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Diurnal variation in freshwater ecoacoustics: Implications for site-level sampling design

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Abstract

1. Ecoacoustic methods are increasingly used to monitor the state of populations and ecosystems. In freshwater environments, they present the clear advantages of being non-invasive, reducing bias, and providing continuous observations instead of only limited sampling snapshots in time. However, similar to standard bioassessment methods, temporal variation and choice of indicators can greatly influence ecoacoustic assessments, highlighting the importance of sampling and analysis design.

2. In this study, we quantified diurnal variation in underwater sound and its effect on sampling regimes for two waterholes in the Einasleigh River, Northern Australia. Recording continuously for 6 days, and subsampling 5 s every 10 min, we found 22 distinct sounds that were emitted by fish, Hemiptera and Coleoptera as well as another 22 of abiotic or unknown origin.

3. Through rarefaction analyses, we found that subsampling the data to 60% of the recorded sound events resulted in capture of most of the 44 identified sound types. Temporal heterogeneity—patchy sound events through time—needs to be considered when maximising detected sound events. Reducing the sampling interval from every 10 min to half-hourly or hourly had a much greater effect on capturing all sound types compared to the number of days recorded or the length of the recording. Overall, only 10–20% of the sound events need to be annotated for most sound types to be described; for example, restricting analysis of the days recorded to only three and the recording interval to 0.5–1 s. Acoustic indices were dominated by three main event types—a diurnally flowing creek, a nocturnal chorus of Hemiptera, as well as a dawn chorus of terapontid fishes.

4. We conclude with two key messages: First, a select group of informative signals can be monitored using very simple methods—namely, converting an audio stream into indices using freely available software. Second, however, to detect less acoustically dominant sound events, manual annotation or single call processing will still be needed. While these findings are encouraging, similar analysis will need to be conducted within other freshwater ecosystems before general conclusions about optimal sampling regimes can be drawn.

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1 | INTRODUCTION

Acoustics, as a tool to monitor and assess ecosystems, is gaining traction globally (Servick, 2014). These techniques are not new; bird and amphibian research has used acoustics in monitoring extensively for over 40 years (Laiolo, 2010; Mossman, Hartman, Hay, Sauer, & Dhuey, 1998; Obrist et al., 2010). Likewise, cetacean research has used acoustic monitoring, including long-term listening stations, since the late 1970s (Sousa-Lima, Norris, Oswald, & Fernandes, 2013). Advantages of acoustic approaches include continuous long-term monitoring in the absence of an observer, monitoring of areas that are difficult to access, and the ability to verify and validate data even years after measurement (Frommolt, Tauchert, & Koch, 2008). In recent years, the *single species* focus of bioacoustics has morphed into more holistic science—the field of ecoacoustics (Sueur & Farina, 2015)—which sees the soundscape as a data source for information about the ecology of populations, communities, and landscapes (Sueur & Farina, 2015).

Bioacoustics in freshwater systems has existed for two millennia—the first record can be attributed to Aristotle, who in his *Historia Animalium* (Aristotle, 500BC/1910) described the sound production mechanisms of major soniferous fish families with surprising anatomical accuracy. A large body of freshwater bioacoustic studies exists, but is dispersed among disciplines. Most of these have been either anatomical or behavioural studies (see Ladich, 2015 for an up-to-date comprehensive overview). While described in single publications, reference sounds and descriptive call characteristics are not readily accessible in archives such as the Cornell Library or the Berlin Animal Sound Archive. Nevertheless, about 10 years ago, multiple groups in the U.S.A. started a new initiative to use passive acoustics as a monitoring tool in freshwater habitats (Luczkovich, Mann, & Rountree, 2008; Rountree et al., 2006). As this study will show, integration of biological knowledge into ecoacoustic assessments is vital to the design of freshwater acoustic monitoring methods.

Most ecoacoustic analyses for environmental monitoring utilise either single species approaches or holistic soundscape analysis. Acoustic single species monitoring has been used extensively in terrestrial systems to track trajectories of endangered birds (Grava, Mathevon, Place, & Balluet, 2008; Holmes, McIlwrick, & Venier, 2014), bats (Murray & Kurta, 2004), and anurans (Willacy, Mahony, & Newell, 2015). In the marine realm, apart from applications in cetacean research and conservation (Klinck et al., 2012; Mellinger et al., 2007), acoustic monitoring has also been applied to fish (Erisman & Rowell, 2017; Hernandez et al., 2013) and could potentially be used to survey crustacea, such as spiny lobsters and mantis shrimp (Staaterman, 2016). In freshwater systems, single species monitoring has been used to automate detection of spawning events (Straight, Freeman, & Freeman, 2014) but also to detect presence of invasive fish such as Tilapia (Kottege, Jurdak, Kroon, & Jones, 2015). Automatic algorithms

to detect and monitor bioacoustics events are species-specific and perform better when customised manually, rather than using commercial software (Digby, Towsey, Bell, & Teal, 2013). If the aim of a monitoring programme is to detect change in communities or habitats, the need to identify single species sounds would be a key disadvantage as sounds will have to be individually characterised and counted.

The second set of techniques evaluates the soundscape, often by calculating acoustic indices instead of quantifying single sound events. These indices are analogous to ecological community metrics, such as richness, diversity, and evenness (Farina, Buscaino, Ceraulo, & Pieretti, 2014; Sueur, Farina, Gasc, Pieretti, & Pavoine, 2014). Soundscape approaches were developed in a terrestrial setting (Pieretti, Farina, & Morri, 2011; Sueur, Pavoine, Hamerlynck, & Duvail, 2008) and have been used to monitor birds (Depraetere et al., 2012; Lellouch, Pavoine, Jiguet, Glotin, & Sueur, 2014) but also marine environments, mainly reefs (Harris, Shears, & Radford, 2016; Kennedy, Holderied, Mair, Guzman, & Simpson, 2010). Ecoacoustic indices are just beginning to be used in freshwater systems, for example, a recent study by Desjonquères et al. (2015), who investigated the acoustic properties of freshwater ponds in France with both indices and single calls. A second study (Geay et al., 2017) has used an acoustic index to estimate bedload transport in rivers. In this paper, we will use both of these ecoacoustic approaches: annotated single calls from a subsample, and a variety of ecoacoustic indices.

To anyone familiar with the dawn chorus of birds, considering diurnal variation in acoustic surveys is intuitive. Ecoacoustic studies on diurnal variation have been conducted in recent years (Farina et al., 2014), one of them explicitly aimed at optimising sampling regimes (Pieretti et al., 2015). However, the latter study was only focussed on acoustic indices. To our knowledge, there is no published study that has (1) considered diurnal variation of single calls and ecoacoustic indices simultaneously; and (2) examined diurnal variation of ecoacoustics in freshwater communities.

This study describes three main approaches to investigate the design and analysis of ecoacoustic monitoring of the study site:

1. Description of diurnal variation in both acoustic events and acoustic indices,
2. Comparison of the efficiency of automatic and manual methods of acoustic diversity estimation to highlight major acoustic events, and
3. Estimation of optimal sampling design by testing the loss of information resulting from different sampling strategies (varying number of days, duration of recordings, and intervals between recordings).

To achieve this, we analysed temporal variation in underwater sound across the 6 days in two ways. First, we subsampled the calls using different strategies, including sampling effort, targeted times of

TABLE 1 Summary of rarefaction analyses

Rarefaction objective	Randomisation analysis conducted
Sampling effort—number of calls annotated	Sampling 0%–100% of original calls in 0.5% increments
Sampling effort—sample time	Sampling 0.5–5 s of each 5 s block
Sampling repeat—number of days	Sampling all combinations of 1, 2, 3…6 days
Sampling interval	Sampling every 10, 20, 30 … 360 min

day and subsampling different combinations of the 6 days. Second, we calculated five acoustic indices and analysed their total variation as a function of recording duration.

2 | METHODS

2.1 | Study area

The Einasleigh is a tropical river, which flows into the Gulf of Carpentaria, North Queensland. The Gilbert–Einasleigh system is the largest river system in northern Australia in a monsoonal climate. The river typically flows during the wet season (January–March), then slowly contracts to a series of waterholes. We recorded acoustic activity in two connected waterholes (18.116994S, 143.965225E) from 19–24 August 2016, starting and ending at 1:33 p.m. Waterhole 1 (approximately 4 m in diameter and 80 cm deep) was connected to waterhole 2 (approximately 10 m long, 4 m wide, 1 m deep) by a small creek section that was flowing daily between 2 and 8 p.m. We started recording 18 hr after a full moon. We used two Aquarian Audio H2a hydrophones (sensitivity: −180 dB re: 1V/μPa) that were mounted 20 cm below the water surface and continuously recording in the field using a Zoom H2 recorder set to maximum gain (10) at 44.1 kHz/16-bit. To count the number of fish species in the waterholes, we used WaterWolf V1 underwater cameras—footage was manually analysed.

2.2 | Sound event annotation and classification

As it was impossible to annotate the entire recording fully (we estimate that a million sound events were present in the 6-day recording), we trialled different subsampling regimes. We settled on subsampling 5 s every 10 min, as this seemed to capture most sounds in our trials. We annotated 8,097 sound events in the recordings—compared with 2,793 annotated by Ruppé et al. (2015) and 2,446 annotated by Desjonquères et al. (2015). The start and end times of each sound event were annotated in Adobe Audition CC 2015.

As with the studies mentioned above, we were unable to definitively link the annotated sounds to particular species, but they were classified into sound types. To keep the categories consistent within a single observer, the first run of classification and annotation was conducted by one of the authors (E.D.) followed by a full revision

by two of the authors (S.L. and E.D.) in which 130 initial sound types were consolidated to a final 44. Similar to Desjonquères et al. (2015), classification into different sound types was conducted by simultaneously evaluating visual and aural cues in Adobe Audition CC 2015—classes were defined by grouping sound events with similar frequency, duration and periodicity. We were then able to categorise into five classes as follows: (1) fish; (2) coleoptera; (3) hemiptera; (4) unknown biological; and (5) environmental. We split the calls of Terapontid fishes into four classes using a statistical classification (see Supporting Information Appendix S1). Similarly, hemiptera and dytiscid beetles have distinct stridulation patterns of which we have reference recordings for several (but not all) of the taxa that we recorded in isolation (see Supporting Information Table S1, Supporting Information Figure S1). Hemiptera display a sharper, higher pitched *zipping* sound (see Supporting Information Audios S1, S2, and S3c) while the reference beetles we collected sonify with a duller scraping sound (see Supporting Information Audios S4 and S5). In addition to our own reference recordings, we based the classification on a previous study by one of the team members (Desjonquères et al., 2015). Each sound event was then annotated by start and end time.

2.3 | Rarefaction of sound events

After we classified the 8,097 sound events into 44 sound types, we calculated rarefaction curves by subsampling within the classified dataset (see Table 1). To determine total sampling effort needed to detect all sound types, we randomly picked 5-s blocks and counted the number of captured sound types, sampling between 0% and 100% of the total annotated time. To quantify the potential loss of sound types by not sampling over 24 hr, we counted the number of sound types in 4-hr bins. We split the dataset into six 4-hr blocks centred around midday and midnight and capturing dusk and dawn in one block (2–6, 6–10, 10–14, 14–18, 18–22, 22–2). We calculated median, 25th and 75th percentile within each of the blocks for the 6 days. This was then graphed as box plots.

To determine the interacting effects of sample duration, duration of interval between samples and number of days recorded on the number of sound types captured, we employed different rarefaction regimes. We first reduced the sample duration within each 5-s block, varying sample duration from 0.5 to 5 s in increments of 0.5. We calculated all possible combinations of 1, 2, 3 … 6 days and increased the sampling interval in increments of 10 min, between 10 and 360 min. For intervals >10 min, we randomised the start time to get the maximum number of permutations. For all of these rarefaction analyses, we calculated 100 permutations of the sample combinations.

2.4 | Acoustic indices

Using the R packages seewave (Sueur, Aubin, & Simonis, 2008) and soundecology (Villanueva-Rivera, Pijanowski, & Villanueva-Rivera, 2016), we calculated five acoustic indices (Table 2)—restricting

TABLE 2 Acoustic indices used in the analysis

Index	Description/rationale
M (Depraetere et al., 2012):	Median of the amplitude envelope—an indicator of overall sonic activity
H (acoustic entropy index; Sueur, Pavoine, et al., 2008)	Measures diversity across frequency bins and time
ACI (acoustic complexity index; Pieretti et al., 2011)	Measures spectrogram complexity within frequency bins
$ACI_{500-1,000\,Hz}$ (ACI between 500 and 1,000 Hz)	ACI within the activity window of the soniferous fish
$ACI_{5-20\,kHz}$ (ACI between 5 and 20 kHz)	ACI within the activity window of the insect choruses

ourselves to α-indices to simplify the time-series analysis. With an FFT window of 512, we used a 60 s sample of frequencies between 0 and 20 kHz every 2 min. The subsampling was conducted as the final GLMM models (see below) proved very computationally intensive and we could reduce computational time. This yielded a total of 4,311 observations; eight observations were missing as they corresponded to times where an SD card and/or battery was being swapped.

To investigate the effect of time on the five index values in the pools, we used generalised linear mixed models (GLMM; Baayen, 2008) with a Gaussian error structure and identity link function, similar to Desjonquères et al. (2015). To examine the daily cyclic effects of time on the richness, we transformed time into a 24-hr circular variable and included its sine and cosine in the model (Cox, 2006). Since the effect of time may have differed between the two pools if they hosted different species, we included the interaction between pond and the sine and cosine in the model. Recording day was included as a random effect. To keep the type I error rate at the nominal level of 5% (Schielzeth & Forstmeier, 2008), we included all possible random slopes components (sine and cosine of time within both transect point and recording day and pond within recording day) as well as respective correlations between random slopes and intercepts. As an overall test of the fixed effects, we compared the full model with a null model lacking the fixed effects but comprising the same random effects structure as the full model (Forstmeier & Schielzeth, 2011) using a likelihood ratio test. Models were stable, as assessed by comparing the estimates derived by a model based on all data with those obtained from models with the levels of random effects excluded one at a time. The variance inflation factors (Miles, 2014) for a standard linear model excluding random effects and interactions were 1 for sine and cosine of time, as well as pool indicating that there was no collinearity issue.

3 | RESULTS

Our final classification contained five types of fish sounds, comprising distinct calls (see Supporting Information Appendix S1) and noises that we classified as feeding sounds as observed by underwater video. The classification of feeding sounds was derived from a pilot study in which we had filmed two species of Terapontidae feeding and rustling around the hydrophone (Supporting Information Videos S1 and S2). Additionally, other biological sounds were classified into six sound types classed as aquatic Hemiptera, 10 sound types classed as aquatic Coleoptera as well as one sound of unknown origin (Supporting Information Table S1, Supporting Information Figure S1). The remaining sound classes were either physical processes (flow, sediment movement, wind) or sounds suspected to be of terrestrial origin, such as bird calls. While terrestrial sounds were more audible in the shallower waterhole 1, the total number of biological sound types from fish, Hemiptera and Coleoptera was substantially higher in waterhole 2.

3.1 | Rarefaction of sound events

The accretion curves for both waterholes plateaued at about 60% of our observations (Figure 1a). However, when keeping the audio channels separate, more effort would have been needed to guarantee completeness in capturing sound types, especially in the second pool (Figure 1b). Figure 2 demonstrates that completeness would be far from achieved when sampling for limited hours only. The highest sound type richness in an interval was 24—representing slightly more than half of all observed types—in the morning hours between 6 and 10 a.m., while we observed 14 or fewer distinct sounds during samples from two periods, 6–10 p.m. and 2–6 a.m.
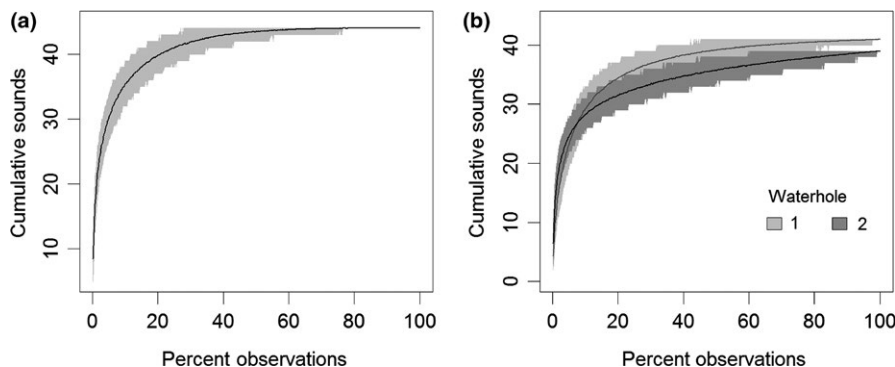

FIGURE 1 Accretion of identified sounds recorded in two connected waterholes in northern Australia, in relation to proportion of sampling time analysed. Curves are shown (a) for the two waterholes combined and (b) for each individual waterhole. Grey whiskers are 95% confidence intervals
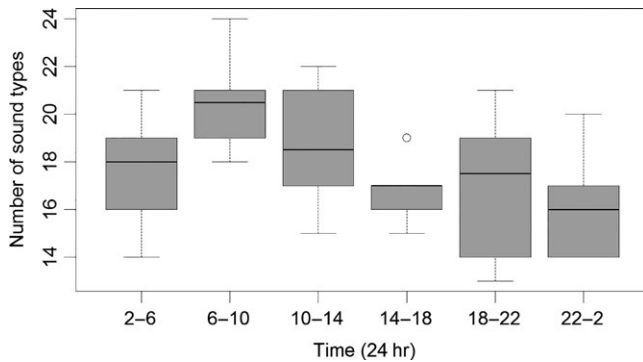
FIGURE 2 Sound richness recorded in two connected waterholes, showing median, interquartile and extreme values for 4-hr bins across a 24-hr period

Interval between recordings was the main driver in the accretion curve (Figure 3a,b). When varying both the number of days and the recording time from 0.5 to 5 s and plotting against the recording interval, the fastest drop-offs occurred when the interval was increased from 10 to 20 or 30 min. Once the interval had increased to 60 min, between 8 and 10 sound types were missed (18%–23%). Both recording time and the number of days recorded had a lesser effect, with recording time hardly noticeable. Even with only 0.5 s recorded per 10 min interval, 40 calls would still be recovered on average, missing only four (9%). Similarly, dropping from 6 to 3 days would be hardly noticeable, with still 40 sound types detected (also missing 9%). Single days would reduce the average number of detected call types by 30%.

The shape of the day/recording time relationship (Figure 3c) has consequences for the amount of effort needed for different levels of precision. While the full recording schedule (6 days at 5 s every 10 min) has 8,097 sound events, 99.8% of sound types on average can be retrieved when only analysing 2 s every 10 min (see Table 3)—thereby reducing the total number of sound events by close to 50% (4058.9 on average). This is close to being halved again when recording for 1 s every 10 min for 5 days (2121.4 calls/41.9 types). Thus, 39.7 calls (i.e. only 4.3 missing) on average can be identified with only 1215.5 annotated calls (4 days, 0.5 s) and with 11% of the effort (885 calls), still 83% of the sound types (36 types).

3.2 | Diurnal heterogeneity revealed by acoustic indices

All five acoustic indices showed similar patterns of daily variation. M (the median amplitude) had dual peaks for the dominant classes of sound events—the groundwater-fed creek that flowed every day from midday to after dusk (diurnal events between 0 and 4 kHz, Figure 4) and the nocturnal chorus of aquatic Hemiptera that started faintly in nights 1 and 2, but increased steadily over nights 3–6. ACI was dominated by the creek flow, while the targeted bands $ACI_{500-1,000\,Hz}$ and $ACI_{5-20\,k}$ showed additional peaks for soniferous fish (small humps at around 8 am) and the insect chorus (high nocturnal bands from 5 to 15 k, peaking at 2 a.m.).

All five GLMMs revealed significant interactions between circular time and pool (Supporting Information Table S2), indicating that in the two pools acoustic indices reveal daily cycles of acoustic activity (Figure 4). These cycles are not fully in phase for the two pools. Most of the time, the peak of activity occurred earlier in the left pool (See Supporting Information Table S2). Moreover, some indices reveal slightly staggered cycles for the same pool (Supporting Information Table S2, Figure 4).

4 | DISCUSSION

Our study shows that relatively small snapshots can be sufficient to capture sound richness in a tropical river system as shown by the rarefaction curves (Figure 1). However, monitoring applications in this environment should not rely on a single acoustic sample or on acoustic samples from a single time of day. In a similar system, Desjonquères et al. (2015) found differences between both sound richness and accretion rate between different nearby ponds. Ponds with a lower sound richness plateaued out earlier, while full accretion was not reached in the pond with the highest richness. In this study, accretion curves fully plateaued in the combined data and were close to plateauing in the split channels. We suspect that the cause of difference between our study and Desjonquères et al. (2015) is the overall call rate. We identified on average 53.5 sound events in every analysed minute, whereas the French study only found 7.7/min. As with ecological studies of species/area relationships, we recommend that the relationship between habitat diversity, number of species and call diversity should be studied in all habitats in more detail.

We demonstrated that acoustic analysis is highly sensitive to diurnal variation, albeit easier to incorporate temporal aspects into sampling programmes. The first study to highlight temporal issues with optimal acoustic monitoring was conducted almost 20 years ago (Bridges & Dorcas, 2000). As automatic scheduling of recordings was not available at the time, the authors could not recommend an optimal schedule, but only estimate that under the standard protocols, up to 30% of species could be missed. This is consistent with our assessment—as we found that in any 4-hr period, only between 25% and 50% of sound types could be identified (Figure 2). A comprehensive subsampling strategy for ecoacoustics was devised by Pieretti et al. (2015), who—similar to this study—found that in a tropical environment, a 24-hr recording schedule was necessary to capture the main patterns. This is in line with the findings that even in traditional fish surveys, diurnal sampling can be key to taxonomic completeness (Arrington & Winemiller, 2003; Baumgartner, Stuart, & Zampatti, 2008). However, since acoustic methods are more readily conducted continuously than other assessment methods, they are better adapted to accounting for temporal variation.

Our study focused on diurnal variation, showing more variation within than between days but seasonal variation can also be a substantial source of heterogeneity in the data. We recorded for 6 continuous days during the dry season of a monsoonal climate. We expect that for this particular study site the soundscape during the wet season would be significantly different. However, during the dry season, we expect the temporal dynamics to be dominated by lunar
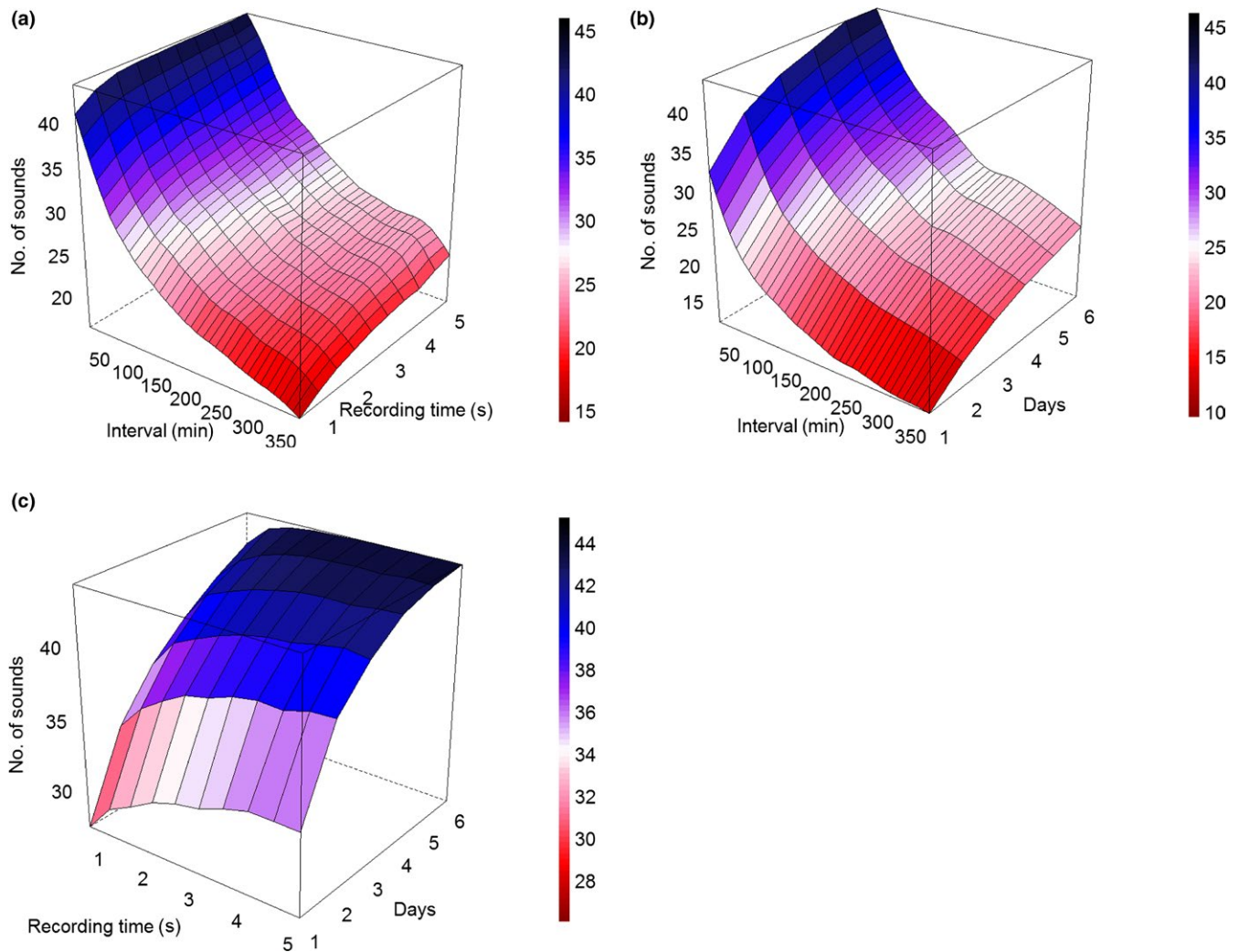
FIGURE 3 Effect of (a) recording interval versus recording time, (b) recording interval versus number of recording days and (c) number of recording days versus recording time on the sounds captured

TABLE 3 Example combinations of times and days recorded when keeping recording interval constant at 10 min. Note that with even 11% of the effort, still 83% of the sound types can be found.

Days recorded	Seconds per subsample	Number of sound events	Number of sound types	Percentage of sound events (%)	Percentage of sound types (%)
6	5	8097	44	100	100
6	2	4058.9	43.92	50.1	99.8
5	1	2121.4	41.91	26.2	95.3
4	0.5	1194	38.63	14.7	87.8
3	0.5	884.9	36.36	10.9	82.6

and diurnal cycles, rather than annual variations, as the water-borne taxa are restricted to isolated waterholes, or relatively short sections of river for which the water flow is above ground. It would therefore be interesting to investigate the potential interplay between diurnal and seasonal variation in freshwater environments.

A key limiting factor to acoustic analyses is the need to manually annotate acoustic events. In freshwater systems where sound types are not as readily known, this can be extremely time consuming. We found that both replication by recording consecutive days, as well as the sample length, were less important than a higher temporal resolution (Figure 3). As sound events are usually patchy—think of a bird chorus that often does not last long—this makes intuitive sense taking shorter samples from more locations (or time slots) will maximise detections. While trading off recording time and temporal resolution
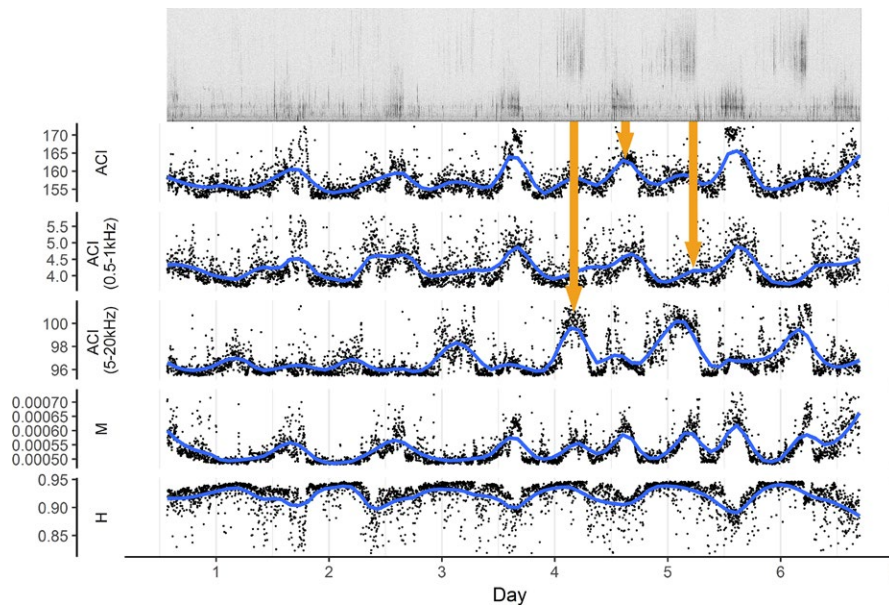
FIGURE 4 Diurnal cycles of the spectrogram and the used indices. Arrows indicate (from left to right): Hemiptera, creek flow, and fish chorus. The blue line is a trend line fitted in R. Grey lines on time axis indicate midnight

does not matter in automated index analysis, it matters greatly when manually annotating acoustic events. We found that to reach near completeness, a 1-s snippet every 10 min for 4 days would result in recovering 95% of calls—while only 21% of the acoustic events would need to be annotated (Figure 4; the diagram). However, even annotating 1,700 events would take a long time, potentially rendering unautomated single call acoustic monitoring prohibitive as a rapid technique (Wimmer, Towsey, Roe, & Williamson, 2013). This will hopefully not be a problem in the future with the advent of fully automated analysis techniques.

Revisiting the bioassessment debates of the late 1990s suggests a potential solution that does not require annotation of full datasets: not all species—or in this case calls—have to be captured for ecological assessment, as long as degradation or other main effects are detectable. Acknowledging that taxonomic completeness is not needed for assessment shifted the effort involved in assessments from full count surber samples that were used earlier, to rapid protocols that usually only needed 5–10% of the identification effort (Chessman, 1995; Metzeling & Miller, 2001), while revealing the same trends. However, determining optimal sampling effort that trades off sensitivity with processing cost depends on the objective of the assessment (Bennett, Rühland, & Smol, 2016; Bennett et al., 2014). Although there have been some advances in the theory of ecoacoustic assessments, we suggest that new frameworks that focus on the monitoring objectives should be developed. While this study develops a framework to evaluate sampling effort required for monitoring programmes, sensitivity analysis for any monitoring programme needs to be conducted before sampling regimes can be implemented.

In this study, we contrast single call analysis with an approach based on ecoacoustic indices. We investigated whether single sound types can definitely influence acoustic indices. The nightly peaks

in ACI (Figure 4) are primarily due to Hemipteran activity—probably from the genus *Micronecta*, for which we recorded an individual (not yet identified to species level) in the laboratory. These peaks do not appear in the first 2 days and increase in intensity on a daily basis, which we attribute to the full moon in the beginning of the recording period. When the moon was below 80% of maximum luminance (according to meteorological data), insect calls started to intensify. Lunar cycles have been widely described in the evaluation of underwater acoustic activity in marine systems: for example, a study of acoustic events on reefs showed that acoustic activity of soniferous fish was highest during quarter moon and new moon periods (Staaterman et al., 2014). While, in this study, we only looked at diurnal cycles, lunar or annual cycles will have to be examined and accounted for in any monitoring programme—standard procedure in other assessment schemes (Hilsenhoff, 1988; Linke, Bailey, & Schwindt, 1999). That M and ACI pick up significant peaks when the Hemipteran taxon with the highest call frequency starts confirms the notion that complexity should not be confused with richness or diversity. Although the effect of snapping shrimp on acoustic indices has been described in marine systems (McWilliam & Hawkins, 2013), dominance of single events on acoustic indices warrants increased discussion and further investigation.

We found the utility of acoustic indices in this study limited to detection of three distinct processes: the sounds of the intermittent stream during the day, the nocturnal insect chorus, and—if appropriate bands are selected—also the fish chorus in the morning. These are picked up in varying magnitudes by several indices. The flow events were captured by $ACI_{500-1,000\,Hz}$ and H (Figure 4). The fish chorus was only captured in the filtered $ACI_{500-1,000\,Hz}$ as an additional hump in the mornings, which confirms the recommendation by Gage and Axel (2014) that analysing bandpass-filtered signals can act as a simple proxy for species detection. The remaining indices

(ACI, M) were sensitive to both the stream flow signal and insect chorus, albeit with varying dominant peaks. The agreement between indices was to some degree unexpected and contrary to other studies that often found no correlation between different indices (Depraetere et al., 2012; Fairbrass, Rennett, Williams, Titheridge, & Jones, 2017; Harris et al., 2016). We explain this by suggesting that the flow noises and nightly insect chorus are such strong signals, they override most other acoustic events.

Unfortunately, no single index picked up the high acoustic richness between 6 and 10 a.m. While correlations between sound type richness and well calibrated acoustic indices have been described in the past (Depraetere et al., 2012; Desjonquères et al., 2015), a lack of correlation is also not unprecedented: Harris et al. (2016) for example, found correlations of acoustic indices with species diversity and evenness, but not with richness. We consider this analogous to the description of rare taxa in conventional sampling and monitoring programmes. Rare taxa are often discarded in biodiversity assessments, as they introduce noise (Linke, Norris, & Pressey, 2008). This is an ongoing issue in all survey techniques for which a potential solution would be automated call detection, a bioacoustic technique demonstrated in freshwater systems on fish (Straight et al., 2014) and frogs (Kottege et al., 2015) which unfortunately needs a large library of currently unavailable reference calls (Linke et al., 2018).

The evident diurnal variation—both in single species calls and acoustic indices—indicates that recording schedules in this environment need to be carefully tailored to the objectives of the monitoring programme. As manual annotation of sound types remains a time-intensive activity, efficient subsampling is an important consideration for practical monitoring applications. Whilst the rarefaction curves in this study have been derived for a particular site, and a particular time of year (dry season in a monsoonal climate), our approach of shorter duration extracts with smaller intervals between them (compared with typical ecoacoustic schedules) may be useful in other contexts for which animal sonifications are short, numerous and temporally clumped. The ecoacoustic indices afforded detection of three types of biophysical process: fish calls, insect choruses, and river flow. The response of these indices to diurnal variation in the dominant sounding taxa suggests that the relationship between sound complexity and species diversity is not straightforward. However, the existence and observability of such temporal dynamics in the soundscape may enable future studies to collect valuable information about animal behaviour patterns, physical dynamics, and interactions between these.

CONFLICT OF INTEREST

There is no conflict of interest.

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REFERENCES

Aristotle, Historia Animalium. (1910). *In* D. A. W. Thompson, The works of Aristotle. Historia animalium: Clarendon Press, Oxford, UK.

Arrington, D. A., & Winemiller, K. O. (2003). Diel change-over in sandbank fish assemblages in a neotropical flood-plain river. *Journal of Fish Biology*, *63*, 442–459. https://doi.org/10.1046/j.1095-8649.2003.00167.x

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/cbo9780511801686

Baumgartner, L. J., Stuart, I. G., & Zampatti, B. P. (2008). Determining diel variation in fish assemblages downstream of three weirs in a regulated lowland river. *Journal of Fish Biology*, *72*, 218–232. https://doi.org/10.1111/j.1095-8649.2007.01696.x

Bennett, J. R., Rühland, K. M., & Smol, J. P. (2016). No magic number: Determining cost-effective sample size and enumeration effort for diatom-based environmental assessment analyses. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 208–215.

Bennett, J. R., Sisson, D. R., Smol, J. P., Cumming, B. F., Possingham, H. P., & Buckley, Y. M. (2014). Optimizing taxonomic resolution and sampling effort to design cost-effective ecological models for environmental assessment. *Journal of Applied Ecology*, *51*, 1722–1732. https://doi.org/10.1111/1365-2664.12312

Bridges, A. S., & Dorcas, M. E. (2000). Temporal variation in anuran calling behavior: Implications for surveys and monitoring programs. *Copeia*, *2000*, 587–592. https://doi.org/10.1643/0045-8511(2000)000[0587:tviacb]2.0.co;2

Chessman, B. C. (1995). Rapid assessment of rivers using macroinvertebrates: A procedure based on habitat-specific sampling, family level identification and a biotic index. *Australian Journal of Ecology*, *20*, 122–129. https://doi.org/10.1111/j.1442-9993.1995.tb00526.x

Cox, N. J. (2006). Speaking Stata: In praise of trigonometric predictors. *Stata Journal*, *6*, 561–579.

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., & Sueur, J. (2012). Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. *Ecological Indicators*, *13*, 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006

Desjonquères, C., Rybak, F., Depraetere, M., Gasc, A., Le Viol, I., Pavoine, S., & Sueur, J. (2015). First description of underwater acoustic diversity in three temperate ponds. *PeerJ*, *3*, e1393. https://doi.org/10.7717/peerj.1393

Digby, A., Towsey, M., Bell, B. D., & Teal, P. D. (2013). A practical comparison of manual and autonomous methods for acoustic

monitoring. *Methods in Ecology and Evolution*, 4, 675–683. https://doi.org/10.1111/2041-210x.12060

Erisman, B. E., & Rowell, T. J. (2017). A sound worth saving: Acoustic characteristics of a massive fish spawning aggregation. *Biology Letters*, 13. https://doi.org/10.1098/rsbl.2017.0656

Fairbrass, A. J., Rennett, P., Williams, C., Titheridge, H., & Jones, K. E. (2017). Biases of acoustic indices measuring biodiversity in urban areas. *Ecological Indicators*, 83, 169–177. https://doi.org/10.1016/j.ecolind.2017.07.064

Farina, A., Buscaino, G., Ceraulo, M., & Pieretti, N. (2014). The soundscape approach for the assessment and conservation of Mediterranean landscapes: Principles and case studies. *Journal of Landscape Ecology*, 7, 10–22. https://doi.org/10.2478/jlecol-2014-0007

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65, 47–55. https://doi.org/10.1007/s00265-010-1038-5

Frommolt, K. H., Tauchert, K. H., & Koch, M. (2008). *Advantages and disadvantages of acoustic monitoring of birds–realistic scenarios for automated bioacoustic monitoring in a densely populated region*. In: *Computational Bioacoustics for Assessing Biodiversity. Proceedings of the Internat. Expert Meeting on IT-based Detection of Bioacoustical Patterns*. BfN-Skripten (pp. 83–92).

Gage, S. H., & Axel, A. C. (2014). Visualization of temporal change in soundscape power of a Michigan lake habitat over a 4-year period. *Ecological Informatics*, 21, 100–109. https://doi.org/10.1016/j.ecoinf.2013.11.004

Geay, T., Belleudy, P., Gervaise, C., Habersack, H., Aigner, J., Kreisler, A., … Laronne, J. (2017). Passive acoustic monitoring of bed load discharge in a large gravel bed river. *Journal of Geophysical Research: Earth Surface*, 122, 528–545.

Grava, T., Mathevon, N., Place, E., & Balluet, P. (2008). Individual acoustic monitoring of the European Eagle Owl Bubo bubo. *Ibis*, 150, 279–287.

Harris, S. A., Shears, N. T., & Radford, C. A. (2016). Ecoacoustic indices as proxies for biodiversity on temperate reefs. *Methods in Ecology and Evolution*, 7, 713–724. https://doi.org/10.1111/2041-210x.12527

Hernandez, K. M., Risch, D., Cholewiak, D. M., Dean, M. J., Hatch, L. T., Hoffman, W. S., … Van Parijs, S. M. (2013). Acoustic monitoring of Atlantic cod (*Gadus morhua*) in Massachusetts Bay: Implications for management and conservation. *Ices Journal of Marine Science*, 70, 628–635. https://doi.org/10.1093/icesjms/fst003

Hilsenhoff, W. (1988). Seasonal correction factors for the biotic index. *Great Lakes Entomologist*, 21, 9–14.

Holmes, S. B., McIlwrick, K. A., & Venier, L. A. (2014). Using automated sound recording and analysis to detect bird species-at-risk in south-western Ontario woodlands. *Wildlife Society Bulletin*, 38, 591–598. https://doi.org/10.1002/wsb.421

Kennedy, E. V., Holderied, M. W., Mair, J. M., Guzman, H. M., & Simpson, S. D. (2010). Spatial patterns in reef-generated noise relate to habitats and communities: Evidence from a Panamanian case study. *Journal of Experimental Marine Biology and Ecology*, 395, 85–92. https://doi.org/10.1016/j.jembe.2010.08.017

Klinck, H., Mellinger, D. K., Klinck, K., Bogue, N. M., Luby, J. C., Jump, W. A., … Schorr, G. S. (2012). Near-real-time acoustic monitoring of beaked whales and other cetaceans using a Seaglider™. *PLoS ONE*, 7, e36128. https://doi.org/10.1371/journal.pone.0036128

Kottege, N., Jurdak, R., Kroon, F., & Jones, D. (2015). Automated detection of broadband clicks of freshwater fish using spectro-temporal features). *The Journal of the Acoustical Society of America*, 137, 2502–2511. https://doi.org/10.1121/1.4919298

Ladich, F. (2015). *Sound communication in fishes* (p. 250). Vienna, Austria: Springer. https://doi.org/10.1007/978-3-7091-1846-7

Laiolo, P. (2010). The emerging significance of bioacoustics in animal species conservation. *Biological Conservation*, 143, 1635–1645. https://doi.org/10.1016/j.biocon.2010.03.025

Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H., & Sueur, J. (2014). Monitoring temporal change of bird communities with dissimilarity acoustic indices. *Methods in Ecology and Evolution*, 5, 495–505. https://doi.org/10.1111/2041-210x.12178

Linke, S., Bailey, R. C., & Schwindt, J. (1999). Temporal variability of stream bioassessments using benthic macroinvertebrates. *Freshwater Biology*, 42, 575–584. https://doi.org/10.1046/j.1365-2427.1999.00492.x

Linke, S., Gifford, T., Desjonquères, C., Tonolla, D., Aubin, T., Barclay, L., … Sueur, J. (2018). Freshwater ecoacoustics as a tool for continuous ecosystem monitoring. *Frontiers in Ecology and the Environment*, 16, 231–238.

Linke, S., Norris, R. H., & Pressey, R. L. (2008). Irreplaceability of river networks: Towards catchment-based conservation planning. *Journal of Applied Ecology*, 45, 1486–1495. https://doi.org/10.1111/j.1365-2664.2008.01520.x

Luczkovich, J. J., Mann, D. A., & Rountree, R. A. (2008). Passive acoustics as a tool in fisheries science. *Transactions of the American Fisheries Society*, 137, 533–541. https://doi.org/10.1577/t06-258.1

McWilliam, J. N., & Hawkins, A. D. (2013). A comparison of inshore marine soundscapes. *Journal of Experimental Marine Biology and Ecology*, 446, 166–176. https://doi.org/10.1016/j.jembe.2013.05.012

Mellinger, D. K., Nieukirk, S. L., Matsumoto, H., Heimlich, S. L., Dziak, R. P., Haxel, J., … Miller, H. V. (2007). Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. *Marine Mammal Science*, 23, 856–867. https://doi.org/10.1111/j.1748-7692.2007.00144.x

Metzeling, L., & Miller, J. (2001). Evaluation of the sample size used for the rapid bioassessment of rivers using macroinvertebrates. *Hydrobiologia*, 444, 159–170. https://doi.org/10.1023/a:1017571200859

Miles, J. (2014). *Tolerance and variance inflation factor*. Wiley StatsRef: Statistics reference online. Hoboken, NJ: John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118445112.stat06593

Mossman, M. J., Hartman, L. M., Hay, R., Sauer, J. R., & Dhuey, B. J. (1998). Monitoring long-term trends in Wisconsin frog and toad populations. In M. J. Lannoo (Ed.), *Status and conservation of midwestern amphibians* (pp. 169–198). Iowa City, IA: University of Iowa Press. https://doi.org/10.2307/j.ctt20q20cw

Murray, S. W., & Kurta, A. (2004). Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). *Journal of Zoology*, 262, 197–206. https://doi.org/10.1017/s0952836903004503

Obrist, M. K., Pavan, G., Sueur, J., Riede, K., Llusia, D., & Márquez, R. (2010). Bioacoustics approaches in biodiversity inventories. *Abc Taxa*, 8, 68–99.

Pieretti, N., Duarte, M. H. L., Sousa-Lima, R. S., Rodrigues, M., Young, R. J., & Farina, A. (2015). Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Tropical Conservation Science*, 8, 215–234. https://doi.org/10.1177/194008291500800117

Pieretti, N., Farina, A., & Morri, D. (2011). A new methodology to infer the singing activity of an avian community: The acoustic complexity index (ACI). *Ecological Indicators*, 11, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005

Rountree, R. A., Gilmore, R. G., Goudey, C. A., Hawkins, A. D., Luczkovich, J. J., & Mann, D. A. (2006). Listening to fish: Applications of passive acoustics to fisheries science. *Fisheries*, 31, 433–446. https://doi.org/10.1577/1548-8446(2006)31[433:ltf]2.0.co;2

Ruppé, L., Clément, G., Herrel, A., Ballesta, L., Décamps, T., Kéver, L., & Parmentier, E. (2015). Environmental constraints drive the partitioning of the soundscape in fishes. *Proceedings of the National Academy of Sciences*, 112, 6092–6097. https://doi.org/10.1073/pnas.1424667112

Schielzeth, H., & Forstmeier, W. (2008). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, 20, 416–420.

Servick, K. (2014). Eavesdropping on ecosystems. *Science*, 343, 834–837. https://doi.org/10.1126/science.343.6173.834

Sousa-Lima, R. S., Norris, T. F., Oswald, J. N., & Fernandes, D. P. (2013). A review and inventory of fixed autonomous recorders for passive acoustic monitoring of marine mammals. *Aquatic Mammals*, *39*, 23. https://doi.org/10.1578/am.39.1.2013.23

Staaterman, E. (2016). Passive acoustic monitoring in benthic marine crustaceans: A new research frontier. In W. W. L. Au & M. O. Lammers (Eds.), *Listening in the ocean* (pp. 325–333). Berlin, Germany: Springer. https://doi.org/10.1007/978-1-4939-3176-7

Staaterman, E., Paris, C. B., Deferrari, H. A., Mann, D. A., Rice, A. N., & D'alessandro, E. K. (2014). Celestial patterns in marine soundscapes. *Marine Ecology Progress Series*, *508*, 17–32. https://doi.org/10.3354/meps10911

Straight, C. A., Freeman, B. J., & Freeman, M. C. (2014). Passive acoustic monitoring to detect spawning in large-bodied catostomids. *Transactions of the American Fisheries Society*, *143*, 595–605. https://doi.org/10.1080/00028487.2014.880737

Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*, 213–226. https://doi.org/10.1080/09524622.2008.9753600

Sueur, J., & Farina, A. (2015). Ecoacoustics: The ecological investigation and interpretation of environmental sound. *Biosemiotics*, *8*, 493–502. https://doi.org/10.1007/s12304-015-9248-x

Sueur, J., Farina, A., Gasc, A., Pieretti, N., & Pavoine, S. (2014). Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acustica United with Acustica*, *100*, 772–781. https://doi.org/10.3813/aaa.918757

Sueur, J., Pavoine, S., Hamerlynck, O., & Duvail, S. (2008). Rapid acoustic survey for biodiversity appraisal. *PLoS ONE*, *3*, e4065. https://doi.org/10.1371/journal.pone.0004065

Villanueva-Rivera, L. J., & Pijanowski, B. C. (2016). Soundecology: Soundscape Ecology. R package version 1.3.2. https://CRAN.R-project.org/package=soundecology

Willacy, R. J., Mahony, M., & Newell, D. A. (2015). If a frog calls in the forest: Bioacoustic monitoring reveals the breeding phenology of the endangered Richmond Range mountain frog (*Philoria richmondensis*). *Austral Ecology*, *40*, 625–633. https://doi.org/10.1111/aec.12228

Wimmer, J., Towsey, M., Roe, P., & Williamson, I. (2013). Sampling environmental acoustic recordings to determine bird species richness. *Ecological Applications*, *23*, 1419–1428. https://doi.org/10.1890/12-2088.1

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