

Long-life remote underwater video reveals dawn cleaning station use in the rare stingray, *Megatrygon microps*

Jennifer Ann Keeping

2350816k@student.gla.ac.uk

University of Glasgow

Jule Buschmann

All Out Africa

Charlotte R Hopkins

University of Hull

David M Bailey

University of Glasgow

Research Article

Keywords: *Megatrygon microps*, cleaning stations, habitat use, video monitoring, species co-occurrence

Posted Date: September 25th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10847101/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Cleaning stations are key ecological sites for elasmobranchs, yet batoid behaviour at these locations remains poorly understood. Using three years of long-life remote underwater video (519 h across 99 recording days) we quantified diel visitation, behaviour and multispecies co-occurrence of the Data Deficient smalleye stingray *Megatrygon microps* at a cleaning station in Tofo Mozambique. From 138 frame entries we distinguished a maximum of 55 individuals. Individual-based daily counts (MaxIND) exceeded single-frame counts ($\text{MaxN} \leq 2$) by a mean factor of 1.48 and up to six-fold, comparable to baited video system studies. Arrivals concentrated at dawn: 24 of 55 individuals (43.6%) first appeared between 06:00 and 07:00, an hour representing 6.3% of effort, giving an arrival rate nearly 9 times that of the rest of the day. Visits were brief and dominated by cleaning (71.7% of individuals). Neither injury status nor accompanying cobia (*Rachycentron canadum*) number explained visit duration once behaviour was accounted for. At 30-second resolution *M. microps* showed no association with manta rays or SCUBA divers. *M. microps* occupancy peaked between 06:30 and 07:00 and diver presence between 11:30 and 12:00, with divers absent entirely before 07:00. Peak *M. microps* cleaning activity is therefore outside the period of routine recreational diving. These results establish Tofo as a predictable cleaning habitat for *M. microps*, one of few known across its Indo-West Pacific range and identify dawn as the period of greatest ecological significance for *M. microps* at this site.

1. Introduction

1.1 Cleaning stations and large batoid clients

Cleaning symbioses are essential ecological interactions on coral reefs, providing wound treatment, parasite removal, and tissue maintenance for clients and sustenance for cleaners (Caves, 2021). More than 100 species of marine fish, along with many types of invertebrates, serve as cleaners for an array of clients including fish, mammals, reptiles, and cephalopods (Gibson & Barnes, 2000). Where cleaners aggregate, they form cleaning stations: focal ecological features of tropical and sub-tropical reefs that structure interactions between client and cleaner species and shape patterns of movement, habitat use and community dynamics (Armstrong et al., 2021; Gibson & Barnes, 2000). The variety of cleaner species present, and the quality of the service they provide, is an important driver of visitation to inshore reefs by wide-ranging pelagic megafauna (Armstrong et al., 2021; Bshary & Schäffer, 2002; O'Shea et al., 2010). Cleaning stations thereby act as ecological hubs, at which multiple client species converge, creating the potential for competition for cleaner services or disturbance-driven displacement (Buschmann et al., 2024; Coward, 2017; Grutter et al., 2003; O'Shea et al., 2010).

Manta spp. (*Mobula birostris* and *M. alfredi*) are among the best-studied elasmobranchs at cleaning stations globally, as cleaning stations are often sites of repeated daily visitation, extended visit duration, and important social and reproductive interactions (Newsome et al., 2024; Perryman et al., 2019; Setyawan et al., 2024; Stevens et al., 2018). In Mozambique, manta rays have been recorded dominating the space around cleaning stations for periods averaging 25.4 min and extending to 4.2 h (Venables et al., 2020). Their cleaning behaviour is sensitive to disturbance: the presence of SCUBA divers alters visit duration, posture and engagement with cleaner fish (Gómez-García et al., 2021) and reduces the probability of manta ray occurrence in the minutes surrounding diver activity (Buschmann et al., 2026).

How long a client remains at a cleaning station reflects both what it is doing there and what it requires from the interaction. In manta rays, visit duration varies with the condition of the individual: animals carrying heavier parasite loads or unhealed tissue damage remain longer, consistent with cleaner–client theory in which demand for cleaning scales with what there is to clean (Grutter, 1995, 1999). Shark-bite injuries are common among large batoids, recorded in 68% of *M. alfredi* in southern Mozambique (Venables, 2020) and 23% in eastern Australia (Couturier et al., 2014), and cleaning stations function as sites of wound care and recovery as well as parasite removal (Pelletier et al., 2023). Whether the same relationship between injury and visit duration holds for a dasyatid has not been examined.

Visit duration may also be shaped by the animals travelling with the client. Hitchhiker species often travel with sharks and rays, a behaviour which is likely to have evolved to provide protection from predators, improve movement efficiency, and increase feeding opportunities, such as accessing prey stirred up from the seafloor or feeding on ectoparasites dislodged during cleaning processes (Kenaley et al., 2019; Saltzman et al., 2026). A hitchhiker (cobia *Rachycentron canadum*) was recorded as following *M. alfredi* in just 6% of sightings in Tofo Mozambique and were never recorded with *M. birostris* (Buschmann et al., 2024). Cobia association with a stingray was first included as an observation in Pierce et al. (2008), who described cobia following a small-eye stingray (*Megatrygon microps*) in Tofo Mozambique, however further global investigation shows a more prevalent relationship between *M. microps* and cobia, reporting up to 40 cobia following a single *M. microps* in Queensland Australia (Keeping et al., 2026).

1.2 The small-eye stingray *Megatrygon microps*

The small-eye stingray *Megatrygon microps* is among the least-known batoids, classified as Data Deficient by the International Union for Conservation of Nature Red List of Threatened Species (herein after IUCN Red List) (IUCN, 2025) and documented at only 19 locations in 10 countries across its range (Keeping et al., 2026). *M. microps* is distinctive among dasyatids, having a broad disc (exceeding 2.2 m disc width) and oscillatory swimming motion and are seen in mid-water, akin to the semi-pelagic mobulids (manta and devil rays), myliobatids (eagle rays) and rhinopterids (cownose rays) as opposed to the majority of bottom-dwelling benthic dasyatids (Pierce et al., 2008; Rosenberger, 2001; Schaefer & Summers, 2005). Long-term diver-based surveys in southern Mozambique have indicated that *M. microps* are rare, patchily distributed, and sighted at low but consistent frequencies, peaking in winter months (Keeping et al., 2021). Whether visitation is also structured within the day is as yet unknown; diel patterning in cleaning-station use has been documented for manta rays in this region (Buschmann et al., 2026; Venables et al., 2020) but not for any dasyatid. Photo-identification work demonstrates that individuals of *M. microps* can be reliably recognised via stable dorsal spot patterns and injuries (Keeping et al., 2020), and movement by photographically-identified individuals has been documented across a 350 km stretch of the Inhambane provincial coastline of Mozambique (Boggio-Pasqua et al., 2019). Identifying predictable hotspots, such as cleaning stations, for this otherwise rarely encountered species provides a unique opportunity to examine its behavioural ecology.

Although several stingray species are known to make occasional visits to cleaning stations, these interactions are typically brief and recorded opportunistically, with no quantitative assessments of visitation patterns or ecological function in the literature (Buschmann et al., 2024; O'Shea et al., 2010; Snelson et al., 1990). *M. microps* has been seen to visit various cleaning stations along the Queensland coastline, such as the SS Yongala shipwreck, off Townsville Australia (Keeping et al., 2026; Meekan et al., 2016), and on the diving reefs in Tofo Mozambique (Keeping et al., 2021; Pierce et al., 2008). The high prevalence of dorsal mucus accumulation, injuries, and tail loss in *M. microps* implies a potentially greater reliance on cleaner fish for maintaining health than in other dasyatids, consistent with its large body size and likely semi-pelagic lifestyle (Grutter, 1999; Keeping et al., 2026, 2020).

1.3 Behavioural inference from long-life underwater video

Remote underwater video (RUV) is increasingly recognised as a powerful, non-invasive method for observing behaviours at ecological hotspots of elasmobranchs, especially threatened or elusive species, for which capture-based surveys pose ethical or logistical challenges (Mallet & Pelletier, 2014). While baited remote underwater video systems (BRUVS) dominate survey efforts globally (Leonetti et al., 2024), un-baited and long-life remote underwater video systems (LL-RUVS) provide a crucial complementary perspective by capturing undisturbed behaviours, such as cleaning and multispecies interactions (Buschmann et al., 2024). Multi-day deployments of LL-RUVS at Tofo Mozambique demonstrate the potential of stationary LL-RUVS to document megafaunal visitation patterns and behaviours with temporal continuity unavailable from diver-based surveys or BRUVS (Buschmann et al., 2026, 2024).

Despite these advances, the analytical frameworks applied to RUVS data have lagged behind methodological innovations. The most widely used metric for estimating relative abundance from video survey data is MaxN, the maximum number of individuals of a species visible within a single frame at any point during a recording (Cappo, 2010). Although

computationally simple and inherently robust to double-counting, MaxN is recognised as a conservative metric that increasingly underestimates true abundance as local density rises, since multiple individuals can occupy a site without ever appearing together on screen, despite using bait to attract target species (Sherman et al., 2018; Whitmarsh et al., 2017). Individual-identification-based alternatives, most commonly termed MaxIND but reported under several functionally equivalent names (e.g. TotN (Stobart et al., 2015), Nmax-A (Bond et al., 2012) and IndN (Gore et al., 2020)), instead track the cumulative number of distinguishable individuals across an entire deployment. Where applied to elasmobranchs, this approach has revealed substantially higher abundances than MaxN alone, by a factor of 1.1 to 2.4 depending on species and the distinctiveness of identifying features (Kohler et al., 2025; Sherman et al., 2018). So far, this approach has only been applied to baited video, in which bait actively attracts animals into the frame. It remains untested whether individual-based counts are equally informative in unbaited footage, where visits reflect natural behaviour rather than attraction to bait. *M. microps* is a particularly suitable species for this comparison, since it is already known that individuals are reliably distinguishable by spot pattern and injury markings (Boggio-Pasqua et al., 2019; Keeping et al., 2020).

Beyond relative abundance estimates, alternative analyses of video footage such as co-occurrence models, remain largely imported from terrestrial camera-trap ecology. For example, multispecies occupancy models (MSOMs; Rota, Ferreira and Kays, 2016) capture spatial co-occurrence using repeated detection histories but typically treat temporal overlap as an adjunct analysis. Emerging terrestrial frameworks emphasise the utility of fixed-interval or time-to-event detections for quantifying conditional co-occurrence, avoidance, or behavioural displacement (Andrade-Ponce et al., 2022). However, LL-RUVS generate continuous, fine-scale time-series data on species presence, unlike motion-triggered imagery from terrestrial camera traps. Therefore, such data should be analysed using segmented footage into time-bin intervals to provide an analogous detection-history structure. This approach retains the high temporal resolution needed to resolve short visitation events (Andrade-Ponce et al., 2022; Rota et al., 2016) and permits competing explanations for apparent co-occurrence or instantaneous displacement to be distinguished within a single framework, a distinction that spatially structured occupancy models are not designed to resolve.

1.4 Aims

This study used LL-RUVS to investigate the occurrence and behaviours of a rare and Data Deficient stingray, *M. microps*, at a cleaning station site in Mozambique. Specifically, this study examines (1) abundance of *M. microps* and patterns of daily cleaning station use; (2) whether visit duration is associated with observed behaviours, injury, or the presence and abundance of hitchhiker species (i.e., cobia); and (3) whether the presence of other large batoids (i.e., manta spp.) and SCUBA divers are associated with the presence of *M. microps* at cleaning stations.

2. Materials and Methods

2.1 Study site and data collection

Two types of remote underwater video (RUV) system were deployed at three cleaning station areas: GoPro™ Hero 4 action cameras and an Open Ocean Camera© (OOCAM; Clear Robotics Limited, Hong Kong). The cleaning station areas were labelled 'north' and 'middle', each approximately 50 m apart on a 26–35 m depth rocky reef ledge, running north to south, at Giants Castle dive site, Tofo Mozambique (Fig. 1). The OOCAM was deployed at the 'middle' station and GoPro™ cameras were deployed at station 'north'. Between July 31, 2021, and October 25, 2023, the remote cameras were recording on 86 non-consecutive days (including 13 days with both cameras operating) between 05:30–18:00, generating 519 h 05 min 15 s of video footage. Of this, GoPro™ cameras contributed 75 h 05 min 15 s across 52 deployments, while the OOCAM system contributed 444 h 0 min 0 s across 7 deployments (Online Resource I). The OOCAM was housed in an acrylic tube equipped with a Sony IMX219 sensor (12.3 megapixels) and a 400 Wh battery pack providing approximately 148 hours of recording capacity. The OOCAM systems were set to 1080p resolution, 15 frames per second (FPS) and a 90° field of view. The GoPro™ systems were set to 1080p resolution, 60 FPS and 170° field of view. The OOCAM system was fitted with a Nauticam vacuum check and leak detection system, attached to a weighted metal frame, and secured to the reef substrate

using ski rope. GoPro™ cameras were mounted in cement blocks similarly secured to the substrate. Underwater visibility varied from between approximately 8 m to 20 m and all identified SCUBA divers and species visible within this range were included in the analysis.

For each deployment, the camera system (OOCAM or GoPro™), date and start and end times were extracted from the log data, and the total recording duration (s) was calculated. All footage was reviewed using VLC Media Player (Version 3.0.18; VideoLan, 2006). All elasmobranch sightings were initially logged by trained analysts who had completed species identification training. Training was delivered by All Out Africa (AOA) staff who held a minimum of an M.Sc. in a marine science discipline. Training comprised classroom-based species identification sessions and supervised in-water familiarisation. All records were subsequently verified by the primary author, consistent with the training protocols of Keeping et al. (2021) and data recording protocols of Buschmann et al. (2026, 2024).

A sighting began when an animal entered the frame, and ended when an animal left the frame and did not re-enter for > 5 minutes (Buschmann et al., 2024; Oliver et al., 2011). However, the same *M. microps* individual was recorded in subsequent sightings within the same recording day if it returned with the same identifying features. A frame entry is a single continuous appearance, from entering to leaving the camera's field of view and visit duration is an upper-bound estimate of an individual's first frame entry to its final frame exit within the day. Only sightings in which the animal could be identified to species level were retained. A new data entry row was used for each elasmobranch and SCUBA diver entering the camera frame. For each sighting, the following data were recorded: species identity, time of entry and exit, individual count, the number of cobia (*Rachycentron canadum*) closely following the elasmobranch (i.e., the cobia remains at a distance of within one body length of the elasmobranch), the presence of SCUBA divers within frame and *M. microps* behaviour. All observed behaviours were classified based on Klimley et al. (2023). Individual *M. microps* were identified from three broad tail length categories (none/short/long), distinctive pigmentation and morphology, the presence and location of shark-bite wounds (defined as semi-circular cut-outs along the posterior pectoral fins; Marshall and Bennett 2010) or the tail was short or absent as a result of a bite wound and rostral deformities (consistent with fishing gear wounds; Keeping et al., 2026).

2.2 Visitation rate and diel pattern

The maximum number of *M. microps* present simultaneously in a frame (MaxN) was recorded for each *M. microps* sighting (Cappo, 2010; Stobart et al., 2015). The maximum number of identified individuals in a single recording day (MaxIND) was estimated following protocols from Sherman et al. (2018) (Online Resource II).

The recording day (05:30–18:00) was divided into 30-minute bins. Recording effort per bin was calculated as the total number of minutes of recording within that bin. Arrivals of *M. microps* per 30 minutes bin were modelled with a negative binomial generalised additive model (GAM) using log recording effort as an offset ("mgcv" package; Wood, 2017), with smoothness selected by restricted maximum likelihood (REML) and a non-cyclic cubic regression spline for time of day. Two specifications were compared by Akaike information criterion (AIC): this continuous smooth, and a two-level step distinguishing an early-morning period from the remainder of the day. Because sunrise at the study site varies seasonally by approximately 85 minutes, arrival times were additionally expressed relative to local sunrise. Sunrise was calculated for each recording date from the site coordinates (23.85° S, 35.54° E) using the NOAA solar position algorithm implemented in the R package "suncalc" (Thieurmél & Elmarhraoui, 2026), and both arrival times and recording effort were re-expressed as hours since sunrise. The step model was then refitted in this frame, and the two parameterisations compared by their maximised likelihood-ratio statistics to establish whether the concentration of arrivals is better described as a fixed clock-time phenomenon or as one anchored to the light transition.

The step threshold was identified from the data, making the resulting test statistic a maximally selected statistic whose null distribution is not that of a conventional likelihood-ratio test (Hothorn & Zeileis, 2008; Miller & Siegmund, 1982). Its significance was assessed by a permutation procedure reproducing the same selection: in each of 5,000 permutations the 55 individuals were redistributed across bins in proportion to recording effort, the likelihood-ratio statistic was evaluated at

every candidate threshold from 06:00 to 17:00 in 30-minute increments, and the maximum retained. The observed maximum was compared against this null distribution, yielding a p-value that accounts for threshold selection.

2.3 Drivers of *M. microps* visit duration

Analyses were restricted to the 46 individuals for which behavioural state, injury status and accompanying cobia count were all recorded; individuals whose tail or flanks could not be clearly assessed were excluded. Visit duration was log-transformed and modelled with a Gaussian GAM ("mgcv" package; Wood, 2017). The primary model included behavioural state, injury status and accompanying cobia count across all 46 individuals; a subgroup model restricted to cleaning individuals ($n = 34$) addressed the specific prediction that injured animals require more extensive cleaning. Model assumptions were checked by inspection of residual and quantile plots, and the influence of individual observations was assessed using leverage and Cook's distance. Because sample size is small and visit duration spans three orders of magnitude, effects were additionally tested by permutation (20,000 permutations), shuffling injury labels and recomputing the difference in mean log visit duration, and shuffling visit duration and recomputing Spearman correlations with cobia count and arrival time.

2.4 Modelling species co-occurrence

To examine the co-occurrence of *M. microps* with other taxa at fine temporal resolution, a 30-second interval presence timeline for each deployment was constructed. This generated an interval-based detection history analogous to the encounter histories used in terrestrial camera-trap co-occurrence frameworks (Andrade-Ponce et al., 2022; Rota et al., 2016) (Fig. 2). A similar strategy was applied to the same dataset by Buschmann et al. (2026) to describe co-occurrence of manta rays (*Mobula alfredi* and *M. birostris*) with SCUBA divers. A 30-second width was selected to match the typical within-frame duration of an *M. microps* sighting (median 26 s, mean 65 s, $n = 138$). Intervals were bounded by the logged start and end of each recording interval, so that no interval spanned a recording gap. Each interval was scored 1 or 0 for the presence or absence of *M. microps*, *M. birostris*, *M. alfredi*, SCUBA divers and other elasmobranchs, each interval representing an instantaneous snapshot of co-occurrence at sub-minute resolution.

The probability of *M. microps* presence in an interval was modelled as a function of the simultaneous presence of each taxon using a binomial GAM ("mgcv" package; Wood, 2017), with a cubic regression spline for time of day to account for diel structure. Consecutive intervals are strongly dependent, since an animal present in one interval is likely to remain present in the next. The model was therefore fitted using `bam()` with an AR(1) correlation structure on the working residuals, reset at the start of each recording interval so that correlation was never propagated across a recording gap (van Rij et al., 2020; Wood, 2017). The lag-1 coefficient $\hat{\rho}$ was estimated as the mean within-interval residual autocorrelation of an uncorrelated fit, and the model refitted at $\rho = 0.40, 0.60$ and 0.80 to confirm that conclusions were not contingent on the correction applied.

The AR(1) structure accounts for serial dependence between adjacent intervals, which is the dominant form of non-independence in these data, but not for the clustering of entire co-occurrence events within a recording day; a deployment-level random effect would address the latter but is poorly identified when the events of interest number fewer than ten per taxon. Conclusions were therefore additionally verified by a block permutation test in which the *M. microps* presence series was circularly shifted within each recording interval, preserving the observed run-length structure of every series and the total number of occupied intervals, so that only the alignment between taxa was randomised.

As with Buschmann et al. (2026), SCUBA diver presence was characterised under two definitions to capture displacement extending beyond direct co-occurrence: a strict definition comprising intervals in which a diver was directly visible, and an expanded definition including any interval within five minutes of a diver sighting together with the first two minutes of each GoPro deployment, to account for disturbance during camera placement. For OOCAM deployments, which remain on the seafloor across consecutive days, the placement window was applied only to the first day of each consecutive-day string.

The minimum time gap between every *M. microps* sighting and the nearest diver sighting within the same recording day was computed to contextualise the temporal scale of any diver effect.

All statistical analyses were conducted using R statistical software version 4.5.2 (R Core Team, 2025) and all *mgcv* (Wood, 2017) GAM model outputs are reported in Online Resource III.

3. Results

Across 99 recording days in 86 non-consecutive days, the camera systems recorded approximately 519 h 05 min 15 s of footage (Online Resource I). *Megatrygon microps* was observed to enter and exit the frame 138 times, yielding a total of 2 h 30 min 0 s in frame. The longest visit duration of an individual *M. microps* was 1 h 34 min 53 s. The median visit duration per individual was 56 s and the mean was 10 min 20 s. SCUBA divers were sighted 56 times (total in frame = 1 h 35 min 08 s), *Mobula birostris* 186 times (total in frame = 1 h 33 min 48 s) and *M. alfredi* 129 times (total in frame = 2 h 30 min 26 s).

During the study, *M. microps* showed a restricted behavioural repertoire within the camera field of view: individuals were observed either cleaning or cruising. Cleaning dominated the observations, accounting for 71.7% ($n = 38$) of the 53 individuals whose behaviour could be recorded, while the remaining 28.3% ($n = 15$) involved rays cruising over the reef without circling back into frame. No feeding or courtship behaviour was recorded within the camera field of view.

Using a generous individual-identification approach, 55 *M. microps* were distinguished across the full dataset. Because no individuals were matched across multiple days, this count should be interpreted as an upper-bound estimate. Among rays for which the posterior body region was clearly visible ($n = 48$), 33.3% had a short or absent tail ($n = 15$), or showed evidence of shark-bite injury ($n = 1$). The only individual recorded with a shark-bite injury was also the individual with the third-longest visit duration (1 h 19 min 24 s, OOCAM; 21 August 2021). No rostral deformities were recorded in any of the 30 individuals in which the rostrum was clearly visible.

3.1 Arrival rate and diel pattern of *M. microps*

Megatrygon microps were recorded in 33 of 99 camera recording days (33.3%). MaxN was 1 in 28 deployments and was 2 in five deployments (GoPro; 5 August 2023 and OOCAM; 23 August 2021, 4 April 2023, 9 May 2023, 17 August 2023). No deployment exceeded two *M. microps* in a single frame.

Of the 33 recording days where *M. microps* were recorded, MaxIND ranged from 1 to 6 (median = 1, mean = 1.67), with more than one individual recorded in 15 of 33 recording days (Online Resource II). The highest MaxIND count was 6 individuals occurring on 22 August 2021 (OOCAM). Across all recording days with *M. microps*, MaxIND exceeded MaxN by a mean factor of 1.48 (maximum 6.00), placing this un-baited dataset within the 1.1–2.4 range previously reported for baited video (Kohler et al., 2025; Sherman et al., 2018).

Megatrygon microps arrived at the cleaning station in a pronounced pulse at first light. Of 55 individuals, 24 (43.6%) first entered the frame before 07:00, an hour accounting for 6.3% of recording effort (Fig. 3). Because sunrise at the study site varies seasonally between 04:58 and 06:22, arrival times were re-expressed relative to local sunrise. No individual arrived before sunrise on any date, despite 7.4 h of pre-sunrise recording effort, and 23 of the 24 early arrivals occurred within 60 minutes of sunrise (range + 4 to + 58 min, SD 19 min).

Modelled in sunrise-relative time, the arrival rate within one hour of sunrise was 8.95 times that of the remainder of the day ($\beta = 2.191 \pm 0.391$, $p < 0.001$, 95% CI 4.16–19.24), the model explaining 57.6% of deviance (Fig. 4a). The equivalent clock-time model gave a closely similar estimate (8.82-fold, 95% CI 3.17–24.55, $p < 0.001$, 48.7% deviance explained, Fig. 4b) and the two classifications differed for a single individual, but the sunrise parameterisation was the more precise, reducing the standard error of the effect by a quarter.

The effect was not contingent on the threshold chosen. Every candidate split between 30 minutes and five hours after sunrise produced an elevated early rate, ranging from 3.2 to 9.7 times the later rate, with the maximum likelihood-ratio statistic at 60 minutes (Table 1). Because the threshold was selected from the data, its significance was assessed by a selection-aware permutation in which the null was given the same freedom to choose its own optimum; the observed statistic was not attained in any of 5,000 permutations ($p < 0.0002$).

A penalised smooth of time of day was reduced by REML to a monotonic decline ($\text{edf} = 1.00$, $\chi^2 = 8.16$, $p = 0.004$), whereas a single step fitted appreciably better (AIC 87.34 against 93.58 for the smooth and 100.63 for a constant rate), indicating that arrival rate falls abruptly after the first hour of daylight rather than declining gradually across the day.

Because all recording before 08:00 was undertaken by the OOCAM system, the analysis was repeated within that camera alone, where the effect was retained (11.63-fold, $p < 0.001$).

The 24 dawn arrivals were distributed across 16 separate recording days spanning 2021 and 2023, with no day contributing more than three. A secondary cluster occurred between 09:00 and 09:30 (10 arrivals), but the dawn threshold remained the strongest single division of the day.

Table 1
Sensitivity of the early-morning effect in *Megatrygon microps* arrival rate to the threshold separating the early period from the remainder of the recording day. For each candidate cut point, arrival rates are given as individuals per hour of recording effort before and after the threshold, together with their ratio and the Poisson likelihood-ratio statistic (LRT) testing a two-rate against a single-rate model. The equivalent clock time analysis places the optimum cut-off at 07:00 (ratio 9.68, LRT 54.36).

Time	n before	Rate before	Rate after	Ratio	LRT
+ 30 min	10	0.552	0.090	6.10	18.03
+ 60 min	23	0.649	0.067	9.74	52.95
+ 90 min	24	0.433	0.067	6.43	38.75
+ 120 min	25	0.331	0.068	4.86	29.81
+ 150 min	25	0.257	0.072	3.58	20.14
+ 180 min	31	0.241	0.062	3.88	24.44
+ 210 min	34	0.204	0.06	3.4	20.17
+ 240 min	38	0.19	0.054	3.53	20.69
+ 270 min	39	0.174	0.055	3.17	16.91
+ 300 min	42	0.169	0.049	3.47	18.26

3.2 Drivers of *M. microps* visit duration

Visit duration differed strongly with behavioural state. Individuals engaged in cleaning remained six times longer than those cruising (6.01-fold, 95% CI 1.78–20.38, $p = 0.005$; Fig. 5a), a median of 138 s against 16 s.

Among cleaning individuals ($n = 34$), those bearing injuries ($n = 11$) showed a median visit duration of 429 s (IQR 34–2,206 s) compared with 77 s (IQR 29–656 s) for individuals with intact tails and no visible bite wounds ($n = 23$). This contrast was not statistically supported, either in the full model (1.84-fold, $p = 0.285$) or when restricted to cleaning individuals (2.57-fold, $p = 0.198$) and was not recovered by permutation ($p = 0.339$). No equivalent difference occurred among cruising individuals

(median 15.5 s injured, $n = 4$, against 18 s intact, $n = 8$), consistent with injury acting on cleaning demand rather than on transit through the site.

Accompanying cobia showed a positive association with visit duration (29% longer per additional cobia, 95% CI 1.04–1.60, $p = 0.020$ across all individuals; 1.30, 95% CI 1.00–1.69, $p = 0.052$ among cleaning individuals). This association rested heavily on a single animal, accompanied by twelve cobia and resident for 5,693 s, and its removal reduced the estimate to 19% longer per cobia ($t = 1.06$; Fig. 5b). A rank-based test found no association (Spearman $\rho = 0.194$, permutation $p = 0.270$), and the relationship was not consistent across the range: a cleaning individual accompanied by at least six cobia remained for only 17 s, while the second- and third-longest-staying rays were accompanied by one and three cobia respectively. Reversing the analysis gave a comparable result (visit duration predicting cobia count, $p = 0.036$), so no direction of effect can be established.

Arrival time did not predict visit duration (Spearman $\rho = 0.079$, permutation $p = 0.655$). The diel rhythm reported above therefore governs when *M. microps* arrives at the station, not how long it remains once there.

Taken as a whole, the model of visit duration among cleaning individuals did not significantly explain variation in visit duration ($F_{2,31} = 2.56$, $p = 0.094$, adjusted $R^2 = 0.086$). Residual variation was substantial, with individual residencies varying by a factor of approximately seven around model predictions (residual SD on the log scale = 1.94)

3.3 Species co-occurrence

The 30-second interval presence timeline comprised 62,270 intervals across all footage. *Megatrygon microps* occupied 419 intervals (0.67%), *M. alfredi* 419 (0.67%), *M. birostris* 328 (0.53%), other elasmobranchs 430 (0.69%) and SCUBA divers 249 (0.40%).

Occupancy of the two taxa peaked at different times of day: *M. microps* interval-level presence was highest between 06:30 and 07:00 (5.92% of intervals) and diver presence between 11:30 and 12:00 (1.89%), an offset of approximately five hours (Fig. 6). Divers were recorded in none of the 4,620 intervals before 07:00, the period in which *M. microps* occupied 4.07% of intervals against 0.40% across the remainder of the day.

After accounting for time of day and within-interval autocorrelation ($\hat{\rho} = 0.863$), neither *M. birostris* (est = + 0.393, SE = 0.377, $p = 0.297$), *M. alfredi* (est = - 0.030, SE = 0.439, $p = 0.945$), divers (est = + 0.063, SE = 0.696, $p = 0.928$) nor other elasmobranchs (est = - 0.802, SE = 0.471, $p = 0.089$) was associated with *M. microps* occurrence; combining the two manta species gave the same result (est = + 0.206, SE = 0.267, $p = 0.441$). *M. birostris* and *M. alfredi* co-occurred in only four intervals ($r = 0.005$), excluding collinearity as an explanation. No coefficient reached significance at any value of ρ between 0.40 and 0.863 (Table 2), and a block permutation test gave the same conclusion for every taxon (all $p > 0.17$).

Direct co-occurrence was rare. *Megatrygon microps* shared four 30-second intervals with *M. birostris*, two with *M. alfredi*, six with divers and three with other elasmobranchs; in each case the number expected had the two series been unrelated was between 1.7 and 6.6, so the observed counts carry little information. All six diver intervals occurred on a single recording day. Widening the definition of diver exposure did not alter this. A ± 5 -minute diver expansion produced 20 overlapping intervals with *M. microps* (8.6 expected, $p = 0.293$), and additionally flagging the first two minutes of each deployment produced the same 20 overlaps (10.1 expected, $p = 0.356$). Seventy-nine of 138 *M. microps* sightings fell on recording days that also recorded divers. On those days the two were separated by a median of 205 min (range 0–440), consistent with the diel offset described above rather than with an absence of opportunity.

During an opportunistic observation, *M. birostris* has been observed altering its swimming trajectory when *M. microps* travel over cleaning sites (J. Keeping, pers. obs.; Fig. 7a). One deployment also recorded *M. microps* and divers in frame together. On 5 August 2023 two *M. microps* individuals cleaned continuously from 09:17:47 to 09:28:10, entering the frame ten times over 10.5 min. A diver adjusted the camera at 09:21:03–09:22:59; both rays remained in frame and cleaning continued. A

second approach at 09:26:50–09:31:13, during which the rays were photographed at close range by several divers (Fig. 7b), coincided with the final appearance of either individual. Neither returned during the remaining 41 min of recording, although *M. birostris* was recorded a further eight times.

Table 2
Sensitivity of AR(1)-corrected coefficients to the assumed autocorrelation parameter ρ .

ρ	<i>M. birostris</i>	ρ	<i>M. alfredi</i>	ρ	Divers	ρ	Other elasm.	ρ
0.40	+ 0.53	0.413	-0.12	0.881	+ 0.90	0.260	-0.39	0.613
0.60	+ 0.46	0.461	-0.06	0.933	+ 0.19	0.864	-0.65	0.402
0.80	+ 0.41	0.374	-0.04	0.940	-0.53	0.632	-0.79	0.164
0.863 (estimated)	+ 0.39	0.297	-0.03	0.945	+ 0.06	0.928	-0.80	0.089

4. Discussion

Across more than three years of remote-camera monitoring, this study provides the first quantitative description of *Megatrygon microps* cleaning-station use. A maximum of 55 individuals were recorded at a single reef complex at Tofo, Mozambique, confirming that this area functions as a hotspot for this globally rare species (Armstrong et al., 2023; Keeping et al., 2026). These observations position *M. microps* alongside manta rays as a large-bodied elasmobranch reliant on cleaner services and reveal a previously undocumented dimension of its behavioural ecology: a pronounced concentration of cleaning station use at dawn.

4.1 Daily patterns of cleaning station use

Megatrygon microps arrived at the cleaning station in a strongly concentrated dawn pulse, where the pre-07:00 arrival rate was 8.8 times that of the remainder of the day. Several mechanisms could generate such a pattern, and the present data cannot distinguish among them. Cleaner fish activity and hunger are typically highest in the early morning, when overnight accumulation of ectoparasites is greatest, and client visitation to cleaning stations peaks correspondingly in a range of reef systems (Caves, 2021; Grutter, 1999). Alternatively, dawn arrival may reflect the end of a nocturnal offshore foraging period, with individuals returning to the reef at first light, a pattern consistent with the semi-pelagic and oscillatory swimming mode of this species (Pierce et al., 2008; Rosenberger, 2001). Reduced predation risk in low light, or avoidance of daytime reef traffic, are further possibilities. Distinguishing these will require either telemetry approaches spanning the nocturnal period or artificially lit camera deployments extending beyond the 05:30–18:00 window used here, which cannot exclude the possibility that cleaning station use continues at night.

Results indicate that *M. microps* uses the monitored cleaning stations primarily on a solitary basis. MaxN was 1 in 28 of 33 positive recording days and never exceeded two, while individual-based daily counts ranged from one to six. For solitary species, MaxN carries almost no variance and cannot track relative abundance, yet it remains the standard metric in remote underwater video (Cappo, 2010; Whitmarsh et al., 2017). Appropriate for a species where individuals are distinguishable, such as *M. microps*, MaxIND exceeded MaxN by a mean factor of 1.48, within the 1.1–2.4 range Sherman et al. (2018) reported from baited video. Recovering a comparable ratio without bait indicates the shortfall is a property of instantaneous sampling itself rather than of the attractant. The cleaning station serves considerably more individuals than any instantaneous count reveals, and the discrepancy is not something baiting was necessary to resolve in this case.

4.2 Behavioural repertoire and functional use of cleaning stations

M. microps displayed a narrow behavioural repertoire within the camera's field of view, restricted to cleaning and cruising. Cleaning dominated, supporting the interpretation that this reef functions primarily as a cleaning site rather than a multi-behaviour hotspot. Capturing a wider behavioural range would require cameras oriented differently, or 360° field of view

systems, which would also address the issue that behaviours occurring outside a fixed field of view are systematically under-recorded.

4.3 Factors affecting visit duration

A third of assessable individuals bore a shortened or absent tail or a visible shark-bite wound, comparable to the global citizen science-sourced sightings of *M. microps* (Keeping et al., 2026). This is lower than injury rates reported for *M. alfredi* in the same region (68%; Venables, 2020) and higher than contemporary estimates for manta spp. in the Maldives (16%; Strike et al., 2022). In manta populations, injury severity has been linked to extended cleaning durations, and cleaning stations serve as sites for wound care, parasite removal and recovery from trauma (Marshall & Bennett, 2010; Pelletier et al., 2023). Injured individuals in the present study did show a longer median visit duration than intact individuals, but the contrast was not statistically supported in any model or by permutation, and the sample of injured, assessable, behaviourally scored individuals was small ($n = 11$). The direction is consistent with cleaner–client theory, wherein individuals with greater parasite loads or damaged tissue exhibit prolonged cleaning bouts (Grutter, 1995, 1999), particularly given the abundant surface mucus characteristic of this species (Keeping et al., 2020); but the present data can only be said to be compatible with that expectation, not to demonstrate it.

No rostral deformities were recorded in any of the 30 individuals for which the rostrum was clearly visible. Such deformities have been observed at appreciable frequency in Australian *M. microps* (Keeping et al., 2026), and their absence here suggests either a regional difference in injury source or a difference in the demographic composition of the two locations.

Behavioural state was the only supported predictor of visit duration: cleaning individuals remained six times longer than those cruising through the frame. Accompanying cobia showed an apparent positive association with visit duration, but this rested almost entirely on a single animal. The prevalence of the association is nonetheless notable. Cobia accompanied 72.0%, with a maximum of 12 cobia, per *M. microps*. This is more than double the 28.4% recorded across global visual records of the species, yet the global mean is 10.4 and a maximum of 40 cobia were reported (Keeping et al., 2026). Two explanations are compatible with this contrast. Continuous video across an entire visit detects at least one accompanying cobia far more reliably than a single photograph, while photographic records are biased toward the large aggregations most likely to be captured and shared; and large aggregations may form in open-water or foraging contexts rather than at cleaning stations, where cobia were consistently few. Both counts are minimum estimates under the same convention, since individuals outside the field of view cannot be excluded (Keeping et al., 2026). These figures differ from those reported for *M. microps* from the same recordings by Buschmann et al. (2024), where cobia accompanied 63% of sightings. The present values derive from a targeted second review of all *M. microps* footage in which the absence of cobia was recorded explicitly, whereas the earlier dataset recorded counts where cobia were present. Values are additionally expressed per individual-day here rather than per pooled sighting.

Whether cobia associations reflect foraging opportunity, hydrodynamic benefit, predator avoidance or some combination cannot be determined from these data (Kenaley et al., 2019; Solleliet-Ferreira et al., 2020). However, given the comparatively rare cobia-manta spp. association from the same dataset in Buschmann et al. (2024), the cobia association appears specific to *M. microps* among the large batoids using these cleaning stations, rather than a general feature of elasmobranch hitchhiker assemblages. A review of the cobia literature does not document this associative lifestyle with marine megafauna at all (dos Santos Júnior & de Nóbrega, 2024), and detailed accounts of stingray–hitchhiker associations remain scarce for large and infrequently observed batoids (de Carvalho-Souza et al., 2025).

4.4 Temporal separation of cleaning station use

At 30-second resolution, *M. microps* presence was not associated with the simultaneous presence of *M. birostris*, *M. alfredi*, other elasmobranchs or SCUBA divers, either before or after adjustment for time of day and within-interval autocorrelation. Instead, the taxa were separated in timing of station use through the day rather than instantaneous avoidance.

The contrast on 5 August 2023 between a brief equipment adjustment, which did not interrupt cleaning, and a sustained close approach, after which neither ray returned while manta rays continued to use the station, is suggestive of a response scaled to the character of the interaction rather than to diver presence as such. As a single sequence it cannot support a general claim, but directed observations of diver–stingray interaction are scarce, and it indicates the form a targeted test would need to take: paired deployments contrasting approach types rather than presence alone.

4.5 Modelling LL-RUVS footage and improvements to study design

By converting continuous LL-RUV footage into 30-second detection histories, this study bridges the conceptual gap between terrestrial camera-trap co-occurrence frameworks (Andrade-Ponce et al., 2022; Rota et al., 2016) and aquatic continuous-footage datasets. Interval-based detection histories and multi-site occupancy models answer different questions, and the trade is one of design rather than of framework. Occupancy models resolve spatial inference at the cost of temporal resolution, and their interaction parameters are poorly recovered below 150–1,000 sites (Cowans et al., 2025; Twining & Kellner, 2026). The interval framework presented here resolves presence at sub-minute scale with effectively complete detection within the field of view, which is what allows temporal segregation to be distinguished from instantaneous avoidance, a distinction no spatial co-occurrence model can make since both processes generate identical spatial patterns. Importantly, the two are not mutually exclusive. Nothing in the interval framework precludes spatial inference: deployment site enters the model as a covariate or random effect in the ordinary way, and site-level attributes such as depth, rugosity, substrate etc. can be tested directly against interval-level presence. The present study could not do so because all recording came from a single reef complex, so site had no variance to contribute. Deployed across multiple stations the same framework would estimate both when a species uses a cleaning station and which stations it selects, within one model. This would combine the temporal resolution demonstrated here with the spatial inference that occupancy designs provide.

Constraints on the present design include image quality and angle, which was insufficient to resolve dorsal spot patterns, so individuals were not matched across days and MaxIND remains an upper bound; higher-resolution sensors would convert this into true individual identification and, with it, estimates of site fidelity and return interval. The field of view was narrow, so behaviours occurring outside a fixed arc were systematically unrecorded; wide-angle or multi-camera arrays would resolve this. Recording was confined to daylight, leaving the possibility that cleaning station use continues at night entirely untested, a material gap given that the strongest result here concerns the first hour after sunrise. Infrared illumination (Hermann et al., 2020), paired environmental sensors and automated detection would extend the same interval-based framework across the full diel cycle at a fraction of the analytical cost, which was entirely manual in the present study.

4.6 Conservation implications for a Data Deficient stingray

The cleaning station complex at Giants Castle reef emerges from these data as a functionally significant habitat for *M. microps*: visited at a specific and narrow time of day, and used by more individuals than instantaneous counts suggest. For a species documented rarely across its range (Keeping et al., 2026) and listed as Data Deficient (IUCN, 2025), the identification of any reliably used site is consequential. The present data provide no evidence that current diver activity displaces *M. microps*, and the temporal separation evidenced above suggests that peak cleaning station use currently falls outside the period of routine recreational diving.

Cleaning stations are spatially discrete, structurally dependent on hard coral outcrops, and support cleaner assemblages that are themselves site-attached (Armstrong et al., 2021; Caves, 2021). Because a single cleaning station serves multiple client taxa, measures protecting the reef structure benefit manta rays, *M. microps* and the cleaner assemblage together, without requiring species-specific regulation or restrictions on when people may dive. In a region where sightings of large elasmobranchs are declining (Auditore et al., 2025; Cullain et al., 2025; Venables et al., 2024), maintaining the structural integrity of these sites may provide conservation benefits disproportionate to their small spatial footprint.

The temporal separation documented between visiting taxa is a description of current conditions: were dive operations to extend earlier into the morning, the buffer it presently affords would narrow, and the absence of a detectable diver effect in this dataset should not be read as evidence that none could arise. Moreover, the sensitivity of *M. microps* to disturbance remains untested; the single close-approach sequence documented here is suggestive but cannot be generalised, and a targeted study contrasting matched deployments with and without diver activity would be required to establish whether a code of conduct is warranted on evidential rather than precautionary grounds.

5. Conclusions

This study provides the first quantitative description of cleaning ecology in *Megatrygon microps*. At the monitored cleaning station, use is concentrated into a narrow dawn window, is primarily solitary, and is dominated by cleaning; visits are brief by comparison with sympatric manta rays, and neither injury status nor hitchhiker load explains their duration once behavioural state is accounted for. At sub-minute resolution the species shows no association with manta rays or divers, and the taxa instead partition the day, with peak *M. microps* activity preceding peak manta and diver presence. The interval-based framework developed here converts continuous underwater video into a detection history analogous to terrestrial camera-trap data while retaining the temporal resolution needed to separate instantaneous displacement from differences in activity timing, a distinction that co-occurrence coefficients alone cannot make. For a Data Deficient species known from few locations, the demonstration that a single reef complex reliably supports dozens of individuals at a predictable hour identifies a conservation priority area as well as a tractable platform for ongoing investigation into the species.

Declarations

Conflict of interests:

The authors declare no conflicts of interest. Declaration of Funding: Funding for this research was provided by the Rufford Foundation (grant numbers 32205-1 and 37616-2) and the University of Gibraltar. The funders were not involved in the study design, data collection, analysis, interpretation, manuscript preparation, or the decision to submit for publication. Data availability statement: All data supporting the findings of this study are available upon request to the corresponding author. Deployment record, MaxN and MaxIND counts and a summary of models are included within the online resources.

Author Contribution

J.K. designed the project, analysed data and wrote the manuscript. J.B. analysed data. C.H. and D.B. assisted in project design and all authors reviewed the manuscript.

Acknowledgement

Fieldwork was conducted with the support of Tofo Scuba Dive Centre. We thank all 647 citizen scientists from the All Out Africa Marine Research Centre who contributed to video analysis, with special appreciation to Britt Floris for singlehandedly reviewing 93 hours of footage. We are also grateful to Florian Schettina and Steven Scagnelli for their expertise in camera repairs and to Rene Cote for the generous donation of a camera. We also thank the reviewers for their valuable feedback, which greatly improved the manuscript.

Data Availability

All data supporting the findings of this study are available upon request to the corresponding author.

References

1. Andrade-Ponce, G. P., Mandujano, S., Dáttilo, W., Farías-González, V., Jiménez, J., Velásquez-C, K., & Zavaleta, A. (2022). A framework to interpret co-occurrence patterns from camera trap data: The case of the gray fox, the bobcat, and the eastern cottontail rabbit in a tropical dry habitat. *Journal of Zoology (London, England: 1987)*, 318(2), 91–103. <https://doi.org/10.1111/jzo.13002>
2. Armstrong, A. O., Armstrong, A. J., Bennett, M. B., Richardson, A. J., Townsend, K. A., Everett, J. D., Hays, G. C., Pederson, H., & Dudgeon, C. L. (2021). Mutualism promotes site selection in a large marine planktivore. *Ecology and Evolution*, 11(10), 5606–5623. <https://doi.org/10.1002/ece3.7464>
3. Armstrong, A. O., Bineesh, K. K., Keeping, J., Manjaji Matsumoto, B. M., & Marshall, A. D. (2023). *Megatrygon microps*. International Union for Conservation of Nature. <https://doi.org/10.2305/iucn.uk.2024-1.rlts.t161582a124510222.en>
4. Auditore, L.-M., Pierce, S. J., Prebble, C. E. M., Flam, A., Marshall, A. D., Venables, S. K., Watts, A., Reeve-Arnold, K. E., Domenico, G., Keeping, J. A., Méndez-Jiménez, A., Riensema, A., Rosero, M., Cumbana, L., Tilley, A., Westling, A., Williams, C., & Rohner, C. A. (2025). A 15-year time series shows major declines in whale sharks in southern Mozambique. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 35(10). <https://doi.org/10.1002/aqc.70224>
5. Boggio-Pasqua, A., Flam, A. L., & Marshall, A. D. (2019). Spotting the ‘small eyes’: using photo-ID methodology to study a wild population of smalleye stingrays (*Megatrygon microps*) in southern Mozambique. *PeerJ*, 7, e7110. <https://doi.org/10.7717/peerj.7110>
6. Bond, M. E., Babcock, E. A., Pikitch, E. K., Abercrombie, D. L., Lamb, N. F., & Chapman, D. D. (2012). Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PloS One*, 7(3), e32983. <https://doi.org/10.1371/journal.pone.0032983>
7. Bshary, R., & Schäffer, D. (2002). Choosy reef fish select cleaner fish that provide high-quality service. *Animal Behaviour*, 63(3), 557–564. <https://doi.org/10.1006/anbe.2001.1923>
8. Buschmann, J., Dissanayake, A., Davies, J. S., Bridges, A., & Keeping, J. A. (2026). Multi-scale use of cleaning stations by manta rays in Mozambique: Insights from remote underwater video surveillance. *Marine Environmental Research*, 107962, 107962. <https://doi.org/10.1016/j.marenvres.2026.107962>
9. Buschmann, J., Roques, K. G., Davies, J. S., Dissanayake, A., & Keeping, J. A. (2024). Novel approach to studying marine fauna: using long-life remote underwater video cameras to assess occurrence and behaviour of threatened and data-deficient elasmobranch species in southern Mozambique. *Frontiers in Marine Science*, 11, 1518710. <https://doi.org/10.3389/fmars.2024.1518710>
10. Cappel, M. (2010). Development of a Baited Video Technique and Spatial Models to Explain Patterns of Fish Biodiversity in Inter-reef Waters [PhD, James Cook University]. <https://researchonline.jcu.edu.au/15420>
11. Caves, E. M. (2021). The behavioural ecology of marine cleaning mutualisms. *Biological Reviews of the Cambridge Philosophical Society*, 96(6), 2584–2601. <https://doi.org/10.1111/brv.12770>
12. Cowans, A., Bigatà, A. B., & Sutherland, C. (2025). Sample size considerations for species co-occurrence models. *Ecology*, 106(8), e70175. <https://doi.org/10.1002/ecy.70175>
13. Coward, T. (2017). Ecology of elasmobranch cleaning stations and the effects of tourism activities in Bateman bay, Ningaloo Reef [Murdoch University]. <https://researchportal.murdoch.edu.au/esploro/outputs/graduate/Ecology-of-elasmobranch-cleaning-stations-and/991005541559107891>
14. Cullain, N., Tibiriçá, Y., Venables, S. K., Rohner, C. A., Tittensor, D. P., & Lotze, H. K. (2025). Declines in sightings and changing visitation patterns of reef manta rays at an important aggregation site in Mozambique. *Environmental Biology of Fishes*, 108(9), 1361–1377. <https://doi.org/10.1007/s10641-025-01729-0>
15. de Carvalho-Souza, G. F., Sparaventi, E., & Echeverría-Sáenz, S. (2025). Interspecific associations of the rare and endangered stingray (*Styracura schmardae*) in Caribbean Sandy-Bottom habitats. *Ecology and Evolution*, 15(11), e72471. <https://doi.org/10.1002/ece3.72471>

16. dos Santos Júnior, A. R., & de Nóbrega, M. F. (2024). Global research performance trends and knowledge gaps on cobia (*Rachycentron canadum*): a scientometric perspective. *Reviews in Fish Biology and Fisheries*.
<https://doi.org/10.1007/s11160-024-09882-y>
17. Gibson, R., & Barnes, M. (2000). Evolution and ecology of cleaning symbioses in the sea. *Oceanography and Marine Biology: An Annual Review*. https://books.google.com/books?hl=en&lr=&id=C15jZPBeqyQC&oi=fnd&pg=PA311&dq=manta+rays+cleaning+stations&ots=NVO5I_fObP&sig=jF_eq2Md-dnwTHmfu1WrxnSflZc
18. Gómez-García, M. de J., Blázquez-Moreno, M. del C., Stewart, J. D., Leos-Barajas, V., Fonseca-Ponce, I. A., Zavala-Jiménez, A. A., Fuentes, K., & Ketchum, J. T. (2021). Quantifying the effects of diver interactions on manta ray behavior at their aggregation sites. *Frontiers in Marine Science*, 8. <https://doi.org/10.3389/fmars.2021.639772>
19. Gore, M., Ormond, R., Clarke, C., Kohler, J., Millar, C., & Brooks, E. (2020). Application of photo-identification and lengthened deployment periods to baited Remote Underwater Video Stations (BRUVS) abundance estimates of coral reef sharks. *Oceans (Basel, Switzerland)*, 1(4), 274–299. <https://doi.org/10.3390/oceans1040019>
20. Grutter, A. (1995). Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Marine Ecology Progress Series*, 118, 51–58. <https://doi.org/10.3354/meps118051>
21. Grutter, A. (1999). Cleaner fish really do clean. *Nature*, 398(6729), 672–673. <https://doi.org/10.1038/19443>
22. Grutter, A., Murphy, J. M., & Choat, J. H. (2003). Cleaner fish drives local fish diversity on coral reefs. *Current Biology: CB*, 13(1), 64–67. [https://doi.org/10.1016/s0960-9822\(02\)01393-3](https://doi.org/10.1016/s0960-9822(02)01393-3)
23. Hermann, A., Chladek, J., & Stepputtis, D. (2020). iFO (infrared Fish Observation) - An open source low-cost infrared underwater video system. *HardwareX*, 8(e00149), e00149. <https://doi.org/10.1016/j.ohx.2020.e00149>
24. Hothorn, T., & Zeileis, A. (2008). Generalized maximally selected statistics. *Biometrics*, 64(4), 1263–1269. <https://doi.org/10.1111/j.1541-0420.2008.00995.x>
25. Keeping, J. A., Caine, A., Hopkins, C., Bailey, D., & Chin, A. (2026). The distribution of a rarely encountered stingray, *Megatrygon microps*, informed by citizen science: A systematic review. *Conservation Science and Practice*, 8(5). <https://doi.org/10.1111/csp2.70264>
26. Keeping, J. A., Milligan, R. J., Reeve-Arnold, K., & Bailey, D. (2021). Trends in sightings of the stingrays of southern Mozambique. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF21013>
27. Keeping, J. A., Reeve-Arnold, K. E., Burns, N. M., Catarina, N., Bailey, D. M., & McNeill, D. C. (2020). Computer-aided photo-identification of a rare stingray, *Megatrygon microps*. *Journal of Fish Biology*, 96(3), 815–819. <https://doi.org/10.1111/jfb.14242>
28. Kenaley, C. P., Stote, A., Ludt, W. B., & Chakrabarty, P. (2019). Comparative functional and phylogenomic analyses of host association in the remoras (Echeneidae), a family of hitchhiking fishes. *Integrative Organismal Biology (Oxford, England)*, 1(1), obz007. <https://doi.org/10.1093/iob/obz007>
29. Klimley, A. P., Porcher, I. F., Clua, E. E. G., & Pratt, H. L. (2023). A review of the behaviours of the Chondrichthyes: a multi-species ethogram for the chimaeras, sharks, and rays. *Behaviour*, 160(11–14), 967–1080. <https://doi.org/10.1163/1568539x-bja10214>
30. Kohler, J., Gore, M., Ormond, R., Mason, K., Veeder, A., & Austin, T. (2025). Combining adequate BRUV deployment times with individual photo-identification improves monitoring of shark populations in the Caribbean. *Oceans (Basel, Switzerland)*, 6(4), 70. <https://doi.org/10.3390/oceans6040070>
31. Leonetti, F. L., Bottaro, M., Giglio, G., & Sperone, E. (2024). Studying chondrichthyans using Baited Remote Underwater Video Systems: A review. *Animals: An Open Access Journal from MDPI*, 14. <https://doi.org/10.3390/ani14131875>
32. Mallet, D., & Pelletier, D. (2014). Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). *Fisheries Research*, 154, 44–62. <https://doi.org/10.1016/j.fishres.2014.01.019>
33. Marshall, A. D., & Bennett, M. B. (2010). The frequency and effect of shark-inflicted bite injuries to the reef manta ray *Manta alfredi*. *African Journal of Marine Science*, 32(3). <https://doi.org/10.2989/1814232X.2010.538152>

34. Meekan, M. G., Trevitt, L., Simpfendorfer, C. A., & White, W. (2016). The piggybacking stingray. *Coral Reefs*, 35(3), 1011–1011. <https://doi.org/10.1007/s00338-016-1429-9>
35. Miller, R., & Siegmund, D. (1982). Maximally selected chi square statistics. *Biometrics*, 38(4), 1011. <https://doi.org/10.2307/2529881>
36. Newsome, R. J., Grimmel, H. M. V., Pouponeau, D. K., Moulinie, E. E., Andre, A. A., & Bullock, R. W. (2024). Eat-clean-repeat: reef manta rays (*Mobula alfredi*) undertake repetitive feeding-cleaning cycles at an aggregation site in Seychelles. *Frontiers in Marine Science*, 11. <https://doi.org/10.3389/fmars.2024.1422655>
37. Oliver, S. P., Hussey, N. E., Turner, J. R., & Beckett, A. J. (2011). Oceanic sharks clean at coastal seamount. *PloS One*, 6(3), e14755. <https://doi.org/10.1371/journal.pone.0014755>
38. O'Shea, O. R., Kingsford, M. J., & Seymour, J. (2010). Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Marine and Freshwater Research*, 61(1), 65–73. <https://doi.org/10.1071/MF08301>
39. Pelletier, N. A., Knochel, A., Stewart, J. D., Froman, N., Smith, T. R., Marshall, G., Abernathy, K., Hawkins, J., & Stevens, G. M. W. (2023). Insight into manta ray behaviour using animal-borne Crittercams. *Behaviour*. <https://doi.org/10.1163/1568539x-bja10242>
40. Perryman, R. J. Y., Venables, S. K., Tapilatu, R. F., Marshall, A. D., Brown, C., & Franks, D. W. (2019). Social preferences and network structure in a population of reef manta rays. *Behavioral Ecology and Sociobiology*, 73(8). <https://doi.org/10.1007/s00265-019-2720-x>
41. Pierce, S. J., White, W. T., & Marshall, A. D. (2008). New record of the smalleye stingray, *Dasyatis microps* (Myliobatiformes: Dasyatidae), from the western Indian Ocean. *Zootaxa*, 1734(1734), 65–68. <https://doi.org/10.11646/zootaxa.1734.1.5>
42. Rosenberger, L. J. (2001). Pectoral fin locomotion in batoid fishes: undulation versus oscillation. *The Journal of Experimental Biology*, 204(Pt 2), 379–394. <https://doi.org/10.1242/jeb.204.2.379>
43. Rota, C. T., Ferreira, M. A. R., & Kays, R. W. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7, 1164–1173. <https://doi.org/10.1111/2041-210X.12587>
44. Saltzman, J., Hlavin, J., Martin, C., Yeager, E. A., & Macdonald, C. C. (2026). Behavioral evidence of predator–predator commensalism: Cobia track and feed on prey disturbed by southern stingrays. *Ethology: Formerly Zeitschrift Für Tierpsychologie*, 132(3), 225–234. <https://doi.org/10.1111/eth.70044>
45. Schaefer, J. T., & Summers, A. P. (2005). Batoid wing skeletal structure: novel morphologies, mechanical implications, and phylogenetic patterns. *Journal of Morphology*, 264(3), 298–313. <https://doi.org/10.1002/jmor.10331>
46. Setyawan, E., Heinrichs, S., & Erdmann, M. (2024). First documented courtship behavior between *Mobula birostris* and *M. alfredi* at a coral reef cleaning station in Misool, Raja Ampat. *Diversity*, 16(6), 319. <https://doi.org/10.3390/d16060319>
47. Sherman, C. S., Chin, A., Heupel, M. R., & Simpfendorfer, C. A. (2018). Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *Journal of Experimental Marine Biology and Ecology*, 503, 80–85. <https://doi.org/10.1016/j.jembe.2018.03.002>
48. Snelson, F. F., Gruber, S. H., Murru, F. L., & Schmid, T. H. (1990). Southern Stingray, *Dasyatis americana*: Host for a Symbiotic Cleaner Wrasse. *Copeia*, 1990(4), 961. <https://doi.org/10.2307/1446479>
49. Solleliet-Ferreira, S., Macena, B. C. L., Laglbauer, B. J. L., Sobral, A. F., Afonso, P., & Fontes, J. (2020). Sicklefing devilray and common remora prey jointly on baitfish. *Environmental Biology of Fishes*, 103(8), 993–1000. <https://doi.org/10.1007/s10641-020-00990-9>
50. Stevens, G. M. W., Hawkins, J. P., & Roberts, C. M. (2018). Courtship and mating behaviour of manta rays *Mobula alfredi* and *M. birostris* in the Maldives. *Journal of Fish Biology*, 93(2), 344–359. <https://doi.org/10.1111/jfb.13768>
51. Stobart, B., Díaz, D., Álvarez, F., Alonso, C., Mallol, S., & Goñi, R. (2015). Performance of baited underwater video: does it underestimate abundance at high population densities? *PloS One*, 10(5), e0127559. <https://doi.org/10.1371/journal.pone.0127559>

52. Thieurmél, B., & Elmarhraoui, A. (2026). *Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*. mirrors.aliyun.com. <https://mirrors.aliyun.com/CRAN/web/packages/suncalc/suncalc.pdf>
53. Twining, J. P., & Kellner, K. F. (2026). Can hierarchical modelling of co-occurrence data provide accurate inference into species interactions? *Methods in Ecology and Evolution*, 17(2), 456–479. <https://doi.org/10.1111/2041-210x.70210>
54. van Rij, J., Wieling, M., & Baayen, R. H. (2020). *Interpreting time series and autocorrelated data using GAMMs* (2nd edn). CRAN. <http://download.nust.na/pub3/cran/web/packages/itsadug/itsadug.pdf>
55. Venables, S. K., Rohner, C. A., Flam, A. L., Pierce, S. J., & Marshall, A. D. (2024). Persistent declines in sightings of manta and devil rays (Mobulidae) at a global hotspot in southern Mozambique. *Environmental Biology of Fishes*. <https://doi.org/10.1007/s10641-024-01576-5>
56. Venables, S. K., van Duinkerken, D. I., Rohner, C. A., & Marshall, A. D. (2020). Habitat use and movement patterns of reef manta rays *Mobula alfredi* in southern Mozambique. *Marine Ecology Progress Series*, 634, 99–114. <https://doi.org/10.3354/meps13178>
57. Venables, S.K. (2020). *Ecology and conservation of a threatened reef manta ray (Mobula alfredi) population in southern Mozambique [Doctoral dissertation]*. University of Western Australia.
58. Whitmarsh, S. K., Fairweather, P. G., & Huveneers, C. (2017). What is Big BRUVver up to? Methods and uses of baited underwater video. *Reviews in Fish Biology and Fisheries*, 27(1), 53–73. <https://doi.org/10.1007/s11160-016-9450-1>
59. Wood, S. (2017). *mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation and GAMMs by REML/PQL*. <https://www.typeerror.org/docs/r/library/mgcv/html/mgcv-package>

Figures

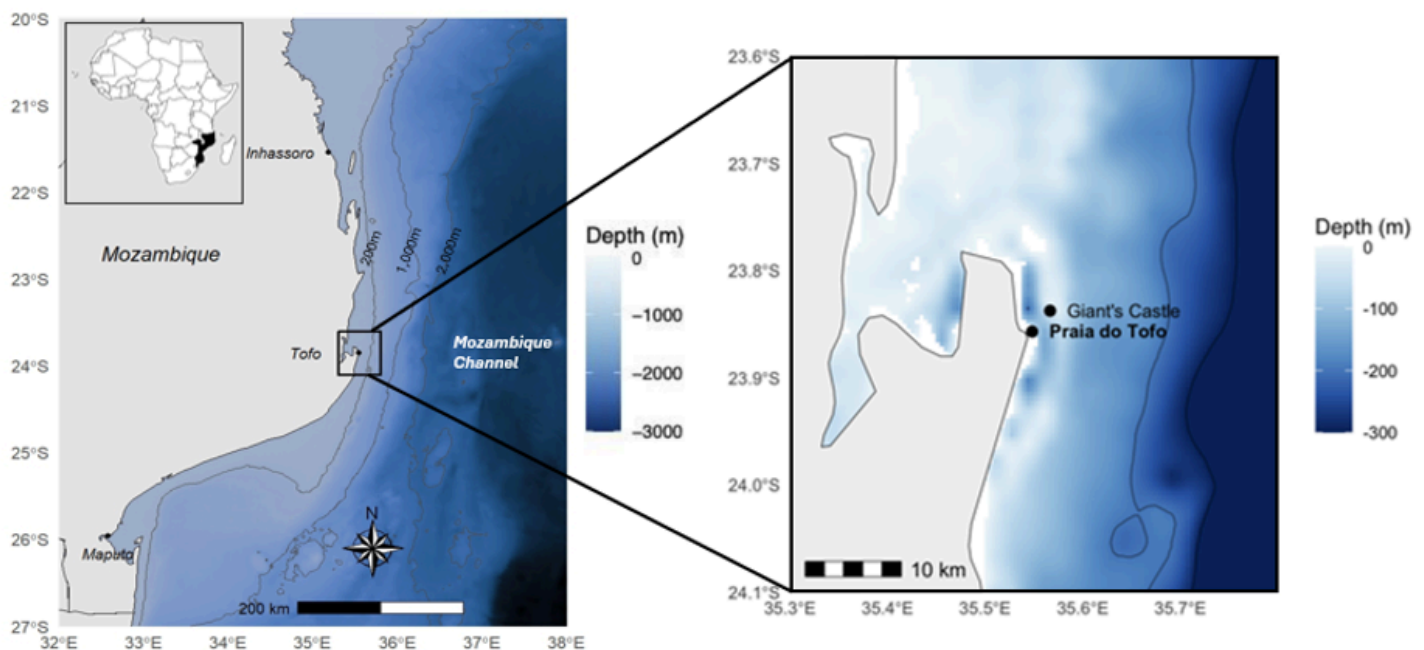


Figure 1

Map of the study region in Mozambique. Left panel: Southern region of Mozambique with the Tofo region in a bounding box. Inset left: country of Mozambique highlighted in black. Right panel: the Tofo region and the Giants Castle dive site.

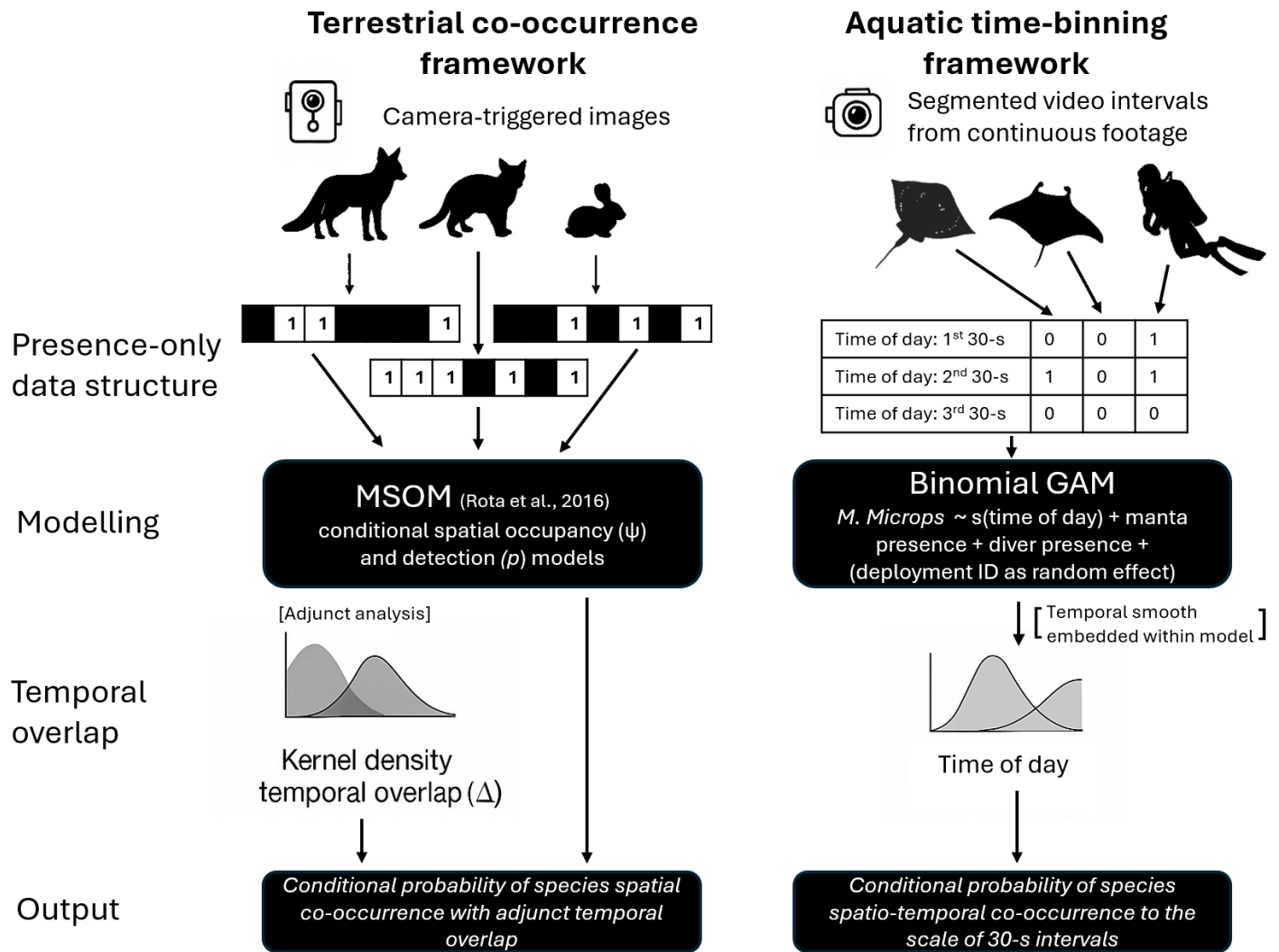


Figure 2

A conceptual comparison between terrestrial multispecies co-occurrence modelling and the aquatic long-life remote underwater video (LL-RUVS) data time-binning framework used in the present study. Left: In terrestrial camera-trap studies, species detections arise from camera-triggered images, producing presence-driven detection histories that feed into multispecies occupancy models (MSOM; Rota et al. 2016), which estimate conditional spatial occupancy (ψ) while explicitly modelling imperfect detection (p). Temporal overlap between species is usually assessed separately via kernel density activity curves (Δ), representing an adjunct rather than an integrated component of the co-occurrence model. Right: Continuous LL-RUVS footage was segmented into 30-s intervals, and each interval was coded for the presence of *Megatrygon microps*, manta spp., and divers. A binomial GAM was then fitted to the interval-level detection data, modelling *M. microps* presence as a function of time of day and manta/diver presence. This framework yields conditional spatio-temporal co-occurrence, integrating diel patterns directly within the model structure and resolving behavioural-scale interactions at 30-s resolution.

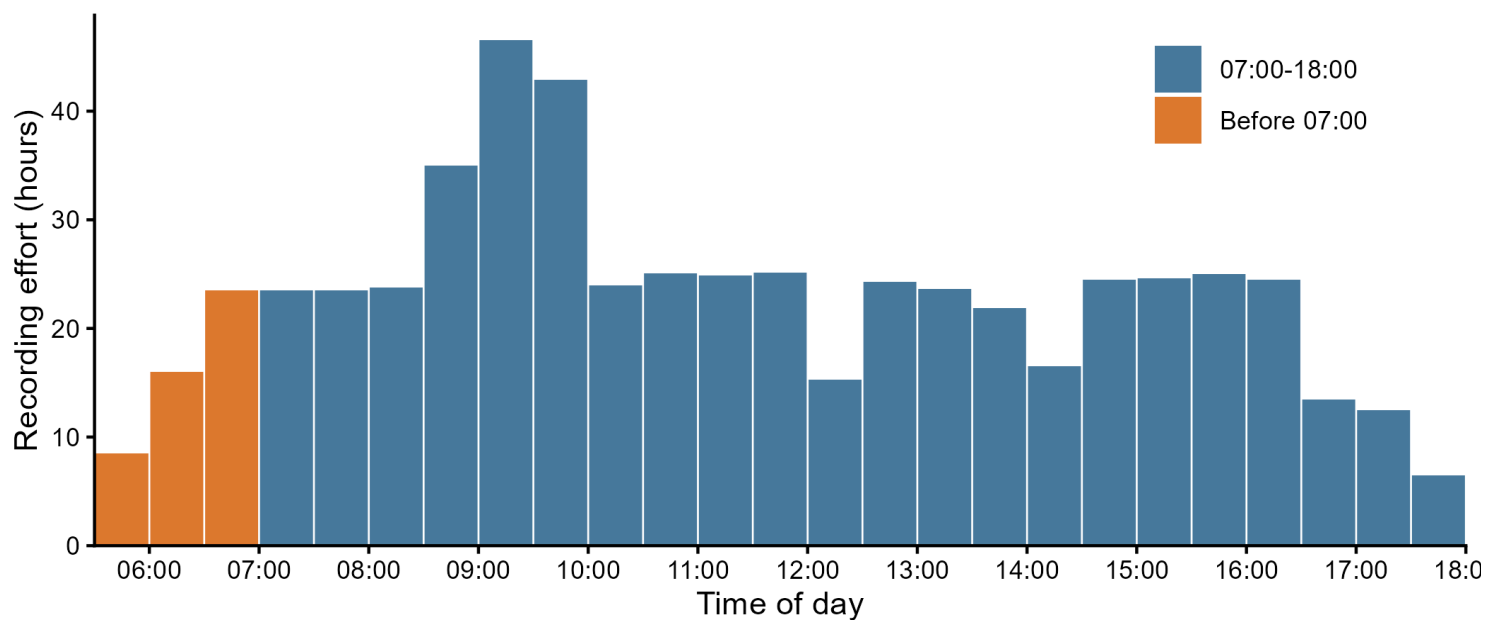


Figure 3

Recording effort per 30-minute interval throughout the recording day (05:30 – 18:00) summed across all recordings (total 519 h 05 min 15 s). Effort ranges from 5.5 h to 40.3 h per bin.

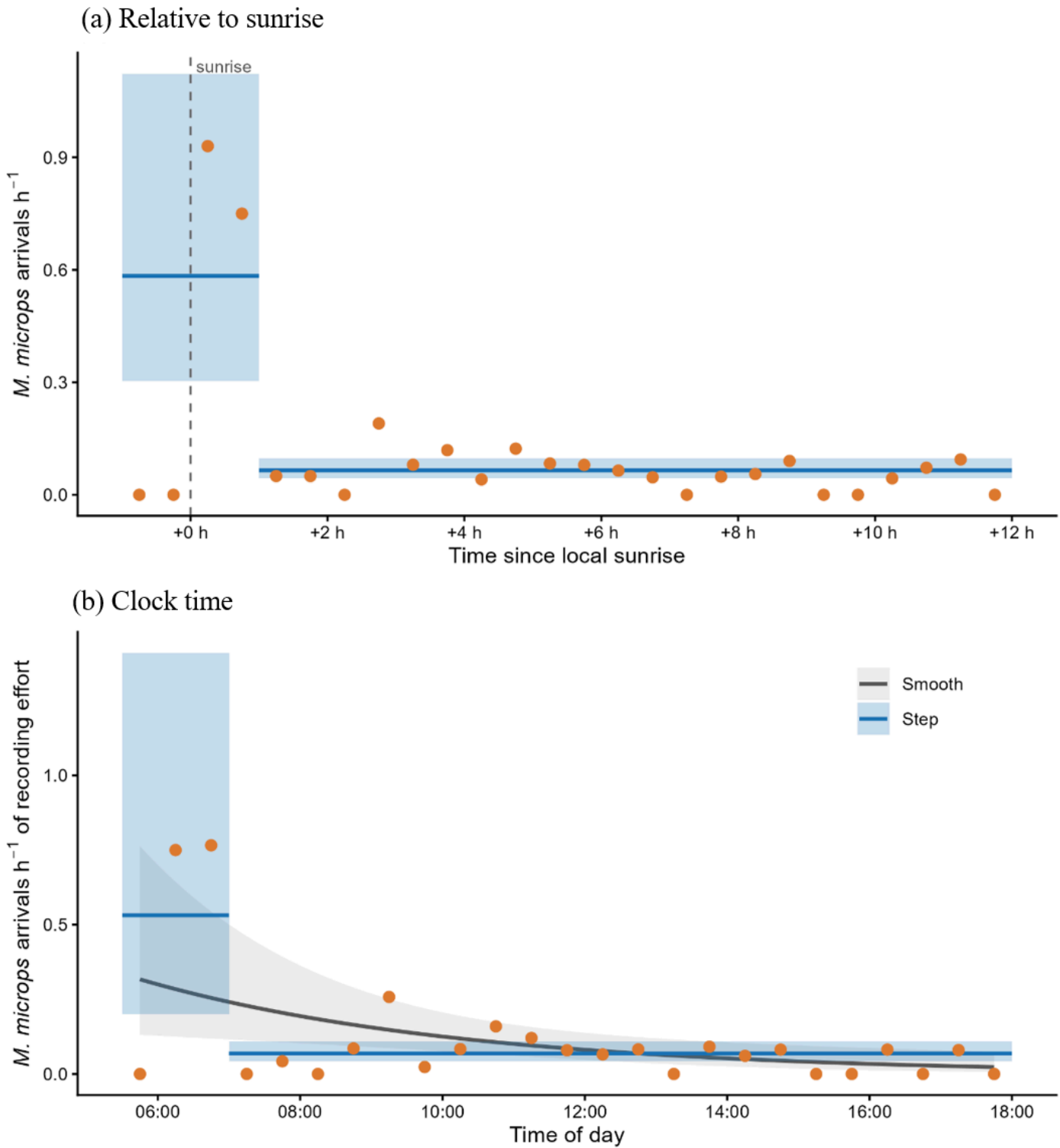


Figure 4

Arrival rate of *Megatrygon microps* per hour of recording effort at Giants Castle reef, Tofo Mozambique. (a) By time since local sunrise, with the step model at +60 min (blue) (b) By clock time, with the fitted negative-binomial smooth (grey) and step model at 07:00 (blue). The dashed line marks sunrise. Points are effort-corrected rates per 30-minute interval; ribbons and shaded rectangles show 95% confidence intervals. No arrival was recorded before sunrise on any date.

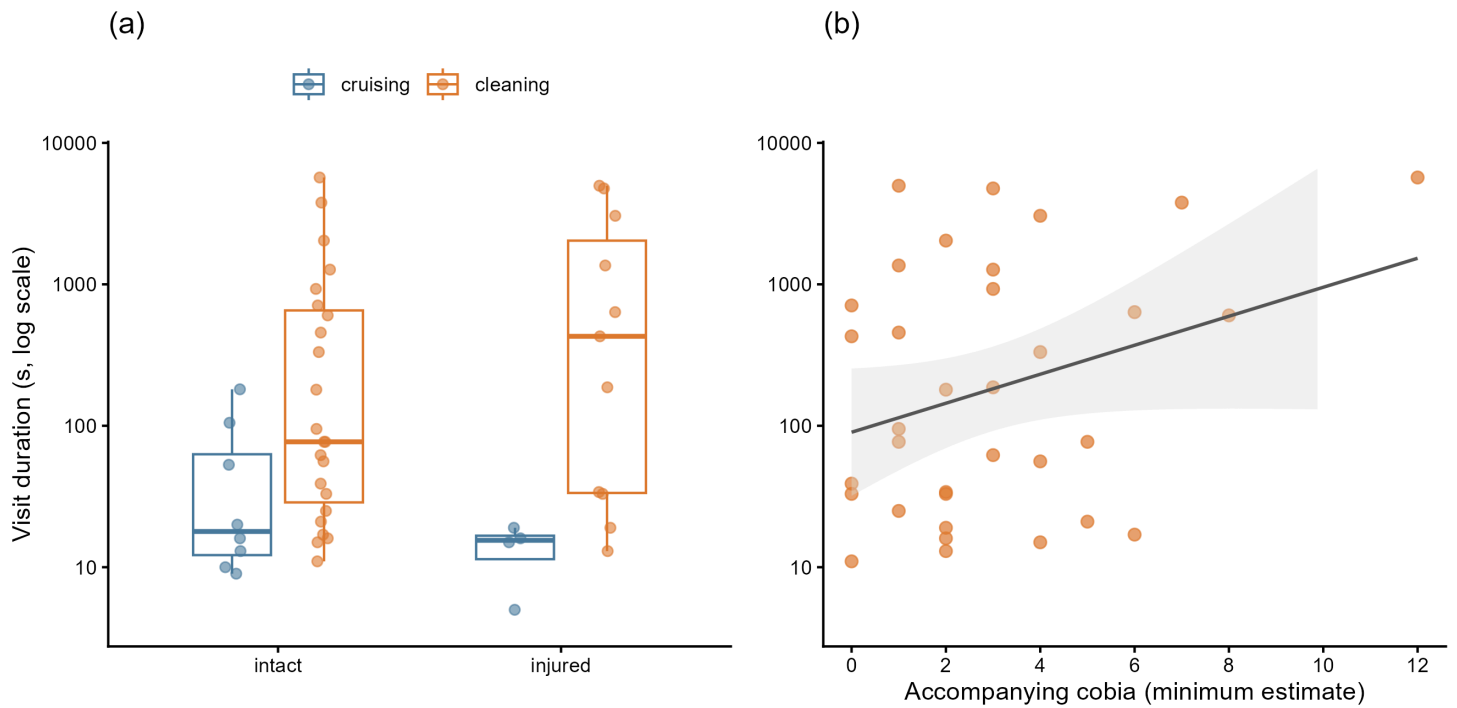


Figure 5

Visit duration of individual *Megatrygon microps* at Giants Castle cleaning station. (a) Visit duration by injury status (shark-bite wound, or short or absent tail) and behavioural state, for the 46 individuals with behaviour, injury and cobia all recorded. (b) Visit duration against the minimum number of accompanying cobia, for the 34 individuals engaged in cleaning; line and shading show a linear fit on the log scale with 95% confidence interval.

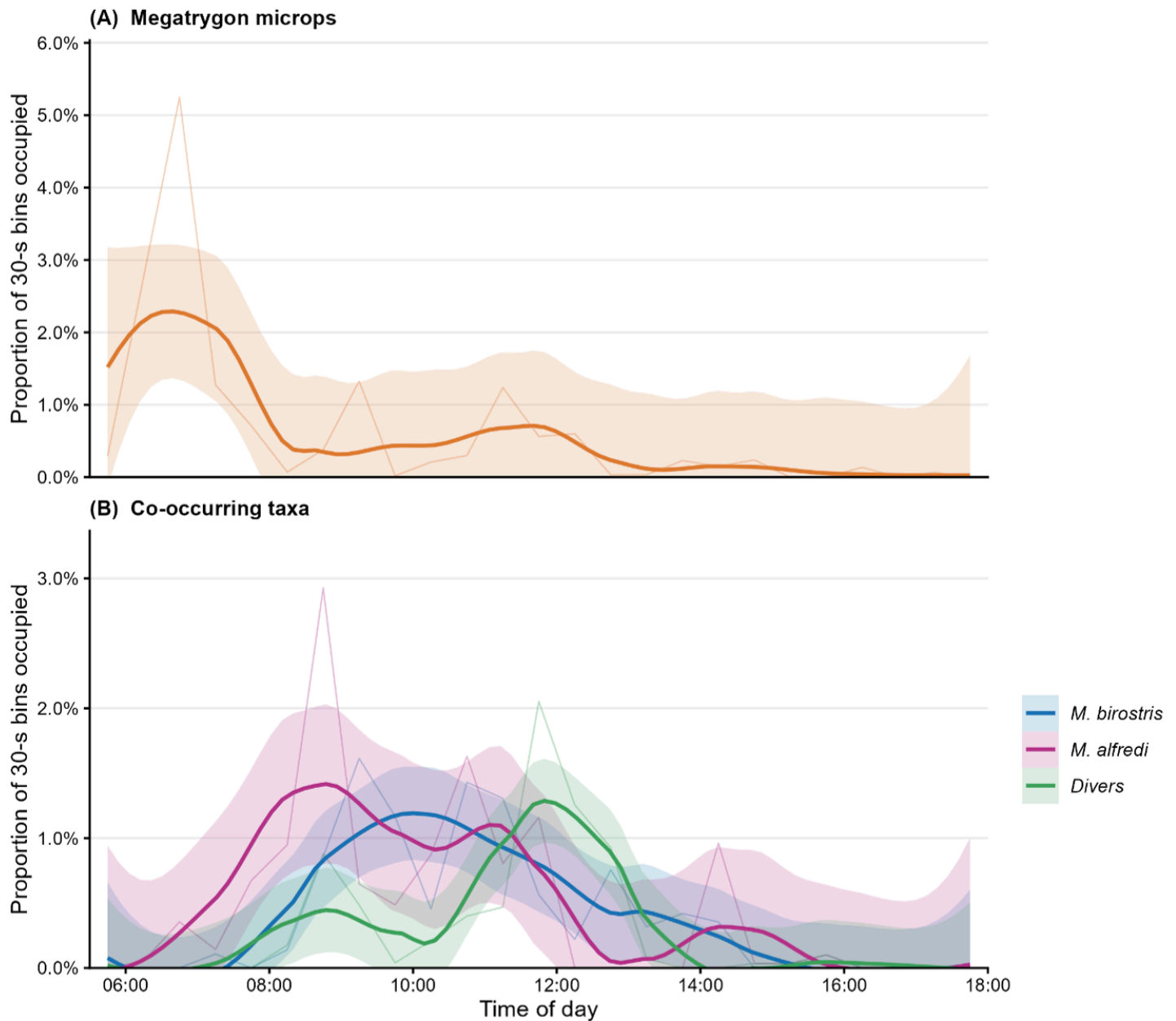


Figure 6

Diel occurrence patterns of *Megatrygon microps* and co-occurring taxa recorded from an LL-RUV at Giants Castle Reef in Tofo Mozambique between 2021-2024. (A) Proportion of 30-second recording intervals in which *M. microps* was present. (B) Equivalent metric for *Mobula birostris* (blue), *M. alfredi* (pink), and SCUBA divers (green). Solid lines show loess-smoothed estimates; shaded ribbon indicates 95% confidence intervals; faint lines show 30-minute interval proportions.

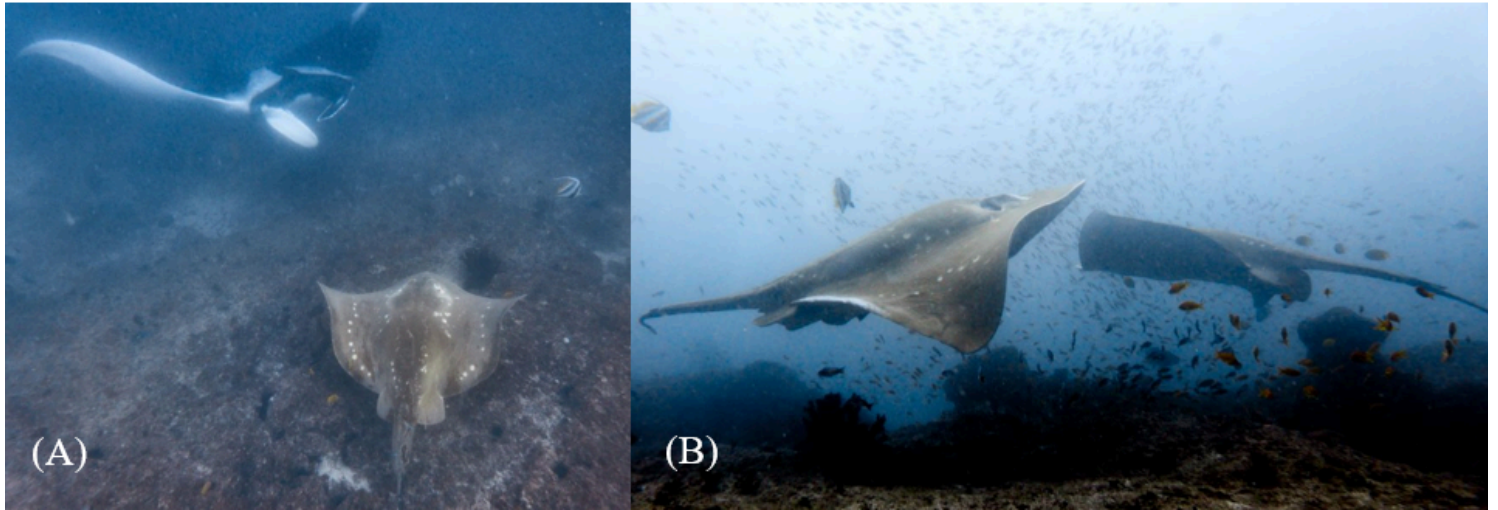


Figure 7

Diver images from the camera deployment site showing (a) *Mobula birostris* (left) and *Megatrygon microps* (right) and (b) two *M. microps* sharing the cleaning station area. Photo Credit: J. Keeping

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [ESMall.xlsx](#)