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Fine-scale spatial and temporal acoustic occurrence of island-associated odontocetes near a mid-oceanic atoll in the northern Indian Ocean

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ABSTRACT: Temporal patterns of oceanic predators can provide valuable information on both lunar and diel influences not just on the distributions of these predators, but also on prey patches that are often difficult to study. Mid-oceanic island chains in the northern Indian Ocean have high odontocete occurrence, but the ecology of these animals is not well characterized. We investigated fine-scale spatial and temporal patterns of island-associated odontocetes using passive acoustic monitoring from January 2019 to January 2020 around Kavaratti Island, Lakshadweep, India. Based on opportunistic recordings in the presence of odontocetes, the majority of the detected whistles were likely made by spinner dolphins *Stenella longirostris*. We identified a resident population whose whistle occurrence was significantly influenced by month, site, and diel and lunar cycles. More acoustic detections were made in the northeast monsoon month of November and fewer during pre-monsoon and southwest monsoon periods. Distinct day–night differences along with fine-scale temporal variability were also observed, suggesting that delphinids use nearshore waters as a daytime resting habitat. Odontocete detections were highest during the new moon period and lowest during the first quarter phase. Detection rates were higher on the south side of the island. Our study shows that solar and lunar cycles modulate odontocete vocal occurrence, presumably through influences on their prey. Similarities of odontocete occurrence around Lakshadweep to other mid-oceanic island chains suggests that an island-associated micronekton community may exist around Lakshadweep that may also be important to other pelagic species targeted by local fisheries.

KEY WORDS: Monsoon · Arabian Sea · *Stenella* · Dolphin · Passive acoustic monitoring · Odontocete

1. INTRODUCTION

In the open ocean, seasonal, diel and lunar cycles influence animal distribution, life history and behaviour at multiple scales, both directly and indirectly (Monterroso et al. 2013, Last et al. 2016, Shaw 2016, Mannocci et al. 2017). One of the clearest examples of animals responding to these cycles is the diel vertical migration of mesopelagic fish and invertebrates of the sound scattering layer, an important prey base in the pelagic food web throughout the world's oceans (Bianchi & Mislan 2016, Aksnes et al. 2017). These cycles also influence the distribution and behaviour of predators (e.g. oceanic cetaceans) of such prey bases (Sims et al. 2006, Benoit-Bird et al. 2009a, Owen et al. 2019). Therefore, understanding temporal patterns of predators can provide valuable information not only on the drivers of predator behaviour but also on prey patches, especially in oceanic regions where prey distributions are often difficult to study directly (Boyd 1996, McMahon et al. 2019).

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Cetacean species and communities have evolved as top predators specialized to ecological niches shaped by underwater topography and associated oceanography (Baumgartner et al. 2001, Praca & Gannier 2008). In pelagic habitats, mid-oceanic islands and seamounts can act as predictable hotspots of prey as a result of the island mass effect, localized upwelling and/or nutrient discharge (Genin 2004, Gove et al. 2016). Some cetaceans inhabiting waters adjacent to mid-oceanic islands take advantage of the mesopelagic boundary layer, a community of mesopelagic micronekton inhabiting the steep slopes around these islands (Reid 1991, Benoit-Bird & Au 2003). This layer potentially plays a critical role in nutrient transfer between neritic and oceanic habitats and is likely to be a significant component of island ecosystem functioning and health (Reid 1991, Lammers et al. 2006, Gove et al. 2016). Species near oceanic islands, such as meso-predators, can be good indicators of prey patches of this distinctive interface zone between open ocean and coral reefs (Benoit-Bird & Au 2003). Unlike some sites in the Atlantic and Pacific Oceans (Norris et al. 1994, Cascão et al. 2020), the occurrence of such species around mid-oceanic island chains in the northern Indian Ocean is not well characterized.

At least 27 cetacean species have been recorded in the Arabian Sea, a tropical ocean basin in the northern Indian Ocean (Ballance & Pitman 1998, de Boer et al. 2002, Afsal et al. 2008). Here, as is the case globally for oceanic odontocetes (toothed whales), the remote nature of the habitat and substantial human resource and funding requirements to monitor oceanic waters have resulted in a relatively poor understanding of Arabian Sea dolphin populations and their ecology. The Arabian Sea is heavily influenced by seasonally reversing monsoonal winds and holds some of the world's largest mesopelagic fish stocks despite harbouring extensive and thick suboxic waters (<0.1 ml l^{-1}; Gjøsaeter 1984, Morrison et al. 1998, Vipin et al. 2012). This semi-enclosed basin is surrounded by densely populated countries with over a fifth of the global human population. Severe anthropogenic pressures, such as fishing, pollution, shipping and a changing climate, have resulted in marine resources being threatened or overexploited and impact cetacean populations and their prey in the region (de Boer et al. 2002, Poloczanska et al. 2016, Avila et al. 2018). Because of this, studies on fine-scale distributions, habitat use and behaviour of odontocete populations in the Arabian Sea are urgently needed (de Boer et al. 2002).

Passive acoustic monitoring (PAM) with fixed recorders deployed off mid-oceanic islands provides a highly cost-effective option to conduct dedicated studies on oceanic cetaceans in regions where resources may be limited (Lammers et al. 2008, Sousa-Lima et al. 2013). In addition to reducing the significant effort that is needed for visual surveys, PAM provides greater temporal coverage and is well suited for long-term monitoring of multiple species (Mellinger et al. 2007). Additionally, it is possible to collect data at night and in rough weather, when visual surveys are extremely challenging. In the south-eastern Arabian Sea, the Lakshadweep Islands, located on the northern end of the mid-oceanic Chagos–Laccadive Ridge, provide relatively easy access to oceanic dolphin populations and are a strategic location to carry out PAM (Fig. 1; Panicker et al. 2020).

The Lakshadweep Archipelago and surrounding waters encompass a mosaic of habitats ranging across several depth strata, including shallow lagoons, coral atolls, submerged reefs, steep island slopes and deep oceanic waters of 1–2 km depth (Pernetta 1993). The Lakshadweep region, in addition to being strongly influenced by the monsoon seasons, is characterized by a seasonal mesoscale eddy feature that develops over the northeast monsoon season called the Lakshadweep High (Shankar & Shetye 1997). These oceanographic features coupled with underwater topography make the area rich in pelagic resources

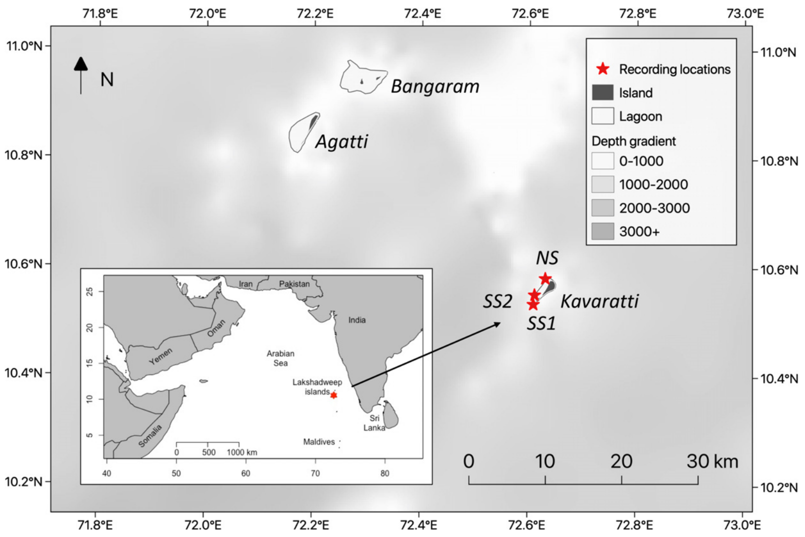

Fig. 1. Locations of hydrophone deployments and the study area (Lakshadweep Islands) in the Arabian Sea

and support a thriving tuna fishery (Nair et al. 1986, Vinay et al. 2017). Silas (1972) identified deep scattering layers in shallow waters near the Lakshadweep Islands that likely consist of euphausiids, myctophids and squids. Nevertheless, the distribution and composition of prey bases such as the mesopelagic boundary layer in these waters is poorly understood.

The Lakshadweep Archipelago was declared an Important Marine Mammal Area in 2019 under the IUCN World Commission on Protected Areas and is therefore recognized internationally as a site of significance to cetaceans that requires protection (IUCN-Marine Mammal Protected Areas Task Force 2021). The area shows high odontocete presence, and records suggest that at least 10 odontocete and 2 mysticete species occur in these waters (Panicker et al. 2020; www.marinemammals.in). Stock and threat assessments of all of these species are lacking in the region. Spinner dolphins *Stenella longirostris* are the most commonly sighted species, followed by bottlenose dolphins (*Tursiops* spp.) and short-finned pilot whales *Globicephala macrorhynchus*. Other odontocete species sighted in these waters include pantropical spotted dolphins *S. attenuata*, striped dolphins *S. coeruleoalba*, Risso's dolphins *Grampus griseus* and false killer whale *Pseudorca crassidens* (Panicker et al. 2020). Here, some cetacean species are associated with islands and higher seafloor slope gradients (Panicker et al. 2020). However, apart from anecdotal records or coarse-scale surveys that were limited in temporal coverage, dedicated fine-scale surveys have not been conducted on odontocete distributions near these islands. Greater temporal coverage would help elucidate whether cetacean communities are resident in the area and the extent over which they occur, which is critical to designing conservation and management plans. Understanding the distribution of island-associated odontocetes can also shed light on the distributions of mesopelagic prey resources, such as the mesopelagic boundary layer community, as cetaceans are known to target dense patches of prey (Benoit-Bird 2004). Odontocetes make a range of vocalisations categorised as whistles, burst pulses and clicks, of which whistles and burst pulses are primarily used for social communication and clicks are used for echolocation, prey detection and navigation.

Here we aimed to understand the occurrence and temporal patterns of island-associated odontocetes using PAM from January 2019 to January 2020 off Kavaratti Island, Lakshadweep, India. More specifically, the objectives of the study were to (1) examine if island-associated odontocete passive acoustic detections occurred year-round; and (2) understand how island-associated odontocete passive acoustic detections correlate with temporal (monthly, lunar, diel) and spatial (site) factors.

2. MATERIALS AND METHODS

2.1. Acoustic recorder deployment

The study was carried out off Kavaratti Island, a one-island atoll with 3.93 km^2 land area in the Lakshadweep Islands (Fig. 1). Divers deployed 2 passive acoustic recorders off the outer reef area (Fig. 1). Two SoundTrap ST-300STDs were used with a flat response from 20 Hz to 60 kHz (±3 dB) with <35 dB re 1 µPa noise floor above 2 kHz and end to end system sensitivities of −176.1 and −176.6 dB V µPa^{-1}. Recorders were anchored using cement blocks on the outer reef flats near the slope (steep oceanic drop offs) on the north and south side of the island at 11 and 18 m depths, respectively (Fig. 1, Table 1). Recorders on the south and north sides of the island were spaced approximately 5 km apart. The southern hydrophone was moved to a depth of 29 m on the slope in mid-November 2019 to reduce noise produced by snapping shrimp (*Alpheus* spp.). South sites 1 and 2 were combined to represent the south site, as these locations were very close to each other (<2 km on the same side of the island). The mean detection distance for tropical odontocetes is ~6.7 ± 3.5 km in deep water (Oswald 2006) but due to the

Table 1. Location, recording periods, duty cycle and depth for each hydrophone deployed off Kavaratti Island in 2019–2020

Site	Recording period	Duty cycle (min h^{-1})	No. of recordings (files/total hours)	Depth (m)
South site 1 (10° 31.98′ N, 72° 36.53′ E)	1 Jan–8 Apr 2019	15	2346/586.5	18
	13 Apr–27 Aug 2019	10	3288/548	18
South site 2 (10° 33.02′ N, 72° 36.67′ E)	17 Nov 2019–5 Jan 2020	15	1200/300	29
North site 1 (10° 34.83′ N, 72° 37.86′ E)	1 Jan–8 Apr 2019	15	2340/585	11
	14 Apr–5 Oct 2019	10	4195/699	11

shallow environment of the deployment and the orientation of the atoll, the 2 locations were unlikely to have sampled the same area. Recorders sampled data at a sample rate of 96 kHz to record a wide spectrum of cetacean whistles (Mellinger et al. 2007). There is a trade-off between duty cycle and battery life; we recorded on a duty cycle of 10–15 min each hour so we could deploy the recorders for at least for 3 to 4 mo at a time (Table 1). The recording duration and location of each hydrophone are given in Table 1 and Fig. 1.

2.2. Recordings and whistle detection

We created long-term spectral averages (LTSAs; time averaged at 5 s with frequency bin size of 1 Hz) from the acoustic recordings retrieved from the SoundTraps using Triton software (Wiggins 2003). We visually searched LTSAs using plot lengths of 1 h and a frequency range of 20 Hz to 48 kHz to identify periods of high bioacoustic activity (whistles) from odontocetes. Upon identifying signals, we chose a subset of whistles to develop a detector. We used the whistle and moan detector implemented in PAMGuard version 2.00.14 beta, with a 1024-point fast Fourier transform, 50% overlap and Hann window (Gillespie et al. 2008, 2013). The detector looked for signals in the frequency band between 2 and 30 kHz with at least 8 dB signal to noise ratio. The detected signals were passed on to the 'Real-time Odontocete Call Classification Algorithm (ROCCA)' module in PAMGuard to collect whistle measurements (e.g. centre frequency) and extract detections as acoustic files (Oswald et al. 2007). We then manually examined detections for all recordings to ascertain true positives and eliminate false positives. Continuous frequency-modulated narrow band sounds (often with harmonics) within 2 and 30 kHz with durations between several tenths of a second to several seconds were accepted as whistles (Oswald et al. 2007). In this study, we specifically focussed on whistles, as clicks were harder to isolate given the high number of snapping shrimp sounds within the same frequency bands.

Cumulative duriation for all recordings from 6 spinner dolphin groups (43.48 min), 3 pilot whale groups (58.67 min) and 1 bottlenose dolphin group (12.6 min) were collected using a dipping hydrophone (SQ26 H1 system, bandwidth 20 Hz to 45 kHz) and a Tascam recorder on an ad hoc basis from a tuna fishing boat between November and December 2019 near Kavaratti Island. The centre frequency of recorded whistles was measured using the 'ROCCA' module to compare with whistle detections from the SoundTrap data.

Ambient noise was calculated by obtaining average sound pressure levels (dB re 1 μPa) for the frequency band between 2 and 30 kHz (the same bandwidth used by the whistle detector) for each recording. We used PAMGuide software to calculate calibrated sound pressure levels (Merchant et al. 2015).

2.3. Temporal patterns

Relative acoustic occurrence for each month (proportion of days with detections in a month), day (proportion of duty-cycled recordings with detections in a day), diel period and lunar phase were calculated for the entire time series and for each site. Seasons were categorized as inter-monsoon (January to March), pre-monsoon (April and May), southwest monsoon (June to October) and northeast monsoon (November and December). Diel periods were categorized as dawn (2 h after nautical dawn which was at 05:00 or 06:00 h local time), day (between dawn and dusk), dusk (2 h before nautical dusk which was at 19:00 h local time), night1 (between dusk and midnight) and night2 (between midnight and dawn). Night was divided into 2 categories to account for any potential inshore–offshore night-time movement of animals that may be reflected in the acoustic occurrence (Benoit-Bird & Au 2003, 2004, 2006). Seasonal changes in daylight regimes are small in this region, hence diel data were not split into seasons. Lunar phase was divided into new moon, first quarter, full moon and third quarter. The times of dawn and dusk as well as lunar days were based on solar and lunar azimuths obtained from the R version 4.0.1 package 'suncalc' (R Core Team 2019, Thieurmel & Elmarhraoui 2019).

2.4. Statistical analyses

A generalized additive mixed model (GAMM) with a binomial distribution and logit link function was used to investigate the relationship between odontocete detections and explanatory variables. The response variable was the presence or absence of at least 1 odontocete whistle during each recording, which dictated the choice of the binomial distribution with a logit link modelling the log odds of success (see Table 1). The explanatory variables were time of day (Hour 1 to Hour 24), lunar day (Day 1 to Day 29), month of the year, and site. An interaction term between lunar day and site was also included to examine site-specific effects of the lunar cycle. An additive model framework was chosen, as time of day and lunar cycle were treated as smoothed terms with a cyclic cubic regression spline to account for the cyclic nature of these predictors and account for a non-linear relationship with the response variable. Smoothness selection was done by using restricted maximum likelihood (Wood 2017). We allowed a flexibility of 23 knots for the time of day variable and 8 knots for the lunar term variable to control the flexibility of the cyclic cubic regression spline. This was further checked with the 'gam.check' function in the 'mgcv' package to ensure there was no overfitting (Wood 2017). Month of the year and site were incorporated as factor terms. We used a mixed model, as an autoregressive moving average correlation structure with a lag of 1 h grouped across sites was incorporated to account for temporal autocorrelation within the response time series.

A generalized linear model (GLM) with a binomial distribution and logit link function was used to examine the relationship between odontocete detections and ambient noise as we expected a linear relationship between the independent and response variable. The response variable was the presence or absence of an odontocete whistle during each recording, and the explanatory variable was the average sound pressure level (between 2 and 30 kHz) for each recording. Data from November 2019 onwards were excluded from this analysis as the hydrophone was placed at a deeper site after this time.

All statistical analysis was done in R version 4.0.1. The GAMM was run using the 'mgcv' package (Wood 2017). An ANOVA table breaking down the estimates, residuals, degrees of freedom, significance tests and p-values for each of the parametric, categorical and smooth terms for both the GAMM and GLM are provided in Table S1 (www.int-res.com/articles/suppl/m683p195_supp.pdf) and Table 2, respectively. Residual analysis, for both GAMM and GLM, including tests for residual temporal autocorrelation, tests for uniformity and tests for heterogeneity, were conducted using a bootstrapping and scaled quantile residual approach via the 'DHARMa' package to check if model assumptions were met (Hartig 2021). Data were not transformed before running either of the models. Multicollinearity between explanatory variables was evaluated using the variance inflation factor (Allison 1999). Goodness of fit was visually determined using a binned residual plot in the 'arm' package for both models and using a Hosmer and Lemeshow goodness of fit test for the GLM to check how well the model fit the data (Hosmer & Lemeshow 2000, Gelman & Su 2021). A chi-squared test of independence was conducted to examine differences in dolphin occurrence across seasons at the north and south sites.

3. RESULTS

3.1. Acoustic occurrence and monthly differences

From January 2019 to January 2020, we obtained a total of 13 369 acoustic data files corresponding to 1413.5 and 1284 h for the south and north site, respectively (Table 1). Odontocete whistles were detected in 465 and 279 recordings, corresponding to 99.5 and 62.7 h, from 179 and 130 d for south and north sites, respectively. Odontocete detections occurred for a higher proportion of days at the south site (62.8% of all sampled days) than the north site (47.6% of sampled days; see Fig. 4a). Although both recorders were unlikely to sample the same area, as mentioned in Section 2, we visually examined spectrograms of whistles detected in the same recording time periods (n = 15 recording files) and found no simultaneous whistle detections between the 2 sites. Of all detections, most whistle centre frequency values lay between 12 and 20 kHz with a mean centre frequency around 15–16 kHz at both sites (Fig. 2a).

Of the 111 spinner dolphin whistles analysed from the dipping hydrophone data, the mean ± SE centre frequency was 14.8 ± 0.23 kHz (6 encounters). The mean centre frequency of short-finned pilot whales (n = 118 from 4 encounters) was 5.20 ± 0.19 kHz, and that of bottlenose dolphins (n = 5 from 1 encounter) was 18.32 ± 0.55 kHz (Fig. 2b). Based on this result, we infer that the whistles detected on the moored hydrophones were mostly spinner dolphins.

Table 2. ANOVA for fitted binomial generalized linear model with a logit link examining the relationship between the presence or absence of odontocete detections and ambient noise (average sound pressure levels). *Significant at $p < 0.05$

	Coefficient	df	Deviance	Residual df	Residual deviance	p
Null				12173	4949.0	
Average sound pressure levels (2–30 kHz)	–0.21	1	126.27	12172	4802.7	<0.005*

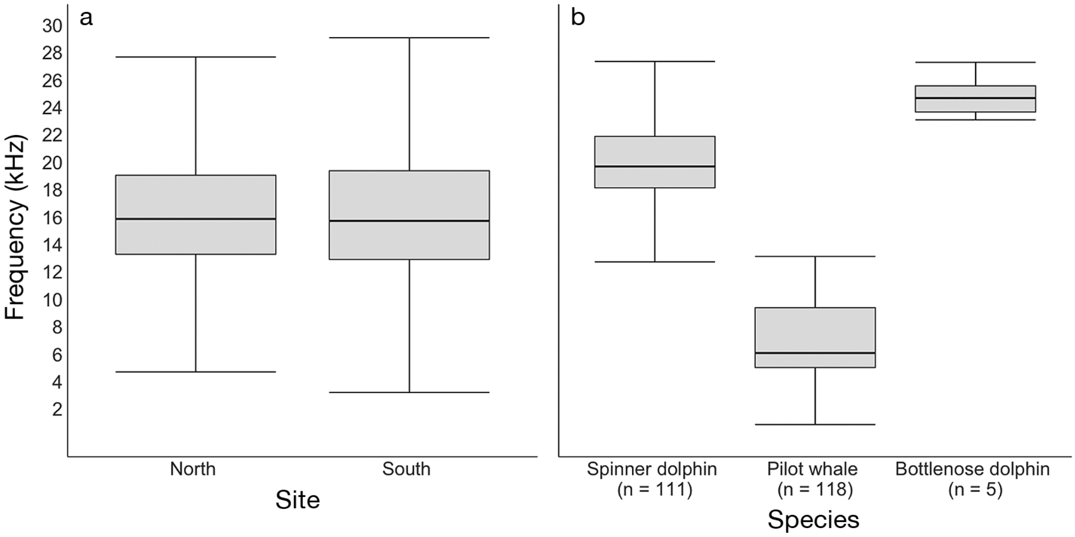

Fig. 2. Centre frequencies showing the minimum, first quartile, median, third quartile and maximum values of the data for (a) odontocete detections from the SoundTrap recordings for the north and south site and (b) spinner dolphin, short-finned pilot whale and bottlenose dolphin whistles collected using the dipping hydrophone

From the moored recordings, we detected delphinid whistles in all sampled months from January 2019 to January 2020 (Fig. 3). At the south site, delphinids acoustically occurred in over 50 % of all sampled days of each month except May 2019 (45.2 %). At the north site, whistles occurred in ≥50 % of all sampled days of each month except from May to September (16.1–48.4 %), which encompasses the southwest monsoon season. There was significant month-to-month variability in delphinid acoustic occurrence as shown by the GAMM (Fig. 4b; Table S1). There were significantly more delphinid detections in November than in any other month (Fig. 4b). Delphinid whistles occurred to a significantly lesser extent during the pre-monsoon months, April and May, and the southwest monsoon months (June, July, September) as compared to the inter-monsoon months (January to March; Fig. 4b). At the north site, there was a higher proportion of recordings with detections per day observed during the northeast and inter-monsoon periods (mean: 8.3 ± 0.88 % recordings per day for November to March) with a lower proportion of recordings with detections per day during the pre-monsoon and southwest monsoon seasons (2.28 ± 0.27 % recordings per day for April to October, $\chi^2 = 126.82$, df = 1, $p < 0.05$; Fig. 3). At the south site, the proportion of recordings with detections per day during the northeast and inter-monsoon periods (7.24 ± 0.72 %) was comparable to the pre-monsoon and southwest monsoon seasons (6.3 ± 0.07 %, $\chi^2 = 1.97$, df = 1, p = 0.16; Fig. 3).

3.2. Diel and lunar patterns

Delphinids were detected in all 5 periods of the day (dawn, daytime, dusk, night1, night2), but there was significant variability in the occurrence of whistle detections between these time periods. The GAMM results showed that delphinid detections were significantly higher during daylight hours as compared to night hours (Fig. 4c). Within the daylight hours, delphinids were detected to a greater extent during dawn hours and late afternoon and to a lesser extent during mid-day periods. This trend was observed at both sites. We observed detections in 10.4 % of all dawn-sampled hours, 7.0 % of sampled hours during the day and 4.8 % of all dusk-sampled hours. The first half of the night (19:00–00:00 h, local time) had the fewest detections (Fig. 4c). We detected whistles in only 1.0 % of all sampled night1 hours and 4.3 % of all sampled hours in night2.

We detected delphinids in all phases of the lunar cycle, but significant variability was observed across lunar days (Fig. 4d). Delphinid detections were most frequent during the new moon period and least frequent during the first quarter. There was a weak non-significant effect of this trend in the north site. At the south site, delphinid detections were most frequent just prior to the new moon period and least frequent just prior to the full moon. At the south site, we observed delphinid detections in 10.2 % of all sampled new moon periods, 7.4 % of all sampled third quarter periods, 4.6 % of all sampled full moon

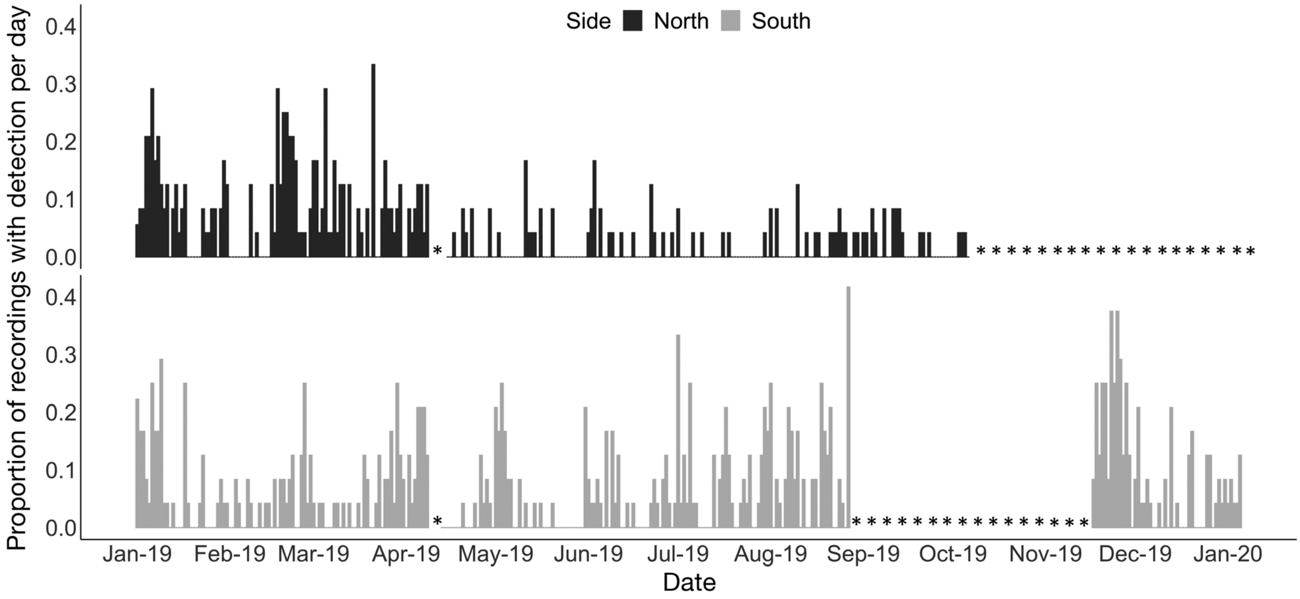

Fig. 3. Proportion of recordings with detections per day at the south and north site. Asterisks show periods where no sampling took place (dates provided in Table 1)

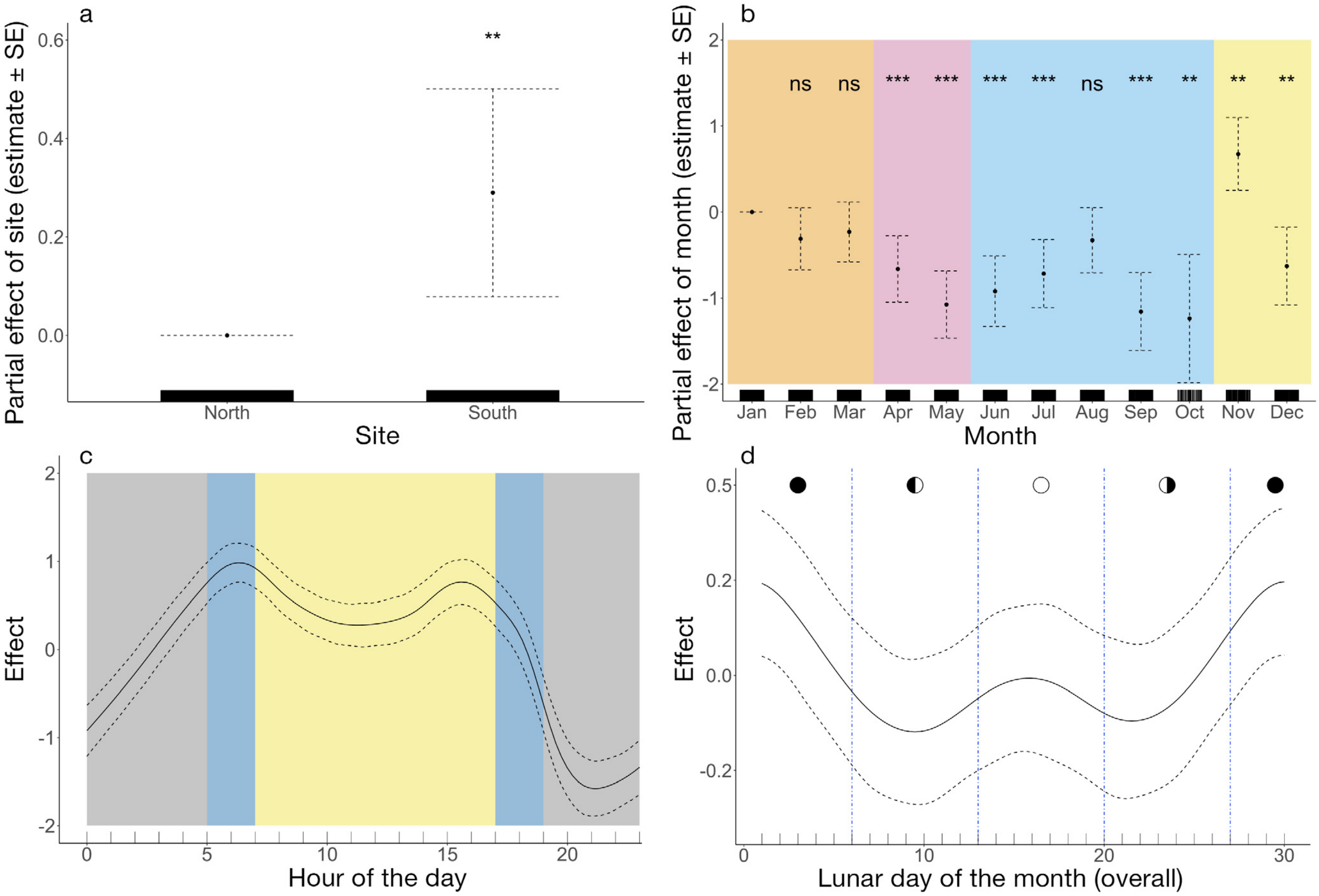

Fig. 4. Response curves and factor effects of a generalized additive mixed model for presence or absence of odontocete detections (from both sites) by (a) site (asterisks show significance with north as the reference) and (b) month of the year (asterisks show significance with January as the reference), $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns: not significant; inter-monsoon is shown in orange, pre-monsoon in pink, southwest monsoon in blue and northeast monsoon in yellow; (c) hour of the day; night hours are shown in grey, dawn and dusk hours in blue and day hours as yellow; (d) lunar day of the month (overall effect); new moon periods are denoted by a black filled circle, the first and third quarter periods by half-filled black circles, and full moon periods in white circle

periods and 4.5% of all sampled first quarter periods. Residual checks for the GAMM showed no residual autocorrelation, and assumptions of the model were adequately met. The GAMM showed a good fit for the data.

3.3. Ambient noise

Mean ambient noise levels (sound pressure levels for the band of 2–30 kHz) during day and night periods are shown in Fig. 5. Ambient noise was highly correlated to time of day due to diel patterns exhibited by snapping shrimp, which was the greatest contributor to this frequency band. Other contributors to this band were not conspicuous acoustically. We examined the effect of ambient noise on delphinid acoustic occurrence using a separate GLM. We found significant correlation between delphinid detections and ambient noise levels (Table 2; Fig. S1). Residual checks for the GLM showed no residual autocorrelation and assumptions of the model were adequately met; however, the Hosmer and Lemeshow goodness of fit test suggested the model was a poor fit for the data ($\chi^2 = 19.81$, df = 8, p = 0.01; see Fig. S2 for the binned residual plot).

4. DISCUSSION

Our study confirms that an island-associated odontocete population, likely spinner dolphins, uses Kavaratti waters year-round over relatively fine spatial (south and north sides of the island spaced approximately 5 km apart) and temporal scales. All sampled seasons and months showed delphinid acoustic occurrence, including during the southwest monsoon season. The year-round presence of delphinids signifies that sufficient prey resources persist near these islands despite intense monsoonal forcing and transient oceanographic features of the region (Pernetta 1993, Shankar & Shetye 1997).

Given the mean centre frequencies and whistle structures of delphinid detections, we conclude that the vocalising animals belong to the family Delphinidae based on broad frequency ranges used by cetacean family groups (Mellinger et al. 2007, Lin & Chou 2015). Panicker et al. (2020) reported that spinner dolphins are the most commonly sighted species in Lakshadweep waters, and sightings increased near islands. This is not surprising, given that spinner dolphins associate with islands and atolls in many parts of the world (Lammers 2019). Our observations of the centre frequency of whistles collected opportunistically with a dipping hydrophone during visual surveys (where species identity was known) support that spinner dolphins are likely to be the major contributor to delphinid whistle detections in our long-term hydrophone data (Fig. 2). Apart from spinner dolphins, it is possible that bottlenose dolphins and/or short-finned pilot whales make up some of the PAM detections, as both of these species have been spotted close to Kavaratti Island during dedicated visual surveys in November and December 2019; however, these species were sighted much less often than spinner dolphins (D. Panicker unpubl. data). Hence we infer that the majority of delphinid whistles detected here were made by resident spinner

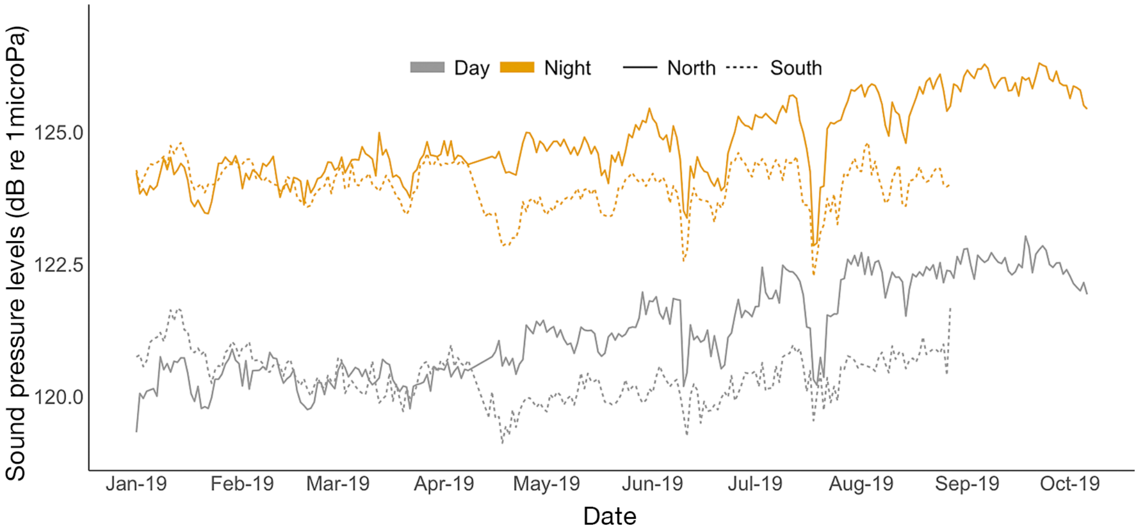

Fig. 5. Daily mean ambient noise levels (2 to 30 kHz band) for day and night periods at the south and north sites. Data from November 2019 onwards are excluded as the hydrophone was placed at a deeper site

dolphins. At our site, PAM could be considered an appropriate proxy for visual survey observations, as shown in other coastally associated spinner dolphin populations (e.g. Heenehan et al. 2016).

Although delphinid acoustic occurrence was persistent throughout the year, there was marked month to month variability in detections. There were more detections in the inter-monsoon and northeast monsoon periods as compared to the pre-monsoon or southwest monsoon periods with the exception of August. In general, seasonal differences in acoustic occurrence may arise from changes in animal abundances, calling rates or a change in ambient acoustic environment (Scheifele et al. 2005, Rouget et al. 2007). Here, the ambient noise is likely to increase in the low frequency bands during the monsoon season when wind and wave noise is higher; however, this is unlikely to impact detections in the high frequency bands where we detected delphinids (Wenz 1962).

Seasonality could modulate delphinid life history characteristics such as calving and movement patterns (Barlow 1984, Smith et al. 2016). For example, in Hawaii, island-associated spinner dolphins show a seasonally diffuse reproductive pattern with a slight bimodal tendency where calving occurs year-round but peaks in late spring and summer and in mid-winter (Barlow 1984, Norris et al. 1994, Lammers 2019). PAM revealed that higher habitat usage coincided with peak calving seasons in bottlenose dolphins in a coastal area in the Mediterranean (La Manna et al. 2014). If a calving peak occurs in Lakshadweep, the monthly variability in acoustic occurrence, such as the increase in detections during November, may be driven by a similar process. Alternatively, there could be seasonal movements between atolls and/or differential seasonal habitat usage on different sides of the islands. Panicker et al. (2020) found an overall increase in odontocete sightings during the northeast monsoon when compared to inter-monsoon periods. That study did not include the southwest monsoon season as the weather is usually too rough to conduct visual surveys. Currently we do not know how frequently, or what proportion of, spinner dolphins move between islands in the region. In the northwestern Hawaiian Islands, such as Midway Atoll, spinner dolphins form stable groups, show strong geographic fidelity, and long-term associates use the same atoll each day for resting, rarely mixing with spinner dolphins from other atolls. This is attributed to the geographic separation and small sizes of remote atolls with limited resting areas (Karczmarski et al. 2005). This is quite different from the highly fluid fission-fusion societies off the main Hawaiian islands (Karczmarski et al. 2005). We suspect spinner dolphin populations in Kavaratti may behave more like populations around Midway Atoll due to the geographic similarity between these locations, as Kavaratti is also a small remote island isolated from other atolls by deep oceanic waters.

We found higher detections on the south side of Kavaratti Island when compared to the north, especially during the southwest monsoon season when detections decreased on the north side of the island. The south side is considered to have more productive fishing grounds, and based on local accounts and personal observations, we found that the majority of local fishers target this area, as it serves as a predictable hotspot for yellowfin tuna *Thunnus albacares*. Yellowfin tuna is closely associated with several oceanic dolphin species such as spinner dolphins and pantropical spotted dolphins presumably due to increased protection from predators or foraging benefits (Scott et al. 2012). Both yellowfin tuna and spinner dolphins may be targeting similar prey at this site (Perrin et al. 1973, Scott & Cattanach 1998, Scott et al. 2012). Alternatively, the south side of the atoll has a wider reef shelf that may provide better daytime resting habitat (Sinha 1994, Condet & Dulau-Drouot 2016). The western side of the island is more exposed to monsoon winds and waves and our north site, located on the northwestern side of the atoll, was more exposed than the south site. This may be why there were fewer detections at the north site during the southwest monsoon, the roughest period of the year. Delphinids occasionally seek out leeward sides of atolls or sheltered areas, particularly for resting (Norris et al. 1994, Lammers 2004). In our study area, we could not sample the leeward side (the eastern side during the southwest monsoon season) of the island due to lack of secure anchoring points for instruments. However, the instrument on the south site was positioned such that it could acoustically detect odontocetes in southeastern waters in addition to the southwestern waters.

We detected dolphins to a significantly greater extent during the daytime, with 2 peaks in whistle detections during dawn hours (around 06:00 h) and late afternoon (16:00 h). Dolphin behaviour and occurrence influence diel whistle patterns (Norris et al. 1994). In several parts of the world, spinner dolphins show distinct day–night movement patterns, whereby animals rest during the day near islands and feed during the night in offshore waters (Lammers 2019). Higher whistle detections during the day have been reported in spinner dolphin habitats near mid-oceanic islands and seamounts (Lammers et al. 2008, McElligott 2018, Cascão et al. 2020). Within daylight hours, spinner dolphin sub-pods typically are more active and aggregate into larger pods during the morning and afternoon when transitioning from foraging to resting or vice versa (Lammers 2019). Whistling behaviour was also observed to be higher during periods of travelling, spreading out and foraging when compared to resting periods (Norris et al. 1994). Lammers et al. (2008) found similar patterns where acoustic detections peaked at 09:00 and 15:00 h local time and dipped just prior to sunset and sunrise near Oahu, Hawaii. If, as we suspect, spinner dolphins are the dominant species contributing to our detected whistles, then we would expect day–night differences in acoustic occurrence to reflect their day–night movement patterns as well. The 2 daytime peaks in delphinid acoustic activity observed in our study may indicate periods before and after which spinner dolphins enter or exit resting states, when dolphins become more active (McElligott 2018, McElligott & Lammers 2021).

In our study, whistle detections decreased markedly during the first half of the night (before midnight) but increased during the second half of the night (until dawn) (Fig. 4). If dolphins foraged within the detection range of the hydrophones at night, then we would expect to detect whistles at night (Norris et al. 1994). Lammers et al. (2008) showed higher detections around 21:00 and 02:00 h at night off Oahu, Hawaii. In the Azores, Cascão et al. (2020) reported that whistle detections were lowest just after sunset and increased linearly towards dawn, similar to our study. McElligott (2018) showed that night-time peaks in acoustic detections varied across site and season. These differences have been attributed to either site variability in the behaviour and distribution of prey species or to the presence of other delphinid species with variable diel patterns (Lammers & Munger 2016, McElligott 2018). Studies in Hawaii have shown that spinner dolphin prey, part of the resident mesopelagic boundary community made up of large myctophids, makes horizontal migrations to shallow inshore waters and then back offshore within the same night and the dolphins closely track these nightly movements to and from shore (Benoit-Bird & Au 2003, 2006, Benoit-Bird 2004). The occurrence, composition and migrations of mesopelagic boundary communities in the northern Indian Ocean is unknown; however there are large myctophid stocks in the Arabian Sea that show distinct diel vertical migrations concentrating in the upper 50 m during the night, and enhanced levels of pelagic biomass as seen in shallow sound scattering layers near coral atolls (Karuppasamy et al. 2010, Vipin et al. 2012, Letessier et al. 2016). Evidence of differential acoustic occurrence within night hours in our study alludes to potential nightly movement patterns of dolphins, and given that spinner dolphins feed at night, possibly their mesopelagic prey as well. Diel variability of whistle detections was observed on both sides of the island, indicating that diel behaviour is unlikely to change over these small spatial scales.

The lunar cycle had an effect on overall delphinid acoustic occurrence. At the south site, detections were highest during the days leading to the new moon and lowest prior to the full moon, whereas at the north site, no significant differences were seen across the lunar phases. Contrary to our study, Benoit-Bird et al. (2009a) found that the relative abundance of spinner dolphins increased with increasing lunar illumination in Hawaii, and that lunar phase is likely to be an important driver of predators that forage on vertically migrating prey. Their study covered both nearshore and offshore areas using visual and active acoustics, whereas our study covered only nearshore areas and did not use multiple methods of investigation. During full moon nights, scattering layers have been observed globally to occur deeper in the water column and are thought to be related to anti-predator behaviour (Prihartato et al. 2016). Benoit-Bird et al. (2009b) showed that scattering layers migrated to shallower nearshore waters during the new moon and remained in deeper offshore waters during full moon periods. If prey behaviour is similar in these waters, perhaps delphinids may be moving further offshore and deeper, beyond our acoustic detection range, during full moon nights and staying nearshore and shallower within the detection range during new moon periods.

We found that dolphin detections were significantly and negatively related to ambient noise (Table 2). Snapping shrimp activity contributed most to the ambient noise in our dataset and showed distinct day–night differences. Dolphin detections also showed distinct day–night patterns in our study, and such patterns have been reported in other studies as well (Lammers et al. 2008, McElligott 2018, Cascão et al. 2020, McElligott & Lammers 2021). Because ambient noise had a strong diel pattern, it is difficult to know if the diel pattern in dolphin detections we observed was caused by true diel differences in behaviour (e.g. occurrence or vocal activity) or by changes in detection probability. We could not include both a day/night factor and ambient noise in our model to elucidate this because those independent variables were correlated (the problem of multicollinearity). However, snapping shrimp acoustic signatures are loud, short in duration and broadband in nature (Everest et al. 1948); since the PAMGuard detector 'de-clicks' (removes clicks from) the data before running the whistle and moan detector (Gillespie et al. 2008, 2013), we think the chances of snapping shrimp clicks directly masking the detection of delphinid whistle occurrence may be negligible (see Fig. S3). Visual spot checks of data files, especially during night periods, also suggest that our estimates of occurrence were unaffected by ambient noise at night. We recommend studies that focus specifically on ambient noise variability, dolphin detections and whistle production patterns to understand this relationship in more detail.

Our study shows that effects of lunar and diel cycles modulate delphinid vocal occurrence and behaviour at fine temporal (hour to hour) and spatial (a few km) scales. Conservation measures for oceanic delphinids need to consider such variability in the region. Our study highlights a poorly understood delphinid population community in the Arabian Sea and provides valuable information on acoustic occurrence of oceanic dolphins in Indian waters. It also presents data from the monsoon season where traditionally *in situ* research has been challenging. Dolphins are protected under Schedule 1 of the Ministry of Law and Justice (1972), but in-country stock assessments, habitat studies and species-specific conservation measures are limited amidst growing anthropogenic threats and changing monsoonal patterns (Kumar et al. 2009, Murakami et al. 2017). This study provides an example of how relatively low-cost techniques, such as PAM with diver-deployable fixed recorders, can be used in resource-poor and remote areas of developing countries to study delphinid occurrence and temporal patterns.

In Lakshadweep, there are plans to develop the tourism sector that would attract high-end luxury-seeking tourists (Kumar et al. 2019). Such plans will inevitably include dolphin-watching tourism. Island-associated delphinids with predictable movement patterns would be a natural target for tourist activities such as dolphin watching or swim-with programmes, as seen in places like the Maldives and Hawaii (Anderson et al. 2012, Wiener et al. 2020). Such dolphin-watching activities, if unregulated, can disrupt resting behaviour or displace animals from preferred habitats (Lusseau 2004, Bejder et al. 2006, Tyne et al. 2018). Delphinid detections in our study are largely made of spinner dolphin vocalisations. Based on spinner dolphin ecology, nearshore areas are likely to be linked to critical resting daytime habitat (Norris et al. 1994). Additionally, we suspect that populations in our study area may be similar to populations off other isolated single-island habitats where site fidelity is high, and resident dolphin populations may be fairly isolated and therefore more vulnerable to anthropogenic disturbances (Karczmarski et al. 2005). Information on the abundance, distribution, and community composition of cetaceans, such as that presented in our study, prior to large-scale tourism is critical to designing adequate regulations in this area and may act as a useful baseline with which to monitor any future trends (McElligott & Lammers 2021). We recommend further fine-scale visual and acoustic studies that can inform policy makers and establish no-go zones, times or seasons in upcoming tourism plans and environment impact assessments.

The presence of an island-associated delphinid community year-round in Lakshadweep suggests that the waters around these islands support micronekton prey of these meso-predators. The diel and lunar variability in delphinid whistle detections that we report is likely to be an indirect effect of the diel and lunar patterns of an island-associated mesopelagic community (Benoit-Bird 2004, Benoit-Bird & Au 2004, 2006, Benoit-Bird et al. 2009a,b). The characteristics of the mesopelagic boundary community associated with the island-slopes in Lakshadweep need to be investigated. In addition to these acoustic occurrence patterns, further visual investigations and prey analysis will help decision makers to prepare data-driven policies that include key species in this important transition zone between deep oceanic waters and reef habitats.

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