








RESEARCH ARTICLE

Reverse diel vertical movements of oceanic manta rays off the northern coast of Peru and implications for conservation

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Abstract

1. An understanding of the vertical movements of elasmobranchs across their range is crucial to defining critical habitat use, its overlap with anthropogenic activities and subsequently managing such interactions.
2. In this study, satellite telemetry was used to investigate the vertical habitat use of three oceanic manta rays (*Mobula birostris*) tagged on the northern coast of Peru.
3. All three oceanic mantas exhibited patterns of reverse diel vertical migration, where vertical movements were significantly deeper at night than the day, as well as an overall preference for surface habitats (< 2 m). High-resolution archival data (3–5 s) from two recovered tags revealed fine-scale behaviours, where individuals predominately remained in coastal surface waters throughout the day, and oscillated up and down through a highly stratified water column at night.
4. Our results suggest that coastal vertical movements were motivated by a combined foraging and thermal recovery strategy, whereby oceanic mantas dived to forage on vertically migrating zooplankton at night and returned to surface waters to rewarm between dives, indicating that the coast of northern Peru may be a foraging habitat for these animals.
5. High use of surface waters here, however, may put oceanic mantas at high risk from several anthropogenic impacts such as entanglement with fishing gear and vessel strikes.
6. Increased sample size and the use of other techniques, such as animal-borne cameras and tri-axial sensors, are required to validate our foraging and thermal recovery hypothesis and confirm this region as a foraging habitat for oceanic mantas.

KEYWORDS

Biologging, Diving behaviour, *Mobula birostris*, Mobulidae, Movement ecology, Peru

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1 | INTRODUCTION

Advances in the affordability and sophistication of electronic tags now allow researchers to routinely document the horizontal and vertical movements of elasmobranchs (Andrzejaczek et al., 2019; Block et al., 2011; Hammerschlag et al., 2011; Stewart et al., 2018). Knowledge of these movements in both dimensions is key to understanding the ecology of these animals in a changing ocean and to improving our ability to understand and manage the interactions of elasmobranchs with anthropogenic activities (Andrzejaczek et al., 2019; Queiroz et al., 2019; White et al., 2019). For example, taxa that spend considerable time in surface waters, such as basking sharks (*Cetorhinus maximus*) and whale sharks (*Rhincodon typus*), are at greater risk of ship strikes (Lester et al., 2020; Pirotta et al., 2019). Limiting shipping activities in important migratory corridors for these species is therefore likely to benefit in conservation efforts for their populations (Pirotta et al., 2019). Similarly, knowledge of vertical movement patterns enables prediction of the susceptibility of elasmobranchs to different fishing gears that vary in their target depths (e.g. Coelho et al., 2015). Furthermore, a holistic understanding of animal movement requires that we need to not only record patterns of movement, but that we also investigate the underlying abiotic and biotic factors that structure them (Nathan et al., 2008).

Studies investigating the movement ecology of the oceanic manta ray (*Mobula birostris*) are currently limited in comparison to those of the closely related reef manta ray (*Mobula alfredi*) (Stewart et al., 2016; Stewart et al., 2018). This is likely due to the relatively sparse distribution of oceanic mantas in offshore habitats which can be difficult to access (Armstrong et al., 2020; Kashiwagi et al., 2011). Given that oceanic mantas have extremely conservative life histories, they face threats such as direct and indirect fishing pressure and are listed as 'Endangered' on the IUCN Red List of Threatened Species (Croll et al., 2016; Marshall et al., 2020), it is vital that we obtain a greater understanding of their movement ecology in order to implement effective conservation strategies. Oceanic manta rays are presumed to be highly migratory due to their large size, pelagic distribution and the lack of population structure found across ocean basins (Hosegood et al., 2020), suggesting that management of populations should take place at an ocean basin scale with international cooperation. In contrast, a recent study on oceanic mantas using satellite telemetry in both Indonesia and Mexico ($n = 18$) revealed restricted patterns of movements and a high degree of residency; suggesting that management strategies would benefit from taking a more local or regional approach (Stewart, Beale et al., 2016). In either scenario, the movement ecology of oceanic mantas needs to be considered and explored at local-regional scales to define critical habitat use and its overlap with human impacts, and subsequently manage such interactions to reduce overall risk to the species.

In the south-east Pacific Ocean, one of the largest recorded oceanic manta ray populations occurs in the productive coastal waters along the border of northern Peru and Ecuador (Hearn et al., 2014). Here, tracking data from nine satellite tags deployed in 2010 and 2011 revealed regional connectivity among the aggregations identified at Isla de la Plata in Ecuador, and oceanic mantas occurring in northern

Peru. The majority of the tagged mantas travelled south from the tagging location at Isla de la Plata to the waters off the coast of northern Peru (a straight-line distance of approximately 250 km), and some tracks ended prematurely in the region where it is thought that at least one individual may have been caught, killed and brought onshore by artisanal fishers in Peru (Hearn et al., 2014). Fortunately, oceanic mantas have since been protected in Peruvian waters following pressure from civil society in Peru, with bans on capture, landing, processing and/or trade of this species in place from 2016 (Ministerial Resolution N° 441-2015-PRODUCE, 2015). Other mobulid rays, however, continue to be targeted by fishers, and, given potential overlaps in vertical and horizontal distributions, oceanic mantas are likely to continue to be caught as bycatch. Indeed, there have been several reports of oceanic mantas being accidentally caught or entangled in fishing gear both before and after the protective legislature was established (Alfaro-Cordova et al., 2017; J. Avila et al., 2012; unpublished data), including descriptions of a dying, pregnant female being brought onshore due to difficulties of disentangling the 6.2-m individual out at sea (Alfaro-Cordova et al., 2017; Alfaro-Shigueto et al., 2012; Cabanillas-Torpoco et al., 2019). There have also been reports of fishers in Peru actively avoiding catching this species due to the large size of individuals increasing their capacity to damage fishing gear, and the substantial effort required to disentangle captured individuals (Ayala et al., 2009). In addition to risk of capture, oceanic mantas in coastal habitats are also threatened by ship strike, collision with other nearshore infrastructure, habitat degradation, pollution, and irresponsible tourism practices (Marshall et al., 2018). Our ability to assess the risk of these threats to the species in northern Peru, however, is challenged by the limited understanding of habitat use of oceanic mantas here.

In this study, we used pop-up satellite archival tags (PSATs) to investigate the vertical habitat use of three oceanic manta rays tagged in the Tumbes region of the northern coast of Peru. Two of these tags were recovered, providing fine-scale data (3–5 s sampling rates) that enabled a detailed examination of the diel vertical movement (DVM) patterns displayed by those individuals. We discuss the likely drivers of the vertical movement patterns, the potential for overlap with anthropogenic activities and the conservation and management implications of our results. Finally, we highlight future directions for continuing work in this region.

2 | MATERIALS AND METHODS

2.1 | Study site and tag deployments

PSAT tags (MiniPAT 348F-00; Wildlife Computers Inc., WA, USA) were deployed on oceanic manta rays (*Mobula birostris*) in May ($n = 1$) and July ($n = 4$) 2018 off the Tumbes region of the northern coast of Peru (Figure 1). Mantas were visually located at the surface by boat-based searches carried out together with local fishermen and externally tagged by free-divers. All tags were leadered according to Wilson et al. (2015). Briefly, leaders consisted of a ~15–17 cm length of 180 kg

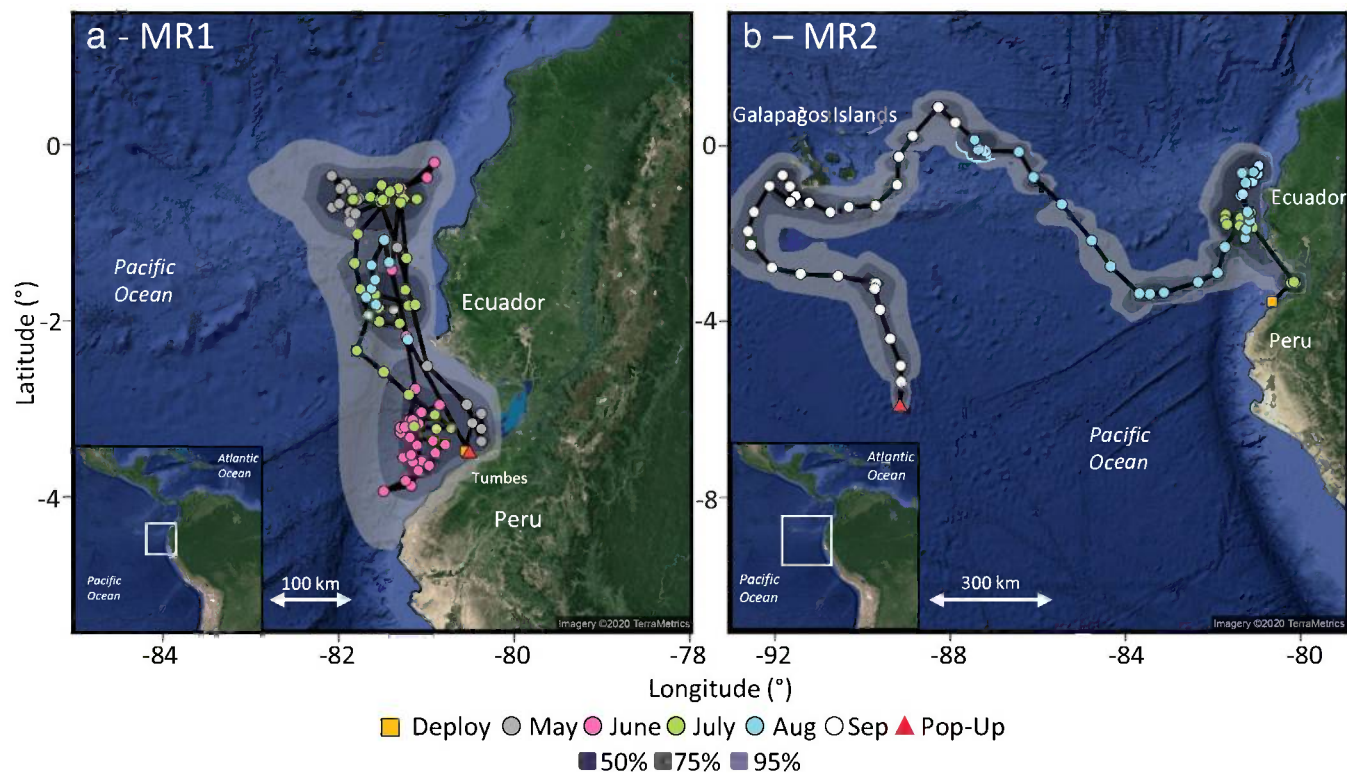


FIGURE 1 Horizontal tracking information from two oceanic manta rays tagged with pop-up satellite tags in the Tumbes region of Peru in 2018. Circles are daily estimates of location derived from transmitted light, depth and temperature data in GPE3 and are coloured by month and deployment and pop-up locations. Inset map indicates location of study region. Polygons represent the merged probability density surfaces for each MiniPAT, with light to dark shades representing 95%, 75% and 50% probability contours. Maps were plotted using ‘ggmap’ in R. Note that the horizontal scale differs between (a) and (b). The most-probable tracks for MR3 can be found in Supplementary Figure 1

monofilament (Moimoi, X Hard) covered with one layer of Aramide and shrink wrap and were attached to the manta via a custom-built titanium dart. Mantas were tagged by a swimmer with a pole in hand, and tags were placed into the dorsal musculature, off the midline of the posterior dorsal surface of each manta ray. PSATs were programmed to sample ambient light levels, ambient temperatures and pressure at 3–5 s intervals and to detach after 90 (May) or 180 (July) days (Table 1). Depth and temperature time series were transmitted at 5-min intervals, and recovery of two tags through collaboration with local community members allowed for the whole archival datasets to be downloaded.

All procedures were approved by the Stanford University Administrative Panel on Laboratory Animal Care (APLAC) under permit APLAC-10765.

2.2 | Track reconstruction

Most-probable tracks were estimated using the tag manufacturer’s proprietary software that utilizes a hidden Markov model (Pedersen et al., 2011; WC-GPE3, Wildlife Computers). This approach considered transmitted light level, temperature and depth data alongside sea surface temperature (SST; NOAA OI SST V2 High Resolution) and

bathymetric constraints (ETOPO1-Bedrock), and calculated a posterior probability distribution that estimated the most likely position of the individual at every time point of the track (Skomal et al., 2017). As we could find no published records of oceanic manta ray speed, the diffusion parameter (i.e. allowable distance moved per day) was set in turn to 1.5, 2 and 3 m s^{-1} for each manta. Resulting outputs from the two longest deployments (MR1 and MR2; >70 days) displayed a similar track for each diffusion parameter, and 3 m s^{-1} was selected as the most likely filter following comparison of GPE3 quality scores (Curnick et al., 2020). For the shorter deployment ($n = 11$ days), resulting tracks varied significantly and were therefore all plotted (Supplementary Figure 1). 50%, 75% and 95% probability density surfaces were also calculated for each individual by averaging the 12-h probability density surfaces generated by GPE3 and resampling the 0.25° GPE3 grid at a resolution of 0.0125° with bilinear interpolation using the packages ‘ncdf’ and ‘raster’ in R. The resulting tracks and probability density surfaces were subsequently plotted using ‘ggmap’ and ‘ggplot2’ in R.

2.3 | Processing depth and temperature data

Igor Pro ver. 8.0.3.3 (Wavemetrics, Inc. Lake Oswego, USA) and the R Statistical Environment (R Core Team 2020) were used for

TABLE 1 Summary details from PSAT deployments on oceanic manta rays *Mobula birostris* in Peru

MRID	MR1 ^a	MR2	MR3 ^a	MR4 ^b	MR5 ^b
TOPPID	5218001	5218005	5218007	5218006	5218008
Tag Code	17P0599	17P0607	17P0549	17P0664	17P0546
Date deployed	9-May-2018	18-Jul-2018	19-Jul-2018	18-Jul-2018	20-Jul-2018
Sex	Unknown	Male	Unknown	Male	Unknown
Deploy latitude (°)	-3.48	-3.56	-3.54	-3.55	-3.61
Deploy longitude (°)	-80.56	-80.65	-80.63	-80.62	-80.66
Date pop-up	8-Aug-2018	29-Sep-2018	29-Jul-2018	-	-
Pop-up latitude (°)	-3.51	-5.94	-3.90	-	-
Pop-up longitude (°)	-80.51	-89.15	-80.87	-	-
Track duration (days)	92 ^c	72	11	-	-
Sampling frequency of pressure data (s)	3	300	5	-	-
Mean depth ± SD (m)	5.2 ± 7.9	11.1 ± 23.3	8.9 ± 12.3	-	-
Median depth (IQR) (m)	1.8 (2.8)	4 (13.5)	1.8 (12.7)	-	-
Maximum depth (m)	82.7	648	61.1	-	-
Mean temperature ± SD (°C)	25.0 ± 1.8	21.8 ± 2.0	22.5 ± 1.6	-	-
Temperature range (°C)	17.1–27.6	6.8–25.1	17.2–24.6	-	-
Average SST (°C)	25.8 ± 0.5	22.5 ± 1.6	23.4 ± 0.3	-	-
TΔ – surface and 10–15 (°C)	2.6 ± 0.9	NA	1.4 ± 0.5	-	-
Mean VV (± SD) (m s ⁻¹)	0.37 ± 0.28	NA	0.19 ± 0.16	-	-
Diving ratio (± SD) (%)	12.4 ± 4.0	NA	25.1 ± 9.5	-	-

MRID: manta ray individual. Mean vertical velocity (VV) excludes periods where mantas are level swimming.

^aTag recovered and archived dataset downloaded.

^bTag did not report.

^cSignificant pressure sensor drift following the 3 June 2018 on MR1.

processing, analysing and plotting pressure and ambient temperature data. Data were first trimmed to the attachment period, with detachment from an individual identified by the depth time-series recording a constant near-zero depth for >12 h, shortly followed by the initiation of Argos data transmissions. For one deployment, where significant drift in the depth sensor was observed (MR1), the depth and temperature time series were cut short, with depth sensor drift validated by a lack of equivalent change in the temperature record (Supplementary Figure 2). For another deployment, where the manta moved offshore (MR2), maximum daily depth and most-probable positions were used to split the depth time series into 'inshore' and 'offshore' phases. Daily mean SST was calculated as the mean temperature encountered by the tagged individual in the uppermost 5 m of the water column each day (Andrzejaczek et al., 2018; Brewster et al., 2020). Due to the water column being highly stratified throughout the deployment period (i.e. > 0.5°C difference between 5 and 10 m depth), mixed layer and thermocline depths could not be discerned.

For recovered data, vertical velocity (VV) was calculated by taking the difference of depth between successive points and dividing by the sampling frequency (3 or 5 s) to obtain an estimate in m s⁻¹. VV was then used to split the depth record into vertical swimming phases

('ascending', 'descending' and 'level swimming'). Ascents and descents were defined where VV exceeded an absolute value of 0.05 m s⁻¹ for more than 10 s, and level where this value was not exceeded (Whitney et al., 2016). The proportion of time spent moving vertically (ascending and descending), termed the 'diving ratio', was also calculated for each day, as well as each diel period within each day, by determining the percentage of time spent vertically moving within the respective period (Andrzejaczek et al., 2018).

2.4 | Data analysis

The R package 'suncalc' was used to determine times of sunrise and sunset (Thieurmel & Elmarhraoui, 2019), and subsequently split the data into diel phases. Daily lunar illumination data were also obtained using the 'suncalc' package. A paired Student's *t*-test was used to compare mean day- and night-time depths and diving ratios for each individual (following tests for normality). This test was also applied separately to the 'inshore' and 'offshore' phases of the track for MR2. Linear least-squares regression was used to assess the relationship between mean nightly depth and daily lunar illumination for one individual where time-series data exceeded 1 month (MR2).

3 | RESULTS

3.1 | Deployment summary

Five PSAT tags were deployed on free-swimming oceanic manta rays in northern Peru in 2018 and together collected 175 days of data (Table 1). Three tags remained attached to the mantas for 92 (MR1), 72 (MR2) and 11 (MR3) days. The longest manta track was a 3-month deployment that remained attached as programmed (MR1). This tag was recovered from a beach ~7 km SE of the tagging location allowing the entire archived dataset to be downloaded (Figure 1(a)). However, this tag experienced significant depth sensor drift resulting in only 25 days of usable pressure data (Table 1; Supplementary Figure 2). Two tags, deployed in July, recorded 72 (MR2) and 11 (MR3) days of data successfully but both released prematurely. Pop-up locations for these two tags were ~1000 km ESE offshore (MR2; Figure 1(b)), and ~50 km SW (MR3; Supplementary Figure 1) from the deployment location, respectively, with the tag from MR3 also being recovered. Two tags did not report (MR4 and MR5; Table 1).

Vertical habitat use was heavily skewed to the surface 2 m for all three mantas, with a median depth over the whole track of less than 5 m recorded by each individual (Table 1; Figure 2). MR1 and MR3 did not exceed maximum depths of 85 m, while MR2 spent 0.65% of its time at depths >100 m, reaching a maximum depth of 648 m (Table 1). A reduction in daily mean SST between the May and July tag deployments was also accompanied by a decrease in mean daily temperature encountered by tagged mantas. MR1 recorded an average SST of $25.8 \pm 0.5^\circ\text{C}$ and mean temperature of $25.0 \pm 1.8^\circ\text{C}$, while MR2 and MR3 recorded average SSTs of $22.5 \pm 1.6^\circ\text{C}$ and $23.4 \pm 0.3^\circ\text{C}$ and mean temperatures of $21.8 \pm 2.0^\circ\text{C}$ and $22.5 \pm 1.6^\circ\text{C}$, respectively (Table 1, Supplementary Figure 3). The water column was highly stratified in the archival datasets retrieved from MR1 and MR3, with the mean difference between surface waters and depths of 10–15 m exceeding 1°C for both individuals, and temperature differentials of up to 10°C for single dives recorded (Figure 3).

3.2 | Regional movement

MR1 and MR3 appeared to remain on, or close to, the continental shelf for the duration of the tag deployments (Figure 1(a); Supplementary Figure 1). The most-probable track and probability surface indicated that MR1 moved north along the coast of Ecuador following tagging, moving back and forth between the Tumbes aggregation site and the coast of Ecuador several times (Figure 1(a)). Track model outputs for MR3 differed significantly between diffusion parameters (maximum allowable daily speed) input to GPE3; however, all show the manta remaining predominately coastal, and moving from the coastal waters of Peru to Ecuador (Supplementary Figure 1). Both tags popped off and were recovered within 50 km of the tagging location.

MR2 underwent larger scale movements (>500 km) moving north following tagging in mid-July, spending approximately 1 month on the continental shelf off southern Ecuador (Figure 1(b)). After this point,

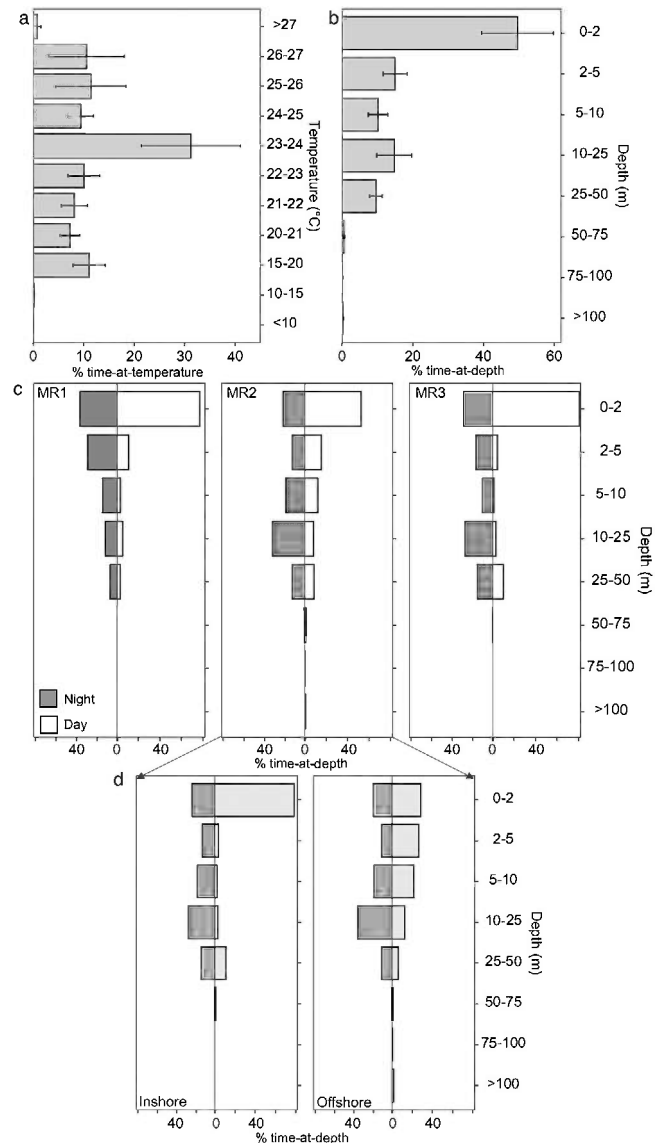


FIGURE 2 Summarized time-series data from PSATs deployed on three oceanic manta rays *Mobula birostris*. (a) and (b) Time-at-temperature and time-at depth for all individuals combined. Error bars represent standard error. (c) Time-at-depth for each individual manta ray. (d) Diel time-at-depth at inshore and offshore phases for MR2

the most-probable track indicated that MR2 headed in a general west-erly direction, making frequent deep dives >200 m in depth, until reaching the Galapagos Islands in early September (approximately 1300 km WNW of the tagging site) and subsequently heading south to where the tag pop-up transmission occurred (approximately 530 km SSE of the Galapagos Islands). Transmitted depth data recorded regular movements between the surface and >50 m depth until the 26th of September, indicating the tag was still attached to the active individual until at least this point (e.g. Supplementary Figure 4E). Deep dives recorded by the transmitted time series were brief (<1 h), with a maximum depth of 648 m reached during a 50-min V-shaped dive that took place just after moving off the continental shelf. Despite such deep movements, MR2 maintained a predominately shallow

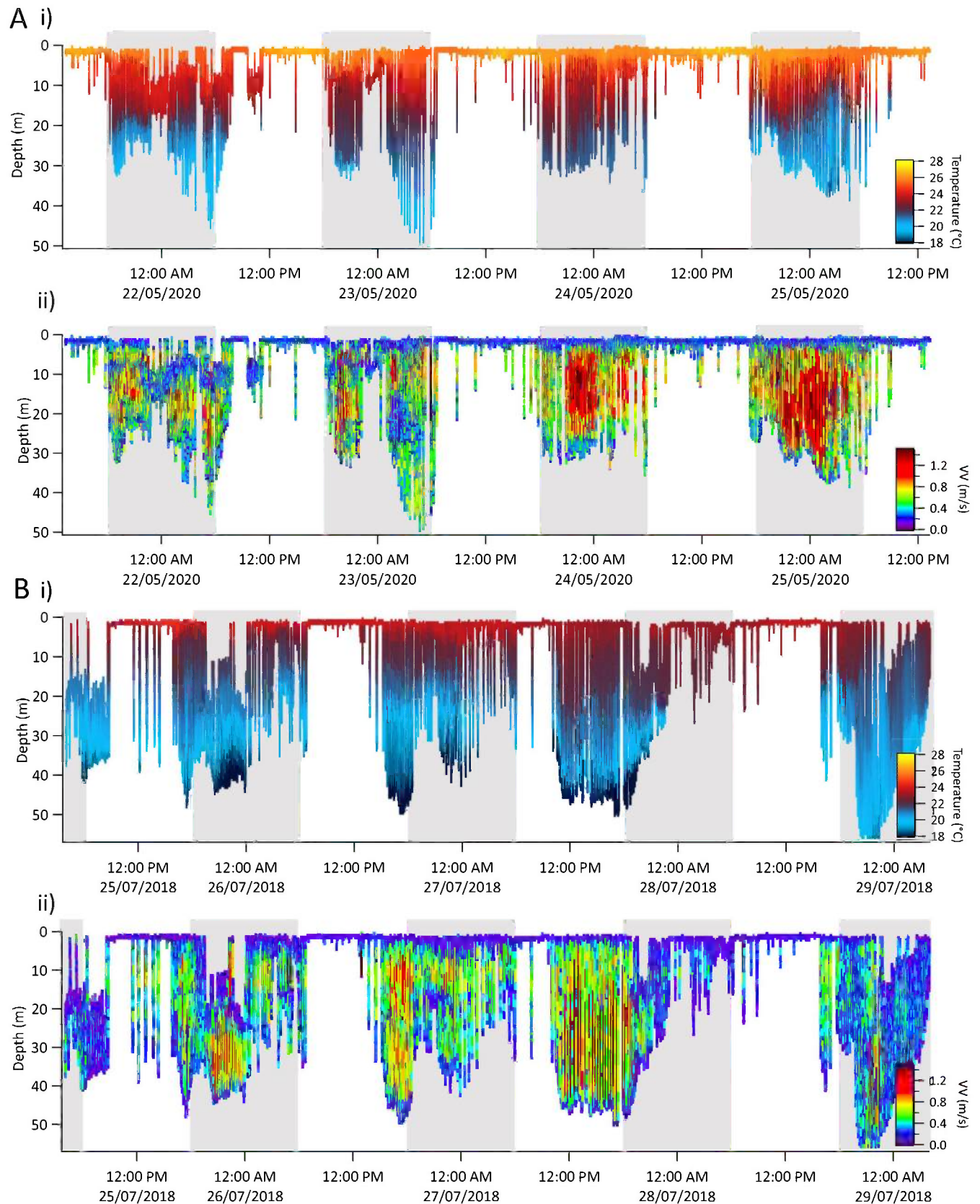


FIGURE 3 Representative archival time-series data from two oceanic manta rays: (a) MR1 and (b) MR3. Plots display diving behaviour and are coded to visualize (i) temperature ($^{\circ}\text{C}$) with depth and (ii) VV (m s^{-1}) with depth. Background shading indicates day (white) and night (grey) periods

TABLE 2 Statistical results for vertical movements from three MiniPAT-tagged oceanic manta rays *Mobula birostris*. Student's *t*-tests compare mean depths (mean \pm SD) and mean diving ratio between day and night. Tests were also performed separately for the inshore and offshore phases of MR2. Diving ratio could not be calculated for MR2 due to lower sampling resolution. * $p < 0.05$

MRID	Depth (m)		t-test for equality of means			Diving ratio (%)		t-test for equality of means		
	Day	Night	df	t	p	Day	Night	df	t	p
MR1	3.5 \pm 6.4	6.7 \pm 8.7	26	-4.6	<0.001*	6.8 \pm 4.8	17.5 \pm 6.0	26	-7.8	<0.001*
MR3	5.6 \pm 11.5	11.7 \pm 12.0	10	-3.4	0.007*	13.7 \pm 8.3	35.7 \pm 10.6	10	-8.4	<0.001*
MR2	9.7 \pm 29.4	12.9 \pm 16.5	54	-2.1	0.04*	Not applicable				
Inshore	6.2 \pm 12.9	12.0 \pm 12.0	26	-4.4	<0.001*	Not applicable				
Offshore	12.9 \pm 38.8	13.7 \pm 19.8	27	-0.2	0.85	Not applicable				

distribution, spending 98% of the time in the top 50 m. In addition, nighttime depth exhibited a weak, but significant, relationship with fraction of the moon illuminated, with deeper depths found during higher lunar illumination ($b = 5.8, r^2 = 0.07, p = 0.03$).

3.3 | Diel vertical movements

All three tagged mantas displayed patterns of reverse DVM, exhibiting significantly deeper movements at night than during the day (Table 2; Figure 2). Differences in diel depth distribution were particularly evident in the surface 2 m, where each individual spent >50% of time during the day, more than double the time spent here at night (Figure 2).

MR2 spent the least amount of time in these surface waters, with a notable reduction in overall percentage of time in the top 2 m from 49% to 32% after moving offshore (Figure 2(d)). After moving offshore, diel differences in mean depth were no longer significant (Table 2). Inshore vertical movements matched those of MR1 and MR3 (Figure 3; Supplementary Figure 4A), while offshore vertical movements displayed high daily variation (Supplementary Figure 4B–4E). This included periods with high surface use and single deep dives (Supplementary Figure 4B), continuous oscillatory dives in the top 50 m (Supplementary Figure 4C), deeper dives during the day (Supplementary Figure 4D) and deeper dives at night (Supplementary Figure 4E).

Recovered PSAT tags from MR1 and MR3 provided archival records that sampled depth and temperature at 3- at 5-s frequencies, respectively, revealing fine-scale reverse DVM and oscillatory behaviours throughout the deployment records for these individuals (Figures 3 and 4; Supplementary Figure 1). Throughout the day, these individuals primarily kept to surface waters (<5 m) with limited vertical movements, while at night, they continuously oscillated up and down through the water column (Figure 3). The amount of time spent moving vertically was significantly greater at night, increasing from 6.8 \pm 4.8% during the day to 17.5 \pm 6.0% at night for MR1 and 13.7 \pm 8.3% to 35.7 \pm 10.6% for MR3 (Table 2). Oscillations were predominantly U-shaped, with the bottom phase often consisting of small-scale bounces <5 m in depth, and dives interspersed with periods of surface swimming (depths <5 m; Figure 4). Small-scale bounce dives were also recorded during surface swimming periods (Figure 4). Mean absolute

VV (excluding periods of level swimming) was 0.37 \pm 0.28 m s⁻¹ and 0.19 \pm 0.16 m s⁻¹ for MR1 and MR3, respectively, peaking during periods of continuous oscillatory swimming and reaching a maximum of 3.5 ms⁻¹ for MR1 and 2.4 ms⁻¹ for MR3. The maximum dive time for prolonged excursions below 10 m was 180 and 134 min for MR1 and MR3, respectively.

4 | DISCUSSION

4.1 | Vertical movements and foraging in oceanic manta rays

Electronic tracking of three oceanic manta rays located in an aggregation site off the coast of northern Peru revealed common patterns of reverse DVM, where vertical distributions are significantly deeper during the night than the day. Data from two recovered tags revealed fine-scale movements, where individuals predominately remained in surface waters (<2 m) throughout the day and oscillated up and down through a highly stratified water column at night. Data from the third tag revealed patterns of reverse DVM inshore, and more variable patterns as the individual moved offshore.

Collectively, our results suggest that coastal vertical movements were motivated by a combined foraging and thermal recovery strategy, whereby oceanic mantas dove to forage on vertically migrating zooplankton at night and returned to surface waters to rewarm between dives. This could either be through moving offshore to shelf-edge habitats at night to forage on mesopelagic sources of zooplankton, as suggested by Burgess (2017) at Isla de la Plata, or alternatively, foraging on demersal zooplankton that emerge from the benthos at night in shallow coastal habitats (Allredge & King 1980). Dives were U-shaped with small-scale (<5 m) bounce dives occurring throughout the bottom phase, potentially consistent with a feeding strategy whereby mantas barrel-roll through dense patches of zooplankton (Stewart et al., 2016), lending support to the former hypothesis of mesopelagic foraging. However, given animal position uncertainty in regard to proximity with bathymetric features, we cannot confirm whether night-time feeding targets demersal or mesopelagic plankton communities. In either scenario, foraging at these depths exposes

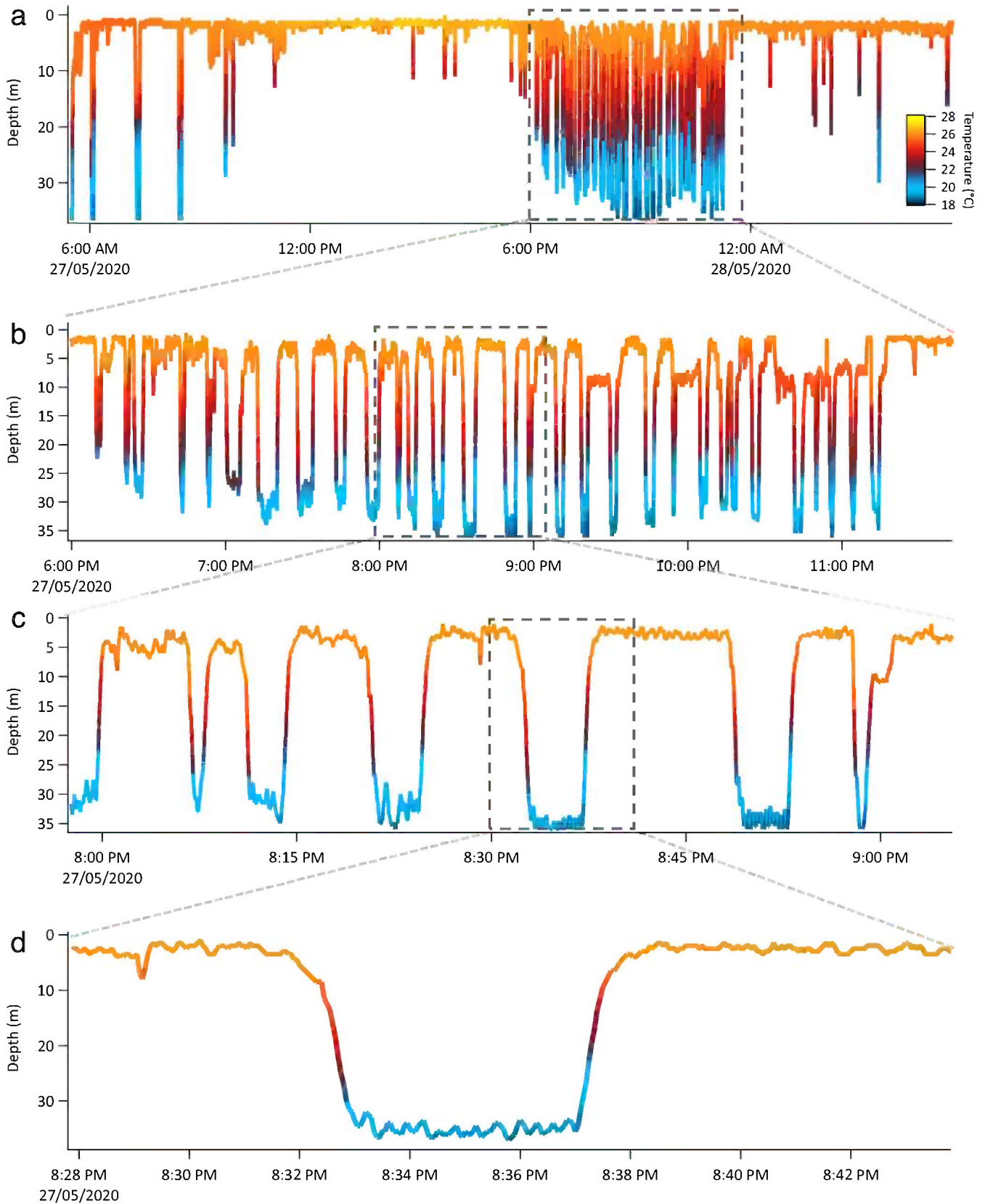


FIGURE 4 Raw archived depth time-series from one oceanic manta ray (MR1) at increasing resolution from (a) to (d). Depth traces are shaded by temperature (°C). Depth time-series are displayed for periods of (a) 24 h, (B) 6 h, (C) 70 min and (D) 16 min

mantas to temperatures up to 10°C cooler than at the surface for durations of up to 3 h, meaning they may need to ascend between dives to rewarm. While their large body size means oceanic manta rays likely exhibit relatively high thermal inertia (Nakamura et al., 2020), slowing the rate at which their skeletal muscle temperature cools with the environment, their cardiac system is expected to cool down much faster due to its close proximity to the gills, where water flows through at ambient temperatures, potentially impacting myocyte contraction and thus aerobic performance. During daytime periods, when zooplankton remain at greater depth or within the benthos and are subsequently inaccessible, mantas can remain in surface waters at preferred temperatures, perhaps foraging, undergoing social interactions, cleaning or cruising (Burgess, 2017; K. Forsberg et al., 2019; unpublished data). It is important to note that internal body temperature, foraging and activity were not directly measured in this study, and it is possible that other processes were responsible for the recorded movement patterns (e.g. hypoxia induced by low oxygen waters, intraspecific interactions, cleaning behaviour). Given available evidence, and until directly validated by other techniques (see the Future Directions section), we predict that foraging and thermal recovery are the most likely explanations for these movement behaviours.

Regional (>100 km) movement patterns and previous studies on foraging ecology of oceanic mantas together suggest that a strategy of nocturnal foraging on vertically migrating zooplankton may be prevalent throughout this region of the SE Pacific. Satellite tags deployed both here and in a previous study (Hearn et al., 2014) are indicative of connectivity between aggregations in northern Peru, Isla de la Plata (Ecuador) and the Galapagos Islands, and therefore the possibility of one regional population. In addition, an extensive study of the foraging ecology of oceanic manta rays at Isla de la Plata using observational methods and molecular techniques revealed limited observations of foraging during daytime periods and that surface zooplankton only contributed a small proportion of dietary intake (Burgess, 2017; Burgess et al., 2016, 2018). Burgess (2017) also suggested that oceanic mantas used the warm, clear surface waters for cleaning behaviours throughout the day, and move offshore, possibly to shelf-edge habitats, to forage on mesopelagic prey sources at night. There was, however, no demersal, benthic or deep-sea bulk stable isotope values available for zooplankton from coastal Ecuador for this study, and therefore the prey source accessed at depth here remains unconfirmed (Burgess, 2017).

As oceanic manta rays move into other habitats and/or other zooplanktonic prey sources become available, individuals may adopt alternate foraging strategies. Isotopic signatures recorded at Isla de la Plata indicated variability in dietary sources among oceanic manta rays (Burgess et al., 2016). Similarly, at the Revillagigedo Archipelago, Stewart et al. (2016) reported a number of distinct foraging patterns that shifted across seasons, including foraging at the surface, in the thermocline, and on vertically migrating zooplankton at depths greater than 100 m. Given errors in geolocation and the small sample size ($n = 3$) and timescale at which manta movements in northern Peru were investigated in this study, we cannot directly assess spatial and temporal shifts in foraging strategies here. Although, one individual

oceanic manta (MR2) moved into offshore waters where it displayed high variability in vertical movement patterns, potentially reflecting changes in behavioural mode (i.e. travel versus foraging) and/or foraging strategy as it moved through different habitats, as observed for white sharks (*Carcharodon carcharias*; Jorgensen et al., 2012). This manta displayed patterns of both normal (deeper during the day and shallower at night) and reverse DVM, behaviours that are indicative of foraging on mesopelagic zooplankton, while also undergoing deep dives (>200 m). In addition, deeper nighttime depths of this manta were associated with higher lunar illumination, possibly following zooplanktonic prey down as they maintain occupancy in preferred isolumes, a pattern consistent with that of reef manta rays (Andrzejaczek et al., 2020; Braun et al., 2014; Couturier et al., 2018). Conversely, deep dives were likely motivated by some other process, given that they were brief (<1 h) and often singular in time. Such vertical movements may represent predator avoidance and/or navigational dives, where vertical gradients in magnetic and electric fields are used to orient individuals during offshore movements (Andrzejaczek et al., 2019; Klimley, 1993). Notably, the first deep dive for this individual was a 50-min dive to 648 m, occurring just after departing the continental shelf. Collectively, vertical movement patterns and associated foraging strategies of oceanic manta rays are likely to be spatially and temporally variable and dependent on available zooplankton prey populations.

4.2 | DVM in filter-feeding elasmobranchs

Variability in diel patterns of vertical movement between habitats is a common theme amongst filter-feeding elasmobranch species (Andrzejaczek et al., 2019). This feeding guild are directly dependent on the daily movements of zooplanktonic prey, who are in turn reliant on prevailing environmental conditions (Hays, 2003). For example, basking sharks tracked in the English Channel displayed patterns of normal DVM in deep, well-stratified waters and reverse DVM in shallow, inner-shelf areas near thermal fronts, with such changes in behaviour between habitats likely mimicking those of zooplankton (Sims et al., 2005). Similarly, locational differences in DVM patterns have been recorded by reef manta rays, with normal DVM recorded around the islands and atolls of the Chagos archipelago (Andrzejaczek et al., 2020), and reverse DVM in both the coastal and offshore areas of the Red Sea (Braun et al., 2014), and the islands and atolls of Seychelles (Peel et al., 2020). Such diversity in foraging modes enables flexibility as these animals encounter spatial and/or temporal changes in the zooplanktonic prey community. In Peruvian waters, zooplankton biomass can be highly variable at short timescales, but is typically higher during austral spring months and moderate upwelling conditions, with a shift in community composition between continental shelf, continental slope and oceanic habitats (Aronés et al., 2019; Ayón et al., 2008). Such spatial-temporal variation could be driving the differences in vertical movement behaviour recorded by MR2 as it moved offshore in late winter to early spring months.

For several filter-feeding species, a critical zooplankton density threshold has been calculated at which the energetic costs of feeding

are balanced or outweighed by energy intake, triggering feeding activity (e.g. basking shark; Sims, 1999, whale shark; Nelson & Eckert 2007, reef manta ray; Armstrong et al., 2016). Although not yet calculated for oceanic manta rays, such a critical threshold may be met at night on SE Pacific coastline habitats, such as the aggregation site in northern Peru, when vertically migrating zooplankton move into the upper extent of their range. Mantas here, however, may be confronted with the physiological cost of foraging in cooler temperatures. This may necessitate returns to warm surface water between foraging bouts to rewarm, a pattern similar to that recorded in whale sharks (Thums et al., 2013), indicating that a high energetic return may be available at depth to offset these oscillatory movements (Armstrong et al., 2016).

4.3 | Management and conservation implications

High use of surface waters by tagged individuals, and connectivity with aggregations on Ecuador's coast and offshore islands, poses a number of challenges for the management and conservation of oceanic manta rays. The high use of surface waters (0–2 m; >50% daytime habitat use) by mantas in this location increases the probability of interaction with fisheries. Although protected in Peruvian waters, oceanic manta rays remain vulnerable to bycatch and/or entanglement by a number of fishing gears, particularly surface drift gillnets and bottom set nets with vessels deploying these gears operating in neritic waters, with the latter reported at depths <50 m (Alfaro-Shigueto et al., 2010), thus overlapping with manta movements reported in this study. Indeed, oceanic mantas continue to be accidentally caught by these fishing techniques (Alfaro-Cordova et al., 2017; Cabanillas-Torpoco et al., 2019). Such interactions also have socio-economic impacts for small-scale fishermen through gear damage and loss of fishing time, with fishermen reporting to lose up to USD 1300 in fishing gear per interaction (Edgardo Cruz and Raúl More, 2020; Personnel Communication). Furthermore, surface swimming also exposes mantas to increased risk of collision with vessels and other nearshore infrastructure (Marshall et al., 2018; McGregor et al., 2019; Pirota et al., 2019).

To reduce the interaction and impacts of such anthropogenic threats, the establishment of protected areas in locations of core area use, where controlled fishing gear use and/or reduced speed limits occur, should be considered. Efforts to mitigate interactions between manta rays and fishing gear should be prioritized, as well as efforts to release incidentally captured individuals. The potential for this site to develop as a community-based manta ray ecotourism hotspot could benefit the socio-economic development of local low-income fishing communities, (O'Malley et al., 2013) as has been recently observed for the whale-watching industry here (Guidino et al., 2020). Adequate protocols for tourism practices, however, should be ensured to avoid negative impacts to manta rays. Behavioral responses to the presence of tourists, boat strike and in the case of dive operators, entanglement with down-lines and lines connected to surface marker buoys, are all risks associated with the development of this industry (Marshall et al., 2018; Stewart et al., 2016; Venables et al., 2016). Anticipating such impacts and developing an enforceable, precaution-driven man-

agement approach and code of conduct for interactions will be of great benefit. As limited tagging has demonstrated connectivity between aggregations in Ecuador and Peru, new protections and management and conservation strategies dedicated to oceanic manta rays need to be established collaboratively in both countries to effectively protect the population, as well as offshore as mantas move through areas beyond national jurisdiction (as in the case of MR2). Lastly, as the coast of northern Peru is in close proximity to a number of river mouths located throughout the Gulf of Guayaquil (Twilley et al., 2001), the aggregation located here is susceptible to a high concentration of plastics and other pollutants, such as mercury, from land-based sources washing into the marine environment (Marshall et al., 2018). Long-term monitoring programs are required to determine the extent of pollution in this region, and increasing awareness of these issues in local communities may help to improve waste management practices (Germanov et al., 2018). More research, however, is required to continue to understand the effects that pollutants have on filter-feeding marine megafauna. Nevertheless, to maximize the effectiveness of the discussed strategies, it is vital that we first spatially and temporally delineate critical habitat use.

4.4 | Future research directions

This study provides a first step in describing patterns of movement and habitat use of oceanic manta rays in northern Peru; however, further work is required to validate the functionality of the recorded behaviours and explore patterns at larger spatial and temporal scales. Animal-borne video cameras are perhaps the best approach to directly validate foraging at depth and determine the source(s) of the zooplanktonic prey (e.g. Stewart et al., 2019), and, when deployed in combination with tri-axial sensors, estimate the energy costs associated with such movement behaviours (Gleiss et al., 2011). Biochemical analyses, such as stable isotope and signature fatty acid analyses, of manta muscle tissue in comparison to different zooplankton functional groups collected in the same area (i.e. near-surface, epipelagic, demersal, mesopelagic) will also assist in determining vertical foraging habitats for these filter feeders, especially when linked with horizontal and vertical movement patterns (Couturier et al., 2013). Sensors recording dissolved oxygen and internal body temperature may help understand the physiological limits of time spent at depth (e.g. Coffey & Holland 2015, Nakamura et al., 2020); however, as acute temperature changes may be affecting cardiac rather than muscle temperature, thermal limits may not yet be able to be tested in a natural setting given available technologies. In addition, further tagging is required to characterize horizontal movement patterns. The deployment of acoustic arrays and concurrent acoustic tagging across the different aggregation sites (i.e. northern Peru, Isla de la Plata and the Galapagos Islands) would be the ideal method to understand connectivity between these regions as well as the potential oceanographic drivers of movement patterns (e.g. Peel et al., 2019); however, deployment and maintenance costs can be expensive and time consuming. Further long duration deployments of satellite tags will also help fill this knowledge gap but are currently limited by deployment duration.

Increasing the sample size of satellite tag deployments on oceanic manta rays across coastal aggregations of the SE Pacific on an annual scale will also help elucidate if behaviours recorded in this study are characteristic of the population. Three mantas in this study were tracked across just 4 months of 1 year, and therefore recorded behaviours may not be representative of the region on an annual scale. Seasonal changes in productivity and thermal stratification of the water column, for instance, may impact both zooplankton communities and manta movements. Similarly, annual variation in primary productivity as a result of the El Niño Southern Oscillation (ENSO) may also impact patterns (2018 was a neutral year on the ENSO index), with El Niño conditions being associated with warmer SSTs, nutrient depleted waters and declines in planktonic biomass (Espinoza-Morriberón et al., 2017). At Isla de la Plata, for example, annual variation in manta sightings was correlated to the ENSO, with a decrease in sightings in El Niño years hypothesized to be a result of a reduction in food availability during these periods (Burgess, 2017). In addition, the long distance movement (> 1000 km) recorded here by one individual from northern Peru to the Galapagos Islands represents one of the longest documented movements made by an oceanic manta ray, with previous tracks from other locations indicating far more limited movements (Stewart et al., 2016). Further work is needed to determine if this is a typical pattern of individuals in this population, and if so, investigate the processes underlying these patterns. Furthermore, tagging across a representative cross section of the population at the different aggregation sites, particularly individuals of both sexes and a range of reproductive states and sizes, will enable better characterization of movement patterns and habitat use across the life history of these animals (Andrzejaczek et al., 2019).

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AUTHORS' CONTRIBUTIONS

KF, RS and BB conceived the ideas and designed methodology; RS, KF, NA, MC and WP collected the data; SA analysed the data; SA and BB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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