Effects of subsampling of passive acoustic recordings on acoustic metrics

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Passive acoustic monitoring is an important tool in marine mammal studies. However, logistics and finances frequently constrain the number and servicing schedules of acoustic recorders, requiring a trade-off between deployment periods and sampling continuity, i.e., the implementation of a subsampling scheme. Optimizing such schemes to each project's specific research questions is desirable. This study investigates the impact of subsampling on the accuracy of two common metrics, acoustic presence and call rate, for different vocalization patterns (regimes) of baleen whales: (1) variable vocal activity, (2) vocalizations organized in song bouts, and (3) vocal activity with diel patterns. To this end, above metrics are compared for continuous and subsampled data subject to different sampling strategies, covering duty cycles between 50% and 2%. The results show that a reduction of the duty cycle impacts negatively on the accuracy of both acoustic presence and call rate estimates. For a given duty cycle, frequent short listening periods improve accuracy of daily acoustic presence estimates over few long listening periods. Overall, subsampling effects are most pronounced for low and/or temporally clustered vocal activity. These findings illustrate the importance of informed decisions when applying subsampling strategies to passive acoustic recordings or analyses for a given target species. © 2015 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution 3.0 Unported License. [http://dx.doi.org/10.1121/1.4922703]

I. INTRODUCTION

Passive acoustic monitoring (PAM) is a widely used tool in marine mammal research concerning primarily spatio-temporal distribution patterns and behavior of vocalizing species (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009; Van Opzeeland *et al.*, 2010). Recent methodological advances have broadened the field of PAM applications to also include abundance estimations for some marine mammals (Küsel *et al.*, 2011; Marques *et al.*, 2011; Ward *et al.*, 2012; Harris *et al.*, 2013). While dependent on vocalizations from the target species, PAM exhibits several advantages over traditional visual surveys, such as the possibility to collect data under poor weather conditions, during darkness and in areas with dense ice cover, allowing marine mammal monitoring in regions and at times otherwise inaccessible (both logistically and financially) (e.g., Mellinger *et al.*, 2007). In particular, autonomous passive acoustic recorders are the tool of choice for collecting long-term data series in remote areas that are inaccessible to ships during much of the year, such as the Arctic and Southern Oceans (e.g., Širović *et al.*, 2009; Samaran *et al.*, 2010; Stafford *et al.*, 2012; Sousa-Lima *et al.*, 2013; Van Opzeeland *et al.*, 2013). In many cases, logistic and financial constraints determine the frequency at which recorders are serviced, resulting in time spans of up to two to three years between recorder deployment and retrieval (e.g., Širović *et al.*, 2004; Miksis-Olds *et al.*, 2010; Rettig *et al.*, 2013). However, to date, the majority of autonomous recording instruments do not quite feature sufficient capacity in terms of battery life and/or data storage to record continuously for such prolonged deployment periods at high sampling rates (e.g., Rettig *et al.*, 2013).

Nevertheless, as multi-year data are indispensable to capture long-term trends in temporal and seasonal occurrences of species, full coverage of the period between recorder deployment and retrieval is highly desirable. This often requires recordings to be subsampled (e.g., Burtenshaw *et al.*, 2004; Gedamke *et al.*, 2007; Stafford *et al.*, 2012; Rettig *et al.*, 2013), i.e., to be collected at a repetitive pattern of sampling periods and non-sampling periods at a given repetition cycle. Likewise, for human

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screening of comprehensive, continuous data sets, researchers may resort to analyzing subsets of the data to accelerate the analysis process (e.g., Oleson *et al.*, 2007; Van Opzeeland *et al.*, 2010).

Subsampling of a given percentage of time might, however, be implemented in different ways, with the extremes being either many short listening periods (sampling bouts) or few long listening periods. This option immediately gives rise to the question of potential impacts of the subsampling scheme on ecological inferences drawn from the ensuing data which, in turn, leads to the question for the most suitable sampling scheme for a given species. Simply put, if the recording period is limited, for example, to 1 h during a day, one wonders whether sampling once daily for an hour, twice daily for half an hour, or four times a day for 15 min represents the vocal behavior of a given species best.

The choice of a specific subsampling scheme will be driven by the research question, power and storage capacity of the recording equipment and most importantly the desire not to introduce any biases to the data which can be achieved by seeking an optimal sampling scheme based on pre-existing knowledge on vocalization patterns (e.g., Sousa-Lima *et al.*, 2013). Impacts of subsampling are likely to depend strongly on the characteristics of the focal species' vocal behavior: In case of frequent, regular calls, results from subsampled data may remain representative of the respective period. However, if vocal activity occurs rarely or exhibits a distinct diurnal pattern, sampling exclusively at off-periods would result in substantial misrepresentations of the focal species' acoustic presence. Consequently, suitable subsampling requires tuning to the acoustic behavior of the focal species, such as rate and temporal structure of call production.

Acoustic presence (a binary parameter) and call rate (a continuous numeric parameter) are two frequently used metrics to investigate various aspects of marine mammal ecology (e.g., Mellinger *et al.*, 2007; Širović *et al.*, 2007; Van Opzeeland *et al.*, 2013), such as spatio-temporal patterns in occurrence and distribution, locations of feeding or overwintering habitats as well as density estimations (see also Table I and references therein). In turn, an unbiased assessment of a focal species' acoustic presence is essential for descriptions of its occurrence and distribution on spatial and/or temporal scales (Table I).

Continuous passive acoustic recordings of North Atlantic right whales (NARW, *Eubalaena glacialis*) and Antarctic blue whales (ABW, *Balaenoptera musculus intermedia*) were used in this study to investigate the potential impacts of different subsampling schemes on acoustic presence and call rates by comparing the ensuing results with regard to their representativeness.

II. MATERIALS AND METHODS

A. Passive acoustic data acquisition

Continuous passive acoustic data were collected at three different locations. On the Ekström ice shelf at 70° 31′ S, 8° 13′ W, the PerenniAL Acoustic Observatory in the Antarctic Ocean (PALAOA) collects continuous underwater recordings from a coastal Antarctic environment since 2005 with a Reson TC4032 hydrophone, deployed at approximately 160 m depth (Boebel *et al.*, 2006; Kindermann *et al.*, 2008). In the Indian Ocean, southwest of Amsterdam Island ('SWAMS', 42° 59′ S, 74° 35′ E), continuous acoustic recordings were collected from October 2006 to April 2008 with an ITC-1032 hydrophone moored at 1000 m depth (see Samaran *et al.*, 2013 for further details). In Massachusetts Bay, MA, continuous acoustic data were recorded from January 2006 to February 2007 by means of marine autonomous recording units (MARUs) deployed at depths ranging from 41 to 76 m

TABLE I. Acoustic parameters used in the present case study and possible inferences on the focal species' ecology based on these parameters as reported by previous studies.

Parameter	Direct and further inferences	References (exemplary)[a]
Acoustic presence	Occurrence of a focal species at recording location(s) with potential indications on suitability of habitat for overwintering/breeding/feeding/etc.	(Mussoline *et al.*, 2012; Rankin *et al.*, 2005; Samaran *et al.*, 2013; Širović *et al.*, 2009; Stafford *et al.*, 2004)
	Spatial and temporal patterns in distribution of focal species in certain area	(Gedamke *et al.*, 2007;[b] Matthews *et al.*, 2014; Mussoline *et al.*, 2012; Samaran *et al.*, 2013; Širović *et al.*, 2004)
	Diel vocalization patterns	(Mussoline *et al.*, 2012)
	Associations with abiotic or biotic factors	(Burtenshaw *et al.*, 2004)[b]
Vocalization rate	Abundance and density estimations of animals at recording location/in study area	(Marques *et al.*, 2013; Širović *et al.*, 2004)
	Estimation of historical catch numbers of different blue whale populations from calling patterns	(Monnahan *et al.*, 2014)
	Movement/migration patterns of animals	(Samaran *et al.*, 2013; Širović *et al.*, 2004; Širović *et al.*, 2009)
	Diel vocalization patterns	(Matthews *et al.*, 2014; Stafford *et al.*, 2005; Wiggins *et al.*, 2005)
	Associations with abiotic or biotic factors	(Širović *et al.*, 2004; Širović and Hildebrand, 2011)
	Effects of anthropogenic noise on focal species	(Di Iorio and Clark, 2010; McDonald *et al.*, 1995; Melcón *et al.*, 2012)

[a]References were selected exemplarily, mainly representing passive acoustic research on the focal species of this study, i.e., blue whale (*Balaenoptera musculus*) and North Atlantic right whale (*Eubalaena glacialis*).
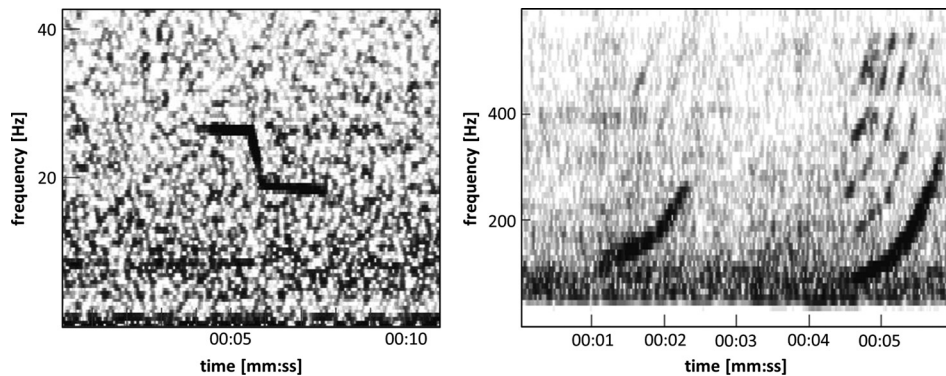[b]Studies based on subsampled acoustic data.

FIG. 1. Spectrogram of Antarctic blue whale Z-call (left panel) and North Atlantic right whale up-call vocalization (right panel). Sound file of NARW up-call was downloaded from http://www.nefsc.noaa.gov/psb/acoustics/sounds.html.

at 10 separate locations throughout the Stellwagen Bank National Marine Sanctuary (see Mussoline *et al.*, 2012 for further details).

B. Focal species and vocalizations

The continuous passive acoustic recordings used in this study contained a variety of marine mammal sounds, yet only ABW Z-calls and NARW up-calls are examined herein. ABW Z-calls (Fig. 1) consist of three components, starting with a constant frequency tone at 27 Hz which lasts for about 8–12 s, followed by a short downsweep to 19 Hz of about 1–2 s duration and a longer (8–12 s) slightly frequency modulated tone at about 18–19 Hz (e.g., Ljungblad *et al.*, 1998; Rankin *et al.*, 2005). The NARW's up-call is a frequency modulated call lasting approximately 1 s with an increasing frequency from 50 to 200 Hz (Fig. 1), which is considered to serve as contact call (Clark, 1982; Parks and Clark, 2007).

C. Passive acoustic data sets

Five data subsets, each comprising seven days, were extracted from the three continuous data sets described in Sec. II A. Each subset is representative of a different pattern of calling behavior including: (1) variable acoustic activity,

(2) clear song sequences, and (3) vocal activity featuring a clear diel pattern.

1. Variable, temporally unstructured acoustic activity with both high and low calling rates

To explore how subsampling may affect data featuring variable acoustic activity, i.e., without any clear song pattern or diurnal trend, two sets from the PALAOA data were chosen on the basis of results from previous analyses of seasonal vocal activity of Antarctic blue whales (Van Opzeeland, 2010) (Fig. 2). Generally, Z-calls are considered to be repeated every 60 to 65 s in patterned sequences ("song") (e.g., Ljungblad *et al.*, 1998; Širović *et al.*, 2004), however, clear song sequences were not present in this selection of PALAOA data. Instead, the acoustic activity was variable with periods of higher and lower calling activity. The selected data were resampled at 6 kHz and ABW Z-call detection was performed visually by manually screening 1-min spectrograms (FFT 8,192 points, Hanning window, time, and frequency resolution 1.3 s, 0.75 Hz) with Adobe Audition 2.0, resulting in call count data at 1-min resolution. "Regime A–high call rate" represented high vocal activity of an average of 55 ± 18 (standard deviation) Z-calls per hour, whereas "regime B–low call rate" represented data with medium vocal activity of 20 ± 8 Z-calls per hour on average.
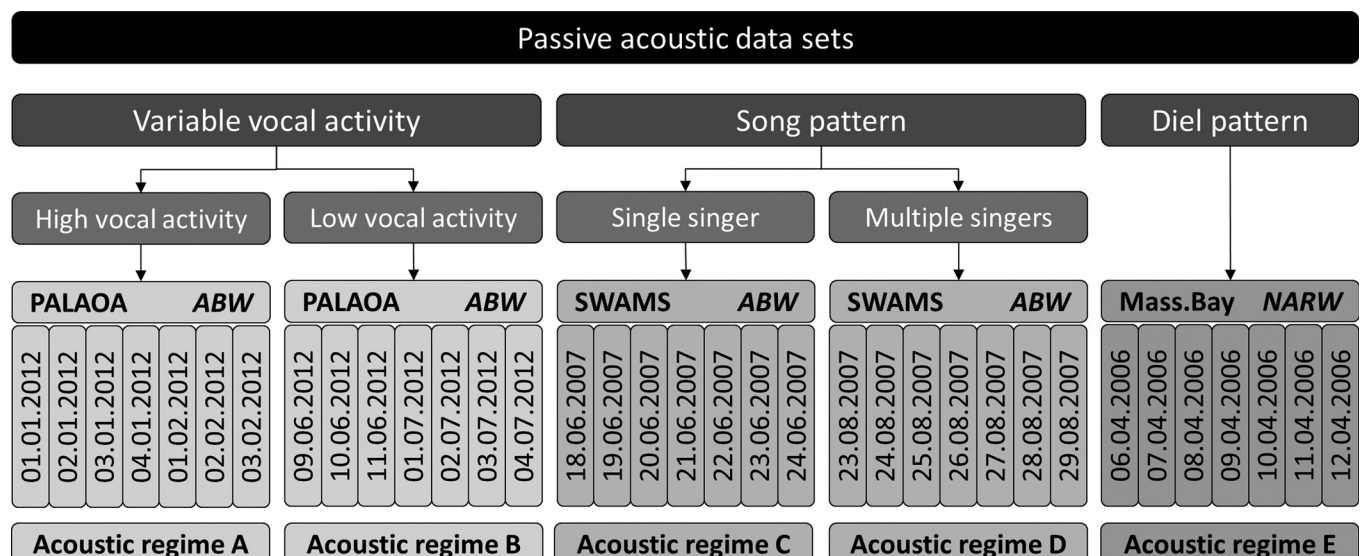

FIG. 2. Passive acoustic data sets used for exploring the effects of different subsampling schemes on call rate and acoustic presence estimation.

No diurnal patterns were evident in these data. Data sets comprised four consecutive days from January and three consecutive days from February (1–4 January 2012 and 1–3 February 2012) for regime A and three consecutive days from June and four consecutive days from July (9–11 June 2012 and 1–4 July 2012) for regime B (Fig. 2). The number of consecutive days was constrained by the presence of noisy periods on some days, caused, for example, by glacier calving. Noisy days were excluded as these potentially affected the reliability of call counts.

2. Structured acoustic activity with clear song sequences by single and multiple individuals

The Indian Ocean data contained sequences of ABW Z-call vocalizations organized in regular song structures. Calls were automatically detected using a template detector in XBAT (Figueroa and Robbins, 2008; see Samaran *et al.*, 2013 for further details). ABW Z-call song featuring inter-call intervals of 60–65 s typically stem from a single calling individual (e.g., Širović *et al.*, 2004) and such events were hence considered as representing single singers. Periods with shorter inter-call intervals are representative of the presence of multiple singers. Seven consecutive recording days from June 2007 (18–24 June 2007) containing individual song were selected to form "regime C–single song," with 17 ± 8 Z-calls per hour on average (Fig. 2). "Regime D–multiple song" comprised a second set of seven consecutive days (23–29 August 2007, Fig. 2) of continuous recordings with 35 ± 22 Z-calls per hour on average, containing ABW song sequences with shorter inter-call intervals (with ∼30% of inter-call intervals ranging between 15 and 45 s). No diurnal patterns were evident in these data.

3. Call activities exhibiting strong diel patterns

The Stellwagen Bank acoustic data, containing NARW vocalizations, were analyzed in XBAT, using a custom-written automated call detection algorithm to detect NARW up-calls (see Mussoline *et al.*, 2012 for further details). Seven consecutive recording days (6–12 April 2006, representing pooled call detections from nine different locations) with distinct diel fluctuations [i.e., increased NARW vocal activity during twilight and at night (Mussoline *et al.*, 2012)]

were selected to comprise "regime E–diel patterns" (Fig. 2). Hourly call rates ranged from 0 to 137 up-calls per hour (mean 12 ± 6 up-calls per hour).

D. Subsampling schemes

Subsampling schemes are defined by their *cycle periods* (τ_c, "sampling intervals") and *duty cycles D,* commonly given in percent but as a fractional number hereinafter (Table II and Fig. 3) The corresponding *listening period* τ_l (i.e., length of a sampling bout) is then given by $\tau_l = D \cdot \tau_c$. In the course of a day, the cycle is repeated $24\,\mathrm{h}/\tau_c = N$ times (*number of cycles per day*), with τ_c usually chosen such that $N \in \mathbb{N}$ (Fig. 3).

The potential repercussions of different sampling schemes are explored in this publication by varying (a) the *cycle period* (τ_c) (or correspondingly the *number of cycles per day N*) and (b) the *duty cycle D*. Table III lists the analyzed combinations of cycling periods and duty cycles that result in full minute listening periods. A given duty cycle D may be realized differently in terms of cycle period and corresponding listening period (rows of Table III), resulting in different sampling strategies (e.g., a single long listening period versus multiple shorter windows distributed evenly over the course of a day).

In PAM studies, commonly little consideration is given to when exactly a cycle period commences within a day, while the start of a listening period mostly matches that of the corresponding cycle period. However, (phase) shifts of either are feasible. Within a cycle period (τ_c) the number of independent (non-overlapping) listening periods equals *1/D*, called the *number or realizations r* hereinafter (Fig. 3). For our statistical analysis of the effects of data subsampling, all possible *1/D* realizations were processed to estimate the variability of call rates and acoustic presence estimations (Table II). This procedure provided $7/D$ (*1/D* realizations times seven days) independent estimates of acoustic presence and call rates per regime, respectively.

1. Daily acoustic presence estimations from subsampled data

For continuous data, a species was considered present if at least one call was evident during a day. For subsampled data, a focal species was considered acoustically present if at

TABLE II. Index of abbreviations and symbols.

Symbol	Definition
τ_c	Cycle period [h], i.e., the interval at which data collection is repeated
N	Number of cycles per day
τ_l	Duration of listening period [min], i.e., the period over which data are acquired continuously
D	$= \tau_l / \tau_c$; duty cycle
1/D	$= \tau_c / \tau_l$; number of independent realizations of a given sampling scheme, i.e., number of listening periods per cycle
d	Metric depicting correctness of acoustic presence determination in subsampled data compared to true acoustic presence in continuous data; $d = 1$ representing correct acoustic presence estimation and $d = 0$ representing incorrect acoustic presence estimation
p_p	Probability to correctly assess acoustic presence of a focal species during the day
p_c	Probability to assess call rate of a focal species within a certain range (i.e., 10%, 50%, and 100%, respectively) of the true call rate

Duty cycle		Cycle period τ_c							No. of independent realizations
D	D [%]	1 h	2 h	3 h	4 h	6 h	8 h	1/D	per regime
1/2	**50.0**	30 min	60 min	90 min	120 min	180 min	240 min	2	14
1/3	33.0	20 min	40 min	60 min	80 min	120 min	160 min	3	21
1/4	**25.0**	15 min	30 min	45 min	60 min	90 min	120 min	4	28
1/5	20.0	12 min	24 min	36 min	48 min	72 min	96 min	5	35
1/6	16.7	10 min	20 min	30 min	40 min	60 min	80 min	6	42
1/8	12.5		15 min		30 min	45 min	60 min	8	56
1/9	11.1			20 min		40 min		9	63
1/10	**10.0**	6 min	12 min	18 min	24 min	36 min	48 min	10	70
1/12	8.3	5 min	10 min	15 min	20 min	30 min	40 min	12	84
1/15	6.7	4 min	8 min	12 min	16 min	24 min	32 min	15	105
1/16	6.3				15 min		30 min	16	112
1/18	5.6			10 min		20 min		18	126
1/20	**5.0**	3 min	6 min	9 min	12 min	18 min	24 min	20	140
1/24	4.2		5 min		10 min	15 min	20 min	24	168
1/30	3.3	2 min	4 min	6 min	8 min	12 min	16 min	30	210
1/32	3.1						15 min	32	224
1/36	2.8			5 min		10 min		36	252
1/40	2.5		3 min		6 min	9 min	12 min	40	280
1/45	2.2			4 min		8 min		45	315
1/48	2.1				5 min		10 min	48	336
1/60	**1.7**	1 min	2 min	3 min	4 min	6 min	8 min	60	420
cycles per day N		**24**	**12**	**8**	**6**	**4**	**3**		

least one call was detected in any of the N listening periods of that day (Table III). Daily acoustic presence was estimated from the call counts in the rth realization in all N cycles of the jth day. If the assessments of acoustic presence from subsampled data and from continuous data matched, the decision was considered correct ($d = 1$), and incorrect otherwise ($d = 0$).

To evaluate the probability p_p of having properly determined the acoustic presence during that day, d was determined for each of the $1/D$ independent realizations r of the listening period per day (Table II). This procedure resulted in $1/D$ independent estimates $d_{r,\mathbf{j}}$ of correctness of presence assessment per day. The probability p_p was calculated from all $7/D$ independent $d_{r,j}$ estimates in each acoustic regime, permitting to establish an average probability of correct acoustic presence determination and its standard deviation ($n = 7/D$) for each sampling scheme:

$$\overline{p_p} = \frac{D}{7} \cdot \sum_{j=1}^{7} \sum_{r=1}^{1/D} d_{r,j}. \tag{1}$$

Between-regime comparisons of the results were conducted for selected duty cycles ($\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{10}$, $\frac{1}{20}$, and $\frac{1}{60}$).

2. Daily call rate estimations from subsampled data

Continuous call count data were subsampled according to the schemes listed in Table III, and hourly call rates $\overline{\gamma}$ were estimated from the call rates γ_i of the rth realization in all N cycles of the jth day:

$$\overline{\gamma_{r,j}} = \frac{1}{N} \sum_{i=1}^{N} \gamma_{i,r,j}. \tag{2}$$

This estimation was accomplished for all possible realizations r of listening periods within a cycle providing $1/D$ independent daily call rates $\overline{\gamma_{r,j}}$ per day (Fig. 4).

To assess the variability of call rate estimates within a given sampling scheme, the ratios of call rates from subsampled data and true call rates from continuous data were calculated for all $\overline{\gamma_{r,j}}$:

$$\mathrm{ratio}_{r,j} = \frac{\overline{\gamma_{r,j}} - y_{\mathrm{true}}}{y_{\mathrm{true}}}. \tag{3}$$

This procedure was repeated for all $1/D$ ratios$_{r,j}$ at each day and resulted in $7/D$ independent estimates per regime providing average and standard deviation of call rate estimations at a given subsampling scheme. As animal abundance estimates from acoustic data strongly depend on the accuracy of call rate assessments, the probability p_c of estimating the actual call rate within a range of 10%, 50%, and 100%, respectively, was calculated (Table II). Results from selected duty cycles ($\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{10}$, $\frac{1}{20}$, and $\frac{1}{60}$) were used for between-regime comparisons.

III. RESULTS

Impacts of different subsampling schemes on daily acoustic presence were evaluated by determining the probability of a correct decision regarding acoustic presence.
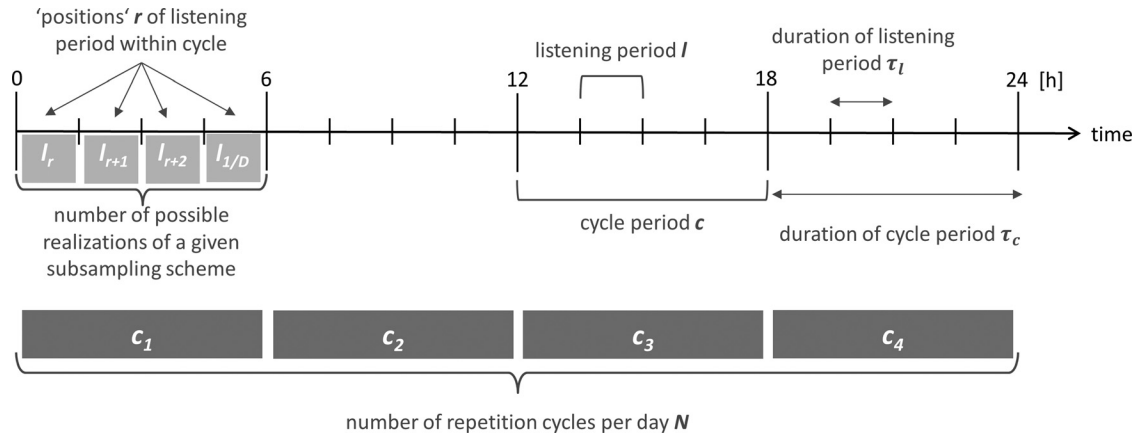
FIG. 3. Exemplary scheme of terms used in the context of subsampling of passive acoustic data.

Subsampling effects on call rate estimates were assessed by considering the probability of call rate estimates better than 10%, 50%, and 100% of the true call rate.

A. Acoustic presence

Analyses of the continuous data sets reveal that ABWs were acoustically present on all days in regimes A, B, C, and D, while NARW up-calls were detected during all days of regime E. The average time-span of hourly acoustic presence varied between regimes, with 24 ± 0 h of acoustic presence per day for regime A and B, 19.43 ± 5.77 h of acoustic presence per day for regime C, 23 ± 2.24 h of acoustic presence per day for regime D and 19.14 ± 2.41 h of acoustic presence per day for regime E.

The probability p_p to correctly assess daily acoustic presence of ABWs and NARWs on the basis of subsampled data was dependent on duty cycle, cycle period and acoustic regime (Fig. 5). While acoustic presence was always assessed correctly for high duty cycles ($D > \frac{1}{4}$), small duty cycles ($D \leq \frac{1}{10}$) underestimated the acoustic presence for some regimes (Fig. 5). Similarly, for a given duty cycle, the probability of estimating presence correctly was smaller for long cycles τ_c (>6 h), i.e., few cycles per day. The repercussions of subsampling also depended strongly on the acoustic regime, i.e., on the vocalization pattern of the focal species. For regimes A, B, and D, subsampling had no or only minor effects on the likelihood of correct presence estimation, even at small duty cycles (Fig. 5). In regime A, acoustic presence was always assessed correctly, regardless of the duty cycle, while in regime B and D presence assessment was correct in at least 97% of cases for all duty cycles (Fig. 5). Contrastingly, effects of subsampling were more pronounced for regimes C and E. While duty cycles of $D > \frac{1}{4}$ did not affect the probability to correctly estimate acoustic presence, this probability decreased at smaller duty cycles for both regimes (Fig. 5). For example, acoustic presence was correctly assessed with a probability of 73% to 90% at $D = \frac{1}{60}$ for regime E, with probabilities decreasing with increasing cycle periods (Fig. 5).
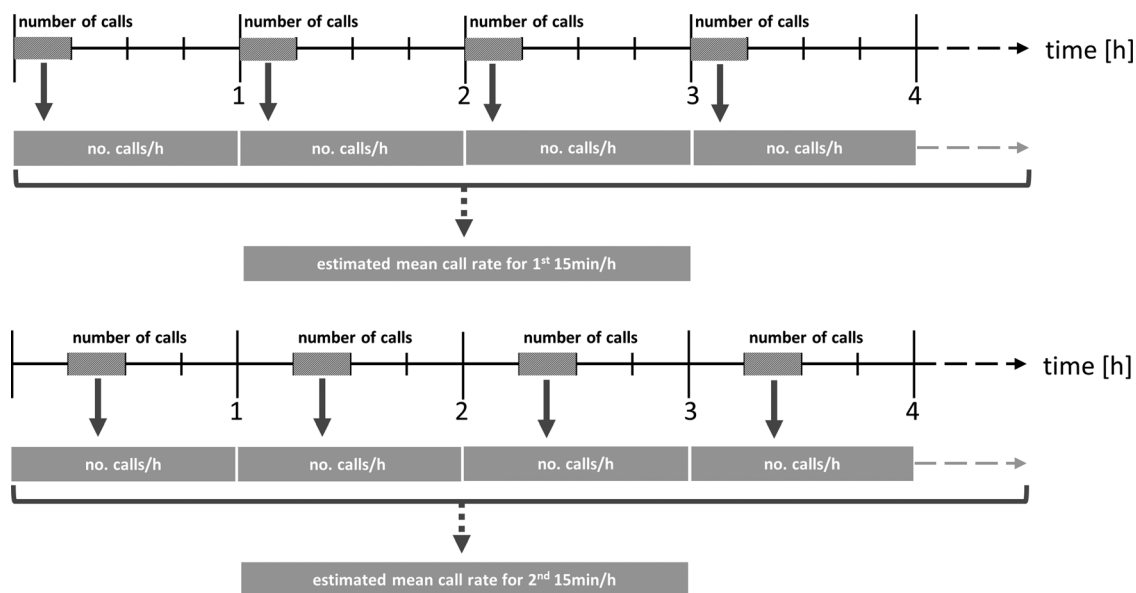

FIG. 4. Exemplary scheme of analysis algorithm to estimate hourly call rates from subsampled passive acoustic data assuming a subsampling scheme of 15 min per hour (DC = [1/4]). Upper panel: first run of algorithm estimating hourly call rates in the first 15 min per hour, lower panel: second run of algorithm estimating hourly call rates in the second 15 min per hour.
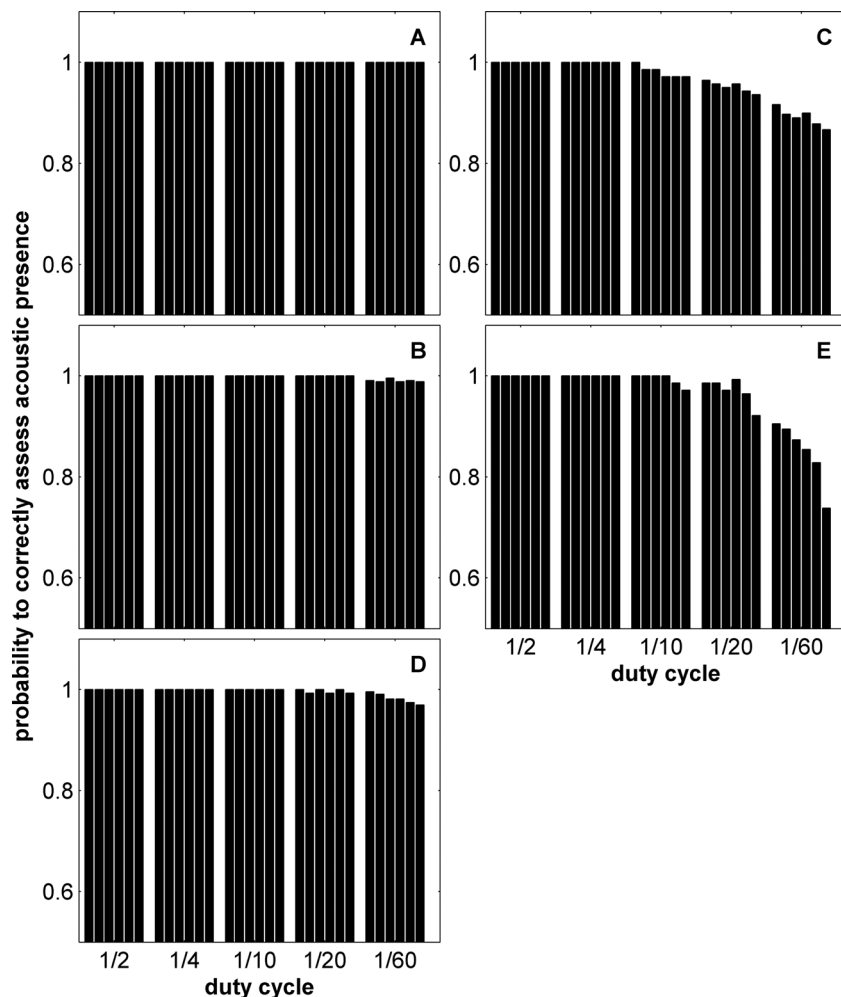
FIG. 5. Between-regime comparisons of probabilities to correctly assess acoustic presence of ABWs and NARWs from subsampled data at different sampling schemes. Letters indicate acoustic regimes with (A) regime A (high ABW call rates), (B) regime B (lower ABW call rates), (C) regime C (single ABW singer), (D) regime D (multiple ABW singers), and (E) regime E (NARW vocalizations with distinct diel pattern). Within a given duty cycle, bars represent different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively).

B. Call rate estimations

The total number of ABW calls detected in the original data sets varied between regimes with 9183 calls in regime A (54.64 ± 17.73 calls per hour), 3353 calls in regime B (19.95 ± 7.96 calls per hour), and 2830 (16.85 ± 8.81 calls per hour) and 5823 calls (34.67 ± 21.65 calls per hour) in regimes C and D, respectively. For regime E, 1945 NARW calls (11.58 ± 6.14 calls per hour) were detected.

Call rates based on subsampled data varied significantly depending on the sampling scheme applied (Fig. 6). Generally, the variability of call rate estimates increased with decreasing duty cycle, i.e., call rates based on subsampling with large duty cycles ($D > \frac{1}{4}$) differed less from the true call rate than call rates based on small duty cycles ($D < \frac{1}{20}$) (Fig. 6). For a given duty cycle, increasing cycle periods τ_c resulted in a higher variability within the call rate estimates, i.e., a more widely spread data distribution and potentially higher deviations from the true call rate (Fig. 6). While this effect was clearly detectable in regime C, D, and E, it was less evident in regimes A and B. In turn, effects of subsampling on call rate estimations also depended strongly on the vocal behavior of the focal species, i.e., the data regime analyzed.

In order to quantify the validity of the call rate estimates from subsampled data, the probability p_c that the call rate estimated from a given subsampling scheme is within a specified range X (with X being 10%, 50%, and 100%, respectively) of the true call rate was assessed (Fig. 7). As expected, the probability to obtain call rate estimates within a certain range of the true call rate depended on the subsampling scheme chosen (i.e., p_c decreased as duty cycle decreased and/or cycle period increased) as well as on the acoustic regime analyzed (Fig. 7). However, effects of subsampling scheme and acoustic regime were much more pronounced at 10% accepted deviation between estimated and true call rates compared to a deviation range of 100%.

The probability p_c to estimate the call rate within 10% of the true call rate was highest for regime A and considerably decreased with duty cycle and cycle period in all regimes (Fig. 7). In regime E, the lowest probability was observed with $p_c < 0.5$ at $D = \frac{1}{2}$ and $p_c < 0.2$ at $D \leq \frac{1}{10}$ (Fig. 7). For estimating the call rates within a 50% range from the true call rate, the probability was highest for regime A with a probability of 1 for all $D \geq \frac{1}{10}$ and of minimally 0.95 at $D \leq \frac{1}{20}$ (Fig. 7). Except for at $D = \frac{1}{2}$ where all call rate estimates were within a 50% range of the true call rate, smaller probabilities were observed for regimes B, C, and D with minimal p_c values of 0.8, 0.55, and 0.76, respectively, at $D = \frac{1}{60}$ (Fig. 7). Regime E exhibited the smallest probabilities at all subsampling schemes analyzed with p_c falling below 0.5 at large cycle periods of duty cycles $D \leq \frac{1}{10}$ (Fig. 7). Finally, the probability to estimate the true call rate
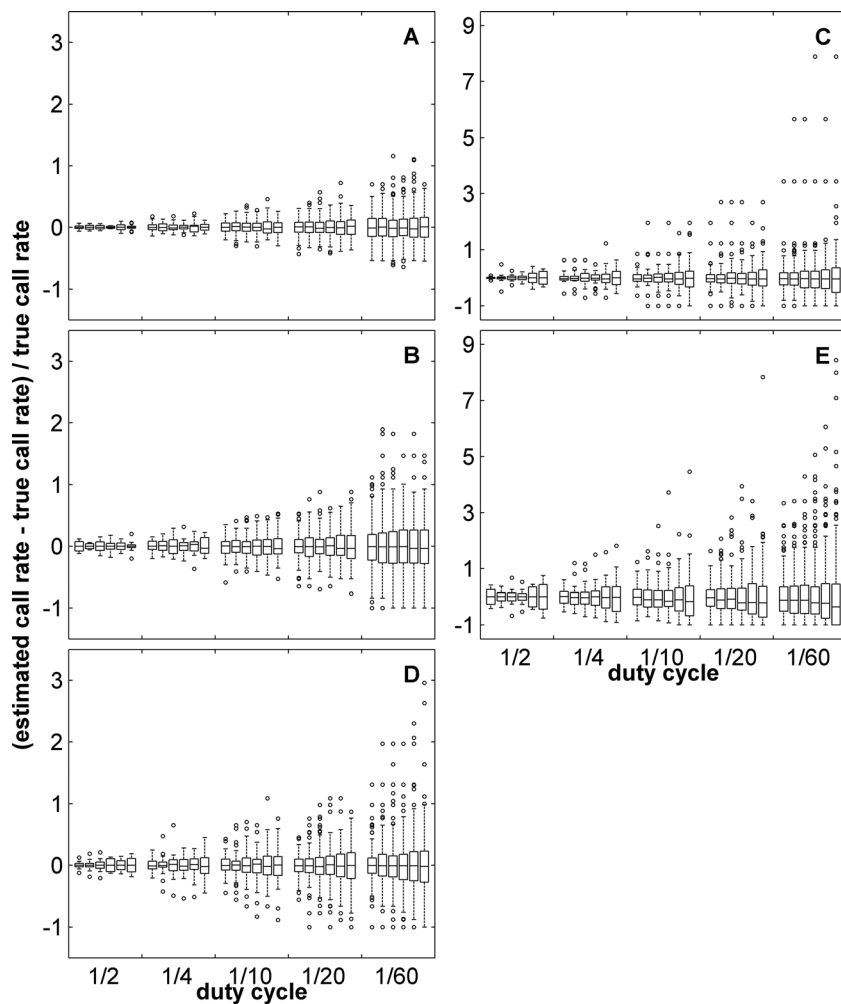
FIG. 6. Between-regime comparisons of ratios of estimated call rates from subsampled data to true call rates at different subsampling schemes. Letters indicate acoustic regimes with (A) regime A (high ABW call rates), (B) regime B (lower ABW call rates), (C) regime C (single ABW singer), (D) regime D (multiple ABW singers), and (E) regime E (NARW vocalizations with distinct diel pattern). Within a given duty cycle, boxplots represent different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively). Note that regimes C and E are differently scaled.

within 100% deviation from the true call rate ranged from 0.97 to 1 for all sampling schemes tested for regimes A, B, and D with little effects of duty cycle and cycle period (Fig. 7). For regime C and E, this probability was smaller for all $D < \frac{1}{2}$ with minimal values of 0.92 and 0.85, respectively (Fig. 7).

IV. DISCUSSION

The present case study shows that subsampling of passive acoustic data can substantially bias acoustic presence estimates or affect the accuracy with which call rates of a focal species are determined, respectively. However, the extent of this effect depends on the subsampling strategy that is applied and the acoustic behavior of the focal species.

A. Overall effect of subsampling acoustic data

Unsurprisingly, large duty cycles generally represented acoustic presence and call rates more accurately than small duty cycles. The acoustic presence of the focal species was increasingly underestimated with decreasing duty cycles. These findings match the trends observed by Riera *et al.* (2013), showing that a duty cycle of $\frac{1}{3}$ resulted in a 24% decline in encounter detections of killer whale calls and a consequent underestimation of the time whales were acoustically present in the data set compared to a larger duty cycle

of $\frac{2}{3}$. In the present study, medium to small duty cycles ($D \leq \frac{1}{10}$) resulted in acoustic presence underestimations of up to 26% for regime E, especially for large cycle periods. These results indicate that temporal clustering of vocal activity is a decisive factor determining the reliability of acoustic presence estimation from subsampled data. In turn, selecting many short samples at short cycle periods may increase the chance of correctly assessing daily acoustic presence, particularly for acoustic data exhibiting strong temporal fluctuation in calling activity.

The accuracy of call rate estimates varied widely across different subsampling schemes without any consistent under- or overestimation of call rates. Deviations from the true call rate were highly variable between regimes and ranged from 100% underestimation to up to 900% overestimation. Generally, the deviation of call rate estimates from the true call rate increased with decreasing duty cycle and increasing cycle periods. This effect was most pronounced in regimes C and E, indicating that the high variability may be a consequence of the (irregular) temporal clustering of calls and/or low calling rates in these regimes.

B. Data regimes

The present study indicates that the organization of vocal activity, i.e., regular (song, regime C and D) or irregular (regime A and B) organization, does not considerably
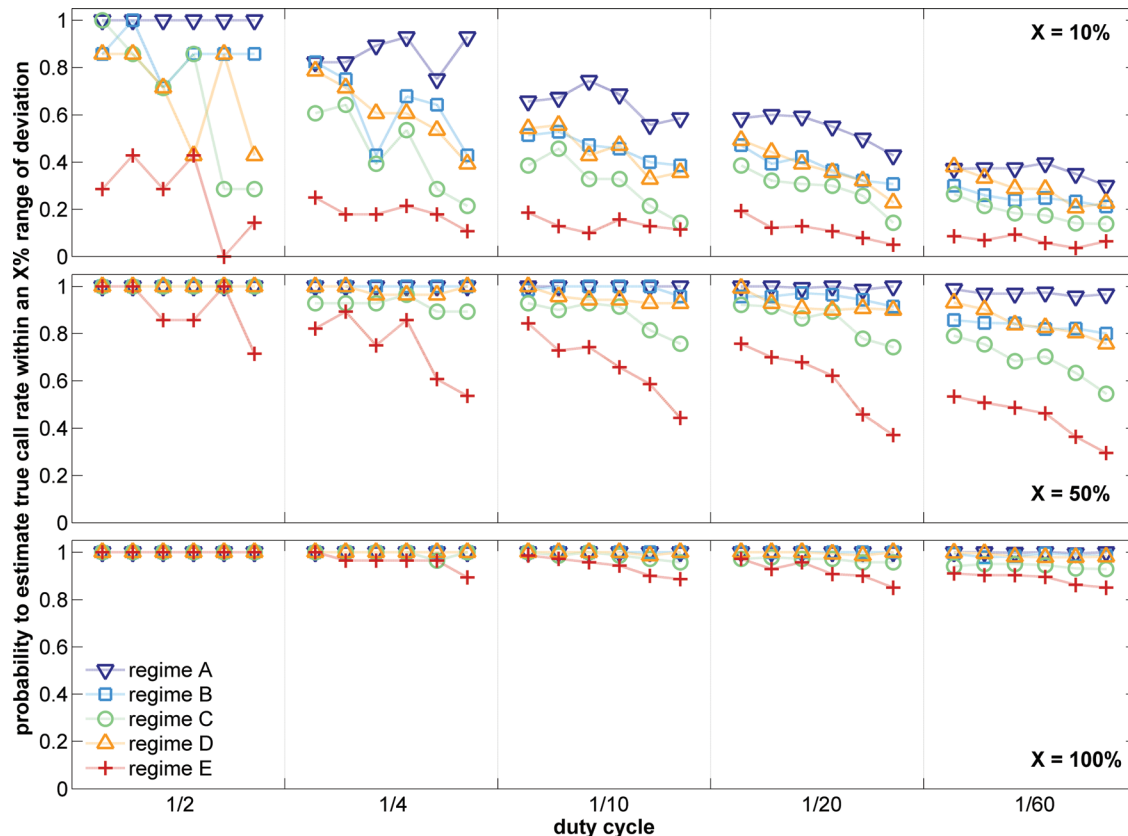
FIG. 7. Between-regime comparisons of probabilities to estimate call rates from subsampled data within a specified range X [with X being 10% (upper panel), 50% (middle panel), and 100% (lower panel), respectively] of the true call rate at different subsampling schemes. Regimes A–E (indicated by different colors) represent different vocal characteristics of the focal species as given in Fig. 6. Within a given duty cycle, markers indicate different cycle periods τ_c (from left to right: 1, 2, 3, 4, 6, and 8 h, respectively).

impact the effects of subsampling. Instead, the calling activity level and potential temporal clustering of the focal species' vocal behavior determine the accuracy with which subsampled data can represent the actual patterns in acoustic behavior. Generally, species with high vocalization rates that call throughout the day are more likely to be detected even with small duty cycles compared to irregularly and/or rarely calling species (Miksis-Olds et al., 2010). This is also reflected in differences in the accuracies of call rate estimates when regime pairs A and B as well as C and D are compared; both basically exhibit the same temporal structure but differ in the frequency of occurrence of calls, showing the more calls, the higher the accuracy of call rate estimates. Highest deviations between estimated and true call rates were observed in regime E, representing vocal behavior with a comparatively low vocalization rate and a distinct diel pattern.

In the context of using passive acoustic data for density estimation of calling animals, highly accurate call rate estimates and/or knowledge on the potential uncertainty of these estimates is crucial, as call rate linearly enters the density estimates (Marques et al., 2013). Under subsampling, most reliable results may be obtained by employing a subsampling strategy that collects short samples at short cycle periods. This will positively affect the accuracy with which cue rates can be assessed as more of the natural variability can be covered by the sampling scheme.

However, subsampling acoustic recordings is not suitable for species vocalizing rarely or to reliably capture unpredictable temporal clusters of acoustic activity, for example, when the species of interest passes the recorder's acoustic range only sporadically. Existing knowledge on the frequency and timing of occurrences of temporal clusters in vocal activity may aid the choice of a subsampling scheme, provided that the patterns in vocal behavior of the focal species are sufficiently well understood.

C. Subsampling strategies

Before deciding on a subsampling strategy, several aspects concerning the research goal need consideration, such as: What is the main purpose of the recording? What is the temporal scale relevant to the investigation (e.g., is collecting multi-year data worth the cost of subsampling to cover the entire deployment period)? What knowledge on acoustic behavior of the focal species is already available, and is this representative for the study area and/or recording season?

Single species studies, for example, investigating acoustic animal density in a given area, might benefit from adjusting the recording parameters as much as possible to the target species. When data storage is the limiting factor, studies investigating low-frequency baleen whale species may decide to lower the sample rate to the minimum required to

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capture only the calls of interest to maximize the time span over which acoustic data can be collected. Alternatively, adaptive subsampling may be considered to selectively capture only the events or species of interest throughout the entire period, although this method is not appropriate to record rarely calling species or short events (e.g., Miksis-Olds *et al.*, 2010; Sousa-Lima *et al.*, 2013). Furthermore, pilot studies during which continuous records are collected in or near the area of interest or information from previous investigations may provide a basis to decide on if and/or which duty cycles are suitable to reliably capture the vocalizations of interest. Recording in a *Matryoshka mode* may provide a solution to collect detailed "snapshots" that can be used to, for example, gauge acoustic animal densities during specific parts of the year. *Matryoshka* mode, referring to the Russian nested dolls, employs continuous or large duty cycles that are again set to cycle over a larger time scale.

For studies aiming to explore acoustic biodiversity or soundscape ecology in an area for which no acoustic records exist yet, it may be inevitable to collect continuous records given that principally all events are of interest. By, for example, continuously collecting a week of data each month, a relatively reliable overview of the event types and species that are (substantially) acoustically present in the vicinity of the recorder may be gained throughout the entire recording time span, depending on the storage and battery capacity of the recording instrument. To reliably capture transiting species or species that frequent the region only sporadically, truly continuous records are the only possibility to collect reliable information. When logistically and financially possible, multiple recorders programmed to record subsequently after the previous one has stopped may allow covering the entire period that the devices are in the water with (near-)continuous acoustic data.

Alongside maximizing the probability of capturing the species of interest, requirements on the acoustic data to answer specific research questions should also be taken into account. For example, humpback whale (*Megaptera novaeangliae*) acoustic presence may be reliably estimated from short samples at short cycle periods data with relatively small duty cycles, however assessing the number of singers and in-detail analyses of song structure require substantially longer samples.

The decision on a certain subsampling strategy is often not primarily (or not at all) driven by biological parameters or considerations. The only recording parameter that in most cases is adapted to meet the specific research objectives is the sample rate, which (when too low) may result in missed call events or species misidentification due to, for example, aliasing (Oswald *et al.*, 2004). The fact that other vocal characteristics of the focal species are not evaluated when deciding on sampling strategies is in most cases not an active decision but rather the result of lacking knowledge on the acoustic behavior for many species (e.g., Mellinger *et al.*, 2007). However, informed decisions on subsampling strategies can only be based on a solid understanding of vocal behavior for which, ironically, a representative acoustic sampling strategy is fundamental. If such information is not available, it may be

preferable to collect continuous samples of limited duration across the year.

Technological developments may sooner or later allow autonomous collection of continuous acoustic records over long time scales with high sample rates, relaxing the need to record in subsampling mode due to instrument limitations. Nevertheless, these extensive data sets also need to be analyzed and stored which are other aspects where subsampling again may come into play. However, in contrast to subsampled recordings, subsampled analyses allow evaluation of the representativeness of the selected sampling strategy by comparisons to the continuous data records, according to the principle applied in the present case study.

V. CONCLUSION

The present case study demonstrates that subsampling acoustic data might have substantial effects on the assessment of acoustic presence and call rate, depending on the vocal characteristics of the focal species. If subsampling at a given duty cycle is mandatory due to logistic constraints, data collection in many short listening periods is preferable. Such sampling scheme results in many sampling cycles per day and hence, enables optimal representation of potential variability in the vocal behavior throughout the day and is best suited for assessments of both acoustic presence and call rate of the focal species.

Vocal characteristics as represented by different acoustic regimes in this study partly affected the accuracy of acoustic presence and call rate estimates from subsampled data. The organization of vocal activity (i.e., in terms of regular or irregular structure of vocalizations) did not markedly affect the results from subsampled data. Contrastingly, differences in vocalization rates had considerable impact on acoustic presence and call rate estimates from subsampled data, with accuracy improving with increasing call rates (in the continuous data). Furthermore, temporal clustering of vocal activity (i.e., diel vocalization pattern) considerably decreased the accuracy with which acoustic presence and call rates were assessed in the present study.

Subsampling during data collection may not be necessary in studies on species vocalizing at low frequencies as the sampling rate may be adjusted to a comparatively low level and in turn, recording continuously during the entire deployment period may be possible. However, subsampling may increasingly become necessary when shifting the focus towards species with high-frequency vocalizations as well as in multi-species studies covering a broad frequency range to investigate an area's acoustic biodiversity or soundscape. While technological advancements concerning power supply and data storage capacities will likely allow acquisition of large (near-)continuous data sets in the near future, human screening of the data will in many cases still be necessary to a certain degree, for example, for verification of automatic detection outcomes, and in turn, may still require subsampling of the total data to be manageable.

Polar oceans are areas where subsampling of acoustic recordings occurs relatively frequently as a consequence of the logistic difficulties of accessing the area. For many

species inhabiting the polar oceans, relatively little is known on acoustic diversity, interactions, and acoustics-based animal densities, whereas gaining insights as to how climate-induced ecosystem changes affect the species in these areas is particularly crucial in the context of monitoring and managing potential changes. Optimizing passive acoustic data collection procedures in terms of sampling strategies lies at the heart of improving the current status of knowledge and providing fundamental information for future management and conservation strategies.

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