

ORIGINAL RESEARCH

Spinner dolphin residency in tropical atoll lagoons: Diurnal presence, seasonal variability and implications for nutrient dynamics

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Abstract

Mobile predators serve important ecological functions, including acting as nutrient vectors between different ecosystems. In coral reefs, pelagic nutrient subsidies are believed to play an increasingly important role under ongoing and projected environmental changes. Here, we combine visual sightings with passive acoustic monitoring to report habitat use and behaviour by cetaceans within atoll lagoons in the Maldives and Chagos archipelagos. We demonstrate that spinner dolphins (*Stenella longirostris*) are the most widely distributed and numerically abundant cetacean inside these atolls (>90% of all individual cetaceans by numbers). Our visual and acoustic observations both provide evidence of a regular diurnal behaviour, where dolphins enter the lagoons during the morning, for day-time resting, and exit during the afternoon, for night-time foraging offshore. Using standard metabolic models and timing of lagoonal residencies, we estimate that a dolphin pod would deposit approximately $288 \pm 17 \text{ kg year}^{-1}$ of nitrogen of primarily mesopelagic origin inside the lagoons. The nitrogen deposited inside an atoll lagoon by a dolphin pod resident year-round will therefore likely enhance coral reef productivity and resilience and suggests that these dolphins play a role in making pelagic energy and nutrients available to coral reefs. The absence of any acoustic detections following the reversal of the monsoon winds suggests that the short-to-medium-term residency of the dolphins is sensitive to seasonal productivity dynamics.

Introduction

Coral reef ecosystems sustain over 6 million people through livelihoods and ecosystem services that are threatened under the current biodiversity crisis (Cinner et al., 2020). On oceanic atolls, coral reefs support elevated biomass and productivity in contrast with their often oligotrophic surroundings, through energetic pathways which remain poorly understood. Mass bleaching events may disrupt benthic energy input from coral symbiosis. There is, as a result, considerable interest in understanding variability in mechanisms that can maintain productivity and functioning under ecosystem stress, such as topographic enhancement (Gove et al., 2016) and pelagic subsidies (Morais & Bellwood, 2019; Skinner et al., 2019). Sea-birds and sharks have been shown to act as vectors of pelagic nutrients (Williams et al., 2018) that may, in the case of sea-birds, enhance production and ecosystem functioning (Graham

et al., 2018). Although cetaceans have long been suspected to act as nutrient vectors between ecosystems ('the whale pump', Roman & McCarthy, 2010), their contribution to coral reef systems remains speculative (Kiszka et al., 2022), in part due to a lack of basic information on prevalence and distribution.

Here, we set out to establish the importance of cetaceans within atoll lagoons, and their potential role in the geographically adjacent and ecologically similar coral reef ecosystems of the Maldives and the Chagos Archipelago (also known as the British Indian Ocean Territory, BIOT) in the central Indian Ocean. Although cetacean prevalence and habitat use within the Maldives is relatively well understood (Anderson, 2005), little is known about the cetaceans of the Chagos Archipelago, in spite of the area offering them the highest protection within the Indian Ocean. The Chagos Archipelago and its 200 nautical mile associated waters was declared a 640 000 km² no-take Marine Protected Area (MPA) in 2010 by the UK government (Hays

et al., 2020). Meanwhile, in the Maldives cetaceans are protected not only by law but also by the fact that local fisheries concentrate on pole-and-line and handline fishing for tuna with most forms of net fishing banned. For cetaceans in the Indian Ocean, the Maldives and Chagos Archipelagoes therefore offer a refuge from most fisheries-related mortality, including bycatch (Anderson *et al.*, 2020). The Chagos Archipelago is difficult to access for fieldwork, and remote monitoring or opportunistic survey platforms are as a consequence potentially of particular value. Insight into cetacean ecology in the Chagos Archipelago following the whaling era (Wenban-Smith & Carter, 2016) stems primarily from opportunistic passive acoustic monitoring (PAM, Marques *et al.*, 2012), from the deep hydrophones installed near Diego Garcia as part of the International Monitoring System (IMS) established under the Comprehensive Nuclear Test Ban Treaty. This has yielded low frequency acoustic recordings of baleen whale vocalizations, attributed to Omura's whale (*Balaenoptera omurai*) and blue whale subspecies (*Balaenoptera musculus* ssp; Cerchio *et al.*, 2019, 2020; Sousa & Harris, 2015; Stafford *et al.*, 2010). Other notable records of cetaceans include samples of sperm whales (*Physeter macrocephalus*) collected in the Chagos Archipelago during the round-the-world voyage of the Research Yacht Odyssey and incorporated into global studies of heavy metal pollution and population genetics (e.g. Alexander *et al.*, 2016; Savery, Evers, *et al.*, 2013; Savery, Wise, *et al.*, 2013; Wise *et al.*, 2009, 2011). In addition, there are sightings predating the implementation of the MPA of delphinids and sperm whales from Spanish and French purse seiner fishing vessels (Escalle *et al.*, 2015).

In this study, we first use visual sightings from multiple sources (from 1992 to 2019) to establish the cetacean species associated with atoll lagoons in the Maldives and Chagos archipelagoes. Next, we combine records of sightings and daily movement behaviour with medium-term (6 months) passive acoustic monitoring (PAM) in order to infer habitat-use and movement patterns across time scales (diurnal and seasonal), in relation to environmental variability. PAM was conducted in the Peros Banhos lagoon, the largest islanded atoll within the Chagos Archipelago, as part of a field trial of surveillance technology aimed at detecting illegal fishing activity. The most abundant cetaceans within Maldivian lagoons are spinner dolphins (*Stenella longirostris*, >90% of individual cetaceans by number) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, <5%; Anderson, 2005). On this basis and in line with understanding of dolphin habitat use around oceanic islands more broadly (Lammers, 2019), we expected spinner dolphins to be an important if not the dominant species associated with atoll lagoons in the Chagos Archipelago, and thus prevalent on the PAM records. Finally, we sought to quantify cetacean contribution to coral reef energy pathways, by estimating the likely quantity of nutrients egested by cetaceans into lagoonal systems, on the basis of species prevalence, habitat use, foraging behaviour, estimates of daily consumption and standard metabolic models. Our results provide insights in the prevalence and behaviour of cetaceans in central Indian Ocean atolls and highlight the likely role of spinner dolphins in sustaining oceanic atoll productivity.

Materials and methods

Visual sightings of cetaceans

We documented cetacean habitat use and behaviour associated with coral atoll lagoons in the Maldives and Chagos Archipelago (BIOT), two geopolitical entities making up the largest section of the atoll chain of the Chagos-Lakshadweep Ridge in the central Indian Ocean (Fig. 1). We used sightings from whale-watching trips, scientific expeditions and enforcement patrols to determine the main species associated with atoll lagoons.

In the Maldives, records from 110 commercial live-aboard whale-watching survey trips were available from two periods: between 1990 and 2002 and between 2010 and 2019, totaling 890 days at sea. All cetacean sightings were systematically recorded during whale-watching trips, from an eye height of about 4 m., as reported elsewhere (Anderson, 2005; Anderson, Sattar & Adam, 2012). The trips covered the entire length of the Maldives Archipelago (Fig. 1a) and were conducted throughout the year (Fig. 2). Each trip included between 1 and 3 experienced observers, assisted by 1–6 inexperienced observers (typically untrained tourists or students). Upon sighting, most groups were approached slowly by the vessels and species identity, behaviour, location and pod size confirmed using binoculars and GPS. Direction of travel was specifically noted for dolphins that were seen near or in atoll channels (i.e. in channels connecting atoll lagoons with the open sea).

In the Chagos Archipelago, sightings were recorded during two scientific expeditions to the Peros Banhos and Salomon Atoll lagoons, in February 1996 and in March and April 2017. Sightings were also recorded during the routine patrols of the BIOT patrol vessel, between February 2015 and July 2017, throughout the year. The primary objectives of the scientific expeditions were to conduct SCUBA surveys of the coral reefs, for reef health and fish community monitoring, and any cetacean sightings were therefore fortuitous. Cetacean sightings were made from small inflatable tenders, either during diver surface intervals in-between dives, whilst waiting for divers to surface or during transit between the mother vessels anchored in the lagoon and dive sites on the outer reef slopes. Diving activities (and therefore opportunity for cetacean sightings) typically started around 08:00 and finished around 17:30. All cetacean encounters were georeferenced using GPS. Species identification and pod size were confirmed when possible, using binoculars. Photographs of cetaceans were taken in 2017 as well, although sightings were not systematically recorded. The patrol-based sightings were recorded by a senior fisheries protection officer (SFPO) during the routine patrols of the BIOT patrol vessel and were made from an eye height of approx. 10 m, by six rotating SFPOs. Coordinates were not always recorded ($n = 12$ not recorded) although location of the pod in relation of the lagoon and atoll were noted in those cases (e.g. 'inside lagoon, NE of entrance towards Ile Passe'). All sightings were made using binoculars and identified with the aid of cetacean guidebooks. Given the opportunistic nature

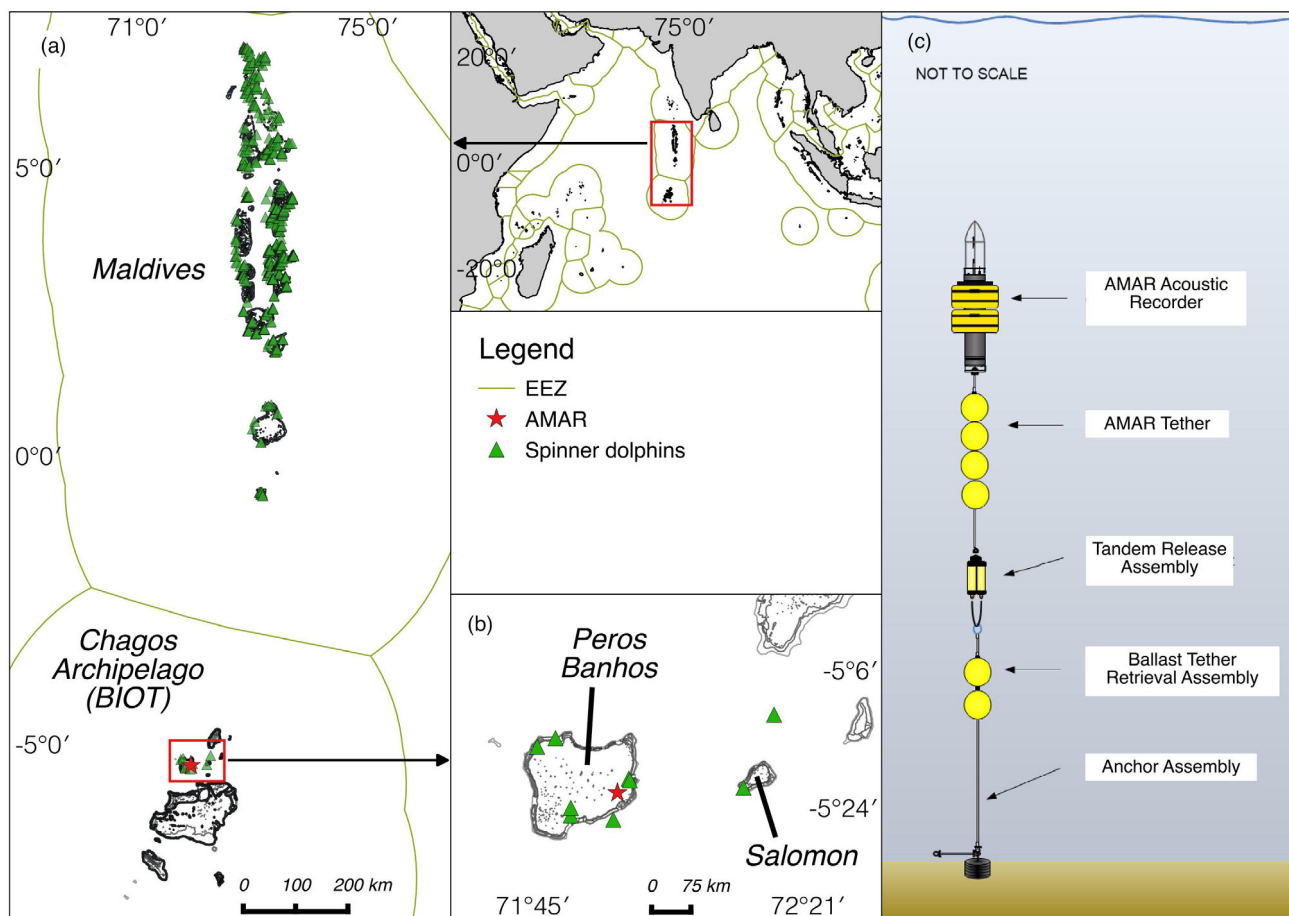


Figure 1 Spinner dolphin sightings ($n = 782$) and passive acoustic monitoring inside atolls in the Maldives and from the Chagos archipelagoes in central Indian Ocean (a), with inset (b) showing location of Autonomous Multi-channel Acoustic Recorder (AMAR) and the Peros Banhos and Salomon Atolls in the Chagos Archipelago. (c) Schematics of AMAR.

of the sightings, the confidentiality of the patrol routes, and the likely differing levels of expertise between the patrol-based observations and the whale-watching trips we do not attempt to account for survey effort, and only use the sightings to determine presence and relative species proportion.

Passive acoustic monitoring

Various enforcement and surveillance technologies are currently being deployed to tackle Illegal Unreported and Unregulated (IUU) fisheries active inside the Chagos MPA (Collins *et al.*, 2021). Here, PAM deployed for IUU surveillance offered the opportunity to investigate habitat use by cetaceans associated with atoll lagoons, although this was not the primary objective of the deployment. An Autonomous Multi-channel Acoustic Recorder (AMAR, JASCO Applied Sciences, Version G3) station was established in Peros Banhos lagoon, Chagos Archipelago, approximately 5 km west of the nearest island of Grand Ile Coquillage at $05^{\circ}22.2'S$, $071^{\circ}56.7'E$ (Fig. 1 b). The AMAR was mounted on a vertical, sub-surface and bottom-anchored mooring, with two flotation clusters and

incorporating a tandem acoustic release pack (Benthos R500) for retrieval (Fig. 1c), with a calibrated GeoSpectrum M36-V35-100 hydrophone. The hydrophone was held at a depth of 20 m, in seabed depth of 25 m and was left to record for 171 days, between 14 April and 1 October 2017. The hydrophone was calibrated with an in-date G.R.A.S 42AA pistonphone (<https://www.grasacoustics.com/>). We offset the manufacturer's calibration curve by the difference between the pistonphone calibration at 250 Hz and the manufacturer's calibration at 250 Hz to obtain the frequency-dependent sensitivities. The sensitivity of the hydrophone was measured at -164.94 dBV/ μ Pa prior to deployment (-165 dBV/ μ Pa nominal). The frequency response of the hydrophone was flat from ~ 50 Hz to $70\,000$ Hz ± 1 dB. One channel recorded low to medium frequencies pertinent to the detection of vessel engine noise in the 10 Hz to 8000 Hz band for a 44% duty cycle, and was not used further in this analysis. A second channel recorded a broader bandwidth up to 375 000 Hz, on a 4% duty cycle (65 s, every 25 min) to capture biological noise, including cetacean vocalizations such as delphinid whistles and echolocation clicks.

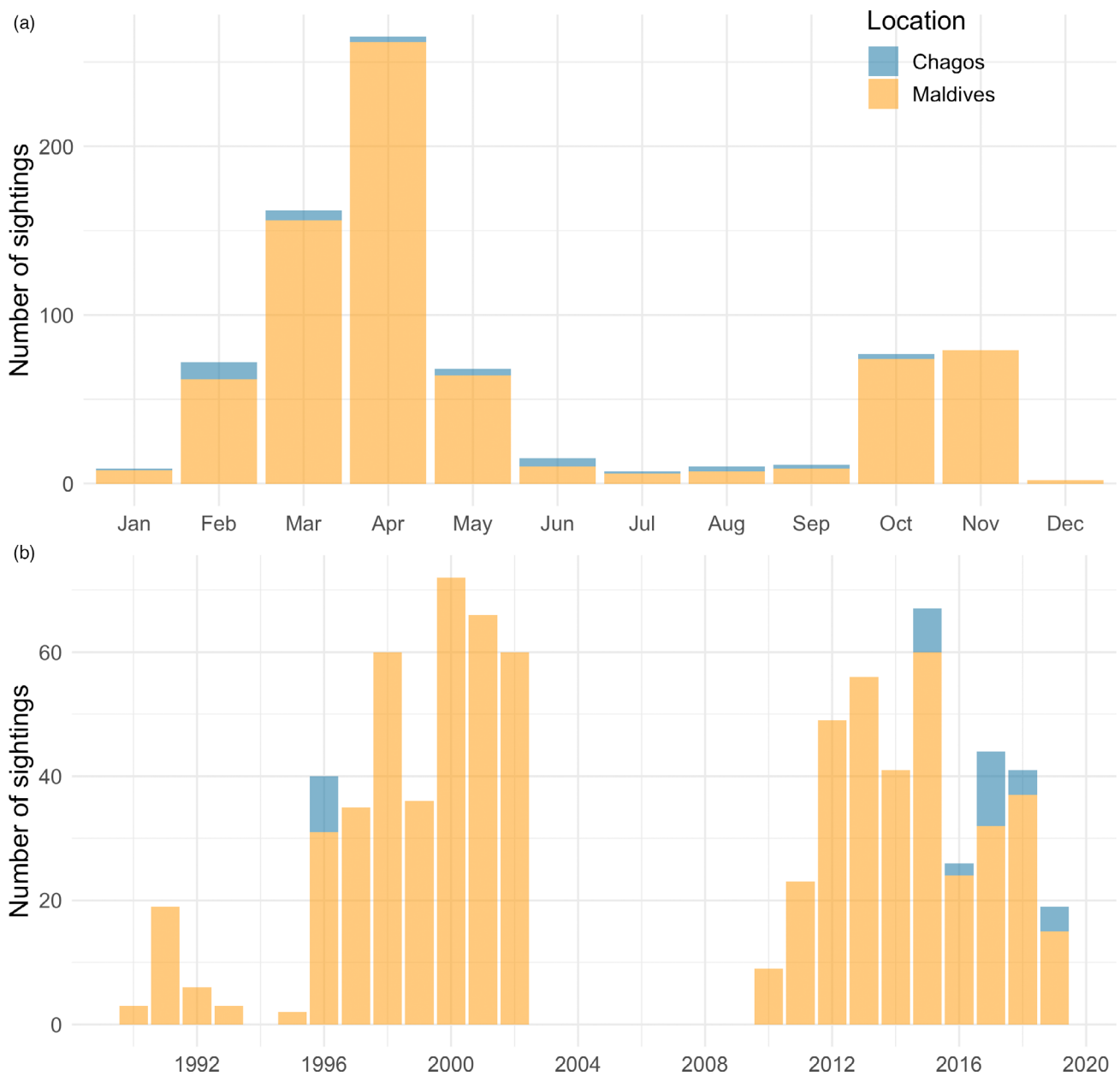


Figure 2 Monthly (a) and yearly (b) number of spinner dolphin sightings in the Maldives and Chagos archipelagoes.

Upon retrieval, the raw audio files were processed in order to detect delphinid whistles using JASCO's PAMlab software. Every file containing at least one positive delphinid whistle detection was validated by visual inspection using Audacity® (Version 3.0.0, Audacity Team, 2021). The site chosen for the initial IUU detection trials was near a lagoon channel as a hypothesized most likely entry site for IUU fishing vessels. The geomorphology of Peros Banhos Atoll displays a characteristically steep peripheral slope outside a ring of islands and submerged reefs, surrounding a relatively shallow lagoon. The lagoon is approximately 20 km across, with highly erratic bathymetry and featuring flat areas of coral sand interspersed

with many coral heads or 'bommies'. This rough sea floor is not particularly conducive to longer-range higher frequency acoustic propagation due to its strongly scattering nature. Propagation modelling of low frequencies sounds, on the basis of topography and expected noise diffusion (Fig. S1) revealed that the lagoon environment supported detections of up to 30 km for vessels within the lagoon, and that detection of noise from outside the lagoon margin was extremely limited due to the shallow marginal bathymetry which acts as an effective barrier to propagation.

Numerically, cetaceans within Maldivian lagoons are dominated by spinner dolphins (*Stenella longirostris*, >90% of

individual cetaceans) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, c. 5% of individual cetaceans; Anderson, 2005). On this basis and in line with current understanding of dolphin habitat use around oceanic islands more broadly (Lammers, 2019), we expected the majority of the cetacean vocalizations to fall within the small cetacean (odontocete) range. We further limit our vocalization analysis to whistles, due to the complexities involved in analysing broadband vocalizations such as clicks (Gillespie *et al.*, 2013). Delphinid whistles were detected according to a set protocol: we used the fast-Fourier transform (FFT) settings for the delphinid whistle contour processing at a 64 Hz resolution and 66% overlap, that is 0.015 s of data, and an advance of 0.005 s. The FFT outputs were concatenated into 5-s long spectrograms that were then normalized using the median sound pressure level in each frequency bin over the 5 s. A normalized amplitude threshold value of 3 was used to detect time-frequency bins that could possibly contain whistles in the normalized spectrogram. Adjacent bins were then joined, and contours were created via a contour-following algorithm. To classify as a delphinid whistle detection, connected contours (normalized over the 65 s of recording) had to be within the range of 4000 to 20 000 Hz and have a duration between 0.3 and 3 s, as these are ranges under which the majority of small cetacean whistle falls (Gillespie *et al.*, 2013). They must also have had total bandwidth greater than 700 Hz but no single bin bandwidth in excess of 5000 Hz. Automatic whistle processing is an evolving field, and any classification protocol is a trade-off between minimizing false negatives and positives (Erbs *et al.*, 2017; Gillespie *et al.*, 2013). Here, our protocol was a trade-off between our primary objective of detecting delphinid presence and the ability of counting all whistles (of lesser priority). For example, our approach meant that constant frequency whistles may be missed. We deemed this acceptable, as in our experience constant frequency whistles are quite rare, and when they do occur, they are mixed with other whistles that do have bandwidth so delphinid presence is still detected. Every 65-s recording flagged as containing a positive whistle detection was manually confirmed to do so post hoc.

Environmental drivers

To examine environmental drivers of cetacean presence in Peros Banhos lagoon, wind direction and speed were both obtained via the R package, 'rWind', each with a resolution of 0.5 by 0.5 degrees latitude and longitude. Chl-a concentration values at two reference stations – west of Peros Banhos (5°28'S, 71°29'E) and east of Salomon (5°28'S, 72°28'E) were extracted using monthly composites of the 4-km Level 4 Global Ocean Chlorophyll (Copernicus-GlobColour) data, generated using E.U Copernicus Marine Service Information (<https://doi.org/10.48670/moi-00100>).

Nutrient cycling

To determine the role cetaceans play on nitrogen deposition in the atoll lagoon, we estimate the nitrogen excretion rate in the

lagoonal environment, on the basis of standard metabolic theory, diet and weight. We limited our analysis to spinner dolphins whose ubiquity and numerical dominance associated with coral atolls suggest a dominant role in nutrient dynamics, and they are known to feed in oceanic waters and rest in lagoons, so are likely sources of pelagic nutrient inputs. We used estimates of daily consumption employing standard metabolic models scaled for assimilation, activity and migratory fasting, following the recommendations of Roman and McCarthy (2010) and Barlow *et al.* (2008). All parameters and calculations are reported in Table 2. We employed average spinner body mass (*M*) for the region (Ilangakoon *et al.*, 2000; Perrin *et al.*, 2005) to calculate the basal metabolic rate (BMR), where $BMR = 293.1 M^{0.75}$. To calculate the field metabolic rate (FMR), we used 3 x BMR. The average daily ration (ADR) was calculated as FMR divided by $(0.8 [3900 Z + 5450 (1-Z)])$, where *Z* is the fraction of crustaceans in the diet, using values from Table 1 in Dolar *et al.* (2003), which yielded an ADR of 3.27 kg day⁻¹ (wet weight). Dolphin prey is typically 2.5% nitrogen, 80% of which is metabolized and therefore egested (Boyd, 1999, Table 2). In the absence of population estimates, we used the average pod size in each region from pod sightings with confirmed identifications, to estimate the order of magnitude of their influence on the nutrient cycle. We deemed this a highly conservative estimate for the absolute amount egested, since several pods may use each atoll each day. Spinner dolphin population abundance estimates for oceanic islands range between 135 (95% CI: 112–163, Moorea, French Polynesia, Oremus *et al.*, 2007) and 631 ± 60.1 [95% CI: 524–761, Hawaii Island 'Big Island' (Tyne *et al.*, 2014)], and it would be tempting to scale up our estimates directly to estimate nitrogen input for these regions. However, many of these populations rest in bays with very different geomorphological and ecological properties than the lagoons in the central Indian Ocean (Karczmarski *et al.*, 2005; Panicker *et al.*, 2022; Young *et al.*, 2017) meaning that the relationship between egested and deposited nitrogen is likely more complicated.

Results

Visual observations

Between 1990 and 2019, we sighted 1250 groups of cetaceans within atolls in the Maldives (*n* = 1212) and in proximity to atolls in the Chagos Archipelago (*n* = 38, Table 1). Spinner dolphins dominated the observations, constituting the most frequently sighted (*n* = 782, 75.5% of all sightings identified to species) and the most numerically abundant species (95.1% of all individuals identified to species by numbers) and were ubiquitous within all atolls in the region (Fig. 1a), consistent with previous records (Anderson, 2005). Estimated group sizes of spinner dolphins were larger in the Maldives (mean number of ind. ± sd, 54.2 ± 2.34) than in the Chagos Archipelago (32.6 ± 1.9). Sightings occurred throughout the year (Fig. 2) although the seasonality of whale-watching activities meant that sightings in the Maldives occurred predominantly in February, March, April, October and November.

Table 1 Cetaceans sightings associated with atoll lagoons in the central Indian Ocean (only sightings from inside the atolls are reported for the Maldives)

Common name	Scientific names	Maldives	Chagos Archipelago
		Number of sightings (and individuals)	Number of sightings (and individuals)
Spinner dolphin	<i>Stenella longirostris</i>	760 (34 175)	22 (652)
Indo-Pacific bottlenose dolphin	<i>Tursiops aduncus</i>	243 (1686)	1 (5)
Unid dolphin		201 (1533)	10 (94)
Risso's dolphin	<i>Grampus griseus</i>	4 (52)	
Pilot whale	<i>Globicephala macrorhynchus</i>		1 (5)
False killer whale	<i>Pseudorca crassidens</i>	1 (25)	
Humpback whale	<i>Megaptera novaeangliae</i>	1 (2)	2(4)
Blue whale	<i>Balaenoptera musculus</i>	2 (2)	
Balaenopteridae			1(1)
Mysticeti			1 (5)
Total		1212 (37 475)	38 (766)

Whistle detections

Automatic whistle detection inside the Peros Banhos lagoon resulted in 618 detections within the small cetacean frequency range (4000 to 20 000 Hz), with whistles exhibiting similar contours to those described by Bazua-Duran (2004) for spinner dolphins (*Stenella longirostris*, Fig. S2). Positive detections occurred on 70 out of 171 recording days (41%). We detected a clear and distinct diurnal pattern of activity, with detections commencing at sunrise (0600–0700), peaking at noon (1200–1300), and ending at sunset (1800–1900, Fig. 3a). Behaviour and direction of travel of spinner dolphin pods (Fig. 3b) show that the timings of vocalizations coincide with the presence of spinner dolphins inside the atolls, since the dolphins enter through reef channels in the morning and leave in the afternoon.

The acoustic observations, lasting from April to October (Fig. 4a), followed the monsoon transition period (March–April), during which the winds in the Chagos Archipelago reverse from predominantly north-westerly (November to March) to south-easterly (April to October). The transition was followed by a sharp rise in median wind intensity (from ~4 m/s to ~6 m/s, Fig. 4b) and by a chlorophyll-a bloom east of Salomon Atoll (Fig. 4c), coinciding with an almost total absence of delphinid detections in Peros Banhos Atoll for approximately 45 days.

Role in nutrient dynamics

We estimate that a single spinner dolphin will egest nitrogen at a rate of 0.0654 kg day⁻¹ and that a dolphin pod of average size will therefore egest nitrogen at an estimated rate of 1294 ± 56 and 778 ± 45 kg year⁻¹ in Maldives and the Chagos Archipelago, respectively (Table 2). On the basis of the timing of entry and exit (Fig. 3), we infer that the dolphins spend roughly 50% of the day inside the lagoons. Further, on the basis of a lack of detections during the period immediately after the monsoon reversal (45 days), we assume that the dolphins are absent from the Peros Banhos lagoon 26% of the time. We further consider that, for purposes of estimating

yearly lagoonal deposits rates, they do not deposit inside the lagoon during this time. We deem this a conservative estimate of total lagoonal deposits, since it is both possible and probable that the dolphins rest inside other atolls during this period (given their dependence on shelter for resting, Tyne *et al.*, 2015), with consequence for nutrient cycling in those lagoons. Assuming a constant egestion rate throughout the day (and that half the day is spent outside the lagoon), a pod of average size in the Chagos Archipelago would deposit 288 ± 17 kg year⁻¹ of nitrogen inside the Peros Banhos lagoon.

Discussion

Spinner dolphins are widely distributed in tropical waters and are often thought of as coral reef associates (Norris *et al.*, 1994). Consistent with this, our results confirm that these species is by far the most abundant cetacean within atoll reefs in the central Indian Ocean. Our observations further confirm that this species exhibits diurnal behaviour with pods spending the day-time inshore in sheltered atoll lagoons and moving offshore into oceanic waters during the night. On the basis of their foraging ecology (Norris *et al.*, 1994; Perrin *et al.*, 2008) and energetic requirements (Tyne *et al.*, 2015), this implies a mechanism by which pelagic productivity is made available to lagoonal ecosystems (up to about 12 kg year⁻¹ nitrogen per dolphin) and suggests a possible factor contributing to the prevalence of pelagic nutrients in the Maldivian atoll reef ecosystem (Skinner *et al.*, 2021).

The whistle detection data in the Peros Banhos lagoon are not, on their own, conclusive evidence that the dolphins there behave in the same way as in the Maldives. However, both the shape and contour of the whistles (Bazua-Duran, 2004), and the diurnal pattern in the detections are highly suggestive of spinner dolphins. Whilst we cannot discount the possibility that some of the acoustic detections stemmed from other delphinid species, we note that in the Maldives the only two delphinid species that occur regularly inside the atolls (>95% of observations; Anderson, 2005) are spinner dolphins and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). The latter occur inside

Table 2 Parameters and steps for estimating nutrient input by spinner dolphins (*Stenella longirostris*) in tropical lagoons

Parameters	Unit	equation	Value	Reference
Average body size (M)	kg	NA	40	(Ilangakoon <i>et al.</i> , 2000)
Basal metabolic rate (BMR)		$BMR = 293.1 M^{0.75}$	4661	(Barlow <i>et al.</i> , 2008)
Field metabolic rate (FMR)		3 x BMR	13 985	(Kjeld, 2003)
Proportion crustacean in diet (Z)	%	NA	7	(Dolar <i>et al.</i> , 2003)
Average daily ration (ADR)	kg day ⁻¹	$\frac{FMR}{(0.8 \cdot (300Z + 9450(1-Z)))}$	3.27	
Proportion nitrogen in prey	%		2.5	(Gaskin, 1982)
Proportion of ingested nitrogen metabolized (and thus egested,	%		80	(Boyd, 1999)
Daily nitrogen egested per dolphin	kg day ⁻¹	ADR * 0.8 * 0.025	0.0654	
Yearly nitrogen egested per dolphin	kg year ⁻¹		23.9	
Yearly nitrogen egested per pod in Maldives	kg year ⁻¹		1294 ± 56	
Yearly nitrogen egested per pod in Chagos Archipelago	kg year ⁻¹		778 ± 45 kg year ⁻¹	
Yearly nitrogen deposit per pod in Chagos Archipelago inside lagoon, accounting for seasonal absence	kg year ⁻¹		288 ± 17	

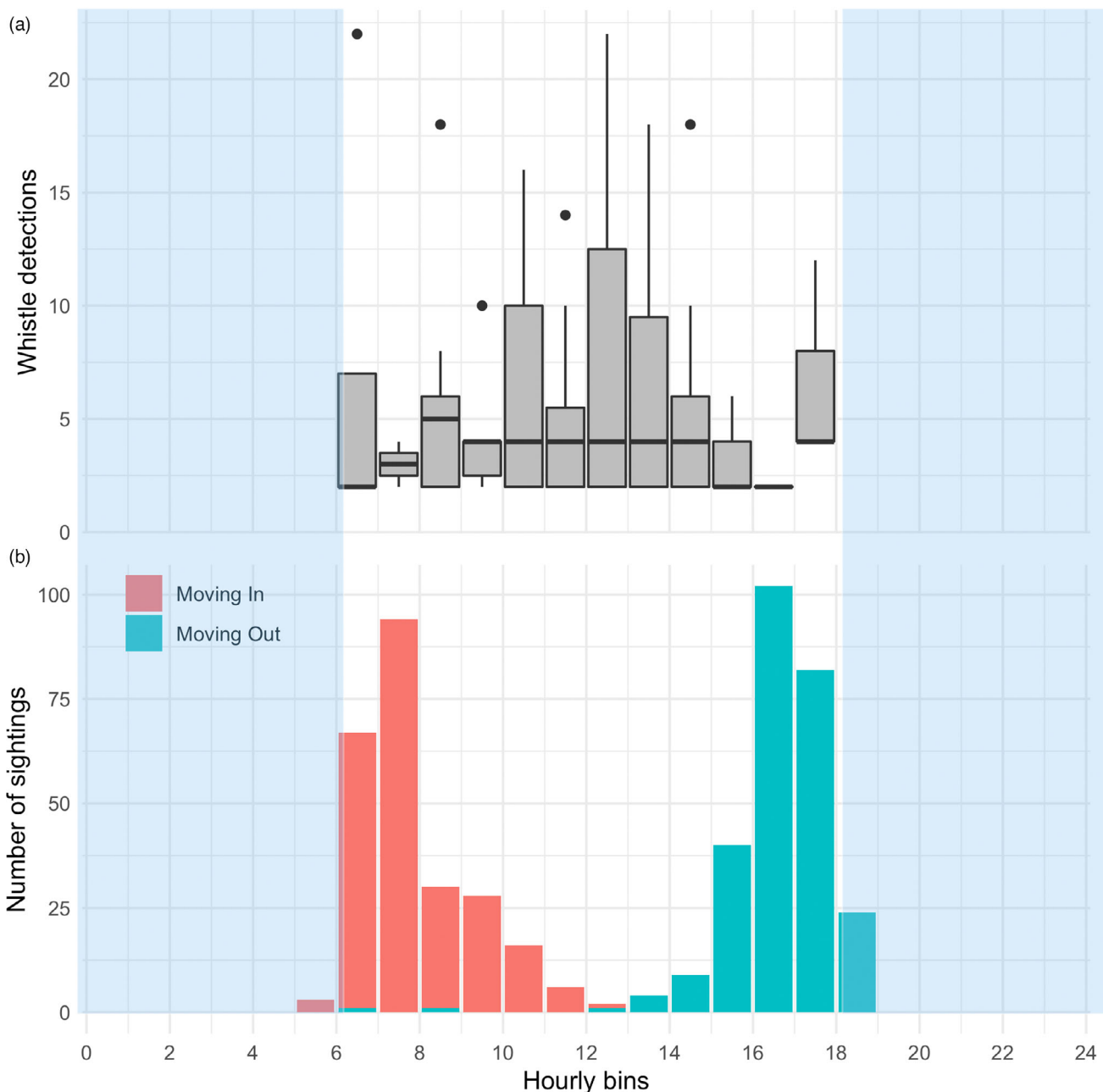


Figure 3 Delphinid whistle detection and spinner dolphin diurnal behaviour in central Indian Ocean atoll lagoons. (a) Delphinid whistle detections within Peros Banhos Atoll lagoon, Chagos Archipelago, showing number of detections per 25 min duty cycle, in hourly bins (median non-zero values, 25% and 75% quantiles). (b) Occurrence and direction of travel of spinner dolphin pods sighted in lagoon channels in the Maldives, by time of day (Moving in = 246, Moving out = 264, Unknown = 110, not shown). Direction of travel was not recorded for sightings in the Chagos Archipelago. Blue shaded areas highlight night hours.

the atolls during both during the daytime and night-time (Anderson, Sattar & Adam, 2012; R. C. Anderson pers. obs.) so we would expect some recordings during the night if this species were responsible for these vocalizations, in contrast with our observations.

Cetaceans have long been hypothesized to function as important nutrient vectors, for example acting as a potential biotic link

between high and low latitudes. In addition, the release of faeces at the surface after feeding at depth is posited to produce a net nutrient flux, creating an upward ‘whale pump’ (Roman *et al.*, 2014). The effectiveness of the pump is highly dependent upon the proportion of total prey consumed at depth, and the proportion of egested nutrients retained within the euphotic layer (Roman & McCarthy, 2010). These proportions are often hard

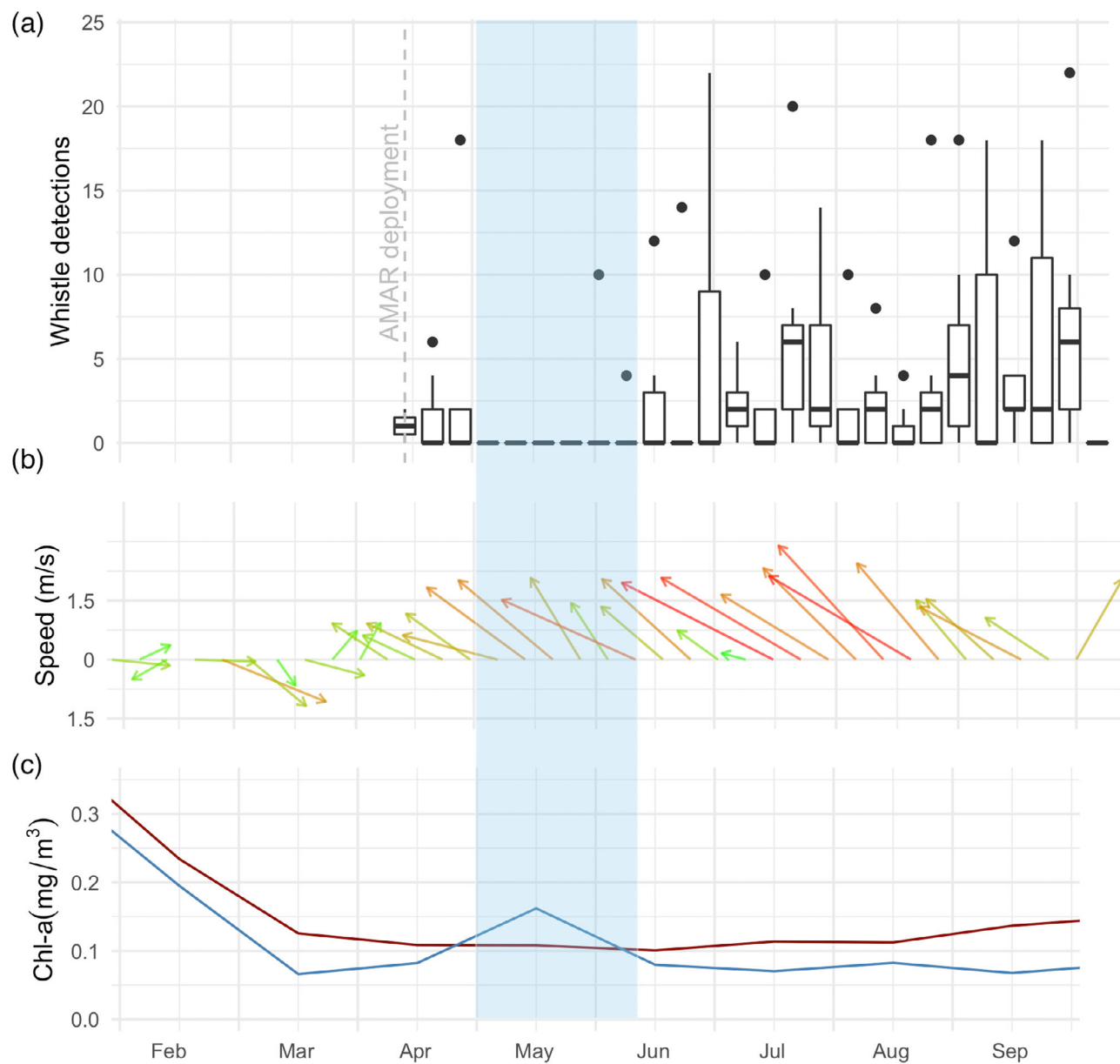


Figure 4 Medium-term delphinid residency and environmental variability within Peros Banhos. (a) Weekly delphinid whistle detections within the Peros Banhos lagoon, from 14th April (note dashed grey line showing start of AMAR deployment) to 1st October 2017 (daily maximum number of detections per 25 min cycle, yielding seven values per week). (b) Wind speed and direction with axes rescaled by a factor of 2 to prevent vector distortion, and (c) chl-*a* concentration at reference stations west of Peros Banhos Atoll (red, 5°28'S, 71°29'E) and east of Salomon Atoll (blue, 5°28'S, 72°28'E). Blue shaded area highlights period of apparent delphinid absence following the monsoon wind reversal (March–April), coinciding with increase in wind intensity and chlorophyll bloom east of Salomon Atoll.

to determine, even though estimates of prey consumption and nutrient egestion rates may be comparatively robust, making the ecological significance of the pump uncertain. Within the context of the atoll lagoon environment, the behaviour of the spinner dolphins is noteworthy in that they are deep diving (up to 400 m, although many dives will likely be shallower) foragers, typically feeding on vertically migrating mesopelagic fish such as *Myctophum* spp and *Diaphus* spp (Dolar *et al.*, 2003), from

outside the lagoons. Their foraging activity (Benoit-Bird & Au, 2009) is distinctly separated from time spent resting (Tyne, Johnston, *et al.*, 2016; Tyne, Loneragan, *et al.*, 2016), which is often spent in sheltered habitats (Tyne *et al.*, 2015), meaning that the proportion of prey of deep origin (and thus from outside the atoll lagoon) is high. The efficiency of this 'dolphin pump' is further strengthened by ecological and oceanographical properties of lagoonal environments which promote nutrient

retention. For example, due to their geomorphology, atoll lagoons are considered nutrient traps (Morell & Corredor, 1993) with high nutrient recycling through bacterial food webs (Falter *et al.*, 2004) or localized plankton productivity (Skinner *et al.*, 2021). Several reef fish species have been observed to associate with spinner dolphins to opportunistically feed on their waste (Sazima *et al.*, 2006), thus potentially ensuring tight trophic coupling.

Recent estimates of pelagic nitrogen input from wildlife taxa into undisturbed coral reef ecosystems include $190 \text{ kg ha}^{-1} \text{ year}^{-1}$ for seabird colonies on islands (Graham *et al.*, 2018), and 94.5 kg day^{-1} for reef shark populations (in Palmyra, Williams *et al.*, 2018). Our estimate of lagoonal deposition for a pod ($288 \pm 17 \text{ kg year}^{-1}$) is therefore of an order of magnitude less than the nutrient input from a seabird colony on a small island [e.g. Middle Brother, $1520 \text{ kg year}^{-1}$ (Graham *et al.*, 2018)]. Such amounts of nitrogen have been shown to significantly impact the functioning and productivity of adjacent coral reef and fish communities, as well as their recovery following mass bleaching events (Benkwitt *et al.*, 2019), so are likely ecologically important. The period following the monsoon reversal in the Chagos Archipelago is noteworthy for the total absence of whistle detections, and a pronounced productivity peak east of the atolls. In the Maldives, under the influence of the seasonally reversing monsoon currents, plankton blooms occur on the seasonally alternating downstream of the atoll chain, with reverberations for higher trophic levels such as manta rays, which forage on these prey blooms (Anderson *et al.*, 2011; Harris *et al.*, 2020). Although little is known of prey-field variability beyond what is known concerning the influence of static features like atolls and seamounts (Letessier *et al.*, 2016, 2021), the magnitude and duration of prey blooms associated with the monsoon reversal in the Chagos Archipelago may be less pronounced than in the Maldives (Anderson, Branch, *et al.*, 2012). In order to take advantage of prey availability in the short-to-medium-term stemming from such productivity patchiness, we would expect spinner dolphin foraging strategies to be dynamic in space and time. We speculate that the absence of whistles may reflect a temporary relocation of the spinner dolphins in order to access more productive areas, such as Salomon Atoll (Rayner & Drew, 1984). Alternatively, the Salomon lagoon is both further enclosed and smaller in size than Peros Banhos, and may therefore offer superior shelter to that of the Peros Banhos lagoon in particular circumstances, for example during periods of adverse weather or under specific wind directions. If this were the case, we would expect relocations to occur primarily in response to weather patterns, and not in response to productivity dynamics, since the dolphins were relocating to seek shelter rather than to improve foraging success. Paired prey-field and dolphin observations that capture both seasonal and interannual processes, such as the Indian Ocean Dipole (Perez Correa *et al.*, 2020), will be required in order to better understand the prevalence and implications of such variability.

The Chagos Archipelago has been identified by the International Union for the Conservation of Nature's Marine Mammal Protected Area Task Force (MMPATF) as an 'Area of Interest', which requires 'enhanced effort for monitoring species of

marine mammals'. Our acoustic recordings have provided novel information given that previous cetacean detections – from deep (~1000 m) hydrophones sampling ~250 Hz installed near Diego Garcia as part of the International Monitoring System (IMS, Stafford *et al.*, 2010) – were from baleen whales outside the atolls.

Recent years have seen increased use of 'patrol-based' monitoring (Dobson *et al.*, 2020), whereby law enforcement activities are harnessed for conservation monitoring, in order to gain scientific insights into illegal activities and wildlife trends. Most examples so far have been terrestrial but marine surveillance technology and patrolling activities have considerable potential, as demonstrated here, and can be particularly valuable in remote and hard-to-survey locations (Hays *et al.*, 2020).

Atoll reefs in the central Indian Ocean are notable for a reliance on pelagic production sources (Graham *et al.*, 2018; Skinner *et al.*, 2019), compared with reefs elsewhere, where benthic productivity may be more important (Hilting *et al.*, 2013). We have hypothesized spinner dolphins as a possible nutrient vector acting by way of their daily commute between offshore foraging grounds and within-atoll resting sites. Our inferences are consistent with observations of elevated pelagic production uptake in lagoonal fish predators in the Maldives (65–88% of production of pelagic origin, Skinner *et al.*, 2019) and adds to a fledgling body of knowledge on cetaceans within the Chagos Archipelago. However, their role in coupling mesopelagic with coral reef systems, and in tropical nutrient cycles, remains speculative and poorly understood.

Spinner dolphins have been considered the most abundant cetacean species in the tropical Indian Ocean (Ballance & Pitman, 1998). They are highly dependent on shelter for resting (Tyne *et al.*, 2015) and exhibit strong partitioning of specific behaviours to particular times of day (Tyne, Johnston, *et al.*, 2016; Tyne, Loneragan, *et al.*, 2016), meaning that they are likely very sensitive to human disturbance. Policies such as a gillnet ban in the Maldives and no-take protection in the Chagos MPA ensure that bycatch levels are low and that spinner dolphins remain common in these regions. Elsewhere, however, spinner dolphins are experiencing what is probably unsustainable mortality through bycatch (Anderson *et al.*, 2020). This, coupled with increased human activities in sheltered bays and atoll lagoons in some areas (Tyne, Johnston, *et al.*, 2016; Tyne, Loneragan, *et al.*, 2016), is likely to compromise their ecological role, warranting monitoring and conservation activities. Further research aiming to establish the role of spinner dolphins in coral reef ecosystems should combine more detailed data on their distribution with that of their likely prey (Letessier *et al.*, 2016), together with functional indicators such as coral growth and fish biomass (Graham *et al.*, 2018). We are to this end expanding our patrol-based observations and acoustic monitoring activities to achieve greater coverage and robust population estimates.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Predicted signal detection range for vocalisation in the small cetacean range by the AMAR in the Peros Banhos lagoon from propagation loss modelling.

Figure S2. Spinner dolphin detections in the Chagos Archipelago. Spectrogram of whistles detected in the Peros Banhos atoll [(a-c) dated the 28th Sept 2017, and (d) dated the 14th June 2017]. Photo of bow riding spinner dolphins in the Peros Banhos lagoon in 2017 [(e) Credit Ronan Roche].