10^{-16}$	0.26	0.06	4.76	1.92×10^{-6}
diel period dawn	0.02	0.08	0.32	0.75	−0.14	0.09	−1.61	0.11
diel period dusk	0.28	0.07	3.99	6.52×10^{-5}	0.30	0.08	3.79	1.48×10^{-4}
diel period morning	−0.13	0.05	−2.62	*0.01*	−0.01	0.06	−0.26	0.79
diel period night	0.25	0.04	6.27	3.66×10^{-10}	0.24	0.04	5.34	9.33×10^{-8}
zero-inflation model coefficients								
season spring	−1.61	0.06	−24.85	$<2.00 \times 10^{-16}$	−1.32	0.07	−18.19	$<2.00 \times 10^{-16}$
season summer	3.65	0.32	11.35	$<2.00 \times 10^{-16}$	3.35	0.32	10.39	$<2.00 \times 10^{-16}$
season winter	−4.80	0.11	−44.68	$<2.00 \times 10^{-16}$	−3.49	0.08	−42.20	$<2.00 \times 10^{-16}$
diel period dawn	0.00	0.13	−0.02	0.99	−0.01	0.14	−0.06	0.95
diel period dusk	−0.47	0.12	−3.79	1.49×10^{-4}	−0.49	0.13	−3.93	8.62×10^{-5}
diel period morning	0.13	0.08	1.63	0.10	0.15	0.08	1.83	0.07
diel period night	−0.66	0.07	−9.50	$<2.00 \times 10^{-16}$	−0.68	0.07	−9.56	$<2.00 \times 10^{-16}$
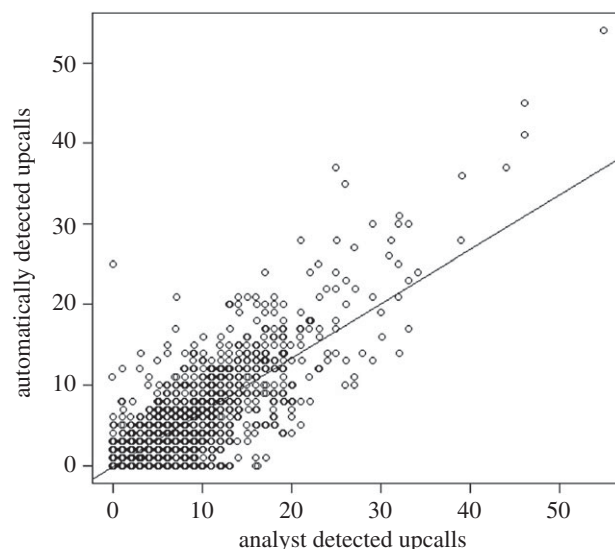
Figure 8. The number of automatically detected *upcalls* per recording versus the number of *upcalls* detected by the analyst. Right whale vocalizations were recorded at the Auckland Islands between July 2011 and May 2012. Best-fit linear regression is shown ($y = 0.6743x - 0.1261$, $r^2 = 0.76$). Points have been jittered by 0.6 to offset and reveal overlapping points.

recorder in the inner part of Port Ross. Also, to be recorded, the whales have to be calling. For these reasons, vocal measures of presence should be considered conservative indicators of SRW presence at the Auckland Islands. It should also be noted that the long periods of silence, in January for example, are presumed to indicate that whales are not present at the Auckland Islands, rather than a change of behaviour that has resulted in the cessation of vocalizations. This is consistent with what is known of seasonal migration behaviour of southern right whales, i.e. offshore foraging in summer and inshore calving in winter [60]. Comparative analyses between autonomous passive acoustic and visual techniques using a solar-powered camera in the Auckland Islands showed that both techniques were comparable for monitoring southern right whale presence [61]. However, while the solar-powered camera was able to record information over a longer period than the battery-limited acoustic recorder, the acoustic recorder was less limited by weather conditions, sea state and light availability.

The vocalization rate in winter was four times that of any other season. Consequently, the ZIM results showed that seasonal variation was the biggest contributing factor to call presence. Strong seasonal trends in call occurrence have been observed in other populations of right whales [37,54]. Seasonal variability in call detection is unsurprising given that right whales migrate between feeding and calving habitats [60]. Taken together, however, the acoustic studies show that right whales are present in particular habitats more often than expected given what was previously understood of their movements.

Upcalls were the most abundant call type detected (33%) and remained so throughout the year. Recent research [58] on NARW vocalizations also found *upcalls* to be the most frequently used call type, although they constituted a higher proportion (49%) of all calls than in this study. This variation in proportion could be the result of comparing two different (albeit closely related) species or because whales were sampled in different habitats. Given that *upcalls* appear to function as contact calls [30,62] it makes sense that they are the most commonly produced call type. *In situ* recordings made in July and August indicate that *upcalls* are made similarly often to *tonal low* and *pulsive* calls [45]. This underscores the value of the much larger dataset provided via autonomous recording.

Previous studies have shown that all right whale species use specific calls in different behavioural contexts [33,34,63] and that the relative proportion of call types varies both seasonally and geographically [46]. In this study, *very high*, *hybrid*, *high* and *gunshot* calls were observed only during a period of between four to six months of the year. This potentially indicates a seasonal change in behaviour, or may simply reflect the low call rates detected outside the main winter period. *Gunshots*, *hybrid* and *high* calls are understood to be related to mating activities [34,63] and the relative proportions of these calls increase during the breeding season [46,64]. The Auckland Islands are the major calving grounds for SRWs in New Zealand waters [41,42], but it is currently unclear where most mating occurs. Despite extensive photo-identification work (Rayment WJ, 2018, unpublished

Table 2. Results of the manual detections (made by an analyst) compared to the automated *upcall* detections for 10% of the total number of acoustic recordings. Data are given for each month separately, except for October to April, where data were combined due to low call rates.

month	number of upcalls manually detected	number of upcalls autodetected	number of true positive (TP) upcalls	number of false positive (FP) upcalls	number of false negative (FN) upcalls	positive predictive value (TP/(TP + FP))	True Positive Rate (TPR) (TP/(TP + FN))
July	183	266	146	113	37	56.1	80.0
August	551	693	455	244	93	58.2	82.0
September	376	488	302	183	74	47.5	81.8
October–April	156	410	135	282	19	16.1	81.8
May	169	173	131	40	38	67.3	72.9
overall detector effectiveness						40.4%	80.4%
						(95% CI: 36.6–44.2)	(95% CI: 76.9–83.8)

data), no female right whale has been seen at the Auckland Islands in the year before giving birth. If the gestation period is about a year, as in SRWs in South Africa [65], the Auckland Islands are not likely to be the principal mating site for SRWs in New Zealand. Further acoustic monitoring and exploration of other areas such as Campbell Island [66] may help locate the main mating habitat for this population.

4.2. Diel variation

Call rates showed a clear diel pattern, with more vocal activity at dusk and during the night than during the day (dawn, morning and afternoon). *Upcalls* showed a similar pattern when examined separately. Mean adjusted vocalization rates, which compensated for the high winter call rates, also exhibited the same diel pattern.

The rate at which right whales call varies with call type, activity of the whales, group composition and group size [33,46,64]. Right whales call more often during twilight and night in winter calving areas [67] and on feeding grounds [54,55,64]. On feeding grounds, the behaviour of NARWs is strongly influenced by the diel migration of copepods, their primary prey [68]. This extends to their vocal behaviour, where an inverse relationship between foraging and call production has been suggested [64]. Daily activity cycles dictated by prey availability have also been observed for other mysticetes and are often linked to the vertical migration of prey [20,53]. Sei whales (*Balaenoptera borealis*) called more frequently during the day when prey was less available and hence the whales were not feeding [22]. The high rate of NARW *upcalls* during twilight periods is considered to be a reflection of prey distribution, i.e. when prey are more dispersed and foraging intensity is lower, call rate increases [55]. There is little evidence of right whales feeding at the Auckland Islands [40] and baleen whales seldom feed while on calving grounds [69]. It is therefore unlikely that vocalization rates at the Auckland Islands are much affected by prey availability. Diel patterns in vocalization rate could also indicate a change in social behaviour or a general increase in activity or communication [33]. In NARWs *gunshot* calls, potentially indicative of mating activity, are most frequent in the late afternoon and evening [70]. Chorusing by humpback whales on wintering grounds in Hawaii increases at night, both in terms of amplitude and the number of whales involved [25]. While there was little change in the relative proportions of different call types throughout the day, SRWs at the Auckland Islands vocalize more at dusk and night. This may be because reduced visual contact in the dark increases the need for acoustic communication, particularly between mother–calf pairs. Risk of predation is likely to be low for SRWs at the Auckland Islands and hence communication at night may not incur the cost it would for other species [71].

4.3. Detection of vocalizations

Throughout the year, *upcalls* were more prevalent than any other vocalization type and were made at all times of the day. Overall they constituted a third of the calls recorded. Particularly given that *upcalls* are produced by both males and females [33,34], they are especially appropriate for automated detection. While there is ongoing development of algorithms to detect other right whale call types [72,73], to date the focus remains on *upcalls* [28,29]. Although no call-positive days were missed by using only an *upcall* detector, the addition of other call types would increase detection probability, particularly when call rates are low.

The strong positive relationship between the manually observed and automatically detected *upcalls*, consistent throughout the year, confirms the utility of the detector. Importantly, however, the false positive detection rate of the automated detector was high, particularly during periods of low vocal activity. The detection threshold of the algorithm could be increased to reduce the number of false positives, but this would also increase the rate of false negatives (missed calls). In our study, false detections were often right whale vocalizations other than *upcalls*. In areas with other mysticetes, false detections will sometimes be species other than right whales. An additional problem is that the true number of calls is never known precisely—detector efficiency can only be compared against a human analyst, an imperfect standard at best [28].

This study has proven the effectiveness of using an autonomous passive acoustic recorder to provide detailed data on vocal behaviour of southern right whales in a remote area seldom visited by vessels. Previously, information on habitat use in this area was limited to visual observations during relatively short visits in the austral winter [40,42,43]. Autonomous recorders have compelling additional benefits: they are viable 24 h a day, are less restricted by bad weather and are much more affordable

than deploying a visual survey team in a remote location for long time periods. Furthermore, different call types might be indicative of different behaviours which may not be apparent from visual observation alone. Additionally, as demonstrated in this study, acoustic data are much more amenable to automated analysis.

In this study, we used PAM to investigate the acoustic ecology and behaviour of SRW at their only known calving ground in New Zealand. SRWs in particular lend themselves to PAM due to their highly vocal nature and extensive vocal repertoire. The year-round monitoring of SRWs at the Auckland Islands expanded upon our current knowledge, revealing that they are at least occasionally present in every month of the year. Call rates in winter were, however, four times higher than any other season, suggesting seasonal variations in density as a result of winter migration inshore to calve. *Upcalls* were the most commonly produced call type proving ideal for automated detection throughout the year. Seasonality was apparent in many other call types, likely indicating a change of behaviour during winter. Call rates exhibited a clear diurnal pattern with higher vocal activity during dusk and night-time, potentially because reduced visual contact increases the need for acoustic communication. This study begins to scratch the surface of temporal variation in the acoustic behaviour of SRWs, but there is much more to be revealed.

References

1. Valdimarsson SK, Metcalfe NB, Thorpe JE, Huntingford FA. 1997 Seasonal changes in sheltering: effect of light and temperature on diel activity in juvenile salmon. *Anim. Behav.* **54**, 1405–1412. (doi:10.1006/anbe.1997.0550)

2. Backwell PR, O'Hara PD, Christy JH. 1998 Prey availability and selective foraging in shorebirds. *Anim. Behav.* **55**, 1659–1667. (doi:10.1006/anbe.1997.0713)

3. Lima SL, Dill LM. 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zoo.* **68**, 619–640. (doi:10.1139/z90-092)

4. Noë R, Bshary R. 1997 The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proc. R. Soc. Lond. B* **264**, 253–259. (doi:10.1098/rspb.1997.0036)

5. Paige KN. 1995 Bats and barometric pressure: conserving limited energy and tracking insects from the roost. *Funct. Ecol.* **9**, 463–467. (doi:10.2307/2390010)

6. Pellegrino AC, Peñaflor MFGV, Nardi C, Bezner-Kerr W, Guglielmo CG, Bento JMS, McNeil JN. 2013 Weather forecasting by insects: modified sexual behaviour in response to atmospheric pressure changes. *PLoS ONE* **8**, e75004. (doi:10.1371/journal.pone.0075004)

7. Gazzola A, Avanzinelli E, Mauri L, Scandura M, Apollonio M. 2002 Temporal changes of howling in south European wolf packs. *Italian J. Zool.* **69**, 157–161. (doi:10.1080/11250000209356454)

8. Burt JM, Vehrencamp SL. 2005 Dawn chorus as an interactive communication network. In *Animal Communication Networks* (eds JW Bradbury, SL Vehrencamp), pp. 320–343. Sunderland, MA: Sinauer.

9. Patricelli GL, Blickley JL. 2006 Avian communication in urban noise: causes and consequences of vocal adjustment. *Auk* **123**, 639–649. (doi:10.1642/0004-8038(2006)123[639:ACIUNC]2.0.CO;2)

10. Schwartz JJ, Ressel SJ, Bevier CR. 1995 Carbohydrate and calling: depletion of muscle glycogen and the chorusing dynamics of the neotropical treefrog *Hyla microcephala*. *Behav. Ecol. Socbiol.* **37**, 125–135. (doi:10.1007/BF00164158)

11. Mougeot F, Bretagnolle V. 2000 Predation risk and moonlight avoidance in nocturnal seabirds. *J. Avian Biol.* **31**, 376–386. (doi:10.1034/j.1600-048X.2000.310314.x)

12. Van Parijs SM, Hastie GD, Thompson PM. 1999 Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season. *Anim. Behav.* **58**, 1231–1239. (doi:10.1006/anbe.1999.1258)

13. Ospina OE, Villanueva-Rivera LJ, Corrada-Bravo CJ, Aide T. 2013 Variable response of anuran calling activity to daily precipitation and temperature: implications for climate change. *Ecosphere* **4**, art47. (doi:10.1890/ES12-00258.1)

14. Fonseca P, Revez MA. 2002 Temperature dependence of cicada songs (Homoptera, Cicadoidea). *J. Comp. Physiol. A.* **187**, 971–976. (doi:10.1007/s00359-001-0267-5)

15. Jacot A, Scheuber H, Holzer B, Otti O, Brinkhof MW. 2008 Diel variation in a dynamic sexual

display and its association with female mate-searching behaviour. *Proc. R. Soc. B* **275**, 579–585. (doi:10.1098/rspb.2007.1500)

16. Janik VM, Slater PJ. 1998 Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **56**, 829–838. (doi:10.1006/anbe.1998.0881)

17. Au W. 1997 Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics* **8**, 137–162. (doi:10.1080/09524622.1997.9753357)

18. Nowacek DP. 2005 Acoustic ecology of foraging bottlenose dolphins (*Tursiops truncatus*), habitat-specific use of three sound types. *Mar. Mamm. Sci.* **21**, 587–602. (doi:10.1111/j.1748-7692.2005.tb01253.x)

19. Mellinger DK, Stafford KM, Fox CG. 2006 Seasonal occurrence of sperm whale (*Physeter macrocephalus*) sounds in the Gulf of Alaska, 1991–2001. *Mar. Mamm. Sci.* **20**, 48–62. (doi:10.1111/j.1748-7692.2004.tb01140.x)

20. Stafford KM, Moore SE, Fox CG. 2005 Diel variation in blue whale calls recorded in the eastern Tropical Pacific. *Anim. Behav.* **69**, 951–958. (doi:10.1016/j.anbehav.2004.06.025)

21. Heimlich SL, Mellinger DK, Nieukirk SL, Fox CJ. 2005 Types, distribution, and seasonal occurrence of sounds attributed to Bryde's whales (*Balaenoptera edeni*) recorded in the eastern tropical Pacific, 1999–2001. *J. Acoust. Soc. Am.* **118**, 1830–1837. (doi:10.1121/1.1992674)

22. Baumgartner MF, Fratantoni DM. 2008 Diel periodicity in both sei whale vocalisation rates and the vertical migration of their copepod prey observed from ocean gliders. *Limnol. Oceanogr.* **53**, 2197–2209. (doi:10.4319/lo.2008.53.5_part_2.2197)

23. Au WW *et al.* 2013 Night time foraging by deep diving echolocating odontocetes off the Hawaiian islands of Kauai and Ni'ihau as determined by passive acoustic monitors. *J. Acoust. Soc. Am* **133**, 3119–3127. (doi:10.1121/1.4798360)

24. Wang Z, Akamatsu T, Wang K, Wang D. 2014 The diel rhythms of biosonar behavior in the Yangtze finless porpoise (*Neophocaena asiaeorientalis*) in the Port of the Yangtze River: the correlation between prey availability and boat traffic. *PLoS ONE* **9**, e97907. (doi:10.1371/journal.pone.0097907)

25. Au W, Mobley J, Burgess WC, Lammers MO, Nachtigall PE. 2000 Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Mar. Mamm. Sci.* **16**, 530–544. (doi:10.1111/j.1748-7692.2000.tb00949.x)

26. Carlström J. 2005 Diel variation in echolocation behavior of wild harbor porpoises. *Mar. Mamm. Sci.* **21**, 1–12. (doi:10.1111/j.1748-7692.2005.tb01204.x)

27. Clark CW, Gillespie D, Nowacek D, Parks SE. 2007 Listening to their world: acoustics for monitoring and protecting right whales in an urbanized ocean. In *The urban whale* (eds SD Kraus, RM Rolland), pp. 331–355. Cambridge, UK: Harvard University Press.

28. Gillespie D. 2004 Detection and classification of right whale calls using an 'edge' detector operating on a smoothed spectrogram. *Can. Acoust.* **32**, 39–47.

29. Urazghildiiev IR, Clark CW. 2006 Acoustic detection of North Atlantic right whale contact calls using the generalized likelihood ratio test. *J. Acoust. Soc. Am.* **120**, 1956–1963. (doi:10.1121/1.2257385)

30. Clark CW. 1982 The acoustic repertoire of the southern right whale: a quantitative analysis. *Anim. Behav.* **30**, 1060–1071. (doi:10.1016/S0003-3472(82)80196-6)

31. McDonald MA, Moore SE. 2002 Calls recorded from North Pacific right whales (*Eubalaena japonica*) in the eastern Bering Sea. *J. Cetac. Res. Manage.* **4**, 261–266.

32. Parks SE, Searby A, Celerier A, Johnson MP, Nowacek DP, Tyack PL. 2011 Sound production behavior of individual North Atlantic right whales: implications for passive acoustic monitoring. *Endanger. Species Res.* **15**, 63–76. (doi:10.3354/esr00368)

33. Clark CW. 1983 Acoustic communication and behavior of the southern right whale. In *Behavior and communication of whales* (ed. RS Payne). Boulder, CO: Westview Press.

34. Parks SE, Tyack PL. 2005 Sound production by North Atlantic right whales (*Eubalaena glacialis*) in surface active groups. *J. Acoust. Soc. Am.* **117**, 3297–3306. (doi:10.1121/1.1882946)

35. Stafford KM, Nieukirk SL, Fox CG. 1999 Low-frequency whale sounds recorded on hydrophones moored in the eastern tropical Pacific. *J. Acoust. Soc. Am* **106**, 3687–3698. (doi:10.1121/1.428220)

36. Širović A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D. 2004 Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep Sea Res. Pt II* **51**, 2327–2344. (doi:10.1016/j.dsr2.2004.08.005)

37. Mellinger DK, Nieukirk SL, Matsumoto H, Heimlich SL, Dziak RP, Haxel J, Fowler M, Meinig C, Miller HV. 2007 Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. *Mar. Mamm. Sci.* **23**, 856–867. (doi:10.1111/j.1748-7692.2007.00144.x)

38. Richards R. 2009 Past and present distributions of southern right whales (*Eubalaena australis*). *NZ J. Zool.* **36**, 447–459. (doi:10.1080/03014223.2009.9651477)

39. Carroll EL, Childerhouse SJ, Fewster RM, Patenaude NJ, Steel D, Dunshea G, Boren L, Baker CS. 2013 Accounting for female reproductive cycles in a superpopulation capture-recapture framework. *Ecol. Appl.* **23**, 1677–1690. (doi:10.1890/12-1657.1)

40. Patenaude NJ, Baker CS, Gales NJ. 1998 Observations of southern right whales on New Zealand's sub-Antarctic wintering grounds. *Mar. Mamm. Sci.* **14**, 350–355. (doi:10.1111/j.1748-7692.1998.tb00726.x)

41. Patenaude NJ. 2000 *Southern right whales wintering in the Auckland Islands. Conservation Advisory Science Notes 321*. Wellington, New Zealand: Department of Conservation.

42. Rayment W, Davidson A, Dawson S, Slooten E, Webster T. 2012 Distribution of southern right whales on the Auckland Islands calving ground. *NZ J. Mar. Freshwater Res.* **46**, 431–436. (doi:10.1080/00288330.2012.697072)

43. Rayment W, Dawson S, Webster T. 2015 Breeding status affects fine-scale habitat selection of southern right whales on their wintering ground. *J. Biogeog.* **42**, 463–474. (doi:10.1111/jbi.12443)

44. Baker AN. 1977 Spectacled porpoise, *Phocoena dioptrica*, new to the subantarctic Pacific Ocean (note). *NZ J. Mar. Freshwater Res.* **11**, 401–406. (doi:10.1080/00288330.1977.9515686)

45. Webster TA, Dawson SM, Rayment WJ, Parks SE, Van Parijs SM. 2016 Quantitative analysis of the acoustic repertoire of southern right whales in New Zealand. *J. Acoust. Soc. Am* **140**, 322–333. (doi:10.1121/1.4955066)

46. Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Van Opzeeland IC. 2009 Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Mar. Ecol. Prog. Ser.* **395**, 21–36. (doi:10.3354/meps08123)

47. Parmentier E, Kéver L, Casadevall M, Lecchini D. 2010 Diversity and complexity in the acoustic behaviour of *Dacyllus flavicaudus* (Pomacentridae). *Mar. Biol.* **157**, 2317–2327. (doi:10.1007/s00227-010-1498-1)

48. Andersson MH, Lagenfelt I, Sigray P. 2012 Do ocean-based wind farms alter the migration pattern in the endangered European silver eel (*Anguilla anguilla*) due to noise disturbance? In *The effects of noise on aquatic life* (eds AN Popper, A Hawkins), pp. 393–396. New York, NY: Springer.

49. Schärer MT, Nemeth MI, Mann D, Locascio J, Appeldoorn RS, Rowell TJ. 2012 Sound production and reproductive behavior of yellowfin grouper, *Mycteroperca venenosa* (Serranidae) at a spawning aggregation. *Copeia* **1**, 135–144. (doi:10.1643/CE-17-620)

50. Wells RS, McHugh KA, Douglas DC, Shippee S, McCabe EB, Barros NB, Phillips GT. 2013 Evaluation of potential protective factors against metabolic syndrome in bottlenose dolphins: feeding and activity patterns of dolphins in Sarasota Bay. *Florida. Front. Endocrinol.* **4**, 139. (doi:10.3389/fendo.2013.00139)

51. Figueroa H. 2012 Extensible Bioacoustic Tool (XBAT), Bioacoustics Research Program, Cornell University, www.xbat.org (accessed 4 June 2014).

52. Charif RA, Pitzrick M. 2008 Automated detection of Cerulean Warbler songs using XBAT data template detector software. Bioacoustics Research Program, Cornell Laboratory of Ornithology Technical Report 08-02. 9 April 2008. Prepared for: US Forest Service San Dimas Technology and Development Center Inventory and Monitoring Program.

53. Oleson EM, Calambokidis J, Burgess WC, McDonald MA, LeDuc CA, Hildebrand JA. 2007 Behavioral context of call production by eastern North Pacific blue whales. *Mar. Ecol. Prog. Ser.* **330**, 269–284. (doi:10.3354/meps330269)

54. Munger LM, Wiggins SM, Moore SE, Hildebrand JA. 2008 North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic recordings in the southeastern Bering Sea, 2000–2006. *Mar.*

Mamm. Sci. **24**, 795 – 814. (doi:10.1111/j.1748-7692.2008.00219.x)

55. Mussoline SE, Risch D, Hatch LT, Weinrich MT, Wiley DN, Thompson MA, Corkeron PJ, Van Parijs SM. 2012 Seasonal and diel variation in North Atlantic right whale up-calls: implications for management and conservation in the northwestern Atlantic Ocean. *Endanger. Species Res.* **17**, 17 – 26. (doi:10.3354.esr00411)

56. Zeileis A, Kleiber C, Jackman S. 2008 Regression Models for Count Data in R. *J. Statist. Software* **27**, 1 – 25. (doi:10.18637/jss.v027.i08)

57. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 Zero-truncated and zero-inflated models for count data. In *Mixed effects models and extensions in ecology with R*, pp. 261 – 293. New York, NY: Springer.

58. Zar JH. 1999 *Biostatistical analysis*, 4th edn. Prentice, NJ: Prentice Hall.

59. Morano JL, Rice AN, Tielens JT, Estabrook BJ, Murray A, Roberts BL, Clark CW. 2012 Acoustically detected year-round presence of right whales in an urbanized migration corridor. *Conserv. Biol.* **26**, 698 – 707. (doi:10.1111/j.1523-1739.2012.01866.x)

60. Kenney RD. 2009 Right whales: *Eubalaena glacialis, E. japonica* and *E. australis*. In *Encyclopedia of marine mammals* (eds WF Perrin, B Würsig, JGM Thewissen). New York, NY: Academic Press.

61. Rayment W, Webster T, Brough T, Jowett T, Dawson S. 2018 Seen or heard? A comparison of visual and acoustic autonomous monitoring methods for investigating temporal variation in occurrence of southern right whales. *Mar. Biol.* **165**, 12. (doi:10.1007/s00227-017-3264-0)

62. Clark CW, Clark JM. 1980 Sound playback experiments with southern right whales. *Science* **207**, 663 – 665. (doi:10.1126/science.207.4431.663)

63. Parks SE, Hamilton PK, Kraus SD, Tyack PL. 2005 The gunshot sound produced by male North Atlantic right whales (*Eubalaena glacialis*) and its potential function in reproductive advertisement. *Mar. Mamm. Sci.* **21**, 458 – 475. (doi:10.1111/j.1748-7692.2005.tb01244.x)

64. Matthews LP, McCordic JA, Parks SE. 2014 Remote acoustic monitoring of North Atlantic right whales (*Eubalaena glacialis*) reveals seasonal and diel variations in acoustic behavior. *PLoS ONE* **9**, e91367. (doi:10.1371/journal.pone.0091367)

65. Best PB. 1994 Seasonality of reproduction and the length of gestation in southern right whales *Eubalaena australis*. *J. Zool.* **232**, 175 – 189. (doi:10.1111/j.1469-7998.1994.tb01567.x)

66. Torres LG *et al*. 2016 Demography and ecology of southern right whales *Eubalaena australis* wintering at sub-Antarctic Campbell Island, New Zealand. *Polar Bio.* **40**, 95 – 106. (doi:10.1007/s00300-016-1926-x)

67. Office of Naval Research. 1997 Northern right whale monitoring project: Final report. Available from Office of Naval Research, Arlington. 66 pp.

68. Baumgartner MF, Lysiak NS, Schuman C, Urban-Rich J, Wenzel FW. 2011 Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. *Mar. Ecol. Prog. Ser.* **423**, 167 – 184. (doi:10.3354/meps08931)

69. Corkeron PJ, Connor RC. 1999 Why do baleen whales migrate? *Mar. Mamm. Sci.* **15**, 1228 – 1245. (doi:10.1111/j.1748-7692.1999.tb00887.x)

70. Parks SE, Hotchkin CF, Cortopassi KA, Clark CW. 2012 Characteristics of gunshot sound displays by North Atlantic right whales in the Bay of Fundy. *J. Acoust. Soc. Am.* **131**, 3173 – 3179. (doi:10.1121/1.3688507)

71. Schmidt KA, Belinsky KL. 2013 Voices in the dark: predation risk by owls influences dusk singing in a diurnal passerine. *Behav. Ecol. Sociobiol.* **67**, 1837 – 1843. (doi:10.1007/s00265-013-1593-7)

72. Urazghildiiev IR, Parks SE. 2014 Objective classification of North Atlantic right whale (*Eubalaena glacialis*) vocalizations to improve passive acoustic detection. *PeerJ PrePrints* **e322v1**, 1 – 27. (doi:10.7287/peerj.preprints.322v1)

73. Baumgartner MF, Mussoline SE. 2011 A generalized baleen whale call detection and classification system. *J. Acoust. Soc. Am.* **129**, 2889 – 2902. (doi:10.1121/1.3562166)

74. Webster TA, Van Parijs SM, Rayment WJ, Dawson SM. 2019 Data from: Temporal variation in the vocal behaviour of southern right whales in the Auckland Islands, New Zealand. Dryad Digital Repository. (doi:10.5061/dryad.ps58g58)