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Understanding cetacean community composition and distribution in Lakshadweep
waters, Northern Indian Ocean

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Abstract

Understanding cetacean community composition and distribution in Lakshadweep waters,
Northern Indian Ocean

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The Northern Indian Ocean (NIO) is a region of high environment variability driven by seasonally reversing winds. The southwest monsoons generate substantial plankton blooms in these tropical waters and shape biogeography of higher trophic levels. Cetaceans in oceanic waters are good indicators of epipelagic and mesopelagic prey bases. This dissertation examines species composition and distribution of cetaceans in a mid-oceanic island habitat in southeastern Arabian Sea. I use passive acoustic monitoring (PAM), which is particularly useful to collect data year-round including night periods and the rough-weather southwest monsoon season when visual surveys are challenging. In Chapter 2, I examine the occurrence and species composition of the cetacean community in the Lakshadweep archipelago via visual surveys using a platform of opportunity. The surveys documented 139 sightings, including eight odontocete species and one mysticete species. Occurrence of cetacean species differed across seafloor slope gradients

and distances to nearest landmass. In Chapter 3, I investigate baleen whale occurrence in Lakshadweep waters using PAM. The study showed occurrence of Central Indian Ocean (CIO; formerly Northern Indian Ocean) acoustic population of blue whales in Indian waters. These results extend the known range of CIO pygmy blue whales about 1000 km north-westward from the waters surrounding Sri Lanka. In Chapter 4, I determined the occurrence and temporal patterns of island-associated odontocetes in Lakshadweep waters using PAM. A resident population, likely to be spinner dolphins, was identified. Whistle occurrence was significantly influenced by month, site, and diel and lunar cycles. Similarities of odontocete occurrence to other mid-oceanic island chains suggest that an island-associated micronekton community may exist around Lakshadweep. In Chapter 5, I characterize dominant sound sources to the shallow water reef soundscape in Lakshadweep and their correlation with local oceanographic parameters across monsoon and non-monsoon months. Four acoustic bands of interest, namely a geophonic band of wind-driven wave sounds and three biophonic bands containing animal choruses, are presented. Low frequency biophonic choruses peaked in inter-monsoon months, while low frequency geophonic sound levels peaked during monsoon months. Choruses showed site-wise variability and correlation with sea surface salinity, chlorophyll-a, and wind speed.

Understanding cetaceans and the underwater soundscape through an oceanographic lens highlight the underlying biological resources and physical drivers in this poorly studied area. This dissertation demonstrates that employing appropriate technology and methodologies can shed light on even highly mobile species (such as blue whales) in challenging conditions. Within the context of a changing climate, the information presented here can provide a baseline to compare with future cetacean and soundscape studies in this region. Furthermore, the dissertation

emphasizes that current plans for tourism development in these islands need to incorporate potential impacts on near-island cetacean communities and on underwater noise.

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DEDICATION

To Achan, for showing me the value of hard work

To Amma, for nurturing my sense of wonder for the natural world

To Rohit, for being my pillar of strength

To Innila, for making my world rich

Chapter 1. INTRODUCTION

Within the Northern Indian Ocean, geographical features and the South Asian monsoons shape ocean physics and biology. Firstly, this water basin is semi-bound by the Asian landmass and therefore lacks connectivity to cold-nutrient rich northern temperate or polar waters like the Pacific or Atlantic Oceans. Secondly, within the Northern Indian Ocean (NIO) annual net evaporation and precipitation patterns are responsible for a salty Arabian Sea (AS) and a relatively fresh Bay of Bengal (BoB; Kumar and Prasad 1997, Shenoi et al. 2002). These two water basins are situated at the same latitudes divided by the Indian subcontinent (Figure 1). Thirdly, two strong monsoons, the seasonal reversal of winds and surface ocean currents drive local oceanographic processes (Pernetta 1993). Monsoon driven upwelling, mixing within the surface layers and mesoscale eddies generate substantial plankton blooms particularly off the Oman and southwest Indian coasts during the boreal summer – these are some of the most biologically productive areas in the world (Lévy et al. 2007). These conditions of high environmental variability influence the biogeography of several trophic levels of animals from plankton to whales (Lévy et al. 2007, Madhupratap & Haridas 1990, Shanker et al. 2019).

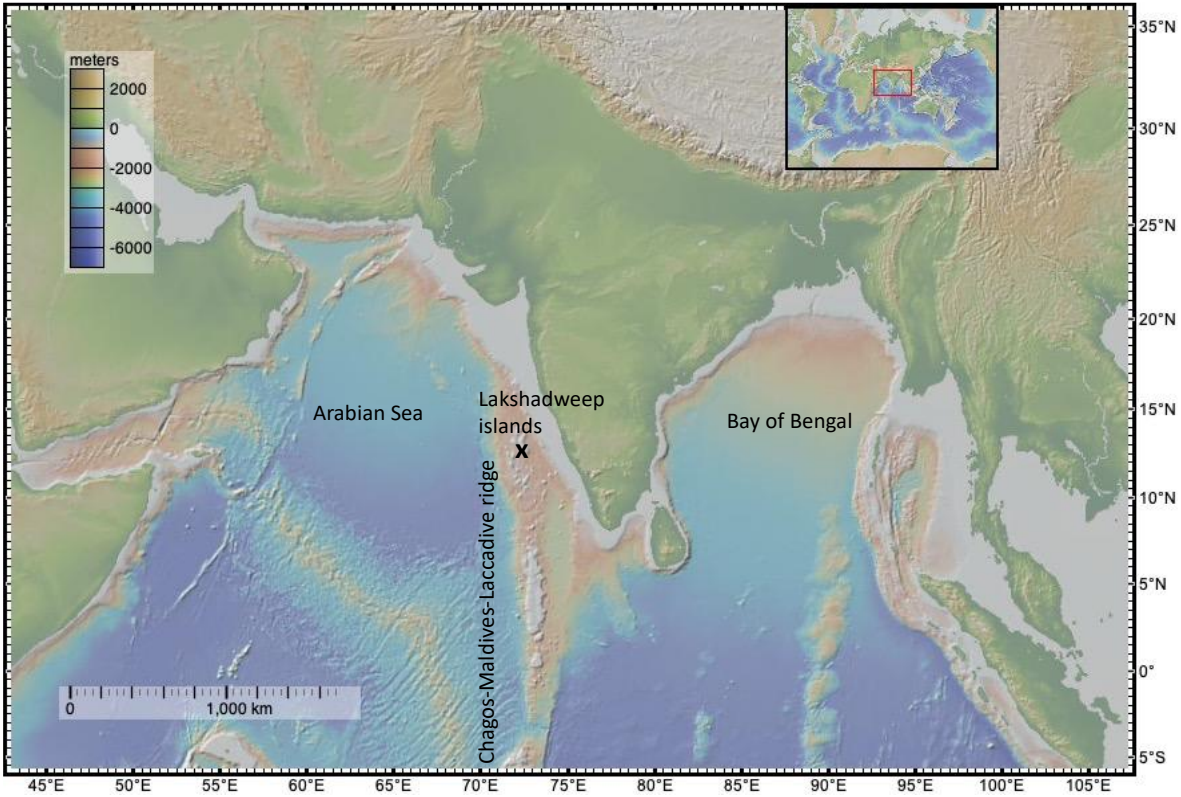


Figure 1.1. Map of the Northern Indian Ocean (GeoMapApp, Ryan et al., 2009).

Oceanic cetaceans associate with epipelagic and mesopelagic prey bases and can be good indicators of the presence of these lower trophic levels. The Arabian Sea has rich cetacean diversity with at least 27 species recorded (Ballance & Pitman 1998, Afsal et al. 2008, Ilangakoon 2012). The unique biophysical environment of the Arabian Sea has resulted in populations of large whales that may be endemic as supported by genetic and life history traits (Mikhalev 2000, Branch et al. 2007, Anderson et al. 2012, Pomilla et al. 2014). For example, pygmy blue whales (*Balaenoptera musculus breviceauda*) in the NIO are reported to form a resident population and have a breeding cycle six months out of phase with whales in the southern Indian Ocean (Mikhalev 2000, Branch et al. 2007). Arabian Sea humpback whales (*Megaptera novaeangliae*) are the world’s most isolated humpback whale population and are non-migratory (Pomilla et al. 2014). In the 1960s illegal Soviet whaling removed hundreds of

whales from NIO waters and the subsequent impact of this whaling is still not fully understood (Mikhalev 2000, Clapham 2016, Cerchio et al. 2020). Although data from these whaling fleets have several uncertainties attached to it, they provide useful information on baleen whale presence and breeding cycles in the NIO (Mikhalev 2000, Branch et al. 2007). Nevertheless, distributions, abundances, and ecological information on mysticete species and oceanic odontocetes are deficient across large areas within the NIO. Prior studies urged in-depth research efforts to shed light on geographic ranges and population connectivity of whales here (Mikhalev 2000, Branch et al. 2007, Redfern et al. 2017). Most studies on odontocetes from oceanic waters within the Arabian Sea are either opportunistic or are limited in temporal scope (e.g., Ballance and Pitman 1998, Afsal et al. 2008, Clark et al. 2012). As a result, we know very little about these populations.

A changing climate and a slew of other anthropogenic pressures within the NIO region emphasize the urgent need to fill some of these gaps in knowledge. Rapid warming of NIO waters is reshaping several key physical, biological, and chemical aspects. For example, the region's oxygen minimum zones (OMZ; ~21% of the world's OMZs are found here) are expanding (Lachkar et al. 2019, Rixen et al. 2020). Marine heatwaves have increased, and altered rainfall patterns are being observed across the Indian subcontinent (Saranya et al. 2022). The intensity, frequency, and duration of tropical cyclones in the Arabian Sea have been rising over the past two decades (Murakami et al. 2017, Deshpande et al. 2021). Such cyclonic storms can drastically increase phytoplankton blooms impacting seasonal biological productivity patterns (Kuttippurath et al. 2021). Surely this will modify spatio-temporal aspects of cetacean prey and therefore, cetaceans. Furthermore, a confluence of complex processes arising from the

region's bathymetry, hydrodynamics and climatology makes this area particularly susceptible to ocean acidification (Panchang and Ambokar 2021). Kaschner et al. (2011) used future projections from the Intergovernmental Panel on Climate Change (IPCC) to caution that marine mammals in the Arabian Sea are some of the most at-risk populations due to rising ocean temperatures.

Countries bordering the NIO hold one-sixth of the world's human population; several of these are low- and middle-income countries with high human densities, especially in coastal areas (United Nations ESA/P/WP/248 2017, The World Bank 2020). Millions of people depend directly on fisheries for their livelihood and food security – large coastal and industrial fishing fleets operate throughout the Arabian Sea (Palomares et al. 2021). Intensive, and often unregulated, fishing has led to crashes in fish populations (potentially cetacean prey) and increases in bycatch and/or entanglements of cetaceans in fishing gear (Pomilla et al. 2014, Belhabib et al. 2019, Anderson et al. 2020, Palomares et al. 2021). Shipping routes near Sri Lanka are some of the busiest globally and blue whale ship strikes are a conservation concern in this area (de Vos et al. 2013, Randage et al. 2014). Presumably, ship noise here, as in other parts of the world, impacts marine mammals and their habitats by altering the soundscape (Hildebrand 2009, Erbe et al. 2019). Furthermore, the region is strategically important for the United States, middle eastern countries, China, Europe and India as all these stakeholders have an active military presence here (Brewster 2018). Finally, economic interests drive increasingly ecologically damaging activities in deep oceanic waters, like deep sea mining, deep sea fishing and oil and gas exploration (Dulip 2003, Akhilesh et al. 2011, Dunn et al. 2018). A comprehensive assessment of threats posed to cetaceans by the host of anthropogenic pressures

discussed here, is wanting. To make such evaluations, we must document baseline cetacean distribution patterns, seasonality, and potential oceanographic drivers for cetacean occurrence within these waters.

For this dissertation, I focus on studying cetaceans that inhabit oceanic waters of the southeastern Arabian Sea (SEAS) within the NIO. SEAS embodies several of the key physical processes reported for the NIO such as wind-driven upwelling, freshwater intrusions from the Bay of Bengal, mesoscale eddies, propagation of Rossby waves and complex bathymetry (Shankar and Shetye 1997, Prasanna Kumar et al. 2004, Lévy et al 2007, Zachariah et al. 2019). As a result, some of the largest phytoplankton blooms within the NIO occur here (Lévy et al. 2007). The occurrence of potential whale prey species such as calanoid copepods and euphausiid species have been reported in the SEAS (Madhupratap & Haridas 1990, Mathew et al. 2003, Shanker et al. 2019). Based on catch estimates, planktivorous fish like oil sardines (*Sardinella longiceps*) dominate the SEAS when compared to other regions in the eastern Arabian Sea (Shanker et al. 2019). Furthermore, large standing stocks of myctophids in the eastern Arabian Sea are likely to form an important prey base for higher trophic levels (Catul et al. 2011).

The Lakshadweep Islands, within the SEAS, are particularly well located for scientific investigations as they provide relatively easier access to oceanic species than from the mainland. These islands are located on the northern end of the mid-oceanic Laccadive-Maldives-Chagos ridge which is an underwater volcanic mountain range extending from 10°S to 15°N. The Lakshadweep archipelago is a union territory of India, consists of 35 islands and is situated approximately 200-400 km from the Indian mainland. These coral atolls, lagoons and islands are

generally smaller than those found in the Maldives with deep oceanic waters between them that range 1-2 km in depth. The islands are densely populated and support a human population of over 64,000 (Lakshadweep Administration, Government of India 2022). Fishing, coconut cultivation and government employment are the main sources of income (Lakshadweep Administration, Government of India 2018). Pole and line tuna fishery, one of the most sustainable forms of fishing, is the biggest fishery in Lakshadweep and has been practiced for decades (Vinay et al. 2017). Currently, there are considerable efforts to promote tourism on the islands by the Lakshadweep administration and the Government of India (Department of Tourism, Government of India 2003, Kumar and Muralidharan 2019). Ongoing development plans aspire to set up a similar model to the Maldivian luxury tourism industry (Kumar et al. 2019). Infrastructure and connectivity needs associated with large-scale tourism development are in the planning stage (e.g., introducing seaplane services, calls for tenders on constructing lagoon villas; Department of Tourism, Government of India 2019, Department of Tourism, Government of India 2021). Scientific experts and local communities have raised serious ecological concerns about these plans (The Wire 2021, Sharma 2021). No assessments on the potential consequences of the proposed large-scale development on cetaceans, their prey, or their habitats have been carried out. One of main obstacles for including cetacean assessments into current and future development plans is the lack of a fundamental understanding of species diversity and distribution in these waters.

Given their large home ranges and remote habitats, studying cetaceans within oceanic waters is often resource intensive and time-consuming. This is a major reason for the dearth of research attention on this group of animals. In this dissertation, I used methodologies that are

cost-efficient and use limited person-power and vessel time. Chapter 2 presents information from visual surveys conducted from platforms of opportunity, while Chapters 3-5 use passive acoustic monitoring (PAM) to better understand the ambient soundscape and its components.

Sound travels further in water than in air and is an effective tool to get information on underwater species. Passive acoustic monitoring (PAM) is used extensively to understand the occurrence and seasonality of vocally active cetaceans (Risch et al. 2014, Buchan and Stafford 2015, Leroy et al. 2018, Dréo et al. 2019, Constaratas et al. 2021, Myers et al. 2021). The suite of PAM methods is especially useful in areas where prior cetacean surveys have not occurred, when resources are low, weather is rough, and study regions are remote. PAM with even one fixed recorder provides occurrence data at a temporal resolution that cannot be matched easily by visual surveys, like night-time monitoring (Mellinger et al. 2007). Since cetaceans use sound extensively to communicate and navigate, this method is well-suited to studying them. Cetaceans make species-specific calls that vary in frequency, duration, and amplitude, making PAM an ideal tool for multi-species studies.

Long-term seasonal patterns in cetacean call detections often act as the first line of investigation for further studies on behavior and habitat use patterns. Temporal analyses of call signals indicate sympatric usage by different species and based on spatial coverage of receivers, can shed light on movement patterns (Risch et al. 2014, Paniagua-Mendoza et al. 2017, Aulich et al. 2019, Shabangu et al. 2019). For example, call types recorded for blue whales (*Balaenoptera musculus*) reveal potential feeding or breeding seasons of a species or even fill gaps in migration hypotheses of the species (Stafford et al. 1999, Paniagua-Mendoza et al. 2017). The temporal

occurrence of call patterns can also aid in identifying the potential oceanographic or prey drivers of cetacean distribution (Širović and Hildebrand 2011, Shabangu et al. 2019).

In the NIO, long-term passive acoustic studies are limited. Central Indian Ocean (CIO) whale call detections in PAM studies south of the equator (e.g., NIO (now referred to as CIO) pygmy blue whale call described in Stafford et al. 2011) demonstrate the need for more studies north of the equator to further explore population connectivity or migration hypotheses. Currently up to four (possibly five) acoustic populations of pygmy blue whales have been documented in the Indian Ocean – an astonishing acoustic diversity for a relatively small ocean basin (Alling and Payne 1985, Alling et al. 1991, Ljungblad et al. 1998, Gavrilov and McCauley 2013, Cerchio et al. 2020, Leroy et al. 2021). Of these, two song types have been recorded in the NIO – the CIO song type and the NWIO song type (Alling and Payne 1985, Alling et al. 1991, Cerchio et al. 2020). Cerchio et al. (2020) emphasizes that apart from the recordings of CIO song type from limited boat-based work off the eastern coast of Sri Lanka (Alling and Payne 1985, Alling et al. 1991), no published records of this song type exist from the Arabian Sea. We know less about odontocete vocalizations than that of baleen whale vocalizations in the oceanic waters of NIO. In the early 80s, Whitehead and Gordon (1986) followed and collected acoustic data from sperm whale groups in Sri Lankan waters during the same expedition, from which the CIO song type was first recorded. Clark et al. (2012) and De Vos et al. (2012) reported acoustic efforts in Maldivian and Sri Lankan waters, respectively, using towed arrays for their surveys. These surveys spanned across a few weeks in 2003 and 2004, and sperm whales (*Physeter macrocephalus*), pilot whales (*Globicephala macrorhynchus*), killer whales (*Orcinus orca*) and

unidentified delphinid species were detected. PAM over longer temporal scales will be particularly useful to fill some of the current gaps in odontocete vocal behavior in the region.

In addition to information on cetaceans, PAM also provides information on the acoustic habitats that cetaceans inhabit. An underwater soundscape consists of biological, anthropogenic and/or geophonic sources at a particular place (Miksis-Olds et al. 2018). It provides observations into temporal variability of these sources (Staaterman et al. 2014). Additionally, it can show how abiotic factors (e.g., wind, ice) may impact biotic factors (e.g., prey, predators; Miksis-Olds et al. 2013). Soundscape ecology is an emerging field with most studies having occurred over the last decade, and primarily conducted in the North Pacific Ocean, Atlantic Ocean and in Australian waters (Lindseth and Lobel 2018). Very few studies have occurred in the NIO, and none of these focus on the mid-oceanic islands. The intersection between soundscape ecology and oceanography will receive growing attention in coming years, and studies within areas of high environmental variability such as the NIO will be illuminating (McKenna et al. 2022).

The overall aim of this dissertation is to investigate spatial and temporal cetacean diversity and distribution in the Lakshadweep waters, within an oceanographic context. Additionally, the dissertation describes the dominant sound sources to the local underwater soundscape and potential oceanographic influences on their temporal variability. An overarching goal of this work is to provide a foundation for future cetacean studies and a baseline to assess threats posed by a changing climate and other anthropogenic pressures in these waters.

In Chapter 2 (Panicker et al. 2020), I present results of cetacean surveys to provide information on which species are present and where they most frequently occur in the Lakshadweep waters. Visual surveys covering over 3,880 km were conducted using platforms of opportunity, namely high-speed passenger ferries that sail between inhabited islands. This chapter was published in *Aquatic Mammals* titled ‘Cetacean distribution and diversity in Lakshadweep waters, India, using a platform of opportunity: October 2015 to April 2016’ in January 2020.

In Chapter 3 (Panicker and Stafford 2021), I collect and analyze low frequency bandwidths through PAM to determine which baleen whales occur in the Lakshadweep waters for a period between December 2018 to January 2020. The study showed the occurrence of the Central Indian Ocean (CIO; formerly known as NIO) acoustic population of blue whales in Lakshadweep, and presented evidence of blue whale songs in Indian waters. The results extend the known range of CIO pygmy blue whales about 1,000 km north-westward from the waters surrounding Sri Lanka, where this song type was first recorded (Alling and Payne 1985, Alling et al. 1991). This chapter was published in *Marine Mammal Science* under the title ‘Northern Indian Ocean blue whale songs recorded off the coast of India’ in April 2021.

In Chapter 4 (Panicker et al. 2022), I expand my analysis to high frequency bandwidths, using the same PAM dataset, to understand acoustic occurrence of island-associated odontocetes in Lakshadweep waters between January 2019 and January 2020. Evidence of a year-round island-associated delphinid community, likely spinner dolphins, inhabiting the waters around Kavaratti atoll is presented. The diel and lunar variability in delphinid whistle detections

suggests these waters support island-associated mesopelagic prey resources. This chapter was published in Marine Ecology Progress Series under the title ‘Fine-scale spatial and temporal acoustic occurrence of island-associated odontocetes near a mid-oceanic atoll in the Northern Indian Ocean’ in February 2022.

In Chapter 5, I analyze the soundscape between 20 Hz and 48 kHz to characterize the main sound sources in the nearshore island waters in Lakshadweep. I report on dominant geophonic and biophonic contributors, their temporal variability, and oceanographic correlates to the observed patterns. These measurements may be particularly useful to compare with future sound measurements in these waters since none exist currently.

In Chapter 6, I conclude by providing key findings and takeaways of the dissertation. I also present recommendations for future research in the region.

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Chapter 2. CETACEAN DISTRIBUTION AND DIVERSITY IN LAKSHADWEEP WATERS, INDIA, USING A PLATFORM OF OPPORTUNITY: OCTOBER 2015 TO APRIL 2016

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2.1 ABSTRACT

Prior stranding records suggest that at least 12 cetacean species occur within the Lakshadweep archipelago, off the southwest coast of India. These islands consist of coral atolls and form the northern part of the undersea Chagos-Laccadive ridge. Distinct oceanographic features, seasonal monsoon cycles, and high productivity make this region a potentially rich cetacean habitat. In this paper, we report findings from the first systematic visual cetacean surveys, conducted from high-speed passenger ferries that sail between nine Lakshadweep islands. The surveys were carried out between October 2015 and April 2016, during both northeast monsoon (October-December) and inter-monsoon periods (January-April). We used a line transect survey framework to record sightings, along with group size estimates. We documented 139 sightings over 3880 km, of which 78 sightings were during systematic survey effort. Eight odontocete species were confirmed from these sightings: *Stenella longirostris*, *S. attenuata*, *S. coeruleoalba*,

Tursiops spp, *Globicephala macrorhynchus*, *Pseudorca crassidens*, *Grampus griseus*, and *Feresa attenuata*. One *Balaenoptera* sp. was also encountered during this survey. *S. longirostris* was sighted the most often (n=22) followed by *Tursiops* spp (n=18) and *G. macrorhynchus* (n=13). We documented significantly higher sightings in the northeast monsoon compared to the inter-monsoon period. Along ferry routes, cetacean species differed significantly from each other with respect to their associations with seafloor slope gradients and distances to nearest landmass. We encountered mixed species assemblages of *G. macrorhynchus* with *Tursiops* sp. and *S. attenuata* with *Tursiops* sp. Given the confirmed high cetacean diversity and occurrence in this region, there is a need for in-depth long-term studies on biogeography, ecology, and population status of cetaceans here.

2.2 INTRODUCTION

In the northern Indian Ocean, seasonal southwest and northeast monsoons play an important role in shaping biological productivity, through intense winds resulting in upwelling processes and/or advection of fresher water from the Bay of Bengal into a hypoxic Arabian Sea (Pernetta, 1993; Prasannakumar et al., 2004). In the open ocean habitat, island archipelagos characterized by steep underwater slopes provide the setting for distinct flow features and eddy formation that aggregate nutrients and plankton (Genin, 2004). Tropical upwelling regions and complex topographies are associated with high fisheries productivity and can be important in sustaining oceanic marine mammal and other higher trophic level populations (Madhupratap et al., 2001; Ballance et al., 2006). The Lakshadweep islands in the Arabian Sea is one such area, located on the northern tip of Chagos-Laccadive ridge. This island chain consists of coral atolls, submerged

reefs, lagoons, and steep slopes amidst deep open ocean waters, providing a mosaic of habitat types for tuna, sharks, corals, seabirds, and cetaceans (Pernetta, 1993).

Distinct mysticete (baleen whale) populations such as the Arabian Sea humpback whales and highly diverse odontocete (toothed whales) populations occur in the northern Indian Ocean (Mikhalev, 1997; Branch et al., 2007; Pompa et al., 2011; Anderson et al., 2012a; Pomilla et al., 2014). Lakshadweep waters are contained within the larger Indian Ocean Whale Sanctuary established by the International Whaling Commission to protect critical breeding populations of large whales (<https://iwc.int/sanctuaries>). Studies report the occurrence of 23 cetacean species from nearby Maldivian waters, 21 species from the western tropical Indian Ocean and 27 species from Sri Lanka and the southeastern Arabian Sea (Ballance & Pitman, 1998; Afsal et al., 2008; Anderson et al., 2012b; Ilangakoon, 2012a). Lakshadweep waters present a data gap in this mosaic of regional marine mammal habitats, and little knowledge exists from this area. Ocean-scale surveys of the Arabian Sea that include Lakshadweep waters or nearby areas, along with other anecdotal reports and stranding and bycatch reports indicate that at least twelve species of cetaceans occur in these waters (Burton, 1941; Alling, 1986; James & Panicker, 1990; Afsal, 2008; Kumarran, 2012; Sajikumar, 2014; <http://www.marinemammals.in>). These reports and the known habitat requirements of tropical cetacean species suggest a potentially high cetacean diversity in the Lakshadweep region (Ballance & Pitman, 1998; Kiszka et al., 2007; Redfern et al., 2017).

The aim of our study was to examine occurrence and species composition of cetacean communities in Lakshadweep waters using a non-scientific platform of opportunity. More

specifically, the objectives of the study were to 1) estimate species diversity and distribution of cetaceans with encounter rates; and 2) to examine the relation of cetacean sightings with season, seafloor depth, seafloor slope gradient and distance to nearest landmass.

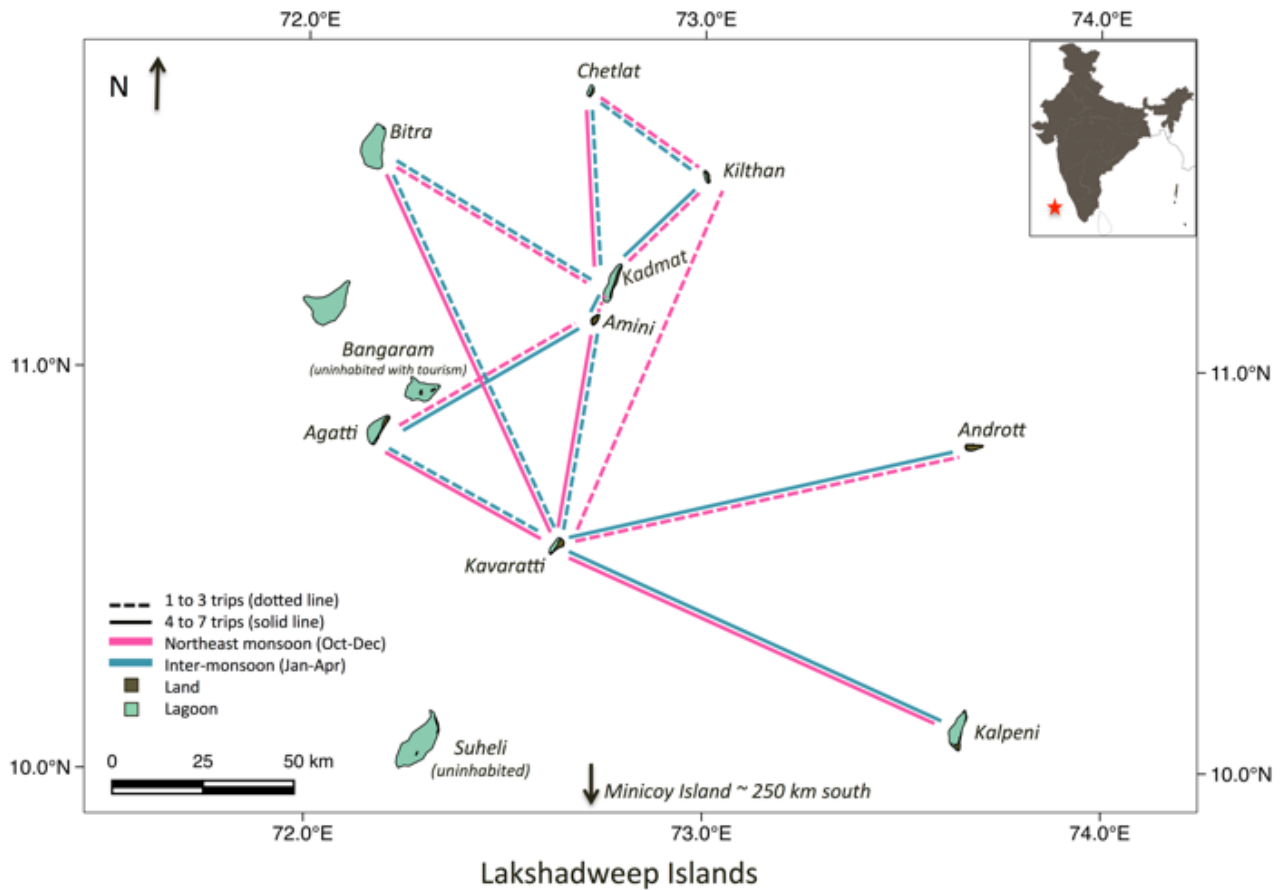


Figure 2.1. Study area map showing schematic ferry routes surveyed from October 2015 to April 2016

2.3 METHODS

The Lakshadweep archipelago, situated between 220-440 km off the southwest Indian mainland, is comprised of 36 islands of which ten are inhabited (Figure 2.1; Kokkranikal et al., 2003). The islands consist of shallow lagoons surrounded by coral atolls leading to open ocean habitats of

depths more than 1.5 km (Varkey et al., 1979; Pernetta, 1993). The region has an active tuna fishery, where over 80% of the total fish catch (>15,000 tonnes per year) comprise of pole and line caught tuna (*Thunnus albacare*, *Euthynnus affinus* and *Katsuwonus pelamis*; Vinay et al., 2017).

Visual vessel-based surveys (Schwarz et al., 2010) were undertaken from government-run passenger ferries that sailed between nine Lakshadweep islands (Figure 2.1). The surveys were in passing mode where the vessel did not stop at or approach cetacean sightings. Two sizes of high-speed vessels were used: 35 m and 32 m length with viewing platforms of 5.8 m and 3.5 m height above sea level, and an average speed of 18.4 knots and 15.2 knots, respectively.

We used a line transect survey methodology framework (Buckland et al., 2001, 2005) for forty-six survey days between October 2015 and April 2016. Three trained observers surveyed from abeam port to abeam starboard using 7x50 handheld binoculars and recorded cetacean sightings, along with group size, instantaneous group behavior, and identification notes with photographs when possible. Species identifications were assigned only when characteristic identification features were seen (as described in Jefferson et al., 2015). We categorized unidentified sightings into unidentified cetacean, unidentified small dolphin (below 2.5 m), unidentified large dolphin (approx. 2.5 to 5 m), unidentified small whale (5 to 10 m), unidentified large whale (above 10 m) or unidentified blackfish (black color, 5-10m and negligible beak structure) based on estimated body size and shape. We recorded minimum, best, and maximum estimates for group size based on actual counts for smaller groups. For larger groups, we counted a section of the group and extrapolated to the area occupied by the larger

group. We report only the best estimate in this paper. The location of the ferry was recorded when a sighting was made within 2 km of the trackline using a Garmin 78s handheld marine GPS. If cetacean groups were encountered when survey effort was suspended, we collected information for these groups and classified these sightings as off-effort. Rough weather, observer fatigue, and returning along an already surveyed track were the reasons to go off survey effort.

Sightings on survey effort were used to calculate encounter rates and test for association with season. These sightings were categorized according to northeast monsoon season (late October to December) or inter-monsoon period (late January to April). All sightings (observed both on- and off-survey effort), were pooled in the analysis to test whether there were differences among species with respect to their associations with seafloor depth, seafloor slope gradient, and distance to nearest landmass along the ferry routes. We extracted seafloor depth from existing datasets on global multi-resolution topography synthesis datasets (GMRT) from the software *GeoMapApp* (Ryan et al., 2009; <http://www.geomapapp.org>) for every cetacean sighting. Slope gradients and distance to nearest landmass were calculated using the spatial analyst toolbox in *ArcGIS 10.5* (ArcGIS, 2011). To examine habitat use and seasonality, we used non-parametric tests as sample sizes were low. All statistical tests were conducted using *R* (R Core Team 2019). Data used for analyses in this study can be accessed through Panicker et al. (2019).

Table 2.1. Route-wise data on sightings, total distance surveyed, encounter rate and surveyed depths. Amini and Kadmat have been combined to the Amini-Kadmat complex as these islands are very close to each other. Surveys were conducted between Amini and Kadmat also.

Route Name	Number of times	Total Distance (km)	Number of Sightings	Encounter rate (No. of sightings per 100 km)	Average depth (m)	Depth range (m)
Agatti-Amini/Kadmat complex	7	387.83	13	3.35	962.71	2-1626
Kavaratti-Agatti	7	330.76	10	3.02	1276.71	95-1865
Bitra-Amini/Kadmat complex	5	279.56	4	1.43	1478.15	11-1939
Kavaratti-Amini/Kadmat complex	7	326.28	6	1.84	839.53	10-1663
Chetlat-Amini/Kadmat complex	7	292.78	2	0.68	1244.07	81-2005
Kilthan-Amini/Kadmat complex	6	212.14	3	1.41	1057.07	6-1918
Kavaratti-Andrott	8	557.69	6	1.08	1516.92	4-2109
Bitra-Kavaratti	7	472.53	10	2.12	1050.06	2-1818
Kilthan-Chetlat	5	174.74	2	1.14	1383.59	112-1979
Kavaratti-Kalpeni	9	705.97	14	1.98	1765.18	215-2297
Amini-Kadmat	9	103.26	4	3.87	250.76	19-691
Kavaratti-Kilthan	1	36.79	4	10.87	1568.97	281-1915

2.4 RESULTS

2.4.1 *Survey effort, number of sightings and encounter rate*

Between October 2015 and April 2016, we surveyed 3880.33 km on routes between the following islands: Kavaratti, Agatti, Kiltan, Chetlat, Bitra, Andrott, Kalpeni, Amini and Kadmat

(Figure 2.1, Table 2.1). The duration of total survey effort was 128 hours and 45 minutes (per day observation: 1.65 ± 0.1 h with range of 0.2 to 3.2 h). All routes were covered during both seasons except for Kavaratti-Kilthan route, which was traversed only once during the northeast monsoon season. For 7 routes, the effort between northeast monsoon and inter monsoon periods was comparable, for another 4 routes, slightly more effort occurred in the inter monsoon period. Beaufort Sea State conditions for 80.6% of the total distance on survey effort were between 0-3 (excellent to good sighting conditions) while 15.5% were at Beaufort 4 (marginal), and 4% at Beaufort 5+ (poor). Surveys were carried out between 0700 and 1730 h. We conducted a total of 78 transits between the islands (Figure 2.1, Table 2.1).

The total number of cetacean sightings was 139 (74 identified to species), with 78 on-effort and 61 off-effort (Figure 2.2; Table 2.2). Of the 78 sightings on-effort, 31 were identified to species. The overall encounter rate of cetaceans was 2.01 sightings per 100 km for the survey effort in the study area. The overall encounter rate of cetaceans based on survey hours was 0.61 sightings per h.

The highest encounter rate was for Kavaratti-Kilthan route (10.87 sightings/100 km; Figure 2.1, Table 2.1); however this route was traversed only once as compared to other survey routes for which 5 to 9 trips were carried out. The routes between Agatti and Amini-Kadmat complex and between Amini and Kadmat also showed high encounter rates; 3.35 and 3.87 per 100 km respectively. The lowest rate of cetacean encounters was between Chetlat and Amini-Kadmat complex (0.68 per 100 km; Figure 2.1, Table 2.1).

Table 2.2. Species recorded during the study period including number of times sighted, group size and depth at sighting location

Species	No of Sightings <i>On & Off effort</i>	Group size		Depth (m)	
		Mean ± SE	Range	Mean ±SE	Range
Spinner dolphin <i>Stenella longirostris</i>	22	96.10 ±35.7	5-600	827.91 ±144.12	5-1870
Striped dolphin <i>Stenella coeruleoalba</i>	5	40 ±10.5	20-70	1733.20 ±143.51	1276-2076
Pantropical spotted dolphin <i>Stenella attenuata</i>	3	76.67 ±37.1	30-150	1662 ±132.03	1481-1919
Bottlenose dolphin (Common & Indo-Pacific Ocean) <i>Tursiops species</i>	18	4.75 ±0.7	1-10	1007.50 ±186.11	10-2107
Risso's dolphin <i>Grampus griseus</i>	7	15.57 ±5.4	2-40	1308.71 ±195.69	198-1664
False killer whale <i>Pseudorca crassidens</i>	4	8 ±4.0	3-20	869.50 ±401.67	101-1618
Short-finned pilot whale <i>Globicephala macrorhynchus</i>	13	17.46 ±3.6	2-40	1351.23 ±137.38	540-2259
Pygmy killer whale <i>Feresa attenuata</i>	1	10	NA	1558	1558
Baleen whale <i>Balaenoptera sp.</i>	1	2	NA	955	955
Unidentified cetacean	5	-	-	-	-
Unidentified small dolphin	20	-	-	-	-
Unidentified large dolphin	34	-	-	-	-
Unidentified large whale	1	-	-	-	-
Unidentified small whale	1	-	-	-	-
Unidentified blackfish	4	-	-	-	-

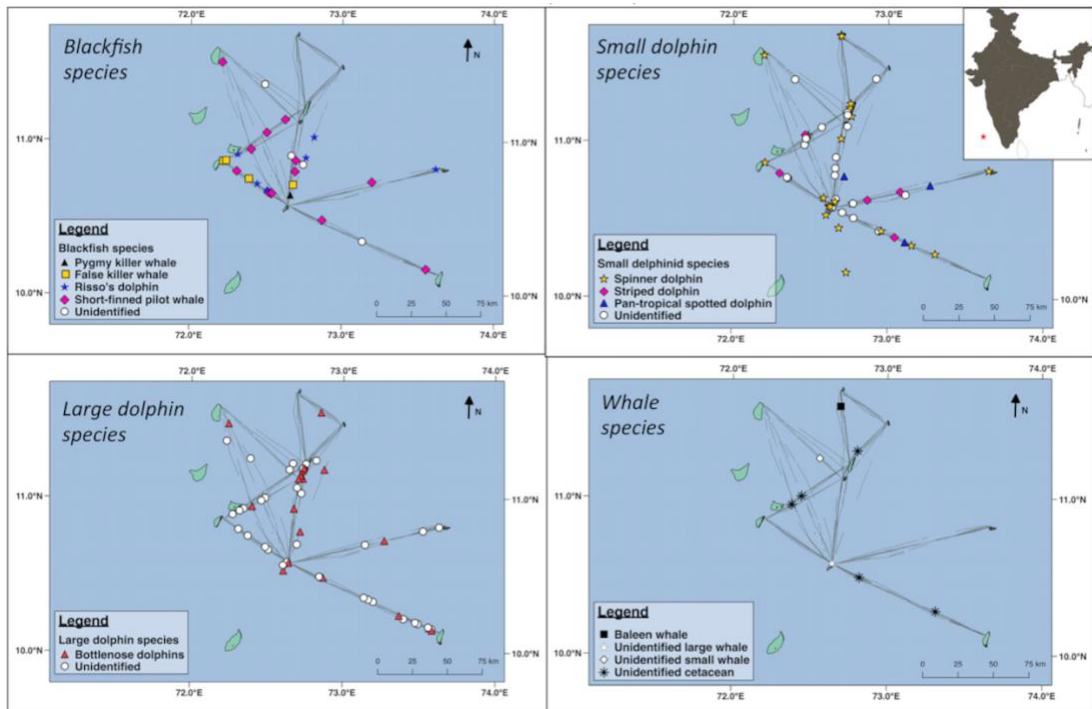


Figure 2.2. Cetacean sightings in the Lakshadweep waters categorized by species and classes. a) blackfish; b) small dolphin species; c) large dolphin species; d) whales and unidentified cetacean species. Faint lines on the map show surveyed tracks.

2.4.2 Species diversity and select species accounts

We identified eight odontocete species and one mysticete genus during the study period (see Table 2.2 for list of species and Figure 2.2 for distribution of sightings). Depth ranges for cetacean sightings ranged from 5 m to 2259 m with a mean of 1179 ± 57.34 m (Table 2.2). The most commonly sighted species was the spinner dolphin (*Stenella longirostris*) with 22 sightings, followed by bottlenose dolphins (*Tursiops* spp) with 18 sightings, and short-finned pilot whales (*Globicephala macrorhynchus*) with 13 sightings.

Spinner Dolphin - Twenty-two sightings of spinner dolphins were recorded. Individuals had a tripartite design, slight falcate to triangular dorsal fins, long beaks with dark beak tips and an eye to flipper stripe, which are characteristic of this species (Figure 2.3a; Jefferson et al., 2015). Large groups of 500 or above were documented on the Kavaratti – Kalpeni route on 2 December 2015 and the Kavaratti – Andrott route on 11 February 2016. Group sizes for all the sightings are provided in Table 2.2. Sightings occurred both in the northeast monsoon (n=8) and inter-monsoon (n=14) periods and varied over a wide range of depths (Table 2.2).

Striped Dolphin (*Stenella coeruleoalba*) - Five groups of striped dolphins were documented (group sizes are given in Table 2.2). Individuals were identified by the light gray spinal blaze protruding into the cape and the dark stripe that runs between the eye and the anal region (Figure 2.3b). In all the sightings, the dolphins were highly acrobatic, and roto-tailing (rotating the tail during a high leap; Jefferson et al., 2015) was observed during one instance. All sightings were in northeast monsoon season except for one in the inter-monsoon period.

Risso's Dolphin (*Grampus griseus*) - Seven groups of Risso's dolphins were sighted. Five sightings were in northeast monsoon season and two in the inter-monsoon period. Individuals were not as heavily scarred or lightly colored as described in Jefferson et al. (2015), however blunt square heads were observed along with other identification features including the vertical crease on the melon (Figure 2.3c). More scarring was observed near the head of individuals than the body (Figure 2.3c). Group size and seafloor depth ranges are provided in table 2.2.

False Killer Whale (*Pseudorca crassidens*) - Four groups of false killer whales were sighted. Three sightings were in the northeast monsoon season and one in the inter-monsoon period. Group sizes and seafloor depth ranges are provided in table 2.2. A sighting in December was on the Kavaratti-Agatti route, where increased aerial display such as breaching, porpoising, and what appeared to be ferry wake surfing was observed. This sighting lasted for 17 min and it was not apparent whether the same individuals were transiting with the ferry. Juveniles were also present with this group (see Figure 2.3c).

Baleen Whales (*Balaenoptera* sp.) - One group of two individuals of *Balaenoptera* sp. were sighted on 7 November 2015 on the ferry route between Chetlat and Amini islands. This sighting could not be confirmed to species (Figure 2.3e). The dorsal fin was falcate and placed further along the back. The blow of the animal was tall and columnar with an estimated large body size comparable to a pygmy blue (*B. m. brevicauda*) or fin (*B. physalus*) whale (estimated by the proportional distance between the blowhole and the dorsal fin). The skin was dark with no mottling. The whales surfaced 3-4 times in succession and the last observed dive was a tail out dive.

Mixed Species Groups - Two mixed species groups were observed. A group of 7 bottlenose dolphins and 4 short finned pilot whales were spotted along the Kavaratti-Bitra route on 6 December 2015. A group of ~150 pantropical spotted dolphins (*S. attenuata*) were observed with at least one bottlenose dolphin along the Kavaratti-Andrott route on 12 March 2016.



Figure 2.3. Cetacean sightings in the Lakshadweep waters categorized by species and classes. a) blackfish; b) small dolphin species; c) large dolphin species; d) whales and unidentified cetacean species. Faint lines on the map show surveyed tracks.

Unidentified Sightings - An unidentified large whale was sighted on Kavaratti to Kalpeni route and its blow was visible from a distance and could have been any of the large whale species. One sighting of an unidentified small whale was recorded between Bitra and Amini island. The

individual was light brown in color, had a falcate fin placed further along the back and surfaced twice. The estimated size range was 5-7m. Number of unidentified sightings in each category has been provided in Table 2.2.

Bottlenose dolphins were not identified to species *T. aduncus* or *T. truncatus* as at-sea identification for these two species is challenging and frequently relies on internal morphology (Hale et al., 2000; Jefferson et al., 2015).

2.4.3 *Cetacean species distribution across season, depth, slope gradients and distance to nearest landmass*

We tested against the null hypothesis that cetaceans were uniformly distributed across northeast and inter monsoon periods after accounting for differences in survey effort using a chi-square goodness of fit test. We found a higher number of sightings (n=51) in the northeast monsoon as compared to the inter-monsoon period (n=27, $\chi^2= 13.984$, df = 1, p-value = 0.002, Figure 2.4). The expected values from chi square goodness of fit test were calculated after accounting for distance traveled in each season (44% and 56% of total survey effort of 3880.33 km in the northeast and inter-monsoon periods, respectively).

We examined whether the cetacean species that we recorded differed with respect to the distance to the nearest landmass, depth and slope gradient at the points they were sighted along the ferry routes. The distance from sightings points to the nearest landmass differed among the species (Kruskal-Wallis $\chi^2= 16.962$, df = 6, p-value = 0.009). Spinner dolphins were observed

closest to land (median 1.82 km) and striped (median 24.72 km) and spotted dolphins (median 43.28 km) were observed furthest from land compared to other species (Figure 2.5). Species also differed in slope gradient at which they were sighted (Kruskal-Wallis $\chi^2= 15.542$, $df = 6$, p -value = 0.016). Spinner dolphins were encountered in relatively higher slope gradients compared to other species and were also found across a wider range from flat to steep slopes compared to the other odontocete species (0.2 to 33.68 percent, median 13.54 percent, Figure 2.5). Striped and spotted dolphins were found in the lowest slope gradients with a median of 1.65 percent and 1.51 percent, respectively. There was no significant difference among species in the depth at which they were sighted along the ferry routes (Kruskal-Wallis $\chi^2= 10.912$, $df = 6$, p -value = 0.091).

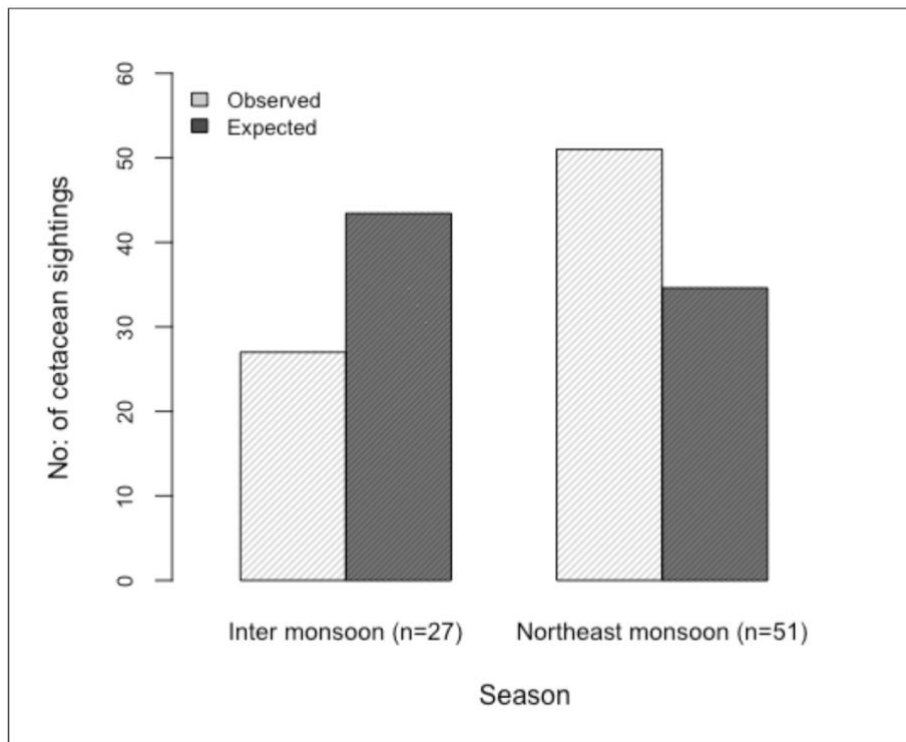


Figure 2.4. Distribution of cetaceans in inter-monsoon (n=27) and northeast monsoon (n=51). Expected values in proportion to distance traveled within each season are 43.41 and 34.59 respectively.

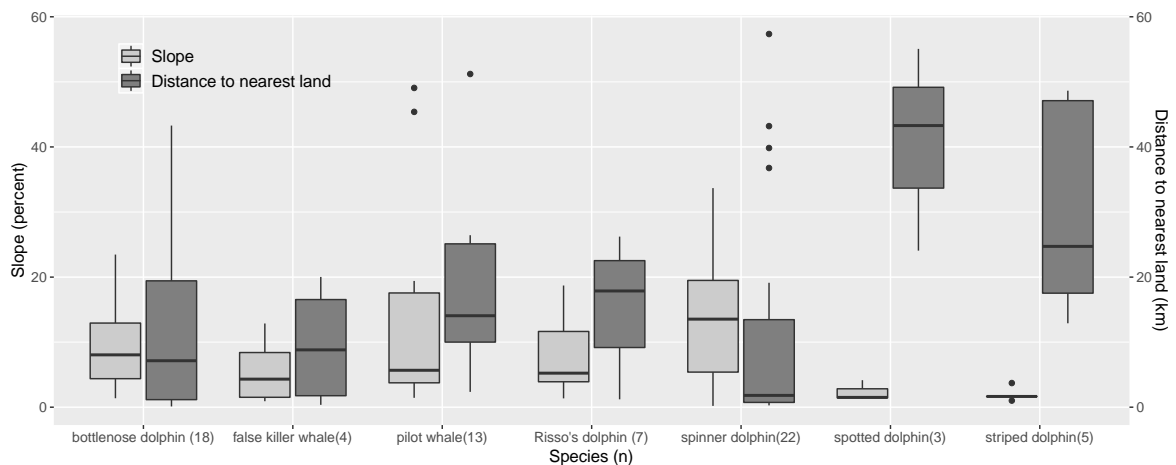


Figure 2.5. Distribution of species ($n \geq 3$) across slope gradients (left axis, light grey boxes) and distance to nearest landmass (right axis, dark grey boxes). Dots are outliers of the data.

2.5 DISCUSSION

Our study used platforms of opportunity provided by ferry services between islands to conduct the first systematic surveys in an otherwise poorly studied region. Using these platforms we have been able to estimate encounter rates and examine differences among species in habitat attributes that they are associated with. A major advantage of using such platforms of opportunity is that it cuts down on costs and helps us to overcome shortages of dedicated and expensive platforms, a common problem in many tropical countries. This, however, also has limitations. We were not able to lay randomized transects or survey areas outside of the ferry routes. We also had to conduct the survey at higher vessel speeds of 18.4 and 15.2 knots/hour than conventionally used by dedicated platforms and were not able to stop or deviate from routes to obtain better identification of cetaceans. Despite these limitations, our study demonstrates that, like other tropical oceanic island complexes such as Hawaii and the Maldives that are characterized by

changing depth profiles, varying ecological niches, and high cetacean usage (Anderson et al., 2012b; Baird et al., 2013), Lakshadweep waters host a diverse tropical cetacean community.

The encounter rate of 2.01 sightings per 100 km recorded during the current study period is lower than encounter rates recorded in some prior marine mammal surveys in nearby waters. Ballance and Pitman (1998) documented 6.02 sightings per 100km in the western tropical Indian Ocean, Ballance et al. (2001) reported an encounter rate of 13.6 sightings per 100 km off Maldives, and Ilangakoon (2012b) recorded an encounter rate of 6.11 sightings per 100km. These studies were dedicated surveys running at lower vessel speeds. Afsal et al. (2008) reported an encounter rate of 0.1 sighting per hour that was lower than our encounter rate of 0.61 sighting per hour. This survey by Afsal et al. (2008) was opportunistic and had fewer observers than our study. Our encounter rate was comparable to the encounter rate of 1.28 sightings per 100km recorded by Alling (1986), although survey effort, vessel type and number of observers differed. In comparison to opportunistic studies such as Afsal et al. (2008), our surveys showed a higher encounter rate, however, our encounter rate was lower than that of dedicated surveys using 25x binoculars such as Ballance and Pitman (1998). Dedicated surveys in this region may improve encounter rate estimates.

Species reported in this study have been previously described in opportunistic sightings in the Lakshadweep region (<http://www.marinemammals.in>; Kumarran, 2012). Peer-reviewed publications chronicle seven species where identification could be verified: Risso's, bottlenose, striped, and spinner dolphins, short-finned pilot whales, sperm whales (*Physeter macrocephalus*) and Cuvier's beaked whale (*Ziphius cavirostris*) (Burton, 1941; Lal Mohan, 1985; Pillai et al.,

1986; James & Panicker, 1990,1994; Afsal et al., 2008; Sajikumar et al., 2014). During a marine fauna study, Nagabhushanam and Rao (1972) recorded the occurrence of common dolphins (*Delphinus delphis*), blue whales (*Balaenoptera musculus*), and killer whales (*Orcinus orca*) as part of their species inventory in Minicoy waters of Lakshadweep but no identification methodology, morphological descriptions, behavioral information or exact locations were provided. This study adds false killer whales, pantropical spotted dolphins and pygmy killer whales to this list. Burton (1941) reported the presence of common dolphin and porpoises in 1935, however these were incorrectly identified and pictorial evidence in the publication shows clear identification features for bottlenose dolphins and Risso's dolphins, respectively.

In this study, we did not classify *Tursiops* spp. to species level as detailed observations and photographs were not available for every *Tursiops* sighting in the field. It appears that both species may occur in Lakshadweep waters as we observed some sightings with robust body type and short beak characteristics and other sightings with a comparatively slender body type and longer beak. Based on our anecdotal notes, it may be a possibility that *T. aduncus* is island-associated and *T. truncatus* occurs offshore. Anderson (2005) noted that both species may occur in the Maldives and observed a difference between the behavior of inshore and offshore bottlenose dolphins there. More investigation in our study area is required to confirm whether one or both species occur in the region.

In the current study, a higher number of sightings occurred during the northeast monsoon season (November-December), suggesting that some species may be using the area seasonally. Seasonal comparisons were conducted between northeast monsoon and inter-monsoon seasons in

this study; our surveys did not cover the southwest monsoon season. Seasonal cetacean usage during northeast monsoon seasons has been documented for Sri Lanka and the Maldives (Broker & Ilangakoon, 2008; Anderson et al., 2012b; Clark et al., 2012; de Vos et al., 2014). Primary and mesozooplankton productivity in the northeast monsoon season is high in offshore regions of the Arabian Sea due to convective mixing and zooplankton community dynamics (Barber et al., 2001; Madhupratap et al., 1996). In contrast, inter-monsoon months can be less productive due to stratification (Barber et al., 2001). In Lakshadweep waters, high mesozooplankton abundance and diversity is observed in December and January (Mathew et al., 2003; Sanu et al., 2014). We hypothesize that some cetacean species may be using this area to exploit such productive conditions in the northeast monsoon season. Cetacean species differed in seafloor slope gradients and with distance from islands in which they were sighted. Spinner dolphins occurred closest to land and across a larger slope gradient. In the Maldivian atolls, spinner dolphins are found nearshore and enter the atolls through reef channels in the mornings and move offshore to feed in the afternoons (Anderson, 2005). Striped and spotted dolphins occurred furthest from land, and also inhabited a narrow slope gradient (flatter topography) in our study. This is similar to findings by Anderson (2005) in the Maldives where striped dolphins were recorded mostly outside atolls in offshore waters. Such differences are likely to reflect niches inhabited by prey species of cetaceans. Habitat analyses in our study used a presence-only approach and tested for how species differed from one another along the ferry routes, hence should be interpreted within this context. Our understanding of habitat preferences of these species in the Lakshadweep region is currently marginal; moreover, sample sizes for some species in our study were low. Therefore to understand habitat use and/or habitat preferences of cetacean species in

Lakshadweep waters, further dedicated surveys covering available bathymetric regimes need to be undertaken.

Mixed species groups comprising of bottlenose dolphins and short finned pilot whales, similar to what we observed, have been recorded in other regions including the western tropical Indian Ocean, eastern tropical Pacific, southern Sri Lanka (Ballance & Pitman, 1998; Hlangakoon, 2012b), and nearby coral atolls such as the Maldives (Anderson, 2005). The second association we documented of pantropical spotted dolphins and bottlenose dolphins appears less common. In some areas such as the Bahamas, Atlantic spotted dolphins associate with bottlenose dolphins regularly and engage in a host of activities such as foraging, play, aggression, and sexual behavior, and potential hybridization (Herzing & Elliser, 2013). Pantropical spotted dolphins commonly occur with spinner dolphins in regions like the Maldives, the Eastern Tropical Pacific, and Hawaii (Perrin et al., 1973; Psarakos et al., 2003; Anderson, 2005). We did not observe this association, which may be due to the 'passing mode' methodology used during our surveys. Qu erouil et al. (2008) suggests mixed species associations in cetaceans might result in some foraging advantages for one or both species. Other reasons could include predator avoidance or social requirements such as play (Herzing & Elliser 2003; Stensland, 2003; Qu erouil et al., 2008). Further research into the behavioral ecology of these mixed species groups across regions would shed light on these theories.

Prior publications have reported instances of small cetacean capture in the Lakshadweep region. Burton (1941) provided a detailed account of a hunt to capture eleven Risso's dolphins on the island of Chetlat for local consumption. Manikfan (1991) documented the hunting of

small cetaceans in the northern Lakshadweep islands for local consumption with harpoons and a drive fishery (also mentioned in Burton 1941) except in Minicoy, where cetaceans are believed to drive fish into the lagoon. Lal Mohan (1985) reported that an estimated 50 dolphins were caught annually across the Lakshadweep islands, except Minicoy. Although our research did not focus on hunting, we feel it is important to share that during the course of our study, targeted hunting was not observed or reported in Kavaratti. While fishermen's accounts indicated knowledge of such practices as isolated events, they stated this practice was largely abandoned by the younger generation after the advent of the pole and line tuna fishery in Kavaratti. Instead, several local reports from Kavaratti and Minicoy stated that dolphins act as cues for fishermen to find tuna shoals similar to the eastern tropical Pacific Ocean (Lal Mohan, 1985; Ballance et al., 2006). The existence and extent of cetacean capture for local consumption across all the islands and the consequence of dolphins being visual aids for tuna fishers (e.g. vessels approaching groups) need to be investigated further.

The most likely candidate for the unidentified *Balaenoptera* sp may be the fin whale based on its apparent body size. The animal seemed too large to be an Omura's (*B. omurai*) or common minke whale (*B. acutorostrata*). Photos taken in succession of a surfacing show the long back coming up after the blow and before seeing the dorsal fin indicating a body size of over 20m (Figure 2.3e shows the last frame of a surfacing with dorsal fin). There are no confirmed records of fin whales in the region and this species is considered rare in low latitudes, with some exceptions (Wade & Gerrodette, 1993). Bryde's whale (*B. edeni*) is another possibility if the large size estimate is disregarded. This species has been sighted in mainland Indian coastal waters and the Maldives (Ballance et al., 2001; Sutaria et al., 2017). Sperm whale,

pygmy blue whale, and humpback whale can be ruled out based on the dorsal fin shape (Figure 2.3e).

In the Arabian Sea, large whales are known to undertake mesoscale movements to meet energy demands (Mikhalev 1997; Pomilla et al., 2014; Branch et al., 2007; Anderson et al., 2012a), but their ranging behavior remains unknown in many areas. There are regional reports of large whales in the Maldives, Sri Lanka, and the west coast of India (James & Panicker, 1990, 1994; Ballance & Pitman, 1998; Afsal et al., 2008; Anderson, 2012b; Ilangakoon, 2012a; Kumarran, 2012; Sutaria et al., 2017). Our surveys had only two observations of large whales; however, anecdotal reports by local fishermen confirm that large whale sightings occur regularly in these waters. Our methodology may have missed whale sightings or any other long-diving species due to availability bias arising from the speed of our platform and 'passing mode' of survey (Barlow, 1999; Williams et al., 2006). There may also be seasonal variations (e.g. southwest monsoon season) in baleen whale presence in the region (Anderson, 2012a). We propose using methods such as passive acoustic monitoring and/or dedicated marine mammal visual surveys for future studies to better understand cetacean occurrence in the region.

Our surveys were conducted from ferries, which served as platforms of opportunity, as the primary purpose of the ferry system is to transport passengers between islands. Ferry routes were linear making it possible for us to survey using a line transect framework in this region, which is otherwise remote and difficult to access (Buckland et al., 2001, 2005). Although the vessel speed and direction was conducive to line transect methodology, we had no control over route design, ferry schedule, speed of travel, or type of vessel used, therefore making it difficult

to compare effort data across the routes. Hence, we have only presented descriptive route information and refrained from making any statistical comparisons .

The Lakshadweep waters are clearly an important area for multiple cetacean species and further surveys are required to provide a robust picture on space-use patterns including those of rare or cryptic species. Oceanographic factors and habitat preferences of cetacean species need to be studied to identify the determinants of distribution in this region. Passive acoustic monitoring would be another relatively cost-effective method to study year-round occurrence, especially during rough weather periods such as the south-west monsoon. As the islands are not currently industrially developed, have limited tourism activities, and practice pole and line tuna fishery, cetaceans in this region may currently face relatively lower or different types of threats than neighboring areas. However, these are likely to change with growing demands from the high-end tourism industry and plans for large-scale tourism expansion (Kumar & Muralidharan 2019). Hence the area needs to be monitored and carefully managed accounting for high cetacean usage near the islands. The high diversity of cetaceans over many months underlines the Lakshadweep region as an important mid-ocean habitat and emphasizes the need for further studies in the region to highlight the biogeography and ecology of cetaceans here.

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Chapter 3. NORTHERN INDIAN OCEAN BLUE WHALE SONGS RECORDED OFF THE COAST OF INDIA

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Blue whales (*Balaenoptera musculus* spp), an endangered species globally, are found throughout the Indian Ocean, including the northern Indian Ocean (NIO) and Arabian Sea (Branch et al. 2007). Blue whales track productive habitats where primary productivity is high and dense aggregations of prey occur (Croll et al. 2005, Branch et al. 2007, Abrahms et al. 2019). The island mass effect, associated upwelling, and nutrient discharge increase productivity near mid-oceanic islands (Genin 2004, Gove et al. 2016). In the NIO, where seasonal monsoons shape ocean life, mid-oceanic islands may act as predictable hotspots for baleen whale prey (Brink et al. 1998, Gove et al. 2016).

In addition to Antarctic blue whales (*B. m. intermedia*), four possible populations of pygmy blue whales (PBW), comprising one or two subspecies to date (*B. m. breviceuda* and *B.m. indica*), occur in the Indian Ocean (Rice 1998, Branch et al. 2007). These have been categorized based on their distinct song types; passive acoustic monitoring has provided most of what we know about the distribution of blue whales post commercial whaling (Stafford et al. 2011, Gavrilov & McCauley 2013, Samaran et al. 2013, Leroy et al. 2016). The so called “acoustic populations” of PBW in the Indian Ocean include the NIO PBW (sometimes referred

to as “Sri Lanka song”, likely *B. m. indica*) (Alling, Dorsey and Gordon 1991), northwest Indian Ocean (sometimes referred to as “Oman song”, Cerchio et al. 2020), southwest Indian Ocean (sometimes referred to as “Australia song,” Gavrilov & McCauley 2013), and southeast Indian Ocean PBW populations (sometimes referred to as “Madagascar song,” Ljungblad, Clark and Shimada 1998). The majority of acoustic studies of blue whales in the Indian Ocean have focused on the southern Indian Ocean and have defined the seasonal and geographic occurrence of PBW acoustic populations south of the equator (Stafford et al. 2011, Gavrilov & McCauley 2013, Samaran et al. 2013). There is considerably less known about the range and distribution of these populations in the NIO and Arabian Sea.

At least some blue whales in the NIO are thought to be resident, with a breeding cycle six months out of sync with Southern Hemisphere blue whale populations (Mikhalev 2000, Branch et al. 2007). Records from illegal Soviet whaling in the 1960s and 1970s showed blue whale catches near Oman, Lakshadweep (India), the southwest Indian coast, Pakistan, and Sri Lanka (Mikhalev 2000, Figure 3.1). Based on catches, sightings, acoustic detections, and strandings across the NIO, Anderson et al. (2012) hypothesized that NIO blue whales feed off Somalia and the southwest Indian and western Sri Lankan coasts during the southwest monsoon (May-October) and disperse to other areas of localized high productivity in the northeast monsoons (December-March), such as the Maldives. Anderson & Alagiyawadu (2019) propose that some part of the population transits through the mid-oceanic Chagos-Laccadive ridge between November and January and again between April and May. Data from blue whales in the NIO suggest that near Sri Lanka, blue whales feed primarily on sergestid shrimp and mysids rather than euphausiids (Alling et al. 1991, de Vos et al. 2018).

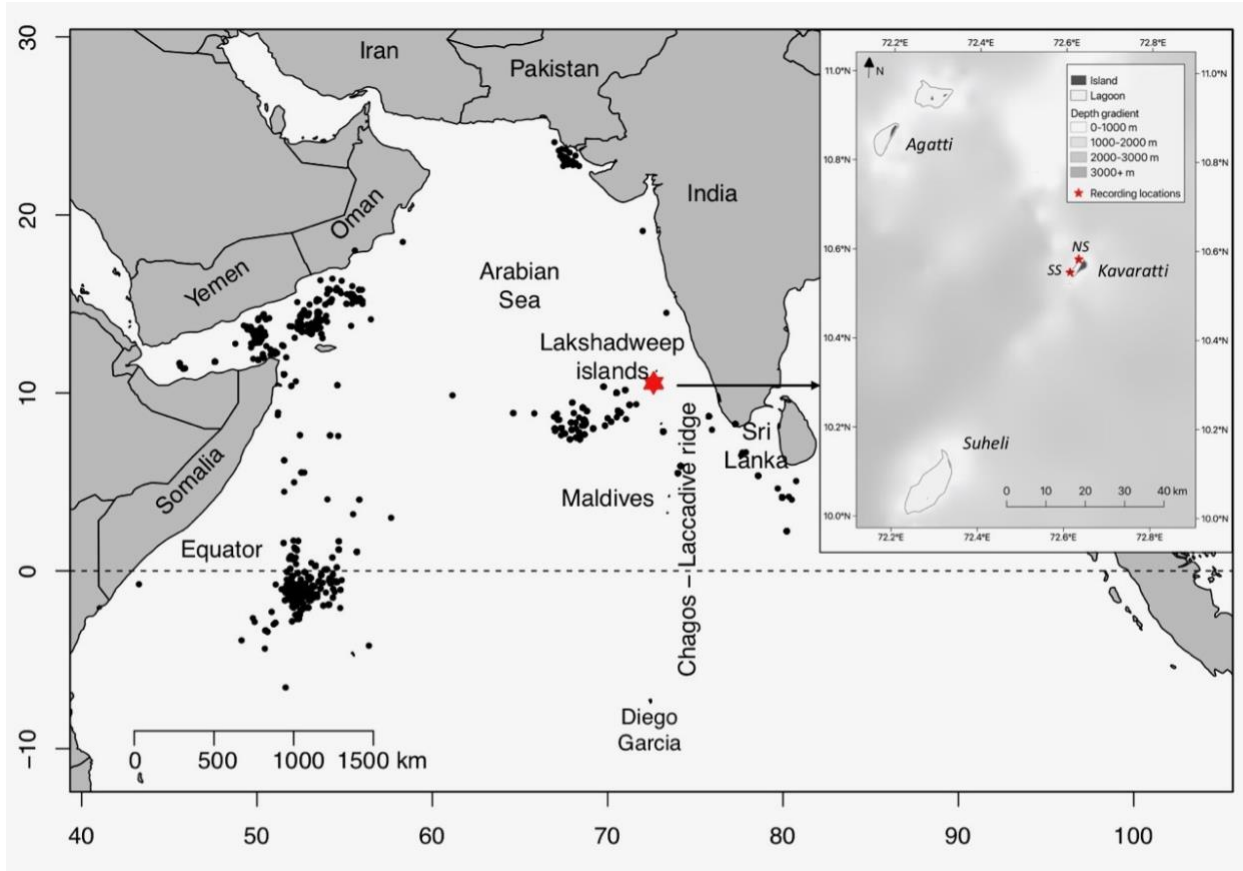


Figure 3.1. Location of hydrophone deployments in the northern Indian Ocean shown by the red star symbol. The black dots are locations of PBW catches from illegal soviet whaling.

Redfern et al. (2017) used environmental modeling to predict that areas near Lakshadweep should be good blue whale habitat during the southwest monsoon (June to September). To determine whether and when blue whales occur in the Lakshadweep region, we examined data from a passive acoustic monitoring study off Karavatti Island, India, from December 2018 to January 2020. The objectives of this study were to assess whether blue whales occur near the archipelago and determine which acoustic population(s) use the area. Secondly, we aimed to determine if there were diel and/or seasonal differences in blue whale song detections. Thirdly, we measured intersong intervals and peak frequency of signals to determine

the minimum number of singing animals present at one time and whether the frequency of the main unit(s) continued to decline as suggested in prior studies (Miksis-Olds et al. 2018). Here, we report on the first acoustic detections of blue whales off the west coast of India.

Divers deployed two passive acoustic recorders (Soundtrap ST-300STDs, bandwidth 20 Hz to 60 kHz) off Kavaratti Island (Figure 1). The recorders were fixed to a cement block that was placed on the seafloor. One recorder was placed on the north side of the island near the slope at 11m depth from December 2018 to October 2019, and another recorder was placed on the south side of the island on the slope at 29 m depth from November 2019 to January 2020. Recording periods and locations of the hydrophones are provided in Table 3.1 and Figure 3.1. Each recorder sampled at 96 kHz on a duty cycle of 10-15 min each hour (Table 3.1). Duty cycle was changed from 15 min to 10 mins per hour from April to October 2019 to ensure the batteries would last through the monsoon season.

Table 3.3. Location, recording periods, duty cycle and depth for each hydrophone deployed off Kavaratti Island from 2018-2020.

Site	Recording period	Duty cycle (min/hr)	# Recordings (files/total hr)	Depth (m)
North site	1 December to 31 December 2018	10	744/124	11
N10° 34.831'	1 January to 8 April 2019	15	2,352/588	11
E72° 37.862'	14 April to 5 October 2019	10	4,200/700	11
South site	17 November 2019 to 5 January	15	1,200/300	29
N10° 33.021'	2020			

E72° 36.671'				
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After retrieval of the Soundtraps, we decimated the audio files to 2 kHz sample rate using *Triton* (Wiggins 2003) and created long-term spectral averages (LTSA; time averaged at 120 s with frequency bin size of 0.1 Hz). We visually searched LTSAs using plot lengths of 10 hr and a frequency range of 20-150 Hz and 20 to 1,000 Hz to identify periods of high bioacoustic activity from baleen whales. From periods with high numbers of NIO blue whale signals identified through LTSAs, we chose a subset of strong and faint whale song units to develop a detector. We ran the detector as just visually examining the data set through LTSAs would only allow a coarse view limited to periods of high singing rates. We used the whistle and moan detector implemented in PAMGuard version 2.00.14beta, with a 4,096 point Fast Fourier Transform with 50% overlap and Hann window (Gillespie et al. 2008). The detector looked for signals in the 90 Hz to 110 Hz band (NIO PBW unit 3, see Figure 3.2) with at least 6 dB signal-to-noise ratio (SNR). This threshold was chosen as it did not give any false negatives with our training set. However, this resulted in a high number of false positives. On running the detector on the entire dataset, we manually examined all detections to eliminate false positives. In the north site, we logged 314 true positive detections and 7,564 false positive detections. In the south site, there were no true positives and 856 false positive detections.

We graded the SNR of PBW song following Sousa and Harris (2015), where Grade 1 had strong songs for which the entire frequency range was visible and showed high SNR (n=138); Grade 2 clearly showed the overall shape of the signal (n=92); and Grade 3 had songs which were identifiable but had otherwise low SNR (n=84). We measured the peak frequency of unit 3

and the intersong interval from only Grade 1 songs. Intersong interval was defined as the time between the start of a song to the beginning of the next song.

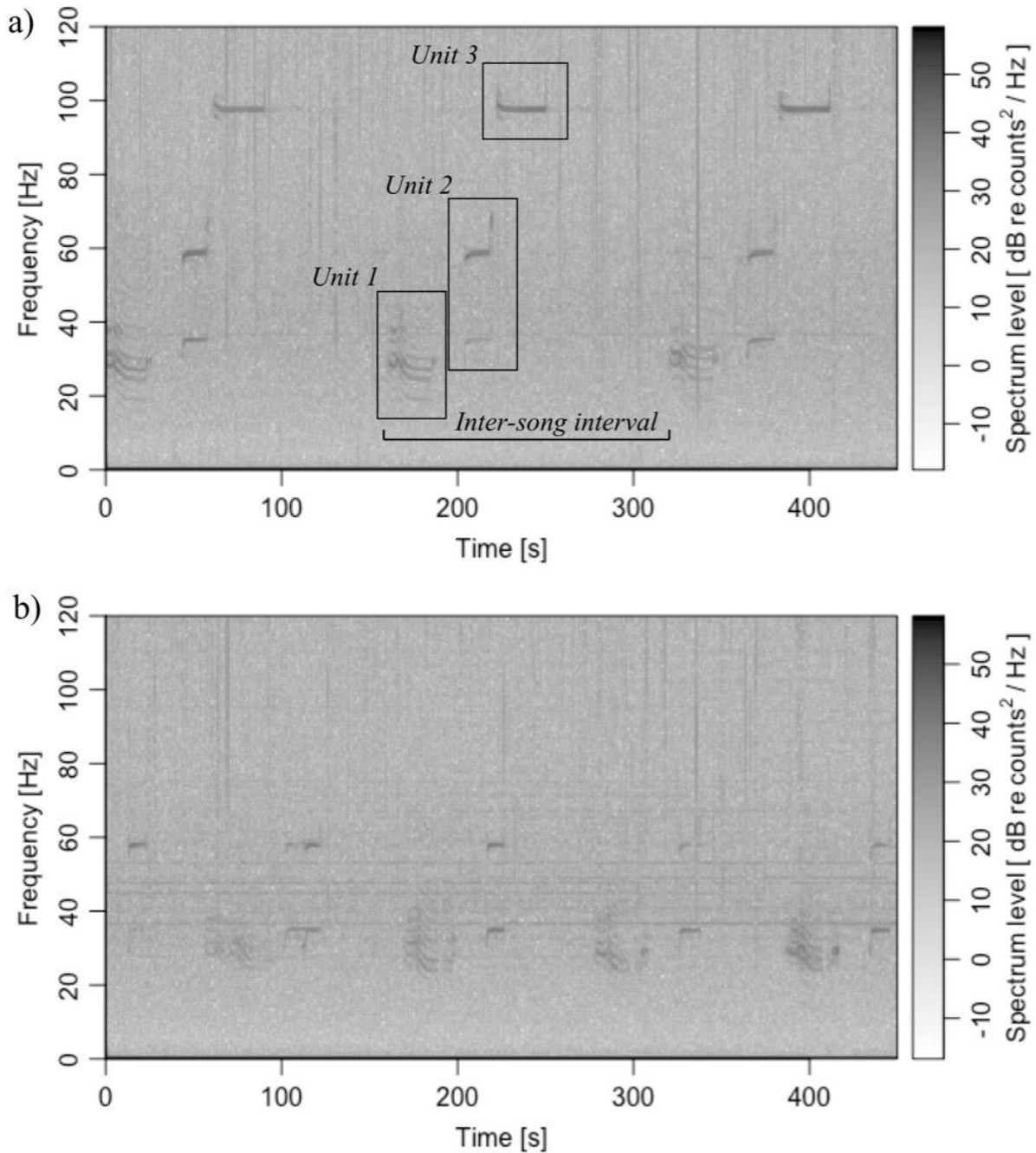


Figure 3.2. Spectrogram of NIO pygmy blue whale songs with all three units recorded on April 28, 2019 and b) examples of songs with only units 1 and 2 recorded on May 27, 2019 (Sample rate 2 kHz, FFT: 4,096, Hann window, 50% overlap).

Relative acoustic occurrence for each season (proportion of days with detections in a season), day (proportion of recordings with detections in a day), and time period (proportion of recordings with detection during dawn, day, dusk, and night hours) were calculated for the entire time series. For example, if 2 recordings in a day showed detections, the proportion per day would be $2/24$ (i.e., 2 of 24 recordings) or 8% of recordings for that day. We conducted chi-squared goodness of fit tests to determine if blue whale acoustic occurrence was equally distributed across seasons: southwest monsoon (June to October), intermonsoon (March to May), and northeast monsoon (December to February), and across time periods: dawn (two hours after dawn nautical twilight), day (between dawn and dusk), dusk (2 hr before dusk nautical twilight) and night (between dusk and dawn). All statistical analysis was done in *R* (R core team 2019). Time of day was based on solar azimuths from the *R* package *suncalc* (Thieurmel and Elmarhraoui 2019).

We detected NIO PBW (hereafter PBW) songs in the acoustic data set. No other blue whale acoustic populations or other baleen whale signals were observed during visual inspection of LTSAs. PBW were detected during 120 recordings of 5,640 recordings at the north site. No PBW vocalizations with unit 3 were detected at the south site which is not surprising since the recorder was in place for only seven weeks, five of which were during a period of the year (December-January) in which few song phrases were recorded in the first year of monitoring efforts.

The majority (69.2%) of PBW detections occurred in April and May during the intermonsoon period, prior to the southwest monsoon (Figure 3.3). During this time, PBW

signals were recorded on over 50% of recordings from some days (Figure 3.4). Apart from these two months, two months in the northeast monsoon (February and December) and three in the southwest monsoon (June, July, and September) had evidence of PBW occurrence (Figure 3.4). For the north hydrophone, we tested against the null hypothesis that all seasons had equal detections and found that the intermonsoon period had significantly higher detections than southwest monsoon or northeast monsoon season ($\chi^2 = 101.9$, $df = 2$, $p\text{-value} < 0.05$).

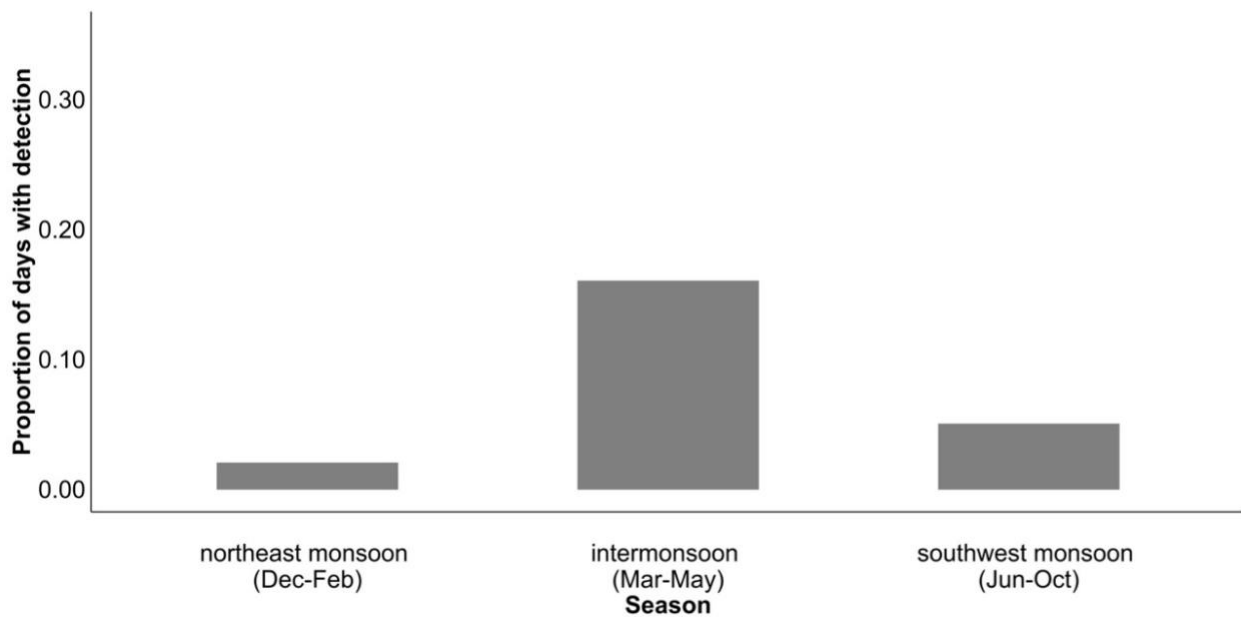


Figure 3.3. Proportion of days with PBW detections across monsoonal seasons for the north site near Karavatti Island.

The NIO PBW song phrase is usually made up of 3 units (Figure 3.2a, Stafford et al. 2011). During manual examination of the LTSAs showing periods of high singing rates, most songs included unit 3. However, in eighteen recordings, on May 27, 2019, June 12, 2019, and July 3, 2019, songs with only units 1 and 2 were observed (Figure 3.2b). We do not believe that unit 3 was too faint to be detected, rather, based on the truncated time between songs, it appears that the whale was omitting unit 3. To determine if this was indeed the case, we examined

few songs overall. Unit 3 is the signal targeted by automatic detection for the NIO song type (e.g., Stafford et al., 2011, Miksis-Olds et al. 2018, Torterotot et al. 2020), which may be why the variation described here has not been reported previously. If modifying the song by leaving units out or adding some in as reported by Joliffe et al. (2019) for SEIO blue whales is a common occurrence, it will not have been noticed in studies that use only unit 3 to detect the presence of NIO PBW. This suggests that these whales occasionally go undetected, as they would have here without detailed examination of the LTSA, which could have implications for conservation actions that require a robust understanding of when and where PBW occur. The songs with just units 1 and 2 were not included in any other analysis in this study. It is difficult to estimate how many songs without unit 3 occurred in this dataset as our detector only targeted unit 3, however, from the visual examination of LTSAs we can report there were no periods of high singing rates where songs had only units 1 and 2.

For the songs that had a unit 3, the peak frequency of this unit was $97.5 \text{ Hz} \pm 0.47 \text{ Hz}$ ($n = 76$ from 5 different recording days). This value is more than 10 Hz lower than reported by Stafford et al. (2011) for data from 2002-2003. Miksis-Olds et al. (2018) documented a decrease in this unit of 5.4% over the decade from 2002-2013 such that in 2013 it was centered at 100.7 Hz. If this decrease was projected from 2013, the expected frequency would have declined a further 3.2% to 97.4 Hz in 2019 which matches the ~97 Hz unit 3 frequency we observed. Clearly, the center frequency of this unit has continued to decline over time. This phenomenon of a gradual decrease in frequency of song units has been recognized in blue whale songs globally, including the Indian Ocean (McDonald et al. 2009, Leroy et al. 2018, Miksis-Olds et al. 2018).

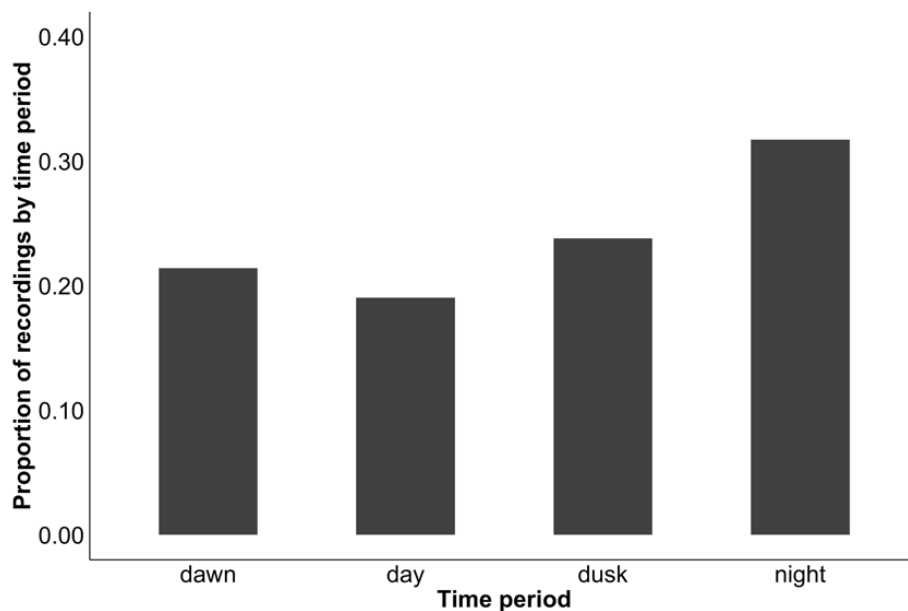


Figure 3.5. Proportion of recordings by period of the day with PBW song units recorded for the north site during the months of April and May 2019.

We examined diel singing patterns in north site data during the months of April and May 2019, as these had the most PBW acoustic detections. The proportion of hours with detections was higher during night, but this was not statistically significant ($\chi^2 = 3.45$, $df = 3$, $p\text{-value} = 0.33$, Figure 3.5). Blue whales exhibit diel variability in acoustic behavior in other locations, and this has been attributed to the diel patterns of their prey, and to seasonal shifts from feeding (night-time singing) to migration (daytime singing) in blue whales (Leroy et al. 2016, Stafford et al. 2005, Oestreich et al. 2020). Unfortunately, we have no prey data from the Lakshadweep region, which would provide more insight into PBW behavior and habitat use patterns in this area.

The seasonal pattern we report here is similar to that observed by Stafford et al. (2011) from Diego Garcia waters where songs peaked during May in 2002 and 2003. From that same

data set, but over a much longer time period, Miksis-Olds et al. (2018) found peaks from May to June in NIO PBW song detections. Our detections were primarily in the intermonsoon periods which is contrary to the predictions of Redfern et al. (2017) that the Lakshadweep region might provide good blue whale habitat during SW monsoons. Anderson & Alagiyawadu (2019) suggested intraregional movement between the eastern and western Arabian Sea and the Chagos-Laccadive Ridge between April and May. If this is the case, it is likely we are detecting animals travelling through, but not remaining in, the Lakshadweep region. NIO blue whale songs have been recorded in all months of the year at different locations in the Indian Ocean (e.g., Samaran et al. 2013), so we believe these animals have a limited seasonal residency in the Lakshadweep region. Another possibility is that the year-round productivity around these islands may provide feeding opportunities during intermonsoon months when other areas in the Arabian Sea may be less productive, as highlighted in Anderson et al. (2012).

In the Arabian Sea, the range and seasonality of pygmy blue whales have not been studied extensively. Here, we provide the first evidence of NIO PBW songs in Indian waters. These results extend the known range of NIO pygmy blue whales about 1,000 km westward from the waters surrounding Sri Lanka. We did not record other blue whale songs during the sampling periods. In the past, fishermen from the region reported seasonal occurrence of baleen whales in Lakshadweep waters (Panicker et al. 2020) and this study confirms that some of these are blue whales. The data deficient status of pygmy blue whales in Indian waters, we believe, is one of the primary reasons for an absence of targeted conservation measures for blue whales in Indian waters. While legislation such as the Wildlife Protection Act (1972) provides broad protection to marine mammals on paper, species-specific conservation and management plans are wanting.

Threats such as climate change (and its impact on the monsoons and primary productivity), underwater noise, and ship strikes are likely to impact blue whales in this densely populated region of the world, and threat assessments are heavily reliant on a comprehensive understanding of the distribution and seasonality of blue whales in Indian waters. For example, environmental impact assessments for large scale tourism development in Lakshadweep waters need to consider that these waters are habitat for endangered blue whales as shown here (Kumar, Muralidharan and Mathur 2019). Continued passive acoustic monitoring efforts in the Lakshadweep region and the greater Arabian Sea, including dedicated visual surveys and prey sampling during April and May, and detection of other blue whale signals such as D-calls, will provide improved knowledge on the occurrence of NIO (and other) PBWs in the northern Indian Ocean and will act as a first step to species conservation and enable managers to make data-driven conservation decisions.

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Chapter 4. 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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4.1 ABSTRACT

Temporal patterns of oceanic predators can provide valuable information on both lunar and diel influences on not just these predator distributions, but also on their prey patches that are often difficult to study. Mid-oceanic island chains in the northern Indian Ocean have high odontocete occurrence, however, 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, 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 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.

4.2 INTRODUCTION

In the open ocean, seasonal, diel, and lunar cycles influence animal distribution, life history and behaviour on 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 ocean (Bianchi & Mislán 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).

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 mesopredators, 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; Gjosaeter 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 world's human population. Severe anthropogenic pressures, such as fishing, pollution, shipping, and a changing climate, have resulted in marine resources being threatened or overexploited and are sure to 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. 4.1, 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 and support a thriving tuna fishery (Nair et al. 1986, Vinay et al. 2017). Silas (1972) show occurrence of deep scattering layers in shallow waters near 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.

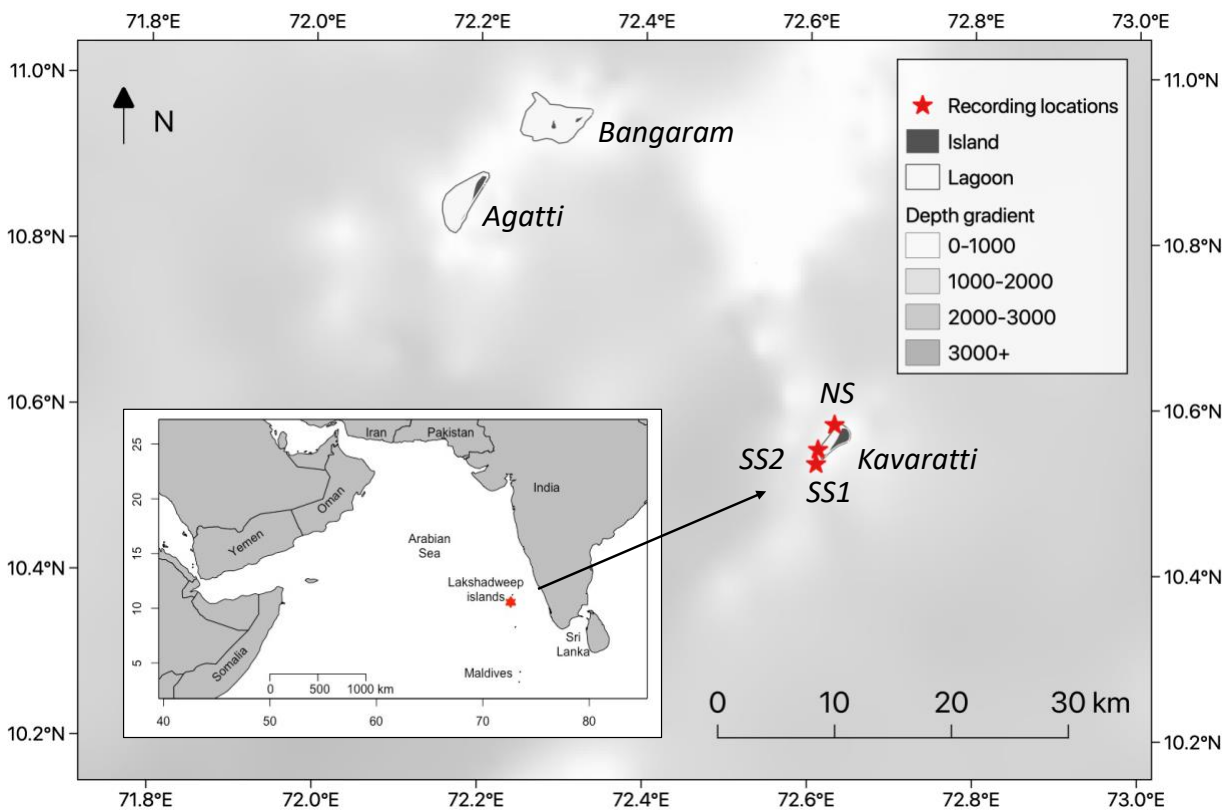


Figure 4.1. Location of hydrophone deployments and the study area in the Arabian Sea.

The Lakshadweep archipelago was declared an Important Marine Mammal Area in 2019 under the IUCN World Commission on Protected Areas, therefore it is recognized internationally as a site of significance to cetaceans and requires protection (IUCN-Marine Mammal Protected Areas Task Force 2021). The area shows high odontocete presence, and records suggest 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 these species are lacking in the region. Spinner dolphin (*Stenella longirostris*) is the most commonly sighted species followed by bottlenose dolphins (*Tursiops* spp.) and short-finned pilot whale (*Globicephala macrorhynchus*). Other odontocete species sighted in these waters include pantropical spotted dolphin (*S. attenuata*), striped dolphin (*S. coeruleoalba*), Risso's dolphin (*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 temporal 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, finding prey and navigation.

Here we aimed to understand the occurrence and temporal patterns of island-associated odontocetes using passive acoustic monitoring 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; 2) understand how island-associated passive acoustic odontocete detections correlate with temporal (monthly, lunar, diel) and spatial (site) factors.

4.3 METHODS

4.3.1 *Acoustic recorder deployment*

The study was carried out off Kavaratti Island, a one-island atoll with 3.93 km² land area in the Lakshadweep Islands (Fig. 4.1). Divers deployed two passive acoustic recorders off the outer reef area (Fig. 4.1). Two SoundTrap ST-300STDs were used with a flat response from 20 Hz to 60 kHz (± 3 dB) with < 35 dB re 1 μ Pa noise floor above 2 kHz and end to end system sensitivities of -176.1 and -176.6 dB V/ μ Pa. 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 m and 18 m depths, respectively (Fig. 4.1, Table 4.1). 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 $\sim 6.7 \pm 3.5$ km in deep water (Oswald 2006) but due

to the shallow environment of the deployment and the orientation of the atoll, the two 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 hr so we can deploy the recorders at least for 3 to 4 months at a time (Table 4.1). The recording duration and location of each hydrophone is given in Table 4.1 and Fig. 4.1.

Table 4.4. Location, recording periods, duty cycle and depth for each hydrophone deployed off Kavaratti Island from 2019-2020.

Site	Recording period	Duty cycle (min/h)	# Recordings (# files/total h)	Depth (m)
South site 1	1 January to 8 April 2019	15	2346/586.5	18
N10° 31.98' E72° 36.53'	13 April to 27 August 2019	10	3288/548	18
South site 2	17 November 2019 to 5 January 2020	15	1200/300	29
N10° 33.02' E72° 36.67'				
North site 1	1 January to 8 April 2019	15	2340/585	11
N10° 34.83' E72° 37.86'	14 April to 5 October 2019	10	4195/699	11

4.3.2 *Recordings and whistle detection*

We created long-term spectral averages (LTSA; time averaged at 5s 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 hr and a frequency range of 20 Hz-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, Gillespie et al. 2013). The detector looked for signals in the frequency band between 2 and 30 kHz with at least 8 dB signal-to-noise ratio (SNR). 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 focused on whistles as clicks were harder to isolate given the high number of snapping shrimp sounds within the same frequency bands.

Cumulative duration 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 μ pa) 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).

4.3.3 *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 (two hours after nautical dawn which was at 5 or 6 am local time), day (between dawn and dusk), dusk (2 hours before nautical dusk which was at 7 pm 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, Benoit-Bird & Au 2004, Benoit-Bird & Au 2006). Seasonal changes in daylight regimes are small in this region, hence diel data was 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 and Elmarhraoui 2019).

4.3.4 *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 one 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 4.1). 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 (REML, 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 `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 hour 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 analysis of variance (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 and Table 4.2 respectively (see Appendix A: Chapter 4 supplementary materials). 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 were evaluated using 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 model to check how well the model fit the data (Hosmer & Lemeshow 2000, Gelman & Su 2021). A chi-square test of independence was conducted to examine differences in dolphin occurrence across seasons in the north and south site.

4.4 RESULTS

4.4.1 *Acoustic occurrence and monthly differences*

From January 2019 to January 2020, we obtained a total of 13369 acoustic data files corresponding to 1413.5 and 1284 h for the south and north site, respectively (Table 4.1). Odontocete whistles were detected in 465 and 279 recordings, corresponding to 99.5 and 62.7 h, from 179 and 130 days for south and north sites, respectively. Odontocete detections occurred for a higher proportion of days in the south site (62.8% of all sampled days) than the north site (47.6% of sampled days; Fig. 4.4a). Although both recorders were unlikely to sample the same area, as mentioned in the methods, 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 two sites. Of all the 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. 4.2a).

Of the 111 spinner dolphin whistles analysed from the dipping hydrophone data, the mean centre frequency was 14.8 ± 0.23 standard error (SE) kHz (6 encounters). The mean centre frequency of short-finned pilot whales (n = 118 from 4 encounters) was 5.20 ± 0.19 SE kHz, and the mean centre frequency of bottlenose dolphins (n = 5 from 1 encounter) was 18.32 ± 0.55 SE kHz (Fig. 4.2b). Based on this, we infer the whistles detected on the moored hydrophones were mostly spinner dolphins.

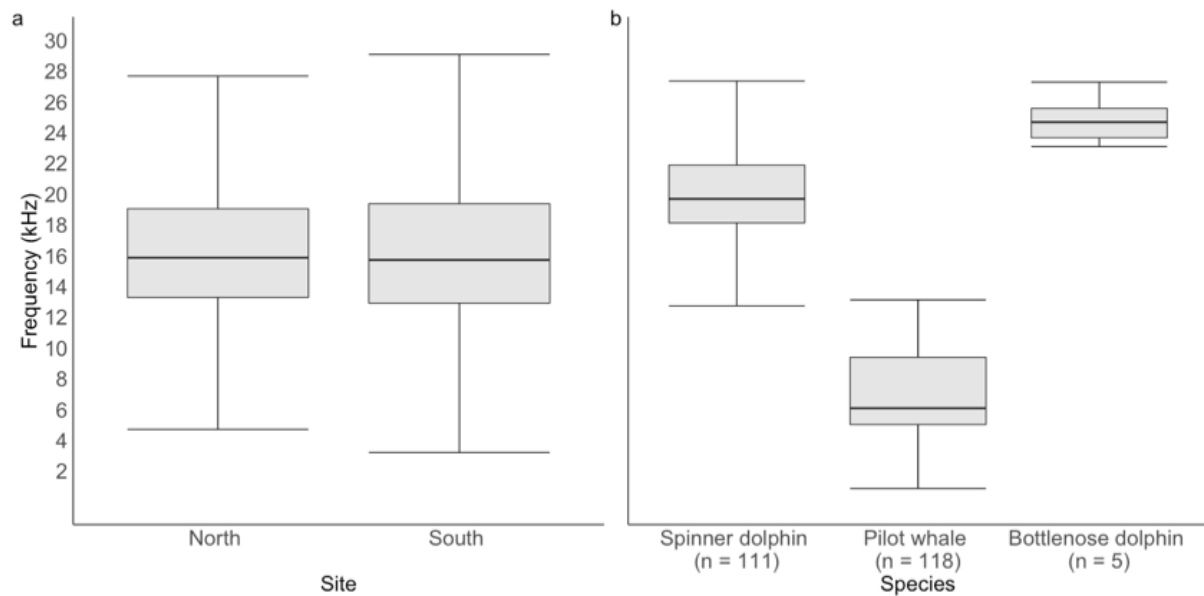


Figure 4.2. Boxplots of centre frequencies showing the minimum, first quartile, median, third quartile and maximum values of the data for a) odontocete detections from the SoundTrap recordings for the north and south site and b) spinner dolphin, short-finned pilot whale and bottlenose dolphin whistles collected using the dipping hydrophone.

From the moored recordings, we detected delphinid whistles in all sampled months from January 2019 to January 2020 (Fig. 4.3). 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 fifty percent or more of all sampled days of each month except from May to September (16.1% to 48.4%), which encompasses the southwest monsoon season. There was significant month-to-month variability in delphinid acoustic occurrence as shown by the GAMM (Table S1 in Appendix A: Chapter 4 supplementary materials, Fig. 4.4b). There were significantly more delphinid detections in November than any other month (Fig. 4.4b). 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. 4.4b). 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 SE % 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 (mean 2.28 ± 0.27 SE % recordings per day for April to October, $\chi^2 = 126.82$, $df = 1$, $p < 0.05$, Fig. 4.3). At the south site, the proportion of recordings with detections per day during the northeast and inter-monsoon periods (mean 7.24 ± 0.72 SE %) was comparable to the pre-monsoon and southwest monsoon seasons (mean 6.3 ± 0.07 SE %, $\chi^2 = 1.97$, $df = 1$, $p = 0.16$, Fig. 4.3).

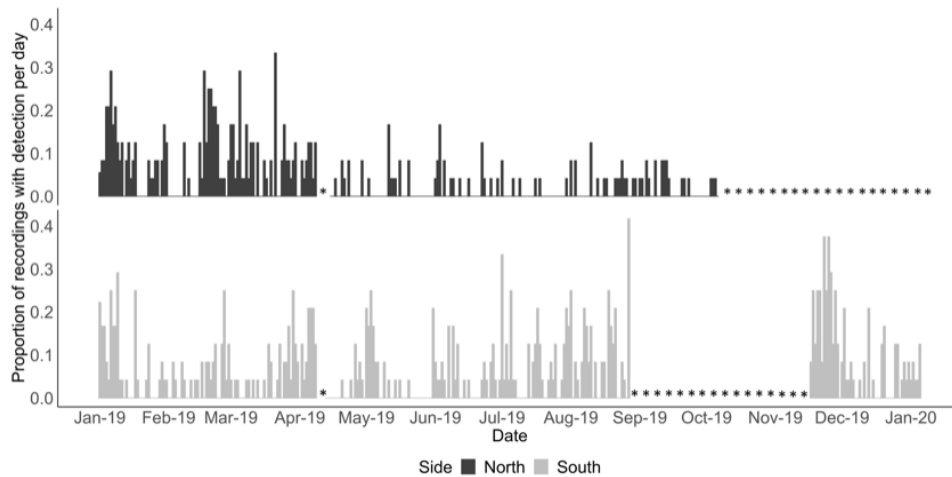


Figure 4.3. Proportion of recordings with detections per day in the south and north site. Asterisks show periods where no sampling took place (dates provided in Table 4.1).

4.4.2 *Diel and lunar patterns*

Delphinids were detected in all 5 periods of the day (dawn, daytime, dusk, night1, night2), however 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. 4.4c). 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 in 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 (7 pm to midnight, local time) had the fewest detections (Fig. 4.4c). 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. 4.4d). 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 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.

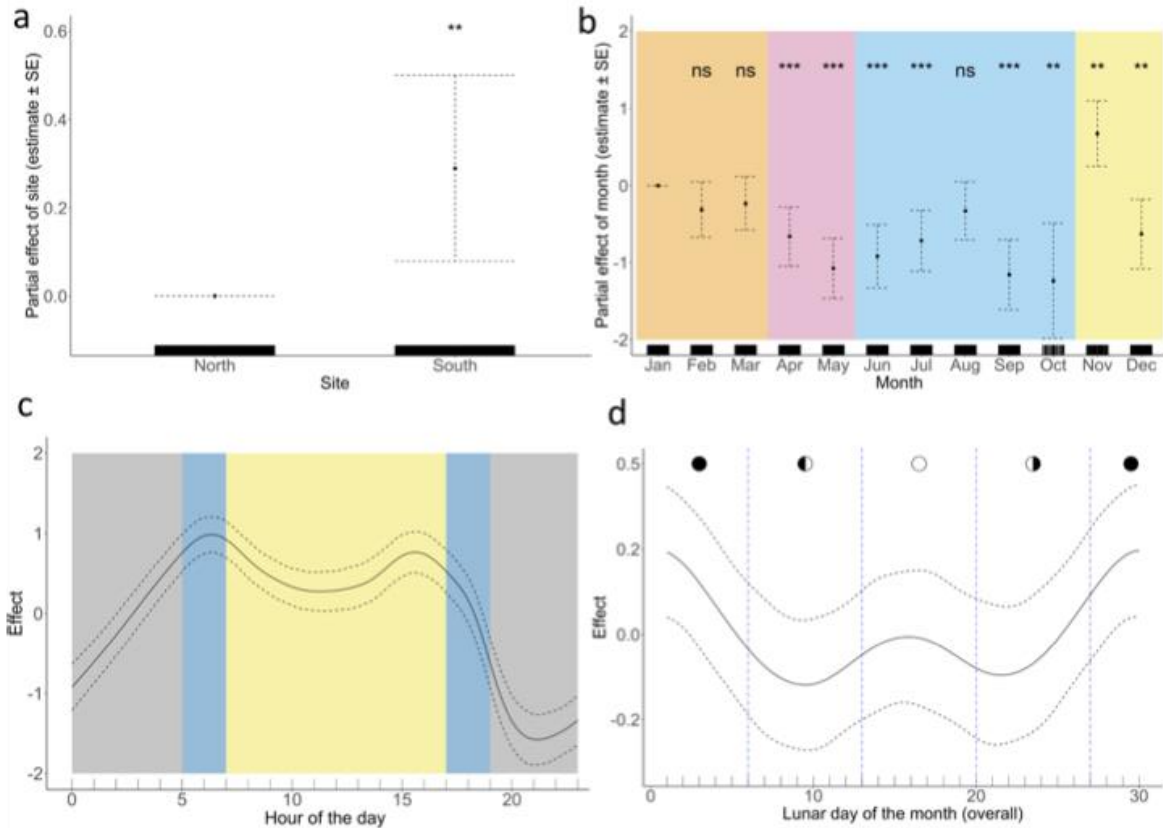


Figure 4.4. Response curves and factor effects of GAMM for presence or absence of odontocete detections (from both sites) with a) site (asterisks show significance with north as the reference); b) month of the year (asterisks show significance with January as the reference), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, 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.

4.4.3 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. 4.5. 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 4.2, Fig. S1 in Appendix A: Chapter 4 supplementary materials). 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 in Appendix A: Chapter 4 supplementary materials for the binned residual plot).

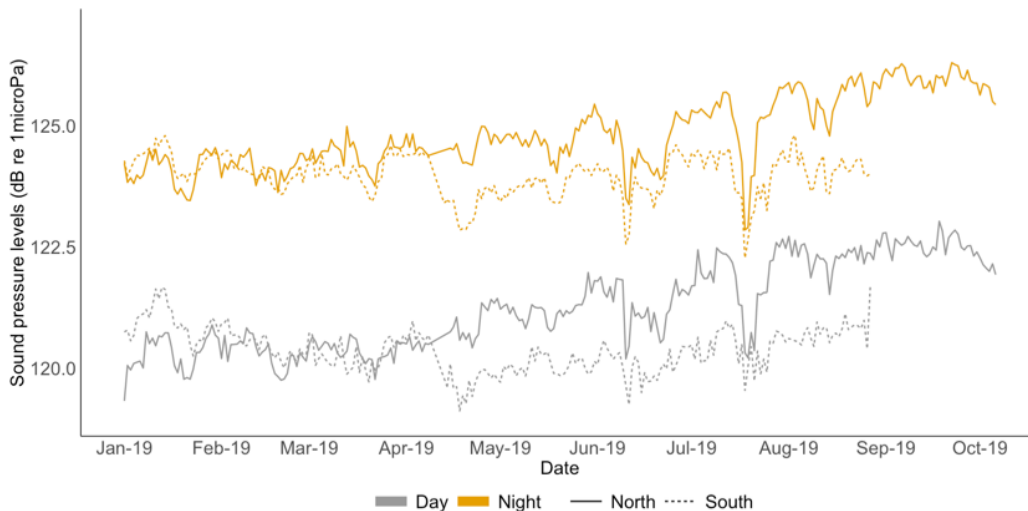


Figure 4.5. Daily mean ambient noise levels (2 to 30 kHz band) for day and night periods at the south and north sites. Data from November 2019 onwards are excluded as the hydrophone was placed at a deeper site.

Table 4.5. ANOVA table for fitted binomial GLM with a logit link examining the relationship between the presence or absence of odontocete detections and ambient noise (average sound pressure levels). Significant terms denoted by *.

	<i>Coefficient</i>	<i>df</i>	<i>Deviance</i>	<i>Residual df</i>	<i>Residual deviance</i>	<i>p-value</i>
Null				12173	4949.0	
Average sound pressure levels (2 to 30 khz)	-0.21	1	126.27	12172	4802.7	<0.005*

4.5 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 year-round prey resources persist near these

islands despite intense seasonal 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 the vocalising animals belong to the Delphinidae family based on broad frequency ranges used by cetacean family groups (Mellinger et al. 2007, Lin & Chou 2015). Panicker et al. (2020) show that spinner dolphins are the most commonly sighted species in Lakshadweep waters, and sightings increased near islands. This is not surprising given 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. 4.2). 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 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 (Panicker, unpubl data). Hence, we infer that the majority of the delphinid whistles that we detected were made by resident spinner dolphins. At our site, passive acoustic monitoring could be considered as 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

except for August. In general, seasonal differences in acoustic occurrence may arise from changes in animal abundances, calling rates or a change in ambient acoustic environment (Rouget et al. 2007, Scheifele et al. 2005). 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 midwinter (Barlow 1984, Norris et al. 1994, Lammers 2019). PAM revealed 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 more productive fishing grounds and based on local accounts and personal observations, we found 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 south-eastern waters in addition to the southwestern waters.

We detected dolphins to a significantly greater extent during daytime with two peaks in whistle detections during dawn hours (around 0600 h) and late afternoon (1600 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 where 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, and foraging when compared to resting periods (Norris et al. 1994). Lammers et al. (2008) found similar patterns where acoustic detections peaked at 0900 h and 1500 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 two 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. 4.4). If dolphins foraged within detection range of the hydrophones at night, then we would expect to detect whistles at night (Norris et al. 1994). Lammers et al. (2008) show higher detections around 2100 h and 0200 h at night off Oahu, Hawaii. In the Azores, Cascão et al. (2020) showed whistle detections were lowest just after sunset and increased linearly towards dawn similar to our study. McElligott (2018) showed 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 the presence of other delphinid species with variable diel patterns (Lammers & Munger 2016, McElligott 2018). Studies in Hawaii show 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, Benoit-Bird 2004, Benoit-Bird & Au 2006). 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 50m during 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 allude to potential nightly movement patterns of dolphins, and given 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 influenced overall delphinid acoustic occurrence. In the south site, detections were highest during the days leading to the new moon and lowest prior to the full moon, whereas in the north site no significant differences were seen across the lunar phases. Contrary to our study, Benoit-Bird et al. (2009a) found that spinner dolphin relative abundance 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 were observed globally to occur deeper in the water column and thought to be related to anti-predator behaviour (Prihartato et al. 2016). Benoit-Bird et al. (2009b) showed 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 detection range during new moon periods.

We found that dolphin detections were significantly and negatively related to ambient noise (Table 4.2). 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 are 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, Gillespie et al. 2013), we think the chances of snapping shrimp clicks directly masking the detection of delphinid whistle occurrence may be negligible (see Fig. S3 in Appendix A: Chapter 4 supplementary materials) 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 Indian Wildlife Protection Act (1972), however 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

passive acoustic monitoring 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 programs, 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 behavior 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 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 prior to large-scale tourism, such as that presented in our study, 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 suggest 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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Chapter 5. TEMPORAL VARIABILITY OF A SOUNDSCAPE NEAR A MID-OCEANIC ATOLL IN THE NORTHERN INDIAN OCEAN

5.1 ABSTRACT

Soundscape ecology in the context of physical oceanographic features is an emerging area of research revealing interactions between physically, biologically and anthropogenically driven sounds and their sources. Soundscapes can shape and reveal distributions of a range of species, from fish larvae to whales, within marine ecosystems. The northern Indian Ocean is a region of high environmental variability driven by seasonally reversing monsoonal winds. The mid-oceanic islands within these waters consist of steep slopes forming a crucial interface between shallow reef and deep oceanic habitats. Studies on soundscape are limited in these waters. The aim of this chapter was to characterize major sound sources off the southern and northern side of the Kavaratti atoll in Lakshadweep islands, India, located at the northern part of the Laccadive-Maldives-Chagos Ridge. A first look at shallow water soundscapes are provided here using passive acoustic monitoring, and how they correlate with satellite-derived oceanographic variables. Geophonic and biophonic sources across different frequency bands are identified with three major choruses – a dusk fish chorus, a midnight chorus that is speculated to be produced by myctophids, and a snapping shrimp night chorus. Low frequency biophonic choruses peaked in inter-monsoon months (January to March), while low frequency geophonic sound levels peaked during monsoon months (June to October) and increased with wind speed. The dusk fish chorus

and the midnight chorus (at the south site) decreased with increasing sea surface salinity, while the snapping shrimp chorus (at the south site) increased with increasing sea surface salinity. Snapping shrimp chorus levels increased with decreasing wind speed. The dusk fish chorus peaked during full and waning moon, and the midnight and snapping shrimp choruses peaked during new moon periods. The sources and patterns described in this chapter will help compare with future soundscape and sound pressure level measurements within this region. This will be useful in the context of a changing climate and for planning future developmental projects on the islands. Reef choruses link with peak larval recruitment, spawning, or feeding activities, and further investigation into the peak calling times reported here will help uncover the function of choruses. Expanding the collection of passive acoustic monitoring data and oceanographic measurements over longer timescales will significantly advance ‘soundscape oceanography’.

5.2 INTRODUCTION

For over a century, sound has been used extensively as a tool to explore the ocean across different spatial and temporal scales (Medwin and Clay 1998). It is designated as an essential ocean variable in the Global Ocean Observing System (IOC 1996, GOOS 2022). Yet, the scientific study of soundscape ecology is a new and emerging field. Most underwater soundscape studies have taken place just over the last decade (Lindseth and Lobel 2018). Understanding soundscapes can provide unique insights into the ocean that reveal occurrence of, and interactions between, physically, biologically and anthropogenically driven sounds and their sources (Miksis-Olds et al. 2018). More recently, the study of soundscapes has revealed that distributions and species compositions within marine ecosystems can be shaped using this

sensory modality (e.g., larval recruitment to neritic habitats; Simpson et al. 2005, 2008). With the widespread use of passive acoustic monitoring and the availability of remotely sensed oceanographic data at similar time scales, exploring soundscapes in the context of local physical oceanographic features is a rapidly-emerging area of research. We anticipate this intersection of soundscape ecology and oceanography will receive growing attention in the coming years (McKenna et al. 2022), and present here the term “soundscape oceanography.” Such studies will, no doubt, raise important questions on the ecological role of geophony in the ocean (Farina et al. 2021). Evolutionary adaptation of soniferous species and distributional responses of a range of marine species, from larvae to whales, to natural sources of non-biological sound will be particularly insightful in the context of a changing climate. Methodology for such studies is also evolving (Farina et al. 2021). To begin to answer these questions, we must first characterize soundscapes within an oceanographic context, in areas of high environmental variability.

The northern Indian Ocean (NIO) is strongly influenced by seasonally reversing monsoon winds (Pernetta 1993). High variability in the physical environment structures marine ecosystems and the biogeography of several trophic levels (Lévy et al. 2007, Madhupratap and Haridas 1990, Shankar et al. 2019). The region is increasingly threatened with climate-induced changes in monsoonal cycles, higher frequency of hurricanes, and coral bleaching events (Arthur et al. 2006, Turner and Annamalai 2012, Murakami et al. 2017). Underwater soundscapes in the NIO have received little attention. Most underwater soundscape ecology studies have focused on the North Pacific Ocean, the Atlantic Ocean and in Australian waters, with a notable emphasis on coral reef soundscapes (Lindseth and Lobel 2018).

Habitats around mid-oceanic coral atolls are heterogenous, topographically complex, and consist of reefs, lagoons, and steep slopes amidst open ocean waters. This heterogeneity is reflected in the wide variety of animal groups that occur here, such as corals, invertebrates, fish, and mammals. The steep slopes off mid-oceanic islands give rise to eddies and upwelling of nutrient rich waters and form a crucial interface of energy transfer between oceanic and neritic habitats (Genin 2004, Levin and Dayton 2009). On coral reefs, soundscapes can reveal dominant seasonal, diel, and lunar cycles of animal distribution and calling behavior, the state of reef health and habitat quality, reproductive patterns, and the role of sound in larval recruitment. For example, Piercy et al. (2014) show that sound pressure levels decrease with decreasing habitat quality in the Philippines, and that an acoustically richer reef propagates sound further out into the open ocean. Additionally, Simpson et al. (2005, 2008) show that natural reef sounds attract higher and more diverse fish larval recruitment. Reef soundscapes also act as a beacon for several other important functional groups such as invertebrates, mollusks, and reef-building coral larvae (Lillis et al. 2015, 2016, Vermeij et al. 2010). Studying soundscapes in the interface between reef habitats and the open ocean provide a unique opportunity to uncover sonic-mediated ecological interactions here.

In addition to biological sources, the influence of physical oceanographic processes (e.g., wind, waves, rain) on ambient sound levels or species' sound-producing behavior can be substantial. Such processes regulate reef soundscapes and animal choruses directly or indirectly. For example, ocean acidification reduces snapping shrimp (*Alpheus* spp.) sound levels and affects larval responses to soundscape cues (Rossi et al. 2016 a, b). Heavy winds reduce the intensity and length of choruses and may act as an important constraint during some seasons (Farina and

Ceraulo 2017). Furthermore, anthropogenic activities can alter soundscapes and reef community structure either directly (e.g., impact of boat noise on coral recruitment; Lecchini et al. 2018) or indirectly (e.g., climate change driven increase in tropical cyclones can impact biophony; Mahanty et al. 2019). Gordon et al. (2018) showed that reefs that are increasingly degraded by climate-induced bleaching and storm damage have reduced acoustic complexity and richness, thereby reducing the settlement rates of juvenile fish, decreasing habitat quality, and leading to further habitat degradation. Such studies emphasize the need to study soundscape ecology within the oceanographic context of an area. In waters where there has been little research attention such as the NIO, it is important to first characterize the reef soundscapes in monsoon and non-monsoon months.

The Lakshadweep islands at the northern end of the Laccadive-Maldives-Chagos ridge are well-located within the northern Indian Ocean to study coral reef soundscapes in the context of monsoonal cycles. There have been very few prior studies of soundscapes in Indian waters. Existing studies are based off the mainland coast that cover short temporal scales of days to weeks, or do not cover the monsoon season (e.g., Mahanty et al. 2018, Chanda et al. 2020, Chary et al. 2020). The aim of this chapter is to characterize major sound sources and how they correlate with local oceanographic parameters across monsoon and non-monsoon months. More specifically the objectives were to 1) identify acoustic bands of interest and describe any major biophonic, anthrophonic, and geophonic sources to the soundscape, 2) determine the dominant temporal drivers for identified acoustic bands of interest and 3) determine how dominant sources correlate with satellite-derived oceanographic variables.

In this chapter, passive acoustic monitoring (PAM) is used to collect data over different temporal scales, including through the rough monsoon weather. The advent of newer and compact acoustic recording technologies coupled with better battery power and larger storage space makes passive acoustic monitoring (PAM) a cost-effective and easier technique to access remote areas like the Lakshadweep islands in India, which would be otherwise logistically challenging and resource-intensive to access.

5.3 METHODS

5.3.1 *Deployment*

Two passive acoustic recorders were deployed off the outer reef area in Kavaratti atoll in the Lakshadweep islands (Fig. 5.1). SoundTrap ST-300STDs with a flat response from 20 Hz to 60 kHz (± 3 dB) were used. The instruments had end-to-end system sensitivities of -176.1 and -176.6 dB V/ μ Pa. A recorder was placed on the north and south sides of the island spaced approximately 5 km apart at 11 m and 18 m water depths, respectively (Fig. 5.1, Table 5.1). The recorders were secured to cement blocks on reef flats near steep slopes. Hydrophones were placed on the reef (rubble and dead coral) since no sandy patches were available nearby. The sample rate was set at 96 kHz to record a wide spectrum of underwater sounds. A duty cycle of 10-15 min each hour was set so the recorders could be deployed for 3 to 4 months at a time (Table 5.1). Acoustic data were collected from January to October 2019. The location and recording periods for each hydrophone are given in Table 5.1 and Figure 5.1.

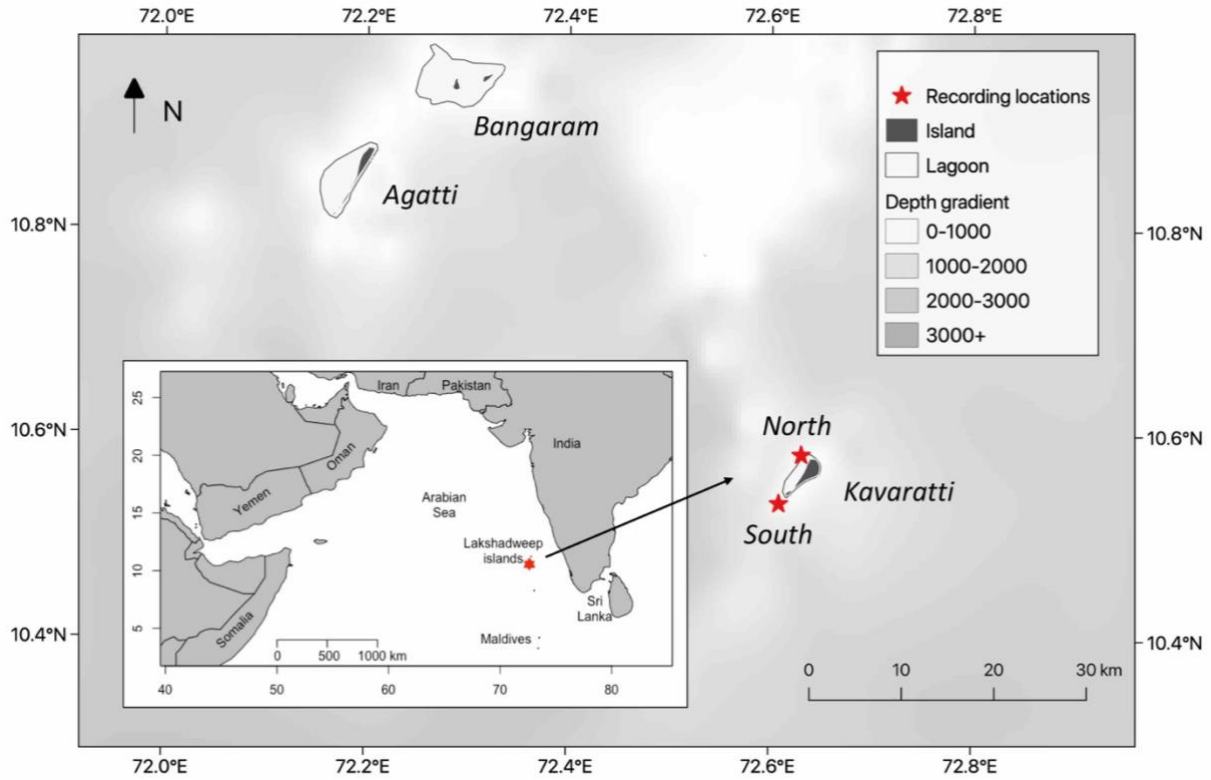


Figure 5.1. Location of hydrophone deployments and the study area in the Arabian Sea.

Table 5.6. Location, recording periods, duty cycle and depth for each hydrophone deployed off Kavaratti Island in 2019.

Site	Recording period	Duty cycle (min/h)	# Recordings (# files/total h)	Depth (m)
South site N10° 31.98' E72° 36.53'	1 January to 8 April 2019	15	2346/586.5	18
	13 April to 27 August 2019	10	3288/548	18
North site N10° 34.83' E72° 37.86'	1 January to 8 April 2019	15	2340/585	11
	14 April to 5 October 2019	10	4195/699	11

5.3.2 Recordings and data processing

Long-term spectral averages (LTSA time averaged at 5s with frequency bin size of 1 Hz) were created from each recording using Triton software (Wiggins 2003) for the frequency band from 20 Hz to 48 kHz. LTSAs (same time and frequency resolution as above) with decimated files of 2 kHz and 12 kHz sample rates were also created to decrease processing time for low frequency signals. We visually searched all LTSAs to identify regions of high energy. The time and frequency scales of spectrograms with high energy bands were expanded to examine signals in detail, and sound sources were identified using existing literature when possible. Four acoustic bands of interest (henceforth referred to as aBOI) based on high energy were identified: 20-100 Hz, 200-600 Hz, 1000-1200 Hz, and 2000-30000 Hz. Details on these bands are elaborated in the results section. Average calibrated sound pressure levels for each recording in an aBOI using PAMGuide software (Merchant et al. 2013) was obtained, resulting in a time series of sound pressure levels (dB re 1 microPa) for each site.

Wavelet analysis was conducted on the time series of sound pressure levels (SPL) for each aBOI using methodology described in Torrence and Compo (1998) with the R package *Biwavelet* (Tarik et al. 2019). A continuous wavelet transform with a Morlet wavelet base was conducted to extract significant periodicities of high SPLs between 2 and ~1024 hours, which included diel and lunar periods. To isolate the timing of diel choruses, time periods in wavelet plots which had significant diel energy were extracted and variability in sound pressure levels was examined graphically. The variability of chorus patterns across seasons was also examined graphically. Seasons were categorized as inter-monsoon (January to March), pre-monsoon (April

and May), and southwest monsoon (June to October). Dawn and dusk periods and lunar days were determined based on solar and lunar azimuths obtained from the R package *suncalc* (Thieurmel and Elmarhraoui 2019).

The relationship between daily mean of sound pressure levels of aBOIs and lunar day and oceanographic data, as described below, was examined using generalized least squares and generalized additive mixed models.

Daily means of sea surface temperature (SST, °C, ~ 5 x 5 km; Stark et al. 2007, Donlon et al. 2012, Good et al. 2022), sea surface salinity (SSS, psu, ~ 8 x 8 km), wind speed (m/s, ~ 25 x 25 km) and chlorophyll-a (Chl, mg m⁻³, 4 x 4 km,) were obtained from the Copernicus Marine Environment Monitoring Service (Dataset access through E.U. Copernicus Marine Service Information 2021) for the Kavaratti region during the study period. Products from CMEMS for SST, wind speed and Chl were calculated from satellite imagery, and for SSS was obtained from satellite imagery and numerical models.

5.3.3 *Statistical analyses*

All statistical analysis was done in R version 4.0.1. (R Core Team 2019). A generalized least square (GLS) model with a Gaussian distribution and identity link was used to investigate the relationship between sound pressure levels of the 20-100 Hz aBOI and *windspeed, season, and site*. A GLS model was chosen to account for the observed heterogeneity of variances across seasons in this aBOI. A repeated analysis of variance (ANOVA) measures was chosen to

investigate the relationship between the daily mean SPLs of the three other aBOIs (200-600 Hz, 1000-1200 Hz and 2000-3000 Hz) with the two categorical variables *season* and *site*. A generalized additive mixed model (GAMM) with a Gaussian distribution and identity link was used to investigate the relationship between sound pressure levels of the three other aBOIs and explanatory oceanographic variables including *windspeed*, *SST*, *Chl*, *SSS*, and *lunar day* (day 1 to day 29) for each site separately. The response variable was the daily mean SPL (average across all recordings per day), which dictated the choice of the Gaussian distribution with an identity link.

An additive model framework was chosen as lunar cycle was treated as a smoothed term with a cyclic cubic regression spline to account for the cyclic nature of this predictor, and to account for a non-linear relationship with the response variable mean SPL. Smoothness selection was done by using restricted maximum likelihood (Wood 2017). A flexibility of 8 knots for the lunar term variable was allowed to control the flexibility of the cyclic cubic regression spline. The residuals and assumptions of the model was further checked with the *gam.check* function in R package *mgcv* to ensure there was no overfitting (Wood 2017). A mixed model was used with an autoregressive moving average correlation structure with a lag of 1 or 2 days to account for temporal autocorrelation within the mean SPL time series.

The GAMM model was run using the *mgcv* package in R (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 all the models is provided in Tables S1-S4 in Appendix B: Chapter 5 supplementary materials. Data were not transformed before

running the models. Multicollinearity between explanatory variables was evaluated using variance inflation factor (Allison 1999).

5.4 RESULTS

5.4.1 *Acoustic bands of interest*

From the long-term spectral averages, visual inspection of spectrograms and literature review, four aBOIs were identified in the dataset; a geophony-dominated band of 20-100 Hz containing wave sounds (Wenz 1962), and three biophony-dominated bands of 200-600 Hz containing a fish chorus (McCauley 2001), 1000-1200 Hz containing a second fish or invertebrate chorus (Radford et al. 2008, McCauley et al. 2016), and 2000-30000 Hz containing snapping shrimp chorus (Everest et al. 1948). Although the choruses extended beyond each of these frequency bandwidths (Fig 5.2), these frequency bands were chosen as they showed the least overlap between these dominant choruses and with other more ephemeral choruses and were visually determined to be most representative of the temporal trends of the chorus.

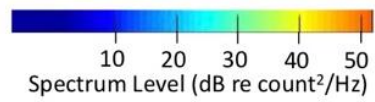
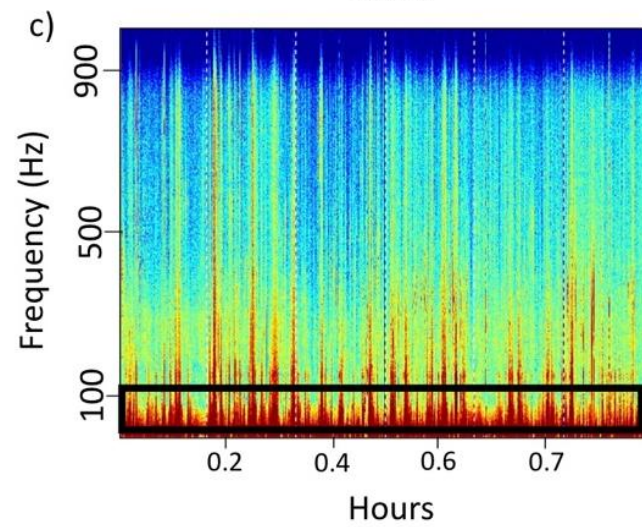
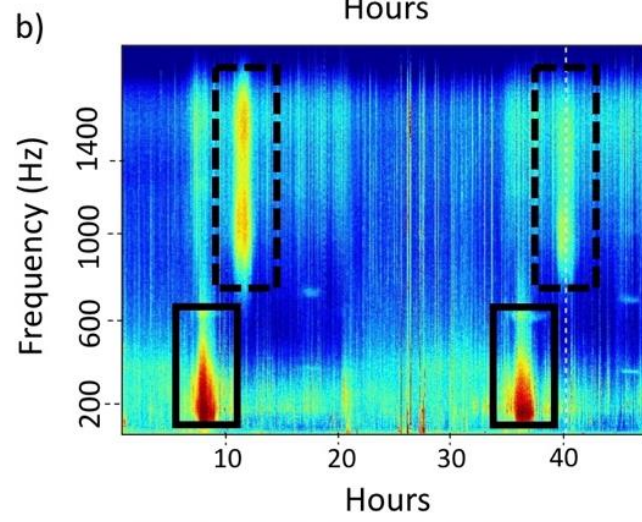
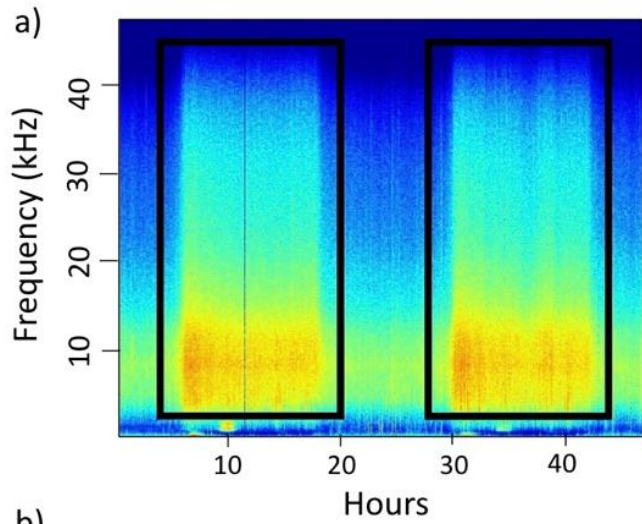


Figure 5.2. Long term spectral averages (LTSA) of acoustic bands of interest and biological choruses within them. a) LTSA spanning two days up to a bandwidth of 48 kHz indicating the snapping shrimp night chorus (black solid box); LTSA spanning two days up to a bandwidth of 2 kHz indicating the dusk fish chorus (black solid box) and the midnight chorus (black dotted box), and c) LTSA spanning 12 hours up to a bandwidth of 1 kHz indicating wind-driven wave sounds (black solid box).

5.4.2 *Identifying temporal patterns in aBOI using wavelet analysis*

Significant periodicities were found in the diel (~24 hours) and/or lunar (~28 days) scales for all aBOI. In the 20-100 Hz band, diel periodicities were not significant, but lunar periodicities towards the latter half of the year were (Fig 5.3a, 5.3b). In the 200-600 Hz band and 1000-1200 Hz band, both diel and lunar periodicities were significant (Fig 5.3c, 5.3d, 5.3e, 5.3f). In the 2000-30000 Hz, only diel periodicities were significant throughout the entire time series (Fig 5.3f, 5.3h). The north and south sites showed similar patterns.

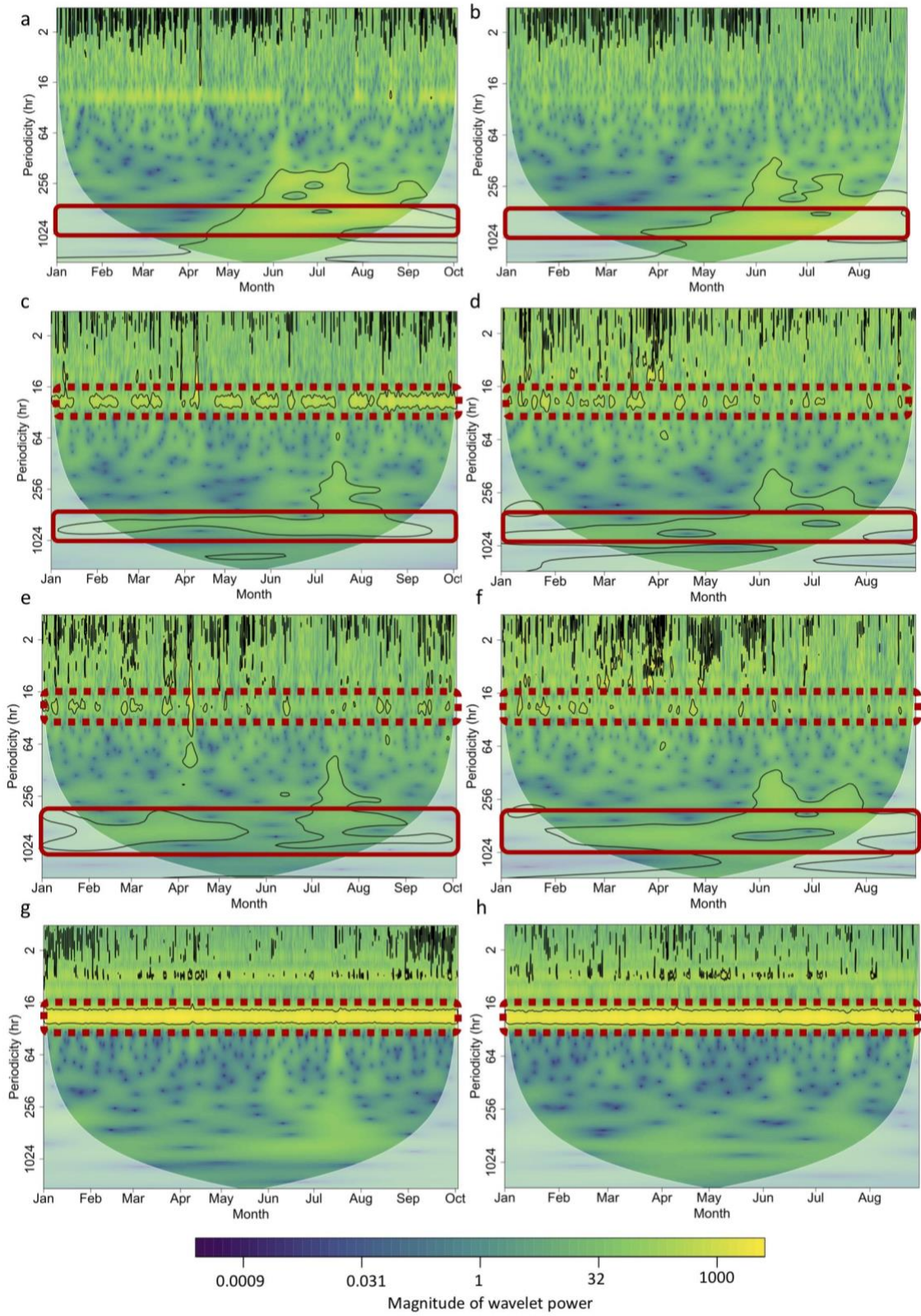


Figure 5.3. Wavelet power spectrum of sound pressure levels in each acoustic band of interest. a) 20-100 Hz in the north site; b) 20-100 Hz in the south site; c) 200-600 Hz in the north site; d) 200-600 Hz in the south site; e) 1000-1200 Hz in the north site; f) 1000-1200 Hz in the south site; g) 2000-30000 Hz in the north site; h) 2000-30000 Hz in the south site. The black contours show regions of significant power in the analysis with a 95% confidence level using red noise as background spectrum. The cone of influence (shaded white areas) shows areas affected by edge-effect artefacts (Torrence and Compo 1998). The dotted red box shows areas of diel periodicity, and the solid red box shows areas of lunar periodicity. The colour bar represents the magnitude of wavelet power. The lighter colours indicate more power at a particular scale, and the darker colours indicate less power at a particular scale.

5.4.3 *Diel patterns of choruses in aBOI*

To identify the times during which choruses occurred, SPLs from the significant portions of the diel periodicity of the wavelet analysis were extracted (Figure 5.3c-h). In the 200-600 Hz band, a dominant dusk chorus during recording periods of 1900 and 2000 local time was identified in both sites (Fig 5.4a; time series of chorus presented Fig S1a in Appendix B: Chapter 5 supplementary materials). In the 1000-1200 Hz aBOI, a dominant midnight chorus during recording periods of 2200 and 2300 local time was identified (Fig 5.4b; time series of chorus presented Fig S1b in Appendix B: Chapter 5 supplementary materials). Within the 2000-30000 Hz band, a night-time peak from dusk to dawn was identified (Fig 5.4c; time series of chorus presented Fig S1c in Appendix B: Chapter 5 supplementary materials).

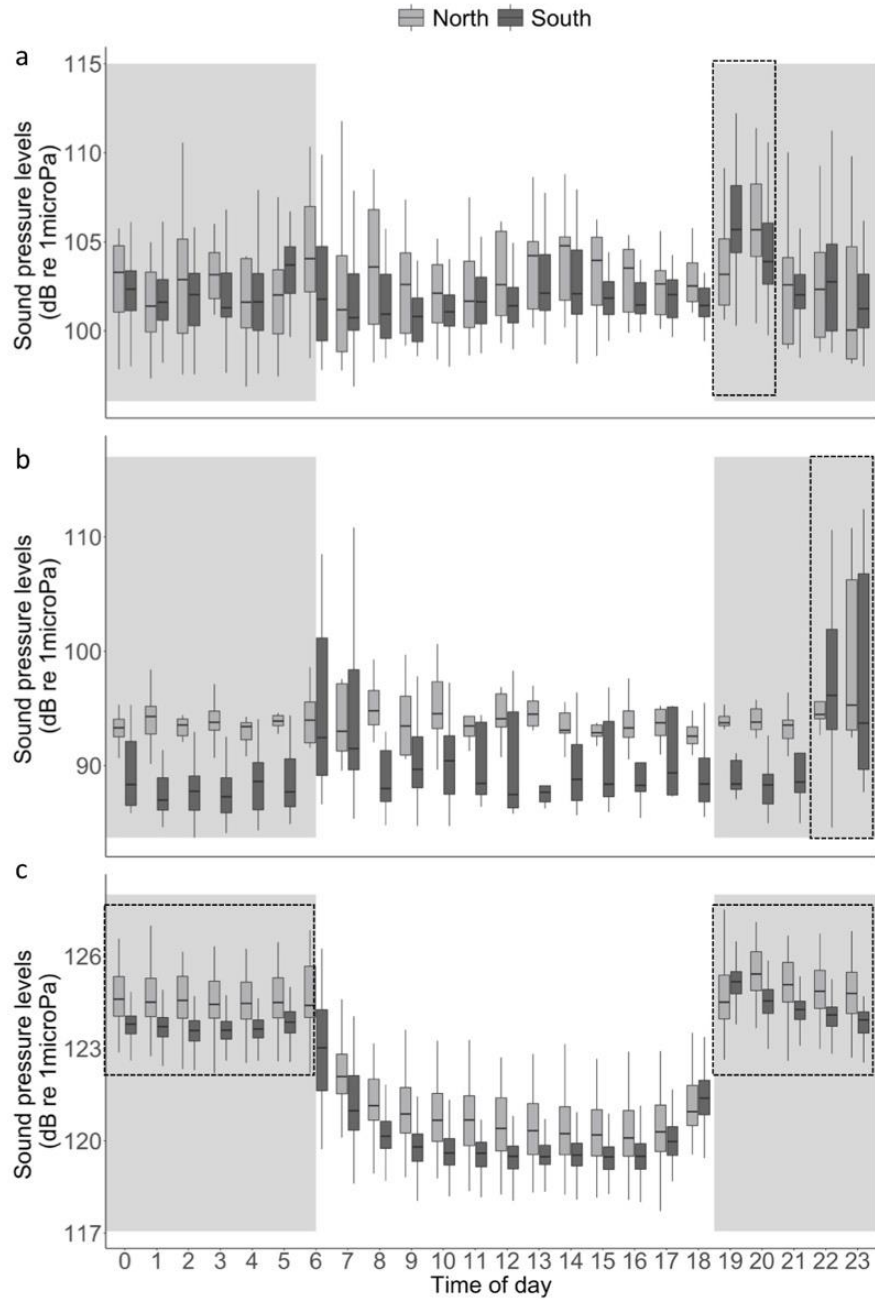


Figure 5.4. Diel patterns of sound pressure levels in significant portions of aBOIs with biological sources in the north and south site. a) 200-600 Hz band; b) 1000-1200 Hz band and; c) 2000-30000 Hz band. Nighttime is shaded. The black dotted boxes indicate the timing of the dominant chorus in each band.

5.4.4 *Seasonal variability of choruses*

All three biologically-driven choruses occurred in each season, although overall sound pressure levels differed. The sound pressure levels for the 200-600 Hz band dusk chorus (1900 and 2000 local time) significantly decreased linearly from inter-monsoon to pre-monsoon to monsoon months for both sites (season: $F_{(1.56, 84.14)} = 58.22$, $p < 0.005$, Fig 5.5a). The south dusk chorus was higher in amplitude than the north dusk chorus (site: $F_{(1,54)} = 248.09$, $p < 0.005$, Fig 5.5a). The sound pressure levels for the 1000-1200 Hz band midnight chorus (2300 and 0000 local time) also significantly decreased across season for both sites (season: $F_{(1.69, 91.42)} = 9.73$, $p < 0.005$, Fig 5.5b). The north midnight chorus was higher in amplitude than the south (site: $F_{(1,54)} = 105.18$, $p < 0.005$, Fig 5.5b). There was no significant seasonal variability in the amplitude of the 2000-30000 Hz snapping shrimp night chorus (season: $F_{(1.91, 94.11)} = 1.511$, $p = 0.23$, Fig 5.5c); however the interaction between site and season was significant (season x site: $F_{(1.42, 78.12)} = 136.79$, $p < 0.005$, Fig 5.5c). There was also a significant difference between the north and south sites for the snapping shrimp night chorus (site: $F_{(1,55)} = 502.42$, $p < 0.005$, Fig 5.5c). The north site night chorus was higher in amplitude than the south site chorus, and linearly increased from the inter monsoon to the southwest monsoon season (Fig 5.5c).

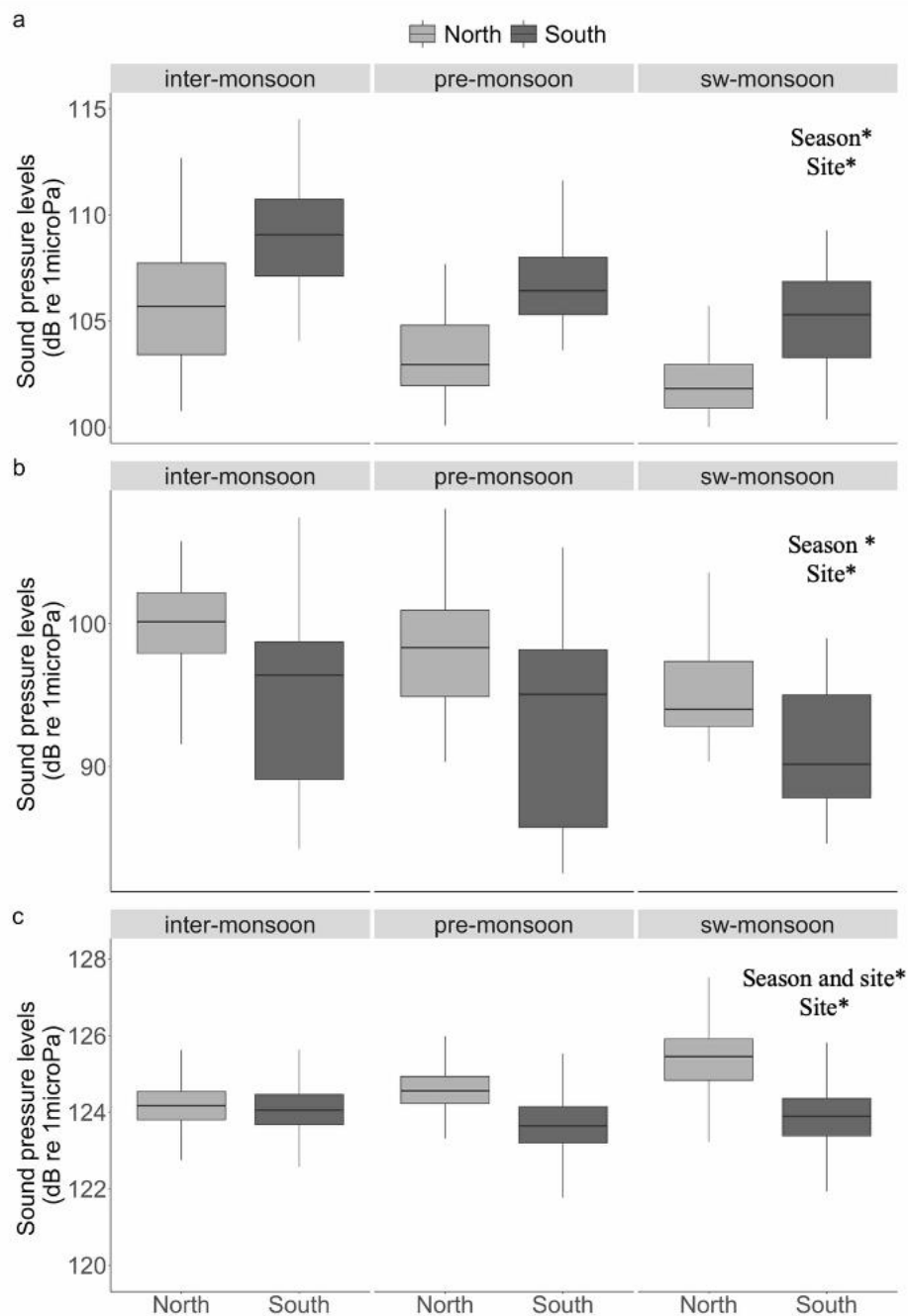


Figure 5.5. Season and site-wise differences of sound pressure levels in significant portions of aBOIs with biological sources in the north and south site. a) 200-600 Hz band; b) 1000-1200 Hz band and; c) 2000-30000 Hz band. Categorical variables that were significant are provided on the top right of the panels.

5.4.5 Geophonic band (20-100hz) across season, site, and wind speed

The GLS model that examined the interaction of wave noise (20-100 Hz band) with respect to the independent variables of *windspeed*, *season*, and *site* accounted for autocorrelation using an autoregressive moving average structure with a lag of 2 days. The interaction between wind speed and southwest monsoon season was significant. At both sites, sound pressure levels increased linearly with increasing wind speeds (Fig 5.6, $p < 0.005$). There was also significant variability between the north and south site; sound pressure levels were higher at the south site than the north site during the inter-monsoon and pre-monsoon months (Fig 5.6, $p < 0.005$). At the north site and south site, there was a 12.4 dB re 1 μ Pa and a 11.0 dB re 1 μ Pa mean increase, respectively, during the southwest monsoon season when compared to the other seasons. The GLS table is provided Table S1 in Appendix B: Chapter 5 supplementary materials. A time series of the 20-100 Hz band is presented Fig S1a in Appendix B: Chapter 5 supplementary materials.

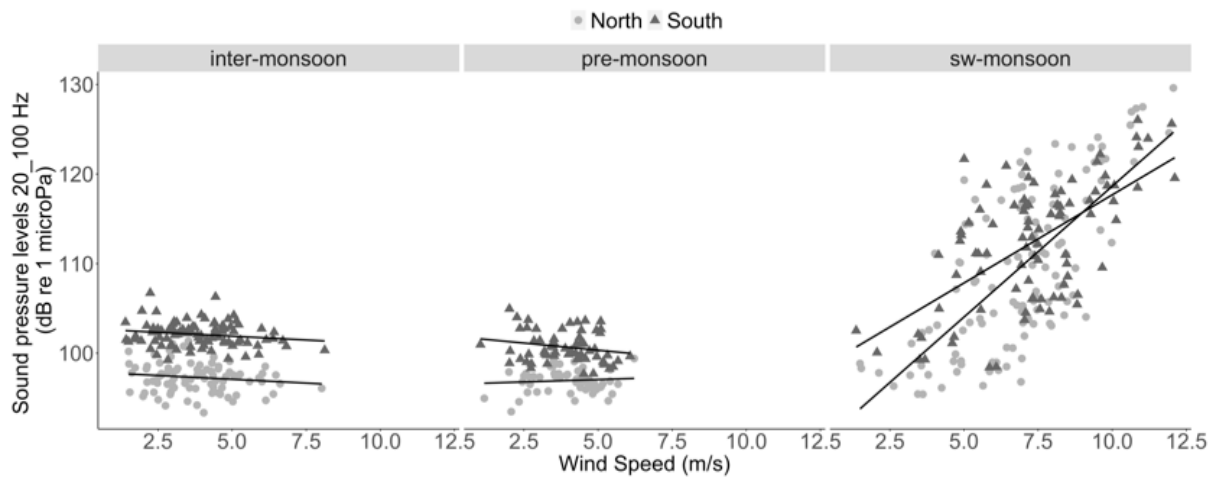


Figure 5.6. Scatter plots of SPL in the geophonic (20-100 Hz) band and wind speed for inter-monsoon, pre-monsoon and SW-monsoon

5.4.6 *Biological choruses and lunar patterns*

A significant relationship between biologically driven choruses within the 200-600 Hz (dusk chorus), 1000-1200 Hz (midnight chorus) and 2000-30000 Hz (snapping shrimp night chorus), and lunar day were found at both sites. The dusk fish chorus was loudest after the full moon and during the waning moon, and quietest during the new moon period (Fig 5.7a, 5.7f, table S2 in Appendix B: Chapter 5 supplementary materials). The midnight chorus was loudest during waning moon and new moon periods, and quietest during the days leading up to a full moon period (Fig 8a, 8f, table S3 in Appendix B: Chapter 5 supplementary materials). The snapping shrimp night chorus was loudest during the new moon period, and quietest during full moon periods (Fig 5.9a, Fig 5.9f, table S4 in Appendix B: Chapter 5 supplementary materials). These patterns were observed at both sites for all three choruses.

5.4.7 *Biological choruses and oceanographic correlates*

The dusk fish chorus in the 200-600 Hz aBOI was significantly and negatively correlated with SSS in both the north and south sites ($p < 0.001$ north, $p < 0.001$ south; Fig 5.7b, 5.7g, table S1 in Appendix B: Chapter 5 supplementary materials). The other ocean variables examined (Chl, SST, and wind speed) did not show any significant relationships with the dusk fish chorus ($p > 0.05$ for each; Fig 5.7c-j). The midnight fish chorus in the 1000-1200 Hz aBOI was significantly and negatively correlated to Chl in the north site ($p = 0.003$), and SSS in the south site ($p <$

0.001; Fig 5.8c, 5.8g, table S2 in Appendix B: Chapter 5 supplementary materials). SST and wind speeds did not show a significant relationship with the midnight chorus ($p > 0.05$; Fig 5.8b, 5.8d, 5.8e, 5.8h-j, table S2 in Appendix B: Chapter 5 supplementary materials). The snapping shrimp night chorus in the 2000-30000 Hz band was significantly and negatively correlated to wind speeds in the north and south site ($p < 0.001$ north, $p < 0.001$ south; Fig 5.9e, 5.9j, table S3 in Appendix B: Chapter 5 supplementary materials). This chorus was also positively correlated to SSS in the south site ($p < 0.001$; Fig 5.9g). Chl and SST did not show a significant relationship with the snapping shrimp night chorus ($p > 0.05$; Fig 5.9b-d, 5.9h, 5.9i, table S3 in Appendix B: Chapter 5 supplementary materials).

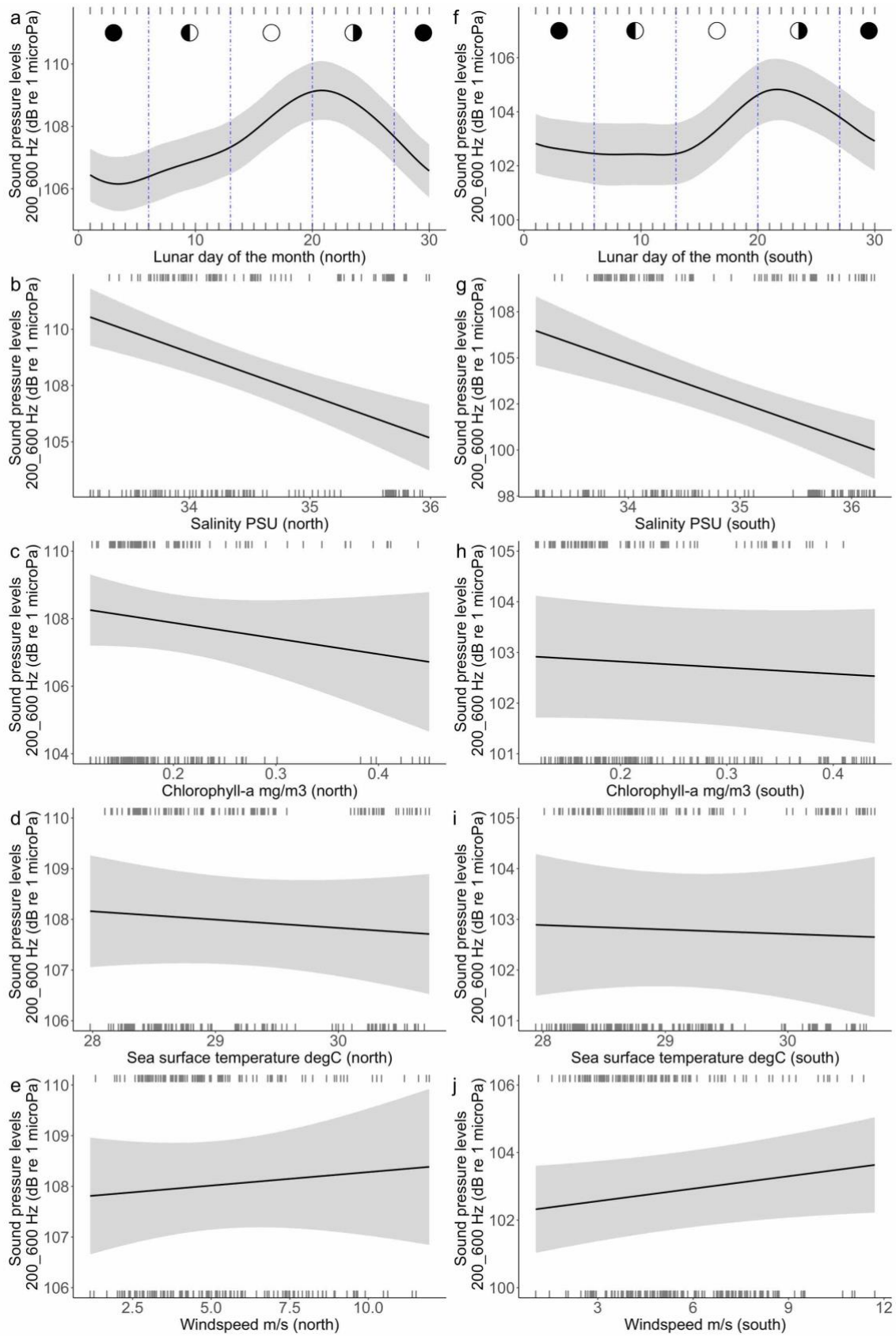


Figure 5.7. Response curves of a generalized additive mixed model for daily mean SPL of the dusk fish chorus (200-600 Hz band) by a & f) lunar day of the month (overall effect); new moon periods are denoted by a black filled circle, the first and third quarter periods by half-filled black circles, and full moon periods in white circle; b & g) daily mean for salinity (psu); c & h) daily mean for chlorophyll-a (mg m^{-3}); d & i) daily mean for sea surface temperature ($^{\circ}\text{C}$); e & j) wind speed (m/s), in the north and south sites respectively.

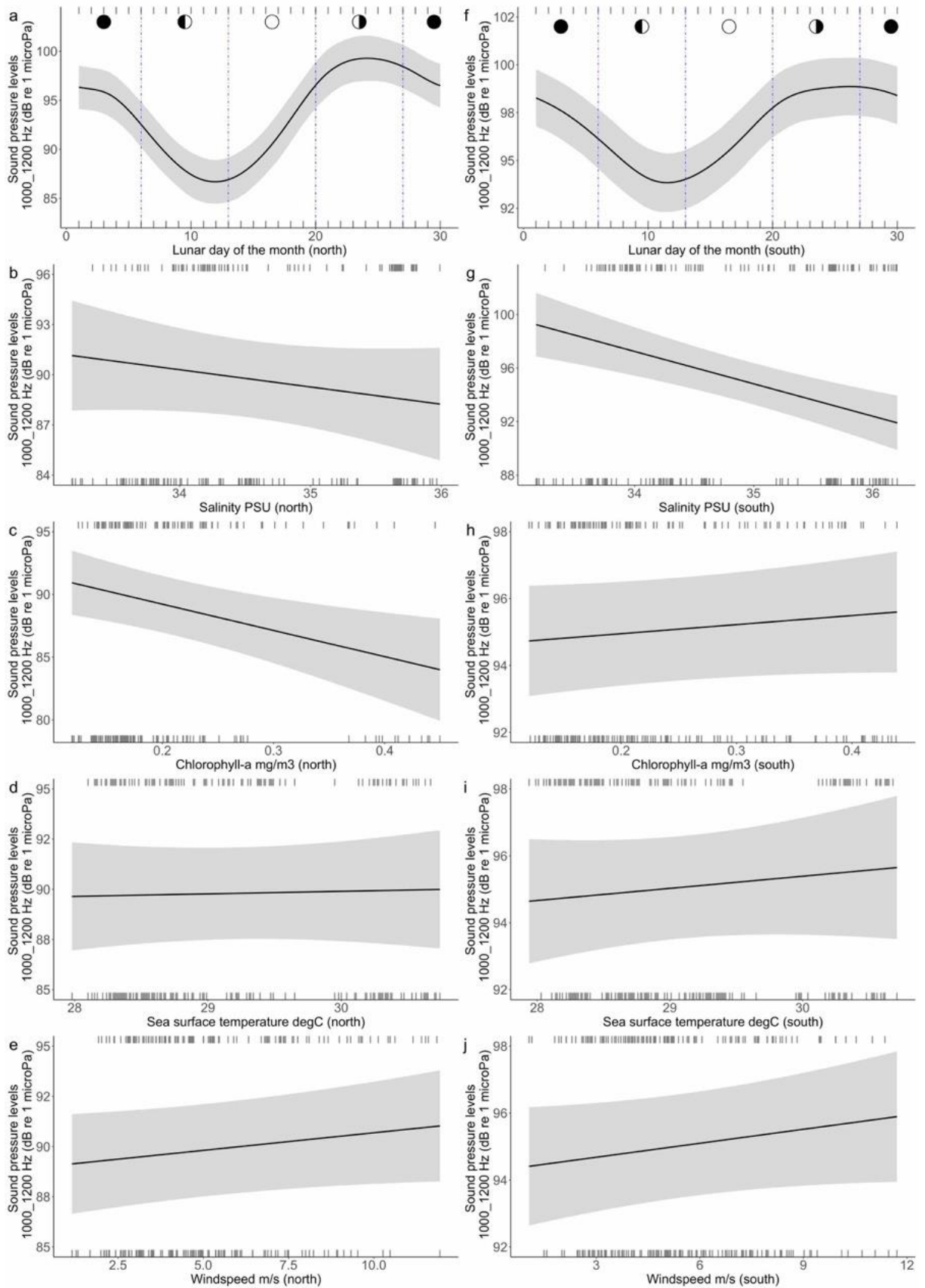


Figure 5.8. Response curves of a generalized additive mixed model for daily mean SPL of the dusk fish chorus (200-600 Hz band) by a & f) lunar day of the month (overall effect); new moon periods are denoted by a black filled circle, the first and third quarter periods by half-filled black circles, and full moon periods in white circle; b & g) daily mean for salinity (psu); c & h) daily mean for chlorophyll-a (mg m^{-3}); d & i) daily mean for sea surface temperature ($^{\circ}\text{C}$); e & j) wind speed (m/s), in the north and south sites respectively.

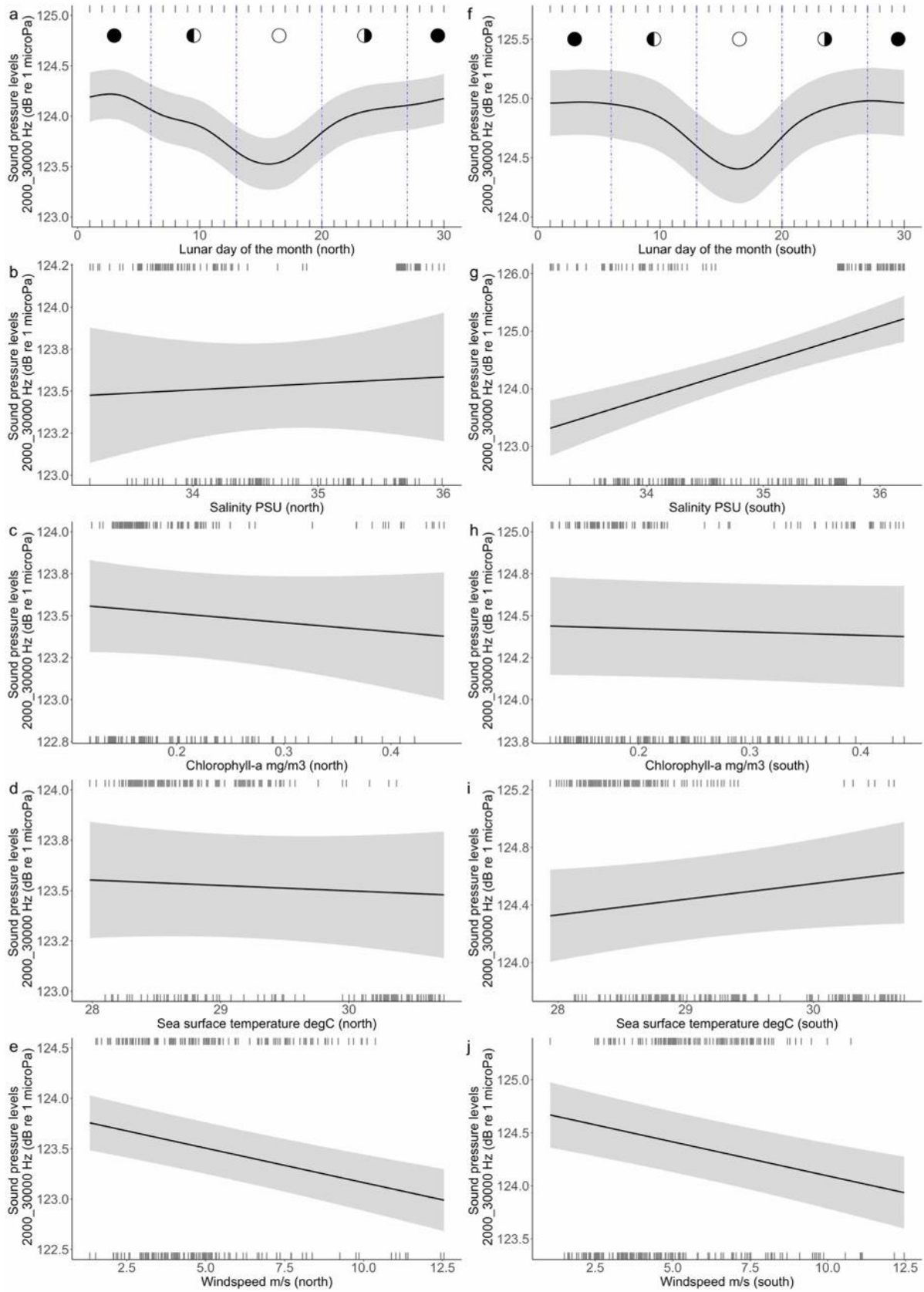


Figure 5.9. Response curves of a generalized additive mixed model for daily mean SPL of the snapping shrimp chorus (2000-30000 Hz band) by a & f) lunar day of the month (overall effect); new moon periods are denoted by a black filled circle, the first and third quarter periods by half-filled black circles, and full moon periods in white circle; b & g) daily mean for salinity (psu); c & h) daily mean for chlorophyll-a (mg m⁻³); d & i) daily mean for sea surface temperature (°C); e & j) wind speed (m/s), in the north and south sites respectively.

5.4.8 *Anthropogenic sources*

The anthropogenic sound observed in the data were motor noise from small fishing vessels and large passenger ferries or ships. Interestingly, boat noise was not conspicuous in the 10-hour plot window scales, LTSAs, time series of the SPLs from the aBOIs or within the wavelet analysis therefore it is not included in the analyses.

5.5 DISCUSSION

5.5.1 *Geophonic band*

Four aBOIs were identified in the soundscape between frequencies of 20 Hz to 48 kHz. The lowest frequency band consisted of primarily a geophonic sound source, whereas the other three bands were made of biophonic sources (Wenz 1962, McCauley 2001, McCauley et al. 2016, Everest et al. 1948). The dominant contributor to the geophonic band was identified to be

shallow-water wind-driven wave sounds (Wenz 1962). A positive correlation between wind speeds and low frequency SPLs is well documented in shallow water settings (Piggott 1964, Kerman 1984, Ma et al. 2005). In our study too, an increase in wind speed resulted in an increase in SPLs in the geophonic band; however, this was significant only during the southwest monsoon season when consistently high wind speeds ($> 5\text{m/s}$) were observed, thereby resulting in large waves (Duxbury and Duxbury 2001). This relationship was absent during low wind speeds ($< 5\text{m/s}$) in the inter-monsoon and pre-monsoon months. Studies exploring the contribution of wind speeds to soundscapes across seasons, especially the monsoon season, are limited in the region. Ramji et al. (2008) show that in shallow waters of the Bay of Bengal, there was an 8 dB (re 1 μPa) increase in low frequency ambient noise spectrum level between summer (southwest monsoon season) and other seasons. In our study, southwest monsoon season showed approximately a 12 dB (re 1 μPa) increase in SPLs when compared to other seasons. Such measurements and comparisons are important in understanding how animals that hear or vocalize within these frequencies perceive their environment (e.g., whale or fish communication, Panicker and Stafford 2021). As expected, the overall seasonal changes within this aBOI were similar in both sites, however there was significant between-site variability in SPLs, despite the recorders being set at a depth difference of only 7 m. The south site showed higher SPLs during the inter-monsoon and pre-monsoon seasons, whereas both sites were comparable during the southwest monsoon season.

5.5.2 *Biophonic bands*

5.5.2.1 Diel patterns and potential sources of choruses

The 200-600 Hz band, containing a fish chorus, occurred predominately just after sunset at 19h00 and 20h00 local time. Dusk fish choruses have been identified in several studies across the Great Barrier Reef in Australia (e.g., McCauley 2001, McWilliam et al. 2018), some of which partly overlap in frequency and temporal characteristics to this one observed in our study (e.g., Chorus I, IV, V in McWilliam 2018, ‘popping chorus’ in McCauley 2001). Some of these choruses have been attributed to soniferous coral reef fish families such as Pomacentridae, Sciaenidae, Serranidae, Batrachoididae, and nocturnal planktivorous fish that include Priacanthidae, Holocentridae, Apogonidae, Pempheridae (McCauley 2001, Lobel et al. 2010, McWilliam et al. 2018). Several other choruses remain unidentified (McWilliam et al. 2018, Parsons et al. 2017). In the visual analysis using LTSAs (Fig 2), the maximum amplitude of the chorus was identified at frequencies of ~150-200 Hz. During night periods, several families of fish that feed on zooplankton emerge and hover over the reef (e.g., Holocentridae, Priacanthidae, Apogonidae and Pempheridae; Helfman 1986). Nocturnal fish vocal behavior is associated with feeding and/or reproductive behavior (Fish and Mowbray 1970), and the function of the chorus identified in this chapter is suspected to be similar. Targeted studies during these calling periods to identify soniferous fish families found in Lakshadweep waters will give further ecological insights into this chorus.

The 1000-1200 Hz aBOI contained a midnight chorus around 0000 local time. Based on frequency and timing characteristics, three potential sources for this chorus were identified from prior studies: myctophids (centered at the 1/3rd octave band at 2 kHz in McCauley et al. 2016), sea urchins (ranging from 800 to 2800 Hz; Radford et al. 2008) or another nocturnal reef fish chorus (e.g., nocturnal planktivorous fish chorus ranging across ~150 Hz to 3 kHz reported in

McCauley 2001 and McCauley 2012). Of these, this chorus is suspected to have a mesopelagic origin due to the following reasons; 1) McCauley et al. (2016) showed that the swim bladders of large (8-10 cm) myctophids resonate at lower frequencies (~1.2 to 2 kHz) in shallow waters (~10m), 2) the chorus was not crepuscular like feeding related sounds of sea urchins (Radford et al. 2008, 2010), 3) the chorus appeared to consist of several short, pulsed signals with no high intensity signals, 4) individual calls could not be isolated from the chorus indicating that the sound sources may be further from the reef, and 5) there were occasional secondary peaks at higher frequencies similar to the evening chorus described in McCauley et al. (2016). Since our recorders were placed in shallow waters adjacent to steep oceanic drop offs, there are possibilities to detect mesopelagic sources during midnight hours. For example, the mesopelagic boundary community consisting of large myctophids are found in shallow waters and closest to shore near midnight hours in other mid-oceanic coral reef sites (Benoit-Bird 2006, Reid et al. 1991). Silas et al. (1972) showed that sound scattering layers occur in shallow waters near Lakshadweep and likely consist of euphausiids, myctophids and squids. Several other studies from this region also show enhanced levels of biomass in shallow sound scattering layers near coral atolls during night periods (Karuppasamy et al. 2010, Letessier et al. 2016). Another possibility could be a source from another reef nearby. Other coral atolls are at least 20 km away from Kavaratti, hence this is unlikely. However, we currently do not know how far these choruses propagate, as this is dependent on a variety of factors such as topography, water characteristics and source levels of the soniferous animals.

The 2000-30000 Hz aBOI containing the snapping shrimp chorus occurred throughout the day with a peak during the entire night period (Johnson et al. 1947, Everest et al. 1948).

Snapping shrimp sounds are used for territoriality, to stun prey, to deter predators and for eusociality (Knowlton and Moulton 1963, Duffy 1996, Bohnenstiehl et al. 2016). Higher night amplitudes have been documented in several study sites in the southern United States, Hawaiian and South Pacific islands (Johnson et al. 1947, Everest 1948, Lillis and Mooney 2018). Other sites including Hawaii, the US Virgin Islands, and off North Carolina, have shown an opposite trend with higher amplitudes observed during day time (Lammers et al. [2008](#), Bohnenstiehl et al. [2016](#), Lillis et al. 2017, Lillis and Mooney 2018). Near the West Bay Reserve, Bohnenstiehl et al. (2016) found shifts between daytime and nighttime peaks based on seasonal variability within the same site. In our study site, nighttime peaks were consistent across different months. This highlights the high variability in general chorusing patterns of snapping shrimp across sites. Given the dominant contribution of snapping shrimp to local soundscapes, it is critical to document such patterns across various habitats and oceanographic conditions.

5.5.2.2 Lunar patterns of choruses

In addition to diel periodicities, all three choruses showed lunar patterns. Several fish and invertebrate choruses are known to be negatively correlated with moonlight (Staaterman et al. 2014, McWilliam et al. 2017, Lillis and Mooney 2018). In our study, the choruses within 1000-1200 Hz and 2000-30000 Hz aBOI were louder during the new moon periods. Lower light levels are hypothesized to reduce predation risk and enhance egg dispersal (McWilliam et al. 2017). Studies have also reported some choruses to show an opposite trend, like the dusk chorus reported in this chapter, where sound levels peaked a few days after the full moon (e.g., chorus V in McWilliam et al. 2017, McCauley 2012). McCauley (2012) hypothesized that nocturnal planktivorous fish may be using increased moonlight to locate prey. Interestingly, in our low

frequency aBOIs (200-600 Hz and 1000-1200 Hz), the two choruses at night peaked at different times (dusk and midnight respectively) and different lunar phases (full/waning moon and new moon respectively) which were relatively exclusive of each other. This partitioning in time within the nocturnal activity phase may be indicative of a competitive relationship (acoustic niche hypothesis) or a predator-prey relationship between these two sources (Kronfeld-Schor and Dayan 2003).

5.5.2.3 Site-wise variability of choruses

An overall increase in nocturnal SPLs, and similar diel and lunar patterns of choruses were observed at both sites, however there were significant differences in the amplitudes of choruses between sites. Reef habitats that are relatively close (a few km) show different underwater sound signatures in other places, and the abundance of soniferous fishes and invertebrates are suggested to be a major contributor to this variability (Radford et al. 2014). In this chapter the dusk fish chorus showed higher SPLs in the south site, whereas the midnight and snapping shrimp chorus showed higher SPLs in the north site. Such differences in sound pressure levels of choruses across the two sites may be reflective of different compositions or abundances of soniferous species or communities.

5.5.2.4 Seasonal differences in chorus levels

A geophonic signature caused by monsoon shallow water wind-driven waves was clearly visible within the 20-100 Hz aBOI. While wind sounds can directly contribute to the sound levels in the other two low frequency bands (200-600 Hz and 1000-1200 Hz), such contribution is likely to be

at much lower sound levels compared to the sound levels of the biological choruses observed in our study (Wenz 1962). In fact, a decrease in sound pressure levels of the choruses was observed within these low frequency aBOIs during the monsoons when wind speeds were the highest. This suggests, in our study area, biophony may be masking the direct contribution of wind to the soundscape at these frequencies. During the monsoon season, there are drastic changes in several physical aspects such as sea surface temperature, water currents, and wind speed (Fig S2 in Appendix B: Chapter 5 supplementary materials), and these may influence a change in the chorusing behavior of soniferous animals. Processes such as recruitment (attracting larvae to the reef) and dispersal (spawning activities) can be challenging with increased and unpredictable changes in current speed. For example, in central Philippines, fish recruitment was low when temperature was lowest and wind strength was highest (Abesamis et al. 2010). If the low frequency choruses reported in this chapter have a reproductive function, decreases in these may indicate that the monsoon is not an ideal season for dispersal of fertilized eggs or recruitment of larvae. Alternatively, if the choruses are driven by feeding behavior, then an increase in sound levels can be expected during the southwest monsoon season because primary and secondary production in nearshore areas of the Arabian sea during this season is generally high (Smith et al 1998, Prasanna Kumar et al. 2000, Fig S2 in Appendix B: Chapter 5 supplementary materials). For the 1000-1200 Hz midnight chorus, which is suspected to have a mesopelagic origin, nearshore currents during the monsoons and the impact of these currents on the behavior of the mesopelagic community need to be assessed (McManus et al. 2008).

5.5.2.5 Oceanographic correlates of choruses

In Lakshadweep waters, higher salinity values correlated with higher water density and sea surface heights (Fig S2 and Fig S3 in Appendix B: Chapter 5 supplementary materials) and are a good indicator of local upwelling processes. Upwelling events are correlated with lower sound production levels in some Atlantic fish species, possibly due to fish movements or reduced calling (Mann and Grothues 2009). In our study as well, the chorus levels in the 200-600 Hz band (dusk chorus) decreased significantly with an increase in sea surface salinity at both the north and south sites. The chorus levels in the 1000-1200 Hz band (midnight chorus) also showed a reduction with increased sea surface salinity at the south site. However, at the north site midnight chorus levels increased with a decrease in chlorophyll-a. This site showed episodic inputs of chlorophyll-a during the non-monsoon months in addition to the sustained increase in chlorophyll-a during the southwest monsoon months observed at both the north and south sites (Fig S2 in Appendix B: Chapter 5 supplementary materials). The role of chlorophyll-a on chorusing animals during these non-monsoon months may explain why this variable was significant only at the north site. High chlorophyll-a measurements are indicative of high phytoplankton biomass. Although such measurements are extensively used to understand distribution patterns of higher trophic levels, there may be spatial or temporal mismatches and lags between primary producers, primary consumers (e.g., copepods) and secondary consumers (e.g., reef fish that feed on zooplankton, myctophids; Grémillet et al. 2008). If the midnight chorus is linked with secondary consumers, then this may explain why there was a negative correlation with chlorophyll-a. The abundance and composition of phytoplankton, zooplankton and myctophids and the interactions between these groups are poorly understood near the Lakshadweep islands.

In contrast, snapping shrimp night chorus levels increased with higher sea surface salinity at the south site. Low salinity levels may impact snapping shrimp habitat negatively thereby reducing snapping shrimp densities and abundances (Butler et al. 1995, Butler et al. 2017). This increase could also be an artefact of increased wind-dependent bubble and spray noise or precipitation, although sound levels of snapping shrimp observed in our study are much higher than typical sound levels attributed to these factors (Wenz 1962). Interestingly at the north site, although snapping shrimp chorus sound pressure levels were higher during the monsoon season when wind speeds are high (Fig S4 in Appendix B: Chapter 5 supplementary materials), the chorus showed a negative correlation with wind speeds suggesting this increase is possibly due to variability in species composition, abundances, and snap rates (Knowlton and Moulton 1963).

5.5.3 *Significance*

This study provides an acoustic view of a coral reef soundscape ranging across multiple frequency bandwidths from a mid-oceanic island ridge in the northern Indian Ocean, where prior soundscape information is lacking. An acoustic habitat context is presented into which results of other single-species or single-taxa acoustic studies from this area can be placed (e.g., Panicker and Stafford 2021, Panicker et al. 2022). Geophonic and biophonic variability is described from a previously undescribed area within the context of high environmental variability. Expanding passive acoustic monitoring of soundscapes over longer time scales (covering several years and multiple seasonal cycles) and correlating this with other remotely sensed data (such as the satellite-based oceanographic measurements presented in this chapter) will provide a critically needed view of ‘soundscape oceanography’ and these important mid-oceanic animals and their habitats.

Several effects of climate change are visible in the Arabian Sea such as increased cyclonic activities, greater varying rainfall patterns, increased acidification, expanding oxygen minimum zones, mass bleaching events and more severe storms (Kumar et al. 2009, Hughes et al. 2017 Murakami et al. 2017, Lachkar et al. 2019). The effect of a changing climate on soundscapes in this region through direct (e.g., changing monsoonal wind patterns that would impact the geophonic band) or indirect ways (e.g., effects on chorusing species), and possible cascading effects are yet to be understood. The aBOIs, sources and patterns described in our study will be useful to compare with future soundscape studies and sound pressure level measurements within this dynamic region, where there are no prior estimates of these parameters.

We provide a sonic snapshot of reef activity during the monsoon season and night periods, when very few studies have taken place on the reef due to challenging dive conditions. This information is crucial for a holistic view of ecosystem functioning. The occurrence, frequencies, and timing of choruses' links with peak larval recruitment, spawning or feeding activities of reef species in other regions (Simpson et al. 2005, 2008, Radford et al. 2008, Lobel 2013). Currently, there is little information on the timing of peak fish larval recruitment and dispersal patterns on local reefs of our study area (Arthur et al. 2006). Further investigation into the identity of these callers or assessing larval recruitment will reveal insights into the function and significance of these choruses. For example, conducting in-situ sampling during peak calling times reported in our study such as dusk or midnight periods in the inter-monsoon season will be illuminating.

At present, vessel activity in the region appears to be limited (e.g., ships, trawlers, purse seiners). Nearshore areas are mostly used by pole and line tuna fishing vessels. While boat sounds were visible in individual spectrograms, they did not occupy a major part of the overall soundscape. No part of this soundscape appeared to be dominated by anthropogenic sources. However, vessel traffic and reef fishing pressure are bound to increase with growing plans for island tourism, mechanized fisheries, and increased connectivity to the mainland (Kumar et al. 2019, Lakshadweep tourism policy 2020). An increase in anthropogenic noise will influence the soundscape of the reefs and behavior of calling animals, and this aspect needs to be incorporated into local development and environmental management plans (Chou et al. 2021, Ferrier-Pagès et al. 2021, Simpson et al. 2022).

5.6 CONCLUSION

This study describes the soundscape, the primary bands of interest based on peak sound pressure levels and the main contributors on a coral reef located adjacent to a mid-oceanic island in an area strongly influenced by the southwest (summer) monsoons. One geophony-dominated band containing shallow-water wind-driven wave sounds and three biophony-dominated bands containing fish and invertebrate choruses is presented. Although anthropogenic sources of vessels were present, they did not play a major role in the overall soundscape. Dusk and midnight choruses at lower frequencies and a snapping shrimp night chorus at high frequencies were identified. Low frequency biophonic choruses peaked in inter-monsoon months, while low frequency geophonic sound peaked during monsoon months. Low frequency geophonic sound

increased with wind speed in monsoon months. The dusk fish chorus (both sites) and the midnight chorus (at the south site) decreased with high sea surface salinity, while the snapping shrimp chorus (at the south site) increased with high sea surface salinity. The midnight chorus (at the north site) decreased with high chlorophyll-a. Snapping shrimp chorus (at both sites) increased with low wind speeds. The dusk fish chorus peaked during the full and waning moon, and the midnight and snapping shrimp choruses peak during new moon periods.

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Chapter 6. CONCLUSION

The main goal of this dissertation was to understand how cetaceans are distributed spatially and temporally across the Lakshadweep waters, an area of high seasonal environmental variability located within the Northern Indian Ocean (NIO). I used cost-efficient methodologies like surveying from platforms of opportunity and passive acoustic monitoring (PAM). PAM is particularly useful to collect data year-round including night periods and the rough-weather southwest monsoon season when visual surveys are challenging. Prior to this dissertation, there were no dedicated cetacean surveys conducted in Lakshadweep waters. The chapters presented here describe the occurrence and seasonality of multiple species in Lakshadweep and place these results within the local oceanographic context. The acoustic habitat is of substantial importance for marine species, ranging from larvae to whales. I describe the dominant sound sources of the local shallow-water soundscape, their temporal variability and oceanographic correlates across monsoon and non-monsoon months. The information within this dissertation provides a foundation for future cetacean and soundscape studies and a baseline to assess threats posed by a changing climate and other anthropogenic pressures in these waters.

A broad-scale view of cetacean occurrence and species composition of Lakshadweep waters was presented in Chapter 2. Over 3,880 km of transects were covered in the archipelago's waters using passenger ferries. I hypothesized that the Lakshadweep Islands sustains a diverse tropical cetacean community because of its complex topography within an open ocean habitat. The surveys confirmed high cetacean diversity and occurrence and set the stage for further in-depth studies in the region. Cetacean sightings were higher during the northeast monsoon season,

as compared to inter-monsoon months. Furthermore, along ferry routes, cetacean species differed from each other with respect to associations with seafloor slope gradients and distances to nearest landmass. Spinner dolphin (*Stenella longirostris*) groups were sighted more frequently on steeper seafloor slopes and closer to islands. Pantropical spotted dolphins (*Stenella attenuata*) and striped dolphins (*Stenella coeruleoalba*) were sighted more frequently in flatter seafloor areas and further from islands. Three cetacean species were added to the existing peer-reviewed literature from Lakshadweep waters, namely false killer whale, pygmy killer whale and pantropical spotted dolphin.

Chapter 2 is published in the journal Aquatic Mammals under the title ‘Cetacean distribution and diversity in Lakshadweep waters, India, using a platform of opportunity: October 2015 to April 2016’ (Panicker et al. 2020). Notably, the results presented in Chapter 2 were used to designate the Lakshadweep archipelago as an Important Marine Mammal Area internationally (IMMA; IUCN-marine mammal protected areas task force 2021). Furthermore, the results from Chapter 2 aided local authorities in proposing a marine mammal conservation team within the Department of Environment and Forests of the Lakshadweep administration of Government of India, which was set up in 2019.

One of the recommendations in Chapter 2 was to carry out PAM so that year-round data could be collected including during the rough-weather southwest monsoon season. This led to subsequent chapters (Chapter 3 and 4), where acoustic occurrence of baleen whales and odontocetes were investigated year-round. Some other recommendations from Chapter 2 are as follows; 1) Conduct finer-scale visual cetacean surveys across available bathymetric regimes

(e.g. near-shore, upper slope, lower slope) and collect co-located oceanographic data (e.g. temperature and salinity profiles of the water column); these surveys were initiated but could not be completed due to the covid-19 pandemic; 2) Investigate the spatial and temporal distribution of two bottlenose dolphin species in Lakshadweep waters - anecdotal observations suggest both *Tursiops aduncus* and *Tursiops truncatus* occur in Lakshadweep waters; 3) Study the interactions of local human population with dolphins - earlier these animals were used for local consumption, and now are used as an aid in tuna fisheries.

Fishers reported occasional occurrence of large whales in Lakshadweep waters. Since we did not have control over vessel speed, the surveys in Chapter 2 were biased against detecting long-diving, cryptic and rare species. Therefore, baleen whales, sperm whales (*Physeter macrocephalus*), and especially beaked whales may have been missed during these surveys. Prior studies suggested that mid-oceanic habitats in the southeastern Arabian sea (SEAS) may act as predictable hotspots of productivity for blue whales in non-monsoon months (Anderson et al. 2012, Anderson and Alagiyawadu 2019). In Chapter 3, using PAM, I present evidence of Central Indian Ocean (CIO, formerly known as NIO) pygmy blue whale (PBW; *Balaenoptera musculus breviceauda*) songs occurring in Lakshadweep waters, mostly during the inter-monsoon months of April and May. No other acoustic population of blue whales, or other baleen whale vocalizations, were detected.

Chapter 3 is published in the journal Marine Mammal Science under the title ‘Northern Indian Ocean blue whale songs recorded off the coast of India’ (Panicker and Stafford 2021). The results extended the known range of CIO pygmy blue whales about 1,000 km north-

westward from the waters surrounding Sri Lanka. The study confirmed that Lakshadweep waters were an endangered blue whale habitat, and received media coverage in India (Uniyal 2021, Ghosh 2021, Jacob 2021). The significance of this habitat to the larger blue whale population in the NIO is yet to be assessed. One limitation of PAM is that we cannot determine animal behavior unless behavior-specific vocalizations are made. I recommend dedicated visual surveys during the months of April and May to determine if whales are feeding or travelling through these islands (Panicker and Stafford 2021). If whales are feeding, I recommend additional surveys focusing on known blue whale prey species such as euphausiids, sergestid shrimps and mysids (Alling et al. 1991, de Vos et al. 2018).

Furthermore, I recommend the expansion of PAM efforts with increased temporal and spatial coverage in this region. This will advance our understanding on diel calling behavior, seasonality and inter-annual variability of baleen whale occurrence including pygmy blue whales in the SEAS. Placing acoustic recorders in deeper waters of the NIO's mid-oceanic habitat (Lakshadweep and Maldives) and off the western Indian mainland is recommended. This will help make comparisons between acoustic occurrence of baleen whales 1) off the mainland and within mid-oceanic habitats 2) across latitudes in the equatorial and northern Indian Ocean, and 3) differing oceanographic conditions observed from remote sensing data (e.g., ARGO floats, satellite data). An increase in deep-water and long-term PAM efforts, as recommended here, will include NIO waters into larger questions of population connectivity and movement patterns of blue whales across the Indian Ocean (e.g., Leroy et al. 2018, Torterotot et al. 2020).

An interesting finding presented in Chapter 3 was that some CIO PBW songs were missing the third unit of the song. This unit is often used to automatically detect the presence of the CIO PBW population (e.g. Stafford et al. 2011, Samaran et al. 2013, Miksis-Olds et al. 2018, Leroy et al. 2018). Jolliffe et al. (2019) reported on variations in the southeastern Indian Ocean pygmy blue whale song. This variation of the CIO PBW song has not been published before. Blue whale song types are generally stable over time, unlike some other baleen whales such as humpback whales and bowhead whales (Payne and Payne 1985, Stafford 2022), which makes this line of investigation particularly interesting. I recommend further study into what the significance of this unit omission is, and the implications of the same.

Occurrence and temporal patterns of an island-associated odontocete community, using PAM, are presented in Chapter 4. A resident population of odontocetes, likely to be spinner dolphins, was identified. The highest number of acoustic detections were recorded during the northeast monsoon month of November. The year-round occurrence of this odontocete community signifies that sufficient mesopelagic prey resources persist near these islands. Higher detections were observed during daylight hours with a peak during dawn and late afternoon hours, suggesting that Kavaratti atoll may be a daytime resting habitat. Detections were most frequent during new moon periods, and least frequent just before full moon periods. Whistles were detected to a greater extent at the south side of the Kavaratti atoll in Lakshadweep waters. Chapter 4 is published in the journal *Marine Ecology Progress Series* in February 2022 under the title ‘Fine-scale spatial and temporal acoustic occurrence of island-associated odontocetes near a mid-oceanic atoll in the Northern Indian Ocean’ (Panicker et al. 2022).

Odontocete species show geographic variability in their whistles (Oswald 2006). A species identification and classification method could not be used in Chapter 4 due to the lack of sufficient training data with known species identity (e.g., Oswald et al. 2007, Rankin et al. 2016). I recommend building an acoustic library of odontocete vocalizations from identified species, through boat-based data collection in Lakshadweep waters or the SEAS. This will aid in identifying and classifying odontocete species in future PAM efforts from this region. Additionally, I recommend further research using visual and acoustic techniques to examine behaviour, hotspot areas and population connectivity of delphinids between islands. Such studies along with contents of Chapter 4 will be valuable to establish regulations for any dolphin-watching activities associated with upcoming tourism plans.

The diel and lunar variability reported in Chapter 4 alludes to a potential inshore-offshore movement of odontocetes and possibly their prey: an island-associated mesopelagic community. I recommend further studies on the mesopelagic boundary community in Lakshadweep waters. This community is likely to play a critical role in nutrient transfer between oceanic and neritic habitats and may have significant implications for the reef ecosystem (Reid et al. 1991). Active acoustic methods using echosounders across the island slope habitat will be particularly useful to characterize this community in Lakshadweep, as done in other regions (e.g., Benoit-Bird and Au 2004, Comfort et al. 2017).

The shallow water soundscape in Lakshadweep waters is examined in Chapter 5. Characteristics of major sound sources, their temporal patterns, and their correlation with local oceanographic parameters across monsoon and non-monsoon months are presented. I identified

four acoustic bands of interest: a geophonic band of wind-driven wave sounds and three biophonic bands containing animal choruses. Low frequency biophonic choruses peaked during inter-monsoon months, while low frequency geophonic sound levels peaked during southwest monsoon months. Dominant choruses occurred during dusk, midnight, and night hours across different frequency bandwidths. I recommend in-situ studies during high calling periods to identify soniferous fish families and document behavior. Such efforts will provide further insight into chorus function.

As expected, the geophonic band was correlated with high windspeeds during the southwest monsoon months. The low frequency dusk (in north and south site) and midnight choruses (in the south site) were negatively correlated with sea surface salinity (used as a proxy for local upwelling processes). The midnight chorus (in the north site) was negatively correlated with the chlorophyll-a (used as a proxy for phytoplankton biomass). I recommend further research on near-island distribution and species composition of zooplankton and myctophid communities. The study of these key prey bases of oceanic and neritic food webs is essential. Expanding PAM of soundscapes over longer time scales and correlating this with oceanographic data (both remote and in-situ) will advance our understanding of how oceanographic processes impact the underwater soundscape in these waters.

Chapter 5 presents a shallow-water soundscape from a mid-oceanic habitat in the NIO, where prior soundscape information is lacking. This chapter provides an acoustic context for single-species or single-taxa studies (e.g., Panicker and Stafford 2021, Panicker et al. 2022). Within the context of a changing climate, the results presented in this chapter will be particularly

useful to compare with future soundscape studies from the region. Presently, a dominant anthropogenic source was not identified in the shallow-water soundscape of Kavaratti atoll. Evolving plans on island tourism, expanding mechanized fishing, and increasing transport connectivity will increase anthropogenic noise (Department of Tourism, Government of India 2003, Kumar et al. 2019). The subsequent effects of underwater anthropogenic noise need to be incorporated in environment assessment plans. Contents of this chapter are being prepared for submission to a peer-reviewed journal.

Understanding cetaceans and the underwater soundscape through an oceanographic lens calls attention to the underlying biological resources and physical drivers in this poorly studied area. For example, the odontocete acoustic occurrence presented in this dissertation not only aids in protecting resident spinner dolphin populations through conservation action, but also highlights a critical need to study island-associated mesopelagic resources that sustain these predator populations year-round. Characterizing the geophonic signature of monsoonal winds on the coral reef soundscape illustrates yet another pathway in which seasonally reversing winds may impact ecological interactions. One major hurdle to conducting studies in this area is the rough weather experienced during southwest monsoons. This study demonstrates that employing appropriate technology and methodologies can shed light on even highly mobile species (such as blue whales) in challenging conditions. Climate change and fast-emerging local anthropogenic pressures make the information presented in this dissertation relevant. Continuing these efforts over several years will contribute to mitigation and management decisions.

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APPENDIX A: CHAPTER 4 SUPPLEMENTARY MATERIALS

Table S1: ANOVA table for fitted binomial GAMM with a logit link (Fig. 4) examining the relationship between odontocete detections presence and absence and smooth terms: hour of the day, lunar day, and interaction between lunar day, month, and site. Regression parameters, standard errors, t-values and *P*-values for the linear and categorical terms such as site, and month are also provided. The model was fit with correlation autoregressive moving average term with lag 1 hour and grouped per site to account for temporal autocorrelation. Significant terms denoted by *. Degrees of freedom, abbreviated to df.

<u>Smooth terms</u>				
	<i>Estimated df</i>	<i>Estimated residual df</i>	<i>F</i>	<i>p-value</i>
Hour of the day	9.922	21	12.27	<0.001 *
Lunar day (overall)	3.334	8	1.049	0.019 *
Lunar day: north site	2.336e ⁻⁰⁵	8	0.00	0.097
Lunar day: south site	2.384	8	1.44	<0.001 *
<u>Parametric terms</u>				
	<i>df</i>		<i>F</i>	<i>p-value</i>
month	11		9.465	<0.001*

site	1		7.245	0.007
<u>Categorical terms</u>				
	<i>Estimate</i>	<i>Std.error</i>	<i>t value</i>	<i>p-value</i>
South site to north site	0.290	0.1077	2.692	0.007 *
Feb to Jan	-0.313	0.184	-1.669	0.090
Mar to Jan	-0.231	0.178	-1.271	0.194
Apr to Jan	-0.663	0.196	-3.307	<0.001*
May to Jan	-1.076	0.198	-5.479	<0.001*
Jun to Jan	-0.921	0.209	-4.156	<0.001*
Jul to Jan	-0.717	0.202	-3.956	<0.001*
Aug to Jan	-0.329	0.193	-1.558	0.081
Sept to Jan	-1.159	0.231	-5.314	<0.001*
Oct to Jan	-1.238	0.380	-3.201	0.001 *
Nov to Jan	0.675	0.216	3.120	0.001 *
Dec to Jan	-0.630	0.2728	-2.769	0.006 *

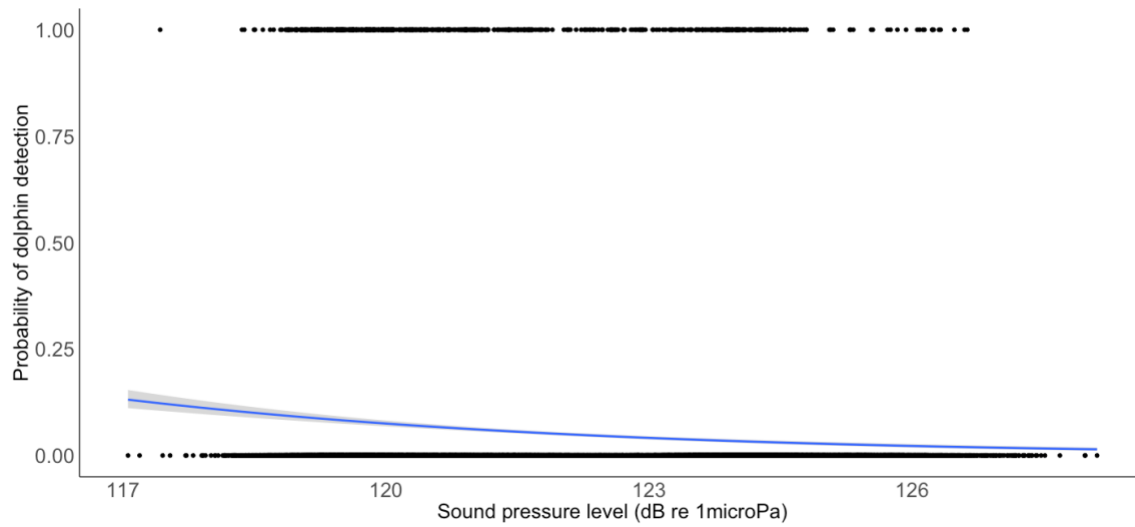


Fig. S1: Model fit of binomial GLM showing raw data points. Response curves of GLM for presence or absence of odontocete detections across sound pressure levels.

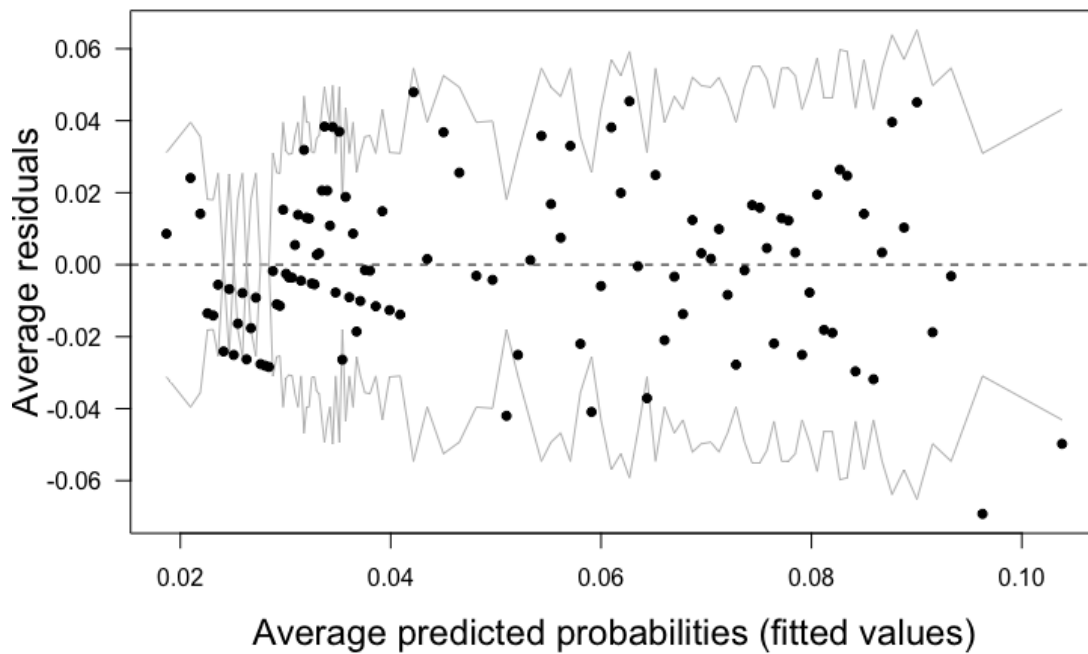


Fig. S2: Binned residual plot for the GLM between residuals and fitted values to assess goodness of fit. Grey lines represent confidence intervals.

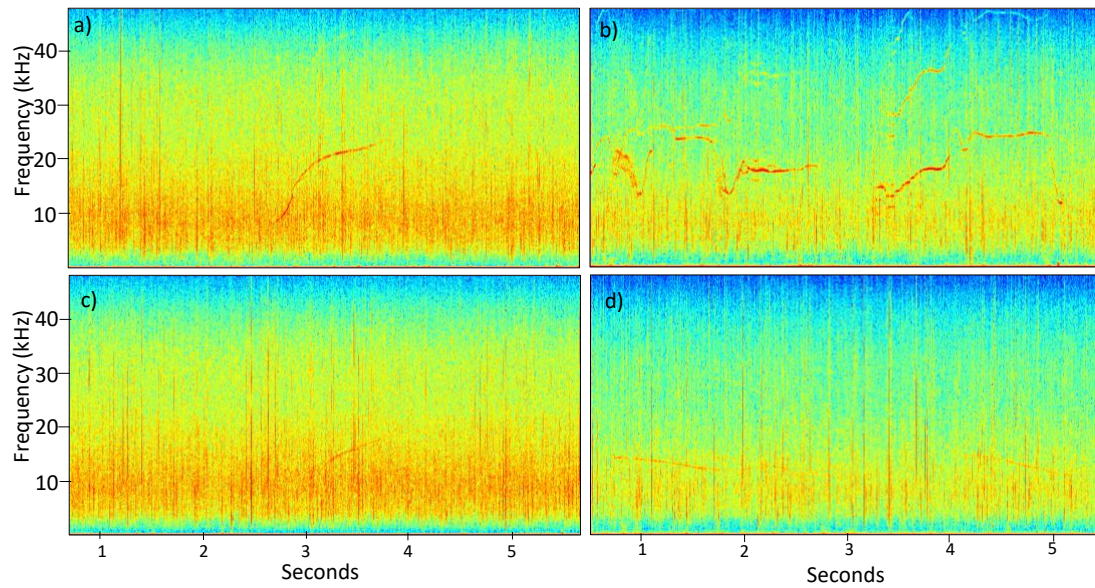


Fig. S3: Examples of spectrogram images of odontocete whistles with relatively a) strong SNR at night b) strong SNR during the day c) weak SNR at night d) weak SNR during the day. The broadband impulsive noise is made by snapping shrimp (Everest et al. 1948).

APPENDIX B: CHAPTER 5 SUPPLEMENTARY MATERIALS

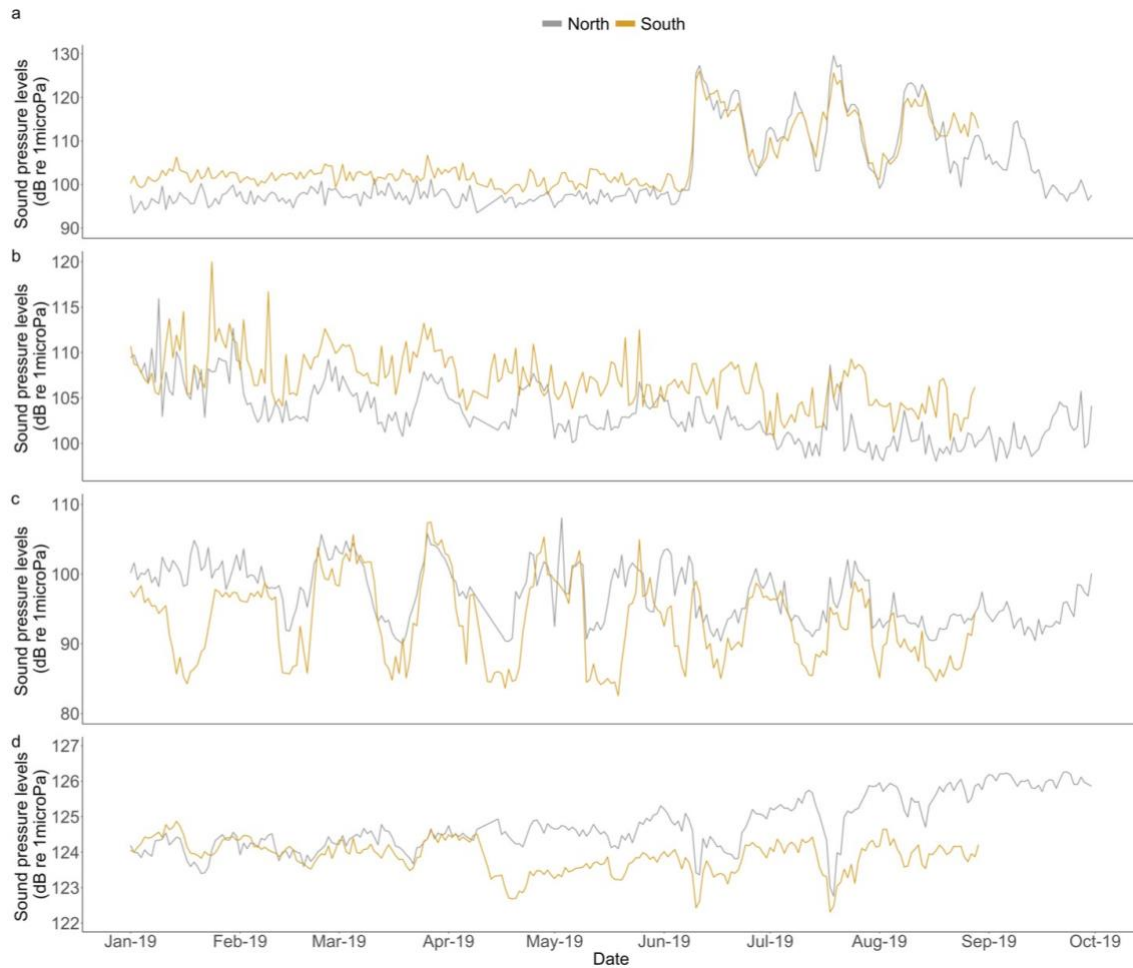


Figure S1: Time series of sound pressure levels within the geophonic band and biophonic chorus periods in the north (grey lines) and south site (gold lines). a) 20-100 Hz band; b) 200-600 Hz band; c) 1000-1200 Hz band and; d) 2000-30000 Hz band.

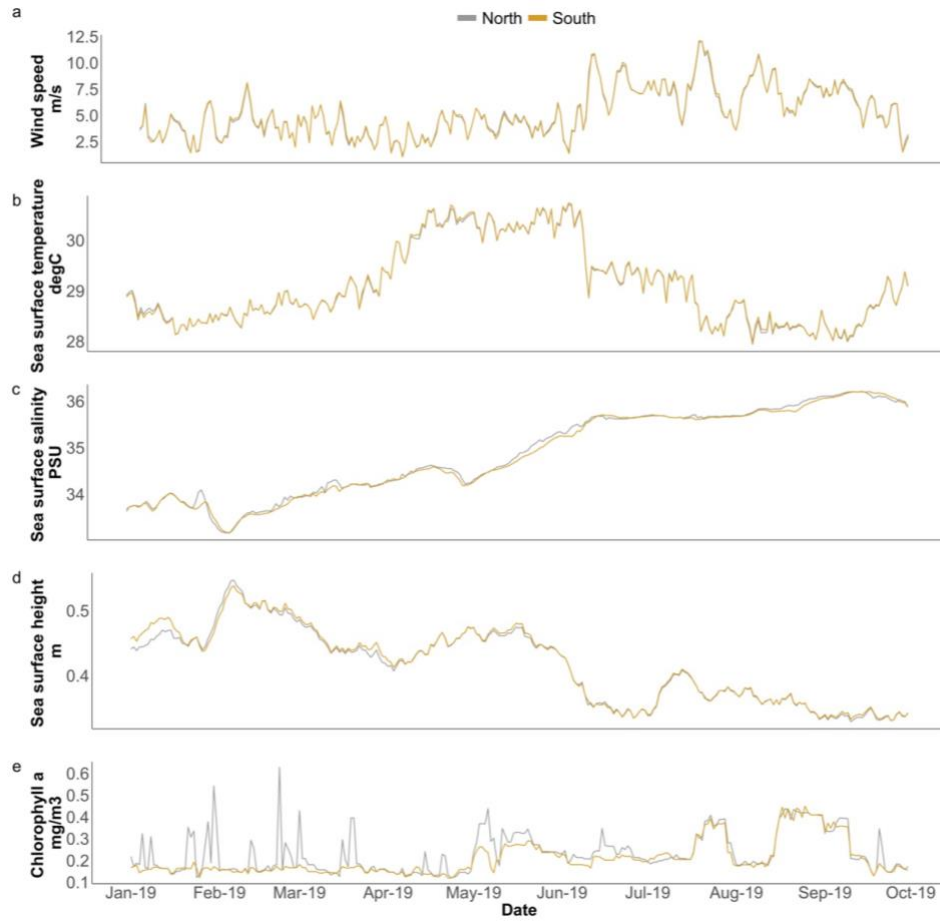


Figure S2: Time series of satellite-derived oceanographic variables in the north (grey lines) and south site (gold lines). a) wind speed (m); b) Sea surface temperature (degC); c) Sea surface salinity (PSU); d) Sea surface height (m) and; e) Chlorophyll a (mg/m³)

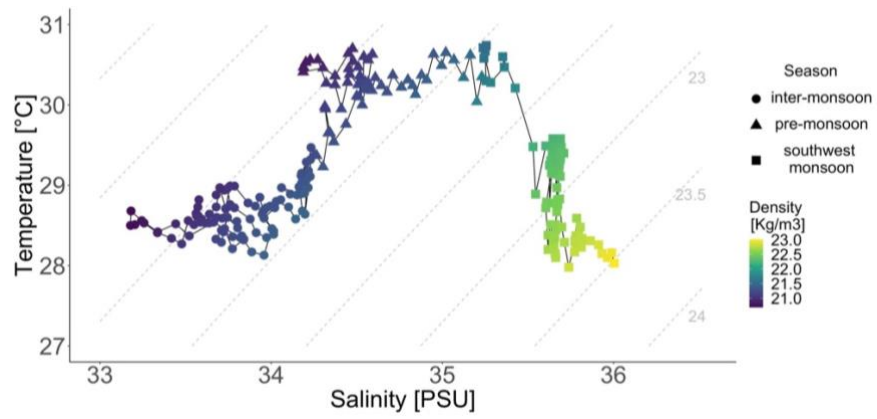


Figure S3: T-S plot based on sea surface temperature and salinity in the south site. Since both the north and south sites had very similar SST and SSS values across the time series, only the south site is plotted here.

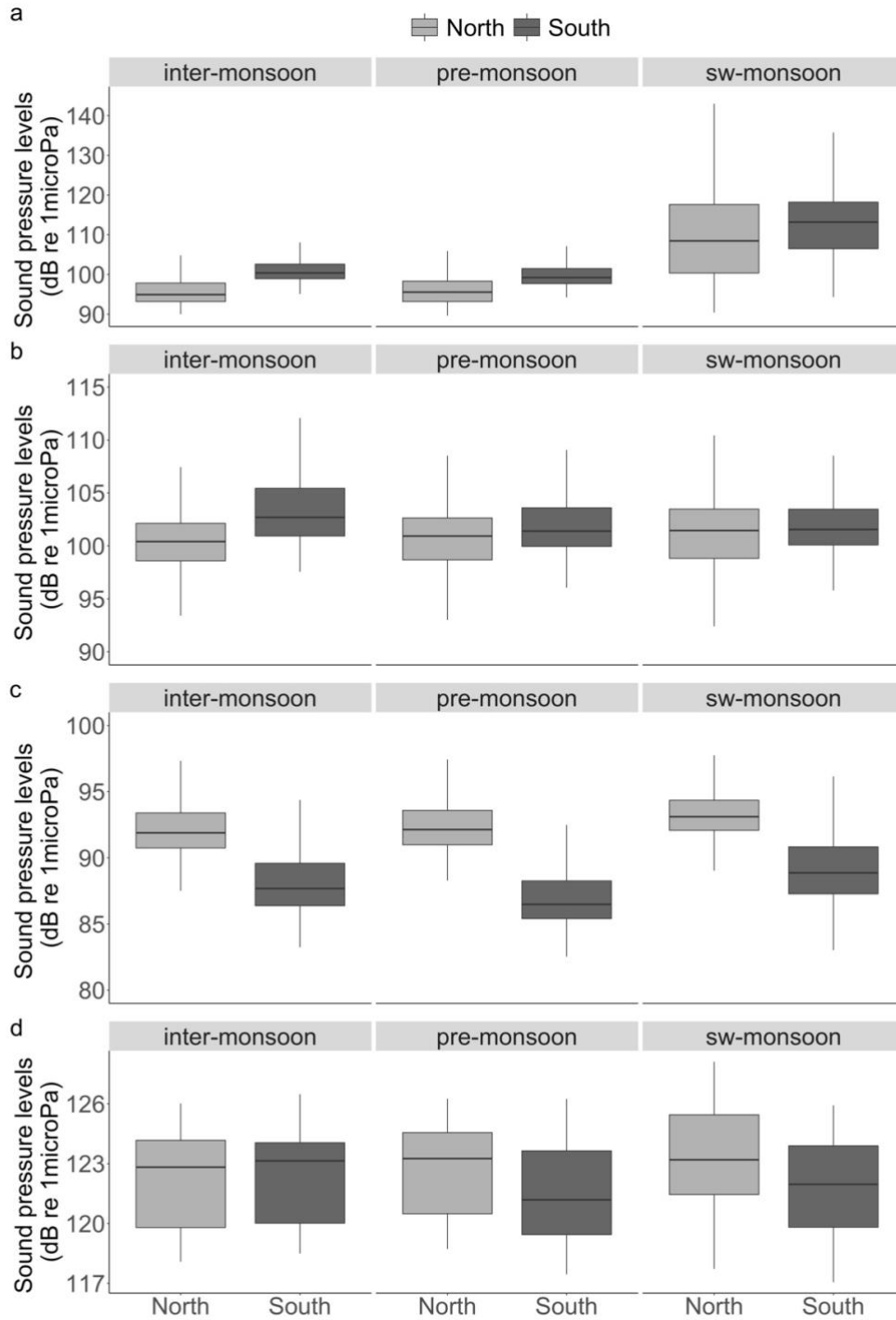


Figure S4: Season and site-wise differences of sound pressure levels of the aBOIs in the north and south site. a) 20-100 Hz band; b) 200-600 Hz band; c) 1000-1200 Hz band and; d) 2000-30000 Hz band.

Table S1: Estimated coefficients, standard errors, t-value and p-value for fixed components of the generalized least squares regression.

	Estimate	Std Error	t value	p value	df
Intercept	98.08	0.66	147.59	< 0.001	
wind speed	-0.12	0.10	-1.13	0.26	1
pre-monsoon to intermonsoon	-1.03	0.86	-1.20	0.23	2
sw-monsoon to intermonsoon	0.42	1.65	0.25	0.80	
South to North site	4.03	0.65	6.18	< 0.001	1
Wind speed x pre-monsoon	0.07	0.18	0.41	0.68	2
Wind speed x sw-monsoon	1.57	0.22	7.25	< 0.001	

Table S2: ANOVA table for fitted gaussian GAMMs with an identity link (Fig. 5.7) examining the relationship between sound pressure levels of the dusk chorus in the 200-600 Hz band and smooth term lunar day in the north and south sites. Regression parameters, standard errors, t-values and *P*-values for the linear terms such as sea surface salinity, sea surface temperature, wind speed and chlorophyll-a are also provided. The model was fit with correlation autoregressive moving average term with lag 1 day and lag 2 days to account for temporal autocorrelation in the north and south site respectively. Significant terms denoted by *. Degrees of freedom, abbreviated to df.

<u>Smooth terms</u>				
	<i>Estimated</i>	<i>Estimated</i>	<i>F</i>	<i>p-value</i>

	<i>df</i>	<i>residual df</i>		
Lunar day (GAMM for north site)	3.193	8	2.892	<0.001 *
Lunar day (GAMM for south site)	3.916	8	2.173	<0.001 *
<u>Parametric terms</u>				
	<i>df</i>		<i>F</i>	<i>p-value</i>
Chlorophyll-a (GAMM for north site)	1		1.441	0.231
Chlorophyll-a (GAMM for south site)	1		0.462	0.497
Sea surface temperature (GAMM for north site)	1		0.342	0.559
Sea surface temperature (GAMM for south site)	1		0.058	0.810
Sea surface salinity (GAMM for north site)	1		24.905	<0.001 *
Sea surface salinity (GAMM for south site)	1		23.718	<0.001 *
Wind speed (GAMM for north site)	1		0.308	0.579
Wind speed (GAMM for south site)	1		3.135	0.078

Table S3: ANOVA table for fitted gaussian GAMMs with an identity link (Fig. 5.8) examining the relationship between sound pressure levels of the dusk chorus in the 1000-1200 Hz band and smooth term lunar day in the north and south sites. Regression parameters, standard errors, t-values and *P*-values for the linear terms such as sea surface salinity, sea surface temperature, wind speed and chlorophyll-a are also provided. The model was fit with correlation autoregressive moving average term with lag 1 day to account for temporal autocorrelation. Significant terms denoted by *. Degrees of freedom, abbreviated to df.

<u>Smooth terms</u>				
	<i>Estimated df</i>	<i>Estimated residual df</i>	<i>F</i>	<i>p-value</i>
Lunar day (GAMM for north site)	5.314	8	10.1	<0.001 *
Lunar day (GAMM for south site)	3.568	8	3.308	<0.001 *
<u>Parametric terms</u>				
	<i>df</i>		<i>F</i>	<i>p-value</i>
Chlorophyll-a (GAMM for north site)	1		8.655	0.003*
Chlorophyll-a (GAMM for south site)	1		1.210	0.272
Sea surface temperature (GAMM for north site)	1		0.043	0.835

Sea surface temperature (GAMM for south site)	1		0.600	0.439
Sea surface salinity (GAMM for north site)	1		1.400	0.238
Sea surface salinity (GAMM for south site)	1		21.39	<0.001*
Wind speed (GAMM for north site)	1		2.237	0.136
Wind speed (GAMM for south site)	1		2.03	0.155

Table S 4: ANOVA table for fitted gaussian GAMMs with an identity link (Fig. 5.9) examining the relationship between sound pressure levels of the night chorus in the 2000-30000 Hz band and smooth term lunar day in the north and south sites. Regression parameters, standard errors, t-values and *P*-values for the linear terms such as sea surface salinity, sea surface temperature, wind speed and chlorophyll-a are also provided. The model was fit with correlation autoregressive moving average term with lag 1 day to account for temporal autocorrelation. Significant terms denoted by *. Degrees of freedom, abbreviated to df.

<u>Smooth terms</u>				
	<i>Estimated df</i>	<i>Estimated residual df</i>	<i>F</i>	<i>p-value</i>
Lunar day (GAMM for north site)	5.060	8	3.256	<0.001 *
Lunar day (GAMM for south site)	4.685	8	2.493	<0.001 *
<u>Parametric terms</u>				
	<i>df</i>		<i>F</i>	<i>p-value</i>
Chlorophyll-a (GAMM for north site)	1		0.822	0.366
Chlorophyll-a (GAMM for south site)	1		0.586	0.445
Sea surface temperature (GAMM for north site)	1		0.207	0.650
Sea surface temperature (GAMM for south site)	1		2.687	0.102
Sea surface salinity (GAMM for north site)	1		0.127	0.721
Sea surface salinity (GAMM for south site)	1		30.960	<0.001*
Wind speed (GAMM for north site)	1		32.143	<0.001*

site)				
Wind speed (GAMM for south site)	1		22.781	<0.001*