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scientific reports

The biological soundscape of temperate reefs in the Wadden sea

Maryann S. Watson[1,2]✉, Annebelle C.M. Kok[1], Ilse van Opzeeland[3,4] &
Britas Klemens Eriksson[1]

Monitoring coastal marine habitats presents many challenges. Often, using multiple approaches to capture different aspects of ecosystems can strengthen the information gained regarding habitat status. The use of passive acoustics to document, describe, and monitor coastal habitats through soundscapes presents one such complementary technique. Marine soundscapes have not yet been described for the Wadden Sea; an ecosystem where reef habitats have experienced major changes over time due to various human-mediated impacts. Recordings at a subtidal shellfish reef and neighbouring sandflat at six 2-week periods over a 14 month period in 2021 and 2022 provide a first catalogue of biotic acoustic signatures in this ecosystem. Furthermore, recordings from two natural reef sites were compared to recordings from two recently deployed artificial reef sites, showing similar patterns of greater biotic acoustic diversity at the natural and artificial reefs compared to nearby sandflats. These results demonstrate that fine-scale differences in habitat soundscapes exist across reef habitats within small geographic scales. This study provides the foundations for further quantitative research using PAM to monitor soundscape dynamics of the Wadden Sea and understanding the role of sound in changing coastal ecosystems.

Keywords Reefs, Soundscape, Passive acoustic monitoring, Coastal, Wadden sea

Coastal ecosystems harbour highly productive habitats that provide specific ecological services to coastal communities, while also confronting various stressors and threats from human activities[1,2]. Monitoring of these marine habitats is therefore crucial to understanding impacts, managing activities, and protecting vulnerable species. However, the marine environment presents many challenges to biodiversity surveys, including the high effort and costs for manual or visual sampling and vessel operations. In addition, physical hurdles in coastal waters, such as variable visibility and light conditions for visual or video-based surveys, as well as harsh weather or hydrodynamic conditions, can preclude regular sampling. In areas of consistent high turbidity there is still a high reliance on extractive sampling methods that often take irregular and seasonally biased snapshots of the biological communities[3]. Developing and testing non-invasive techniques that can collect data autonomously, at large scales with lower investment, is therefore of high priority to support effective management tools to protect coastal biodiversity. In this paper we provide a first baseline for passive acoustic monitoring (PAM) of temperate reefs in northern Europe. We show that PAM can provide an exciting and promising method to monitor coastal habitat characteristics under difficult conditions, providing continuous data on the acoustic activity and composition of marine communities.

Sound is a fundamental part of all ecosystems, and the specific physical features and ecological communities that comprise a habitat result in distinct acoustic patterns, or soundscapes[4,5]. Coastal habitats dominate marine soundscape studies, with much of the efforts to date concentrated on coral reefs, while temperate biogenic habitats (i.e., seagrass, kelp, and shellfish reefs) have received little to no attention in bioacoustic research[6,7]. To date, studies on temperate coastal habitats studies reported higher abundances of fish[4,8] and mobile invertebrate sounds in structured coastal habitats compared to coastal areas that lack these features[9].

Our knowledge of the diversity of marine species that both produce and use sounds is rapidly growing. Sounds produced by marine organisms may be incidental, such as closing shells of bivalves[10], the movements of schooling fish[11], or feeding sounds (e.g., parrotfish or sea urchins)[12,13]. However, sounds are also produced intentionally for communication, prey detection, or for navigation[14,15]. The initial identification of species using passive acoustic monitoring (PAM) often requires a visual confirmation by simultaneous camera captures, visual sightings or catch data of the sound-producing species (e.g., Mouy et al. 2018[16]). For marine mammals, vocal

[1]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, Netherlands. [2]Coastal Systems, Royal Netherlands Institute for Sea Research (NIOZ), Den Hoorn, Noord Holland, Netherlands. [3]Ocean Acoustics Lab, Helmholtz Center for Polar and Marine Research, Alfred-Wegener Institute, Am Handelshafen 12, 27570 Bremerhaven, Germany. [4]Helmholtz Institute for Functional Marine Biodiversity (HIFMB), Carl vonOssietzky University, Ammerlander Heerstrasse 231, 26129 Oldenburg, Germany. ✉email: m.s.watson@rug.nl

repertoires have been relatively well described for the majority of species and acoustic identification based on sound alone is an established method in this field (e.g.,Van Opzeeland et al. 2020[17]). However, for most fish and invertebrate species, these acoustic baselines are still lacking[18]. Documenting and cataloguing sound types and detections across coastal habitats is a key next step in developing PAM[19]. Marine soundscapes may be indicative of biological activity at multiple levels[20]. Therefore, even where sounds cannot be identified to species, descriptions of acoustic signatures has been used to characterize the underwater soundscapes of marine habitats, e.g., reflecting community diversity and its fluctuations over space and time[4,21,22].

Here, we investigated the biological sound assemblages present on subtidal shellfish reefs and adjacent soft-sediment habitats in the western Dutch Wadden Sea. The Wadden Sea is a temperate shallow sea, fringing the southern border of the North Sea. To date, knowledge of the biological soundscape of the Wadden Sea is in its infancy with no prior research that the authors are aware of. We had two goals: (1) describe common biological underwater sound types of this shallow sediment dominated marine system; and (2) add to the body of soundscape research on temperate biogenic habitats, such as shellfish reefs, by comparing the diversity and abundance of underwater sound types to areas without biological structures (bare sand). We tested this by comparing sounds on a subtidal oyster reef and an adjacent bare area over time. We then compared these results with single samplings at another subtidal oyster reef and with two nearby artificial reef sites to confirm both temporal and spatial consistency of effects.

Methods

Site description

The Wadden Sea is a vast temperate tidal soft-sediment dominated ecosystem composed of a mosaic of habitats, including intertidal flats, subtidal banks and gullies, shipwrecks, dykes, harbours, and other infrastructure. It also holds a number of natural shellfish reefs that are mainly intertidal in the present day as most subtidal biogenic reefs have experienced significant historical declines, including seagrass meadows, mussel beds (*Mytilus edulis*) and oyster reefs (historically *Ostrea edulis*, but now dominated by the introduced *Magallana gigas*)[23,24]. These biogenic habitats provide important complex structures and support spawning, feeding and sheltering functions for fish and invertebrates[25–28], and contribute to the coastal mosaic of habitats. Oyster reefs have been found to have distinct soundscapes from neighbouring habitats such as soft-sediment areas[9], making these areas a focal point for our investigation into habitat specific sounds and documenting biological sound types in the Wadden Sea. Compared to the intertidal areas of the Wadden Sea, subtidal habitats, and particularly the mobile communities that use these habitats, are an understudied aspect of this dynamic ecosystem[29].

Reef sound recordings used for this experiment were taken at four subtidal reefs in the in western Wadden Sea (Fig. 1). Natural subtidal oyster reefs are rare throughout the Dutch Wadden Sea. However, based on the local knowledge of fishermen, two oyster reefs were identified in the Marsdiep tidal basin (Nieuweschild, 53.06887, 4.88103; and Kornwerderzand: 53.09392, 5.20231, Fig. 1A). In addition, we could complement this with monitoring at two artificial reef sites which were deployed in April 2022 in the Eilandse Gat tidal basin (trees constructed in pyramids placed in blocks of 9, each pyramid approximately 3 m^3 in size:[30] Keteldiep channel artificial reef: 53.222473, 5.012396 ; and Engelse Vaarwater channel artificial reef: 53.207747, 5.0389429, Fig. 1A). Extremely turbid waters due to large amounts of mobile sediment lead to very low visibility throughout the Wadden Sea;[31] this prevented the use of cameras or other visual methods to survey these sites.

Acoustic recordings

Recordings were collected with SoundTrap 300STD hydrophones (Ocean Instruments, NZ; sampling rate 24 kHz, set at *high gain;* Supplementary Material). Hydrophones were set to record continuously for two weeks. At each site, we recorded soundscapes simultaneously on the reef and at a paired off-reef sand station without any reef structures. The on-reef hydrophones were placed on top of the natural oyster reefs, or in the middle of the groups of artificial reef structures. The off-reef hydrophones were placed at the same depth on the bare sand at a distance of 200 m from each reef site.

Two deployment set-ups were used. At both oyster reef sites, hydrophones were mounted in PVC frames (Fig. 1B) and were deployed using two anchors in the directions of tidal flow; a subsurface buoy ensured that the hydrophone was positioned horizontally approximately 1 m above the seafloor in water depths ranging from 2 to 5 m. At the artificial reef sites where tidal currents can be much stronger within the tidal channels, hydrophones were mounted onto heavy iron frames, here the hydrophone was positioned vertically with the hydrophone facing upward approximately 50 cm above the seafloor (Fig. 1C).

Due to logistical constraints (i.e. weather conditions, accessibility) we were able to be most consistent with deployments at the Nieuweschild site, where recordings at the on- and off-reef locations were taken 6 times over a 2-year period; in April, June, August, and October 2021, and in June and October 2022. A concurrent recording was taken on and off the oyster reef Kornwerderzand in June 2022. At the two artificial reef sites continuous 3-day recordings were taken on and off the reefs at the end of September 2022 as part of the beginning of a longer reef monitoring scheme.

Acoustic analyses

Spectrograms of recordings were manually inspected by the same observer (M.S.W) in RavenPro (Version 1.5, Cornell Lab of Ornithology, Ithaca, New York, USA), with the frequency window of 0–12 kHz, the time range of the view set at 5 min (using a Hann window of 512 samples at 50% overlap), and the brightness and contrast settings for the spectrograms kept consistent. Distinct biological sound types were coded in each recording. Due to the lack of previous work done in the area, sound type codes were developed iteratively, and naming conventions, where possible, were based on previous biological sound typing work (e.g., drum, growl, grunt, knock etc.)[30]. Our goal in this study was not to link sounds to fish species at this time, however sounds produced

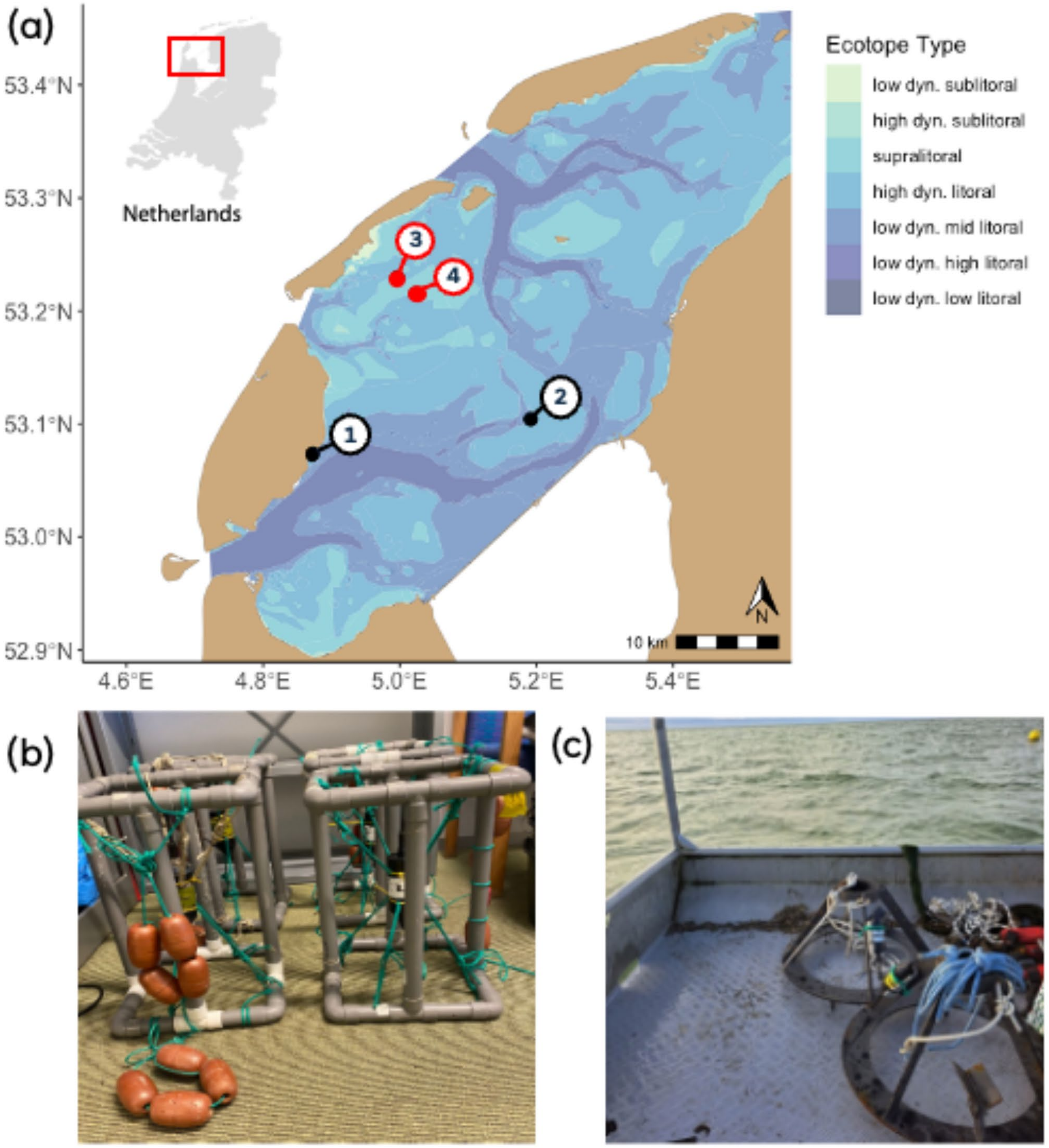

Fig. 1. (a) Map of recording sites: (1) Nieuweschild (2) Kornwerderzand (3) Keteldiep artificial reef (4) Engelse Vaarwater artificial reef. Black circles indicate the shellfish reef sites and red circles indicate the artificial reef sites. Bathymetry data and ecotope classifications from Baptist et al. 2019[32]. Hydrophones suspended in PVC frames used for recordings at sites Nieuweschild and Kornwerderzand, and (c) hydrophones on metal frames used at the artificial reef sites.

by harbour seals (*Phoca vitulina*) were identified to species as part of another study (Willmer et al. In prep)[33] using previous documentation of Sabinsky et al. (2017) and Bjørgesæter et al. (2004)[34,35].

The most commonly found sound types that were identified as being of biotic origin were selected to use for this analysis (i.e., those that were detected > 50 times at all sites). Sound type presence was examined by calculating the proportion of 10-minute samples across the entire recordings in which each sound type was present (*sensu*[36]).

Noise filtering

In PAM analysis, noise is unwanted sound signals that interfere with detections of sounds of interest, and can be of natural and anthropogenic origin[37]. Tidal flow and wave noise had a high influence on background noise in recordings at all sites; noise from rain, vessels and aircraft were also present in the recordings to a much lesser extent. Noise sources were not quantified in this study due to our focus on documenting biological sound sources. Samples with high noise which had insufficient quality for the manual processing (determined to be a threshold SPL of 110 dB) were removed from the analyses. This threshold was found by first selecting five 10-minute samples at low, medium, and high noise periods from 4 recordings at 4 different sites through manual inspection. The broadband means across 100–12,000 Hz were calculated using the Triton software package in Matlab[38,39], inspection revealed that these samples did indeed fall within distinct noise groups (Figure S4). The patterns of broadband noise also followed tidal cycles with slack water being the quietest (Figure S3). The actual detections of sound types within the recordings were then plotted against the broadband mean noise for each 10-minute recording period, where 99% of sound type detections fell below 110 dB. This led to removal of an average of 14% of 10-minute files per recording for the subsequent calculations of sound type presence (Table 1).

Statistical analyses

At the Nieuweschild site, multivariate analysis of sound type proportions was used to investigate differences in the soundscape over time between the on- and off-reef sound types, and between daylight and overnight periods. The test statistic was calculated using PERMANOVA (permutational multivariate ANOVA) with the proportion of 10-minute samples in which each sound type was present as the response variable. Sampling period, daytime (day vs. night) and reef effects (on- vs. off-reef), were included in the model as fixed independent factors. Using a sequential PERMANOVA and entering the sampling period first in the model, meant that the variation depending on sampling period was accounted for in the analysis of day vs. night and reef effects. Each of the six sampling periods was included as a replicate in the analysis. We also illustrated the differences visually by non-metric multidimensional scaling (NMDS) plots. All multivariate analysis used Bray-Curtis dissimilarities as distance measures and the analysis was carried out in RStudio (R version 4.2.2 2022-10-31;[40] using the *vegan* package[41]. We also tested the spatial consistency of the reef effect on sounds by calculating the proportion of total sound type presence in each recording at all four sites. From this we calculated the log response ratio of the reef effect (the natural logarithm of [the total proportion of sound registered on a reef divided by the total proportion of sound registered at their paired off-reef control]). The difference between sound proportions registered on-reef compared to off-reef were then tested statistically using a paired t-test and by calculating the confidence interval for the log-response ratio.

Results

We found 14 biological sound types that were detected 50 or more times across the recording periods. These were categorized as bubble-buzz, chuck, clicks, drum, grunt, growl-buzz, horn, knock, knock-snap, scrape, snap, seal growl, seal "sneeze", and seal "pop" (Fig. 2). The 11 non-seal sound types were used for further analysis to inspect diurnal and seasonal patterns and to compare the on- with the off-reef habitats.

Site	Deployment Number	Stations	Coordinates	Deployment Dates	Number 10-minute samples	Number of 10-minute samples after noise filtering	Proportion of files after filter
Nieuweschild	1	Oyster reef	53.06887, 4.88103	2021-04-12–2021-04-24	2417	2255	0.933
		Sand	53.06939, 4.88254		2741	2306	0.841
	2	Oyster reef		2021-06-02–2021-06-21	2808	2749	0.979
		Sand			2685	2577	0.96
	3	Oyster reef		2021-08-16–2021-09-04	2841	2717	0.956
		Sand			2615	2384	0.912
	4	Oyster reef		2021-10-14–2021-10-25	2615	2384	0.912
		Sand			2773	2506	0.904
	5	Oyster reef		2022-05-22–2022-06-10	2951	2823	0.957
		Sand			2774	2592	0.934
	6	Oyster reef		2022-10-30–2022-11-11	1917	1349	0.704
		Sand			1917	676	0.353
Kornwerderzand	1	Oyster reef	53.09392, 5.20231	2022-05-24–2022-06-12	2884	2809	0.974
		Sand	53.09323, 5.20433		2636	2150	0.816
Keteldiep	1	Artificial reef	53.223001, 5.010292	2022-09-28–2022-09-30	259	244	0.942
		Sand	53.22233, 5.01313		336	221	0.658
Engelse Vaarwater	1	Artificial reef	53.20438, 5.033648	2022-10-11–2022-10-13	306	266	0.869
		Sand	53.207747, 5.0389429		307	272	0.886

Table 1. A summary of the recording site and deployments with the number of 10-minute samples obtained from each recording, and the number and proportion of 10-minute samples that were used for the analyses after applying the noise filtering at 110dB.

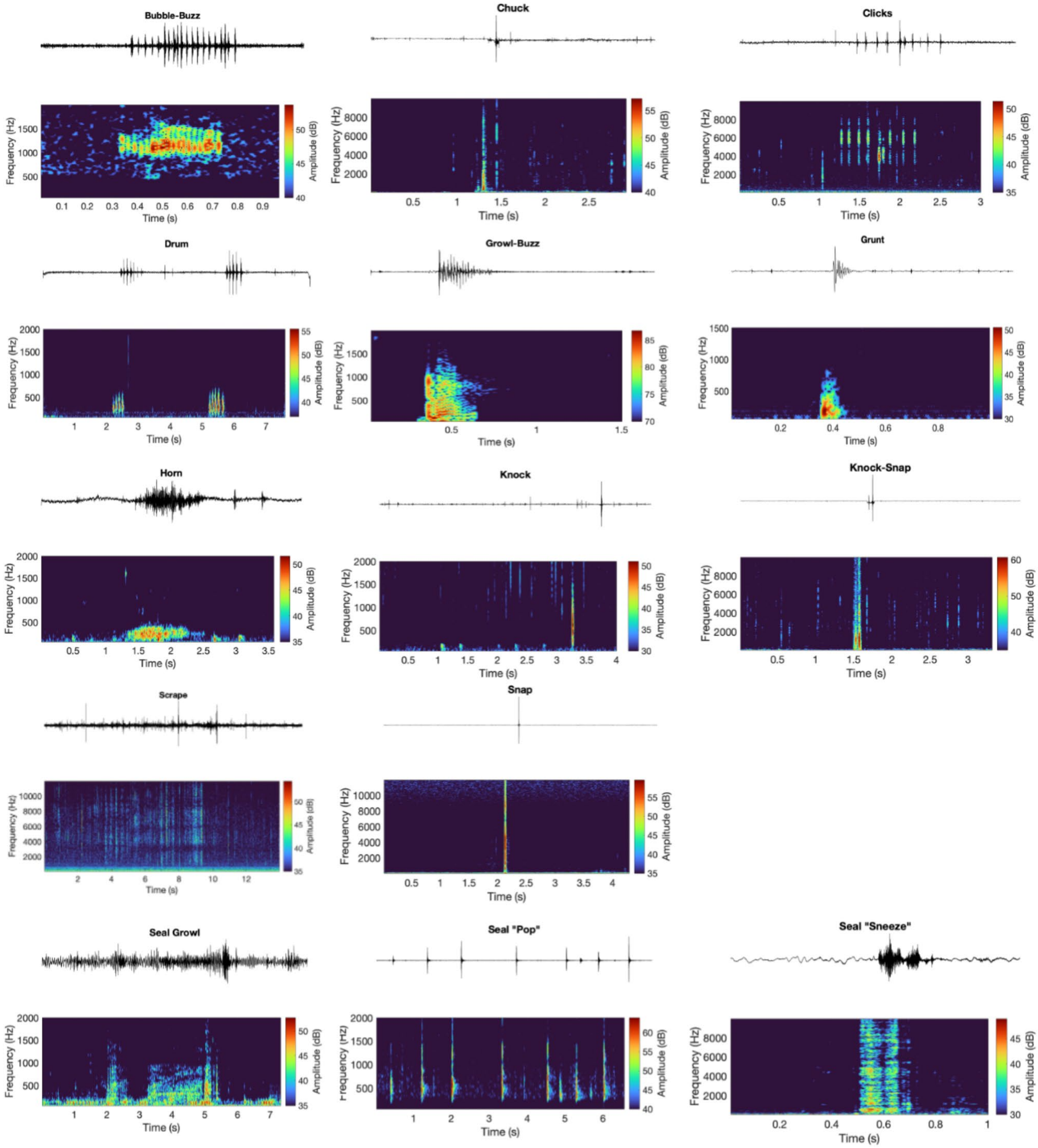

Fig. 2. Waveforms and spectrograms of the most commonly detected sound types. Relatively higher amplitudes are indicated by brighter colours, and relatively lower power by darker colours, and waveforms show relative amplitude. Absolute levels cannot be shown here as the sound files were independently plotted in MatLab using different filtering and modifying settings for each to highlight the structure of each sound type.

Across the 6 two-week recordings at the Nieuweschild site, we detected 3,405 individual biological sounds at the on-reef station (within 15505 10-minute sections), and 896 at the off-reef station (within 15549 10-minute sections; Table 1). Eight sound types were most commonly detected on the reef: chuck, clicks, drum, grunts, knock, knock-snaps, scrape, and snap, while three sound types were most commonly detected off-reef: bubble-buzz, horns and growl-buzz (Figs. 3 and 4). The most common sound types detected at the on-reef station were scrape, snap, and knock (occurring in 1.7% ±0.5, 2.3% ±0.6, and 1.3% ± 0.3 of the recorded 10-minute samples, respectively; mean ± se), while the horn sound type was most frequent at the off reef site (occurring in 1.8% ± 0.7

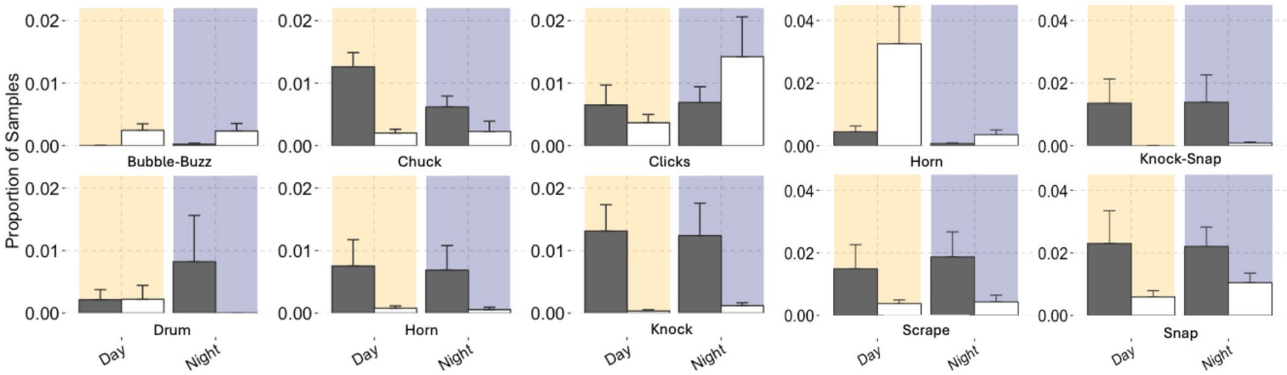

Fig. 3. Sound type presence at Nieuweschild site as proportions of each sound type present within 10-minute samples across two-week recordings at the on-reef station (grey bars) and off-reef station (white bars), proportions are shown as averages across 6 sampling periods taken over two years with standard error bars. The averages are shown as presence during daylight (yellow background) and overnight (blue background) periods.

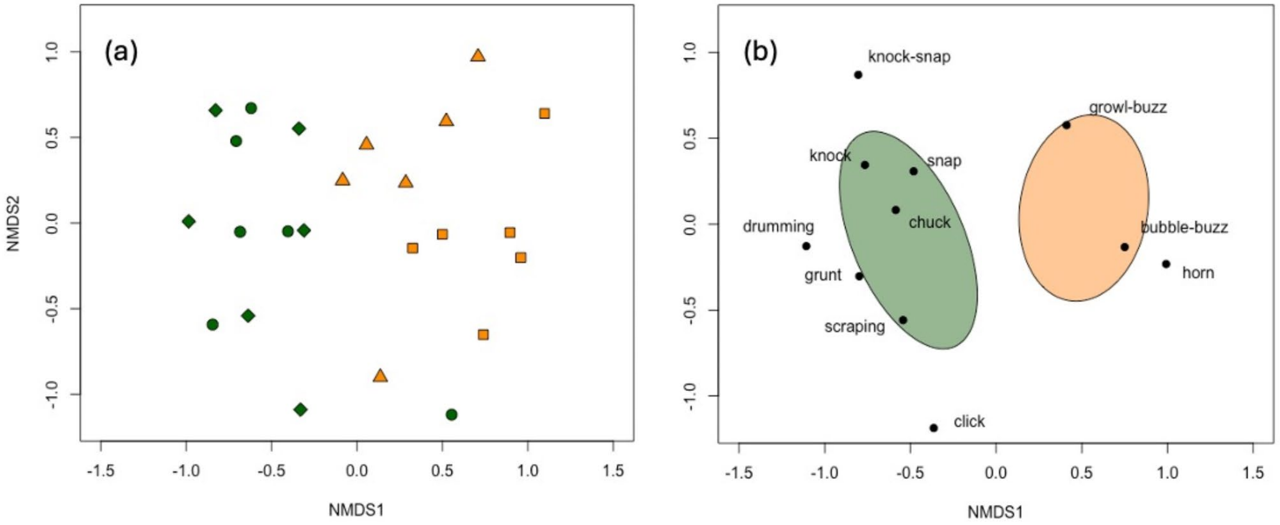

Fig. 4. Non-metric multidimensional scaling (NMDS) plot of the distribution of sound types on-reef and off-reef at the Nieuweschild site. (a) Sample scores for the on-reef recordings during day (green circles) and night (green diamonds), and for off-reef recordings during day (orange squares) and night (orange triangles). The sample scores are based on proportions of distinct sound types for each of six 2-week recordings divided into day and night. (b) Sound scores depicted by their names, showing the distribution of the distinct sound types across the 24 samples (recordings). The shaded circles show the standard deviation around the centroid for the on-reef (green) and off-reef (orange) recordings. Stress of the best solution with 2 dimensions was 0.17.

of the recorded 10-minute samples, mean ± se; Fig. 3). Accordingly, the composition of sounds was significantly different on the oyster reef compared to off-reef over time at the site Nieuweschild (PERMANOVA: $F_{1,16}=9.1$, $p<0.001$; NMDS plot: stress of the best solution with 2 dimensions = 0.17, Fig. 4). There was also a significantly different sound composition depending on day- or nighttime (PERMANOVA, effect of day or night: $F_{1,16}=2.5$, $p=0.023$), with clicks more common during the night and chucks and horns more common during the day (NMDS plot: stress of the best solution with 2 dimensions = 0.17, Figure S2).

All four of the natural/artificial reef stations contained a higher proportion of samples with sounds than at their respective no-reef sand stations (paired t-test: $n=4$, $t=3.2$, $p=0.048$; Fig. 5). The eleven selected sound types were, on average, detected 7 times more often on the reefs compared to their controls (log response ratio: mean = 1.94, ci = 1.65). Also, we found three additional sound types at the artificial reef sites in high abundances (more than 50 times across the recordings at all artificial reef stations) produced by the harbour seal (*Phoca vitulina*): growl, “pop”, and “sneeze” sounds (Figs. 2 and 5).

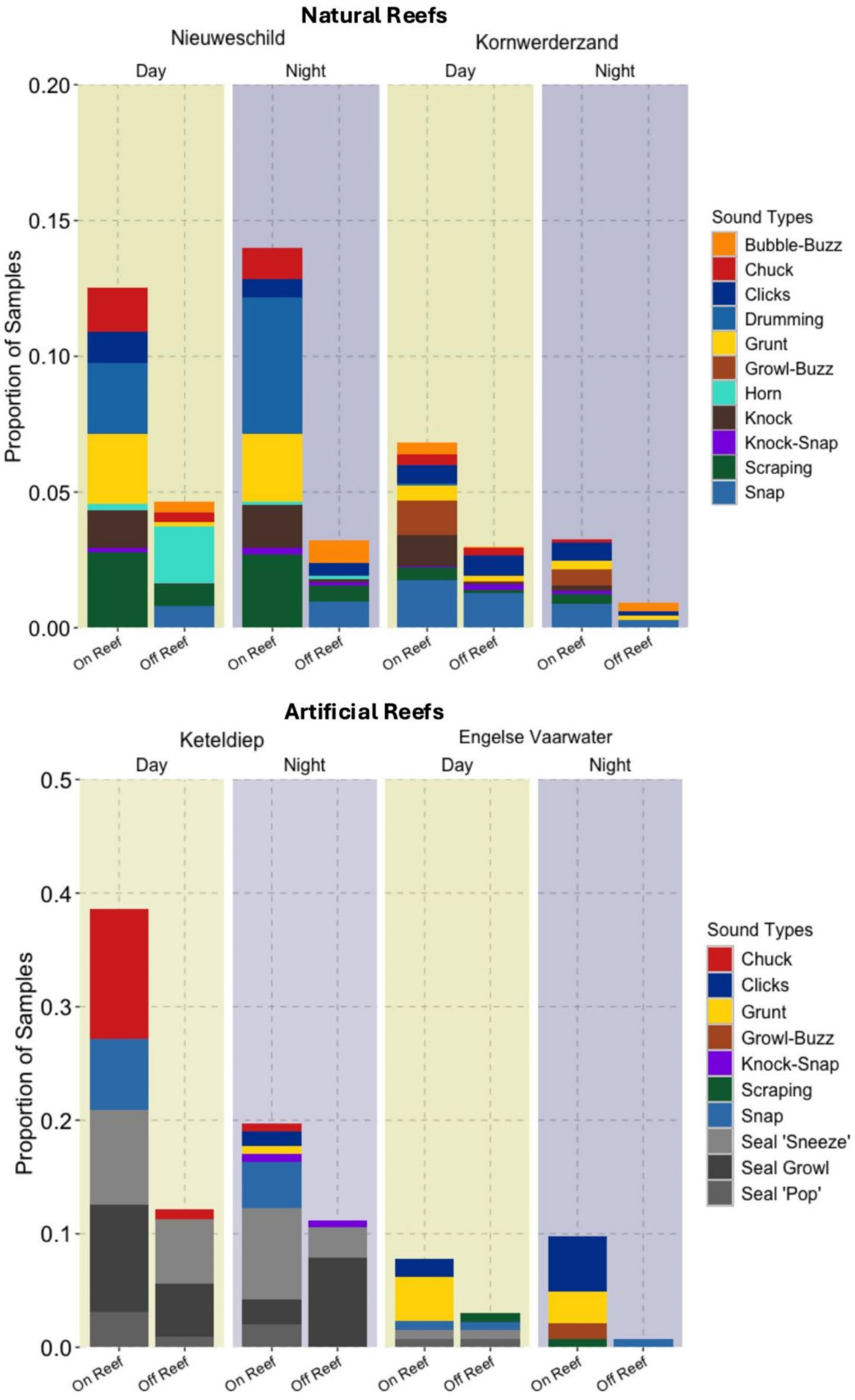

Fig. 5. Sound type presence in 10-minute samples as proportion of the 2-week recordings at the natural reefs Nieuweschild and Kornwerderzand at the on- and off-reef stations, and the 3-day recordings at the artificial reef sites Keteldiep channel and Engelse Vaarwater channel at the on- and off-reef recording stations. The different colours indicate the proportion of the different sound types, shown as presence during daylight (yellow background) and overnight (blue background) periods. Sound types are ordered alphabetically.

Discussion

Understanding and mitigating the rapid changes taking place in coastal ecosystems requires monitoring techniques that give us insights into different aspects of marine communities. Biological soundscape monitoring offers a versatile tool to gauge the sounds present in specific ecosystems and how these vary spatially and temporally[42,43]. Temperate habitats and species have remained a relative gap in studies of soundscapes and descriptions of soniferous species compared to tropical counterparts[7]. Here, we describe the most common biological sound types that characterised subtidal habitats in the western Dutch Wadden Sea; and we show that we can detect distinctly different sound type assemblages between sites. We also show that we can detect close-by differences in soundscapes between habitats by registering consistently higher proportions of sounds on subtidal reefs compared to neighbouring off-reef soft-sediment habitats. This provides the first descriptions of biological sound types and composition of the biological component of the soundscape in the Wadden Sea which will be a baseline for next steps in developing passive acoustic monitoring methods in the region. These results add to a growing body of soundscape studies that show habitats have distinct soundscapes due to their physical and biological make-up[9], and demonstrate that we can use PAM to detect short-range differences in subtidal biological activity.

Biological sound types were more abundant and diverse at the on-reef station than the neighbouring sand habitat at each of the reef sites. Crucial to these comparisons is the detection range of the sounds, i.e., to what extent were the sounds that were recorded on the reefs truly produced by organisms on the reef or could these also be acoustic spillovers from other nearby habitats. Shallow coastal environments have relatively short sound transmission distances - e.g., Biggs & Erisman (2021) found a transmission distance of a fish call to be between 44 and 281 m in a very shallow estuary[44]. The water depths where our hydrophones were deployed were between 2 and 5 m, with on- and off-reef sites test pair distance of 200 m. Differences in sound composition and lack of overlap between neighbouring on- and off-reef test pairs, indicated that soundscapes were qualitatively independent on this scale and reflected true small scale local soundscapes. Dedicated field tests with standardized signals are nevertheless needed and planned to solidify this.

We found a larger acoustic diversity and abundance at the on-reef station than the neighbouring sand habitat at each of the reef sites. This is consistent with findings that the fish and mobile invertebrate communities at reef sites in the Wadden Sea differ from neighbouring soft-bottom habitats[30,45]. Sound type diversity and abundances can also be indicative of community diversity[22], and of habitat status[36]. Extension from this groundwork and description of sound types will be to link these to the mobile communities at these habitats, and to build metrics from these that can support less invasive monitoring methods.

Several sound types were present across reef sites, as well as different sound types present between sites (e.g., the growl-buzz was not detected at the Nieuweschild reef, while the drum was only detected at this site), indicating different levels of biological activity and composition. Some sound types were detected at both the artificial and the natural reefs, albeit in lower abundances at the artificial reefs. Inter-reef acoustic variability within a region was also identified by[9], and highlights some of the finer-scale variation in biological and physical reef characteristics that shape individual reef soundscapes. The reefs (both natural and artificial) recorded for this study represent very different reef habitats with respect to connection to the North Sea, depth, currents, tidal amplitude and many other environmental variables. Therefore, the differences in on-reef sound assemblages between these reef habitats is to be expected. The artificial reefs, which had been deployed for 6 months at the time when the recordings were analyzed for this study had detections of harbour seal vocalizations, including higher detections at the Keteldiep reef site, giving us a picture of top-predator activity at reefs as well. That the small scale differences in soundscapes (on- vs. off-reef) are consistent across subtidal reefs in this area suggests that sound type detections can add value to reef monitoring programs by contributing knowledge of habitat use and activity[21], as well as the impacts of human interventions and the progress of restoration programs.

These results build on several studies showing distinct acoustic patterns at coastal habitats - including tropical coral reefs[46], temperate rocky reefs[5], as well as estuarine habitats comparable to those found in the Wadden Sea[9,21,47]. With the description of biological sound types, we can now look at longer-term patterns, including seasonal and annual patterns, which can also provide insights on potential sources. Furthermore, we can monitor long-term changes in the soundscape, and start building monitoring capacity.

Biological activity at reefs is usually highest overnight, and has been found to be reflected in soundscape patterns with higher sound pressure levels (SPL) and increased number of fish calling[13,47]. Similarly, fish presence at reef habitat in the Wadden Sea has also been found to be significantly higher overnight[45]. The patterns of sound types at the Nieuweschild site also showed trends toward day and night differences in sound type assemblages which may be linked to the species which are active during these periods. However, our recordings took snapshots at each habitat, and increased recording over seasons may further reveal diel patterns with changing behaviours such as species migration and spawning times.

The dynamic environment of the Wadden Sea poses challenges to applying passive acoustic monitoring. Tidal cycles also play a major role in both the activity of marine species as well as the soundscape[48]. There was a high influence of tidal current noise on detections, which was particularly evident at the artificial reef sites which are situated in tidal gullies that experience high current velocities (about 2.5 times higher maximum current speeds at the gullies than near to the Nieuweschild reef, unpublished data). Tidal effects on sound levels have been noted in other estuarine soundscapes, where high tide and falling tide periods have been observed to have greater biological sound levels, possibly also coinciding with better sound propagation at greater water depths[49,50]. These are important considerations for the descriptions of habitat soundscapes in this area, as well as planning for future development of monitoring schemes and recording cycles.

The field of marine ecoacoustics and descriptions of habitat soundscapes is growing rapidly[7]. Sampling schemes and recording rates applied by studies of marine habitat soundscapes vary widely, as do methods applied for analyses of these recordings[43]. Several acoustic indices have been explored for describing aspects of biological communities in marine habitats[51–56], or their utility in distinguishing between habitat types or describing habitat condition[5,57,58]. However, the application of these acoustic indices to recordings in marine environments has had mixed results[22,52,54,59,60]. As reviewed and evaluated by Bohnenstiel et al. (2018), indices can be strongly influenced by particular sound events or a single species[59]. To use passive acoustics as a monitoring tool, it is key to understand how soundscapes change relative to particular habitat characteristics and conditions and how these are reflected within sound metrics and indices. Documenting the sound assemblages which contribute to habitat soundscapes can inform us on how acoustic metrics may be influenced by different sources.

Conclusion

Compounding factors of the loss of 'healthy' habitat soundscapes as well as increasing levels of anthropogenic noise inputs to marine environments are resulting in changing marine soundscapes. This first description of biological sound types at reef habitats in the subtidal Dutch Wadden Sea is a building block toward further development of soundscape monitoring in this ecosystem. Documenting current and potentially changing conditions in the ocean soundscape can provide important information for managing marine ecosystems[61,62].

Data availability

Data is provided within the supplementary information files including example .wav files of sound types identified in this study. Full recordings used for this manuscript can be made freely available upon request after a maximal embargo period of 1 year from publication date. Thus, we provide a short example of each sound in a manageable sound file within the Supplementary Material - and provide contact details for the responsible scientist and a datamanager at the University of Groningen (Britas Klemens Eriksson b.d.h.k.eriksson@rug.nl).

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Author contributions

M.S. Watson carried out the fieldwork, data collection and analyses, and writing. A.C.M Kok contributed to the analyses and writing. I. van Opzeeland contributed to the analyses and writing. B.D.H.K. Eriksson contributed to the statistical analyses and writing.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to M.S.W.

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