



Behavior, site use and demographics of shortfin devil rays, *Mobula kuhlii*, at a newly-discovered cleaning area in South Africa

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Abstract

Many shark and ray species show affinity to specific sites, making these areas critical for their survival. These include cleaning stations: locations on reefs where cleaner fish remove parasites and clean wounds, which is important for maintaining health. Cleaning stations also function as social gathering sites, or resting points, where courtship and mating can occur. In this study, we identify an aggregation site for the shortfin devil ray, *Mobula kuhlii* (Family Mobulidae) within the Aliwal Shoal Marine Protected Area in KwaZulu-Natal (KZN), South Africa, and document their behavior. Remote underwater video was used to collect footage of *M. kuhlii* being cleaned by blue streak cleaner wrasse, *Labroides dimidiatus*. Generalized additive models (GAMs) were used to assess environmental predictors of *M. kuhlii* presence on Aliwal Shoal. Mixed models were used to assess the same environmental predictors and their correlation with mean *M. kuhlii* cleaning duration and number of *L. dimidiatus* bites per second at the identified cleaning station site. *M. kuhlii* were present in 56% of observation days, with group numbers up to > 150 individuals. Sea surface temperature was a significant predictor for *M. kuhlii* presence, while a north to south current was significantly associated with longer mean cleaning durations. These results support findings of mobulid studies in KZN that show increased habitat use during summer temperatures (24–25 °C) and suggest these sites to be important for individual health and social interaction. We hope these findings can be used for development of location-specific management plans to safeguard this Endangered species.

Keywords KwaZulu-Natal · Mobulidae · Aliwal shoal · Marine protected areas · Animal behavior · Generalized additive models · Mixed models

Introduction

Marine cleaning stations are areas of reef where a client (teleost, shark, ray, turtle) visits to have parasites or dead tissue removed by cleaner fish (Limbaugh 1961; Feder 1966; Losey 1972) or shrimps and have been studied for over 70 years. Keyes (1982) first described shark cleaning behavior in an aquarium, observing Atlantic lemon sharks (*Negaprion brevirostris*), Pacific lemon sharks (*N. acutidens*), a bull shark (*Carcharhinus leucas*), sandbar sharks (*C. plumbeus*),

and nurse sharks (*Ginglymostoma cirratum*) being cleaned by the bluestreak cleaner wrasse *Labroides dimidiatus*. Subsequently, this behavior has been documented in free-living elasmobranch species at various locations (Table S1). Most shark and ray (Elasmobranchii) species likely benefit from cleaning services, but only a handful of such species have been observed being cleaned in the wild.

Elasmobranchs are ubiquitously infected by metazoan parasites, such as gnathid isopods and caligid copepods, which can lead to lesions, necrosis, anemia, and respiratory diseases (Caira and Healy 2004). Cleaning behavior can alleviate these effects, and has been linked to better body condition in some fish species when compared to conspecifics who did not have access to cleaning stations (Ros et al. 2020). In addition to providing essential health services, cleaning stations function as social aggregation and courtship/mating grounds for elasmobranchs (Oliver and Kaszo 2015; Stevens 2016; Perryman et al. 2019, 2022a). Individuals or groups of clients repeatedly return to cleaning stations

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seasonally or periodically throughout the year, often displaying long-term affinity to specific sites (Oliver et al. 2011; Germanov et al. 2019; Perryman et al. 2019). Thus, these locations can play a crucial role in the health and reproduction, of many elasmobranch species, serving as habitats to which they consistently return.

The family Mobulidae (*Mobula* spp.) are pelagic/epipelagic, migratory species found circumglobally in tropical, subtropical, and temperate seas (Notarbartolo di Sciara 1987; Stewart et al. 2018). Mobulid species have K-selected reproductive strategies, reproducing by aplacental vivipary, with late maturation and the lowest reported fecundity among elasmobranchs (Dulvy et al. 2014), making them highly vulnerable to exploitation and incidental capture (Couturier et al. 2012; Croll et al. 2016). All mobulids are listed as Vulnerable or Endangered on the IUCN Red List of threatened species as a result of directed capture for the gill plate trade in Asia and incidental capture as bycatch by industrial trawlers, gill nets, seine nets, and longlines throughout their distribution (Croll et al. 2016). *Mobula kuhlii* is listed as Endangered (Rigby et al. 2022) with declines in sighting records of up to 99% being observed in Tofo, Mozambique (Rohner et al. 2017). However, little is known about this species in South Africa, which is the southernmost limit of its range in the Western Indian Ocean (Rigby et al. 2022).

Although known to be heavily parasitized by caligid copepods in KwaZulu-Natal (KZN), South Africa (Lebepe and Dippenaar 2013), the only reported occurrence of *M. kuhlii* at cleaning stations is from the Bazaruto Archipelago, Mozambique (Murie and Marshall 2016) and no such sites are known from South Africa. Other mobulid species including manta rays have been found to inhabit the KZN coastline from Richard's Bay in the north southwards to Port Edward, with significantly more presence in summer and in the area encompassing Aliwal Shoal (Carpenter et al. 2023). Many different mobulid species have been caught in the area (Young 2001). Apart from one study that documented first-time courtship behavior of *M. kuhlii* at Aliwal Shoal (Carpenter and Griffiths 2023), no research on this species has been conducted in the country to date.

In this study we document sightings, habitat use, and behavior of *M. kuhlii* in the Aliwal Shoal Marine Protected Area (MPA), in KZN. This includes the discovery and description of a cleaning station area for this species. As mobulid habitat use is known to be influenced by environmental cues, we used Generalized Additive Models to assess 1) environmental effects (sea surface temperature, current) on the presence of *M. kuhlii* on Aliwal Shoal and 2) cleaning durations on Angels Ledge (AL) cleaning station. Using Remote Underwater Video (RUV) we describe interspecific cleaning behavior and interactions with cleaner fish. The results are informative for understanding fine-scale habitat use of this understudied species.

Materials and methods

Study area

The Aliwal Shoal Marine Protected Area (MPA), is a subtropical sponge and algal reef located four km offshore from the mKomzai River Mouth in KwaZulu-Natal Province (KZN), South Africa (Olbers et al. 2009) (Fig. 1). The reef is influenced by the dominant south-flowing Agulhas Current, which brings warm, nutrient-poor water from the Mozambique Channel; as well as by wind-driven eddies and subsequent upwellings which bring in nutrient rich and productive waters (Heydorn et al. 1978; Hutchings et al. 2002). Aliwal Shoal is renowned for its biodiversity, and specifically, as a site for encounters with rare and threatened sharks, such as the ragged tooth shark (*Carcharias taurus*) and tiger shark (*Galeocerdo cuvier*) (Dicken et al. 2006; Dicken and Hosking 2009). An area covering 18.3 km of coastline and 126 km² of ocean was designated an MPA in 2004, to prevent anchoring and mooring of vessels, and extraction of marine resources (Marine Living Resources Act No. 18 of 1998, Government Gazette No. 26433, South Africa 2004). The study area was in the Crown Area Restricted Zone, which is approximately 1 km long, and 280–890 m wide, encompassing an area of 2.1 km² (Bosman et al. 2005), with an average depth of 12.5 m, but reaching as shallow as 6 m (Bosman et al. 2007).

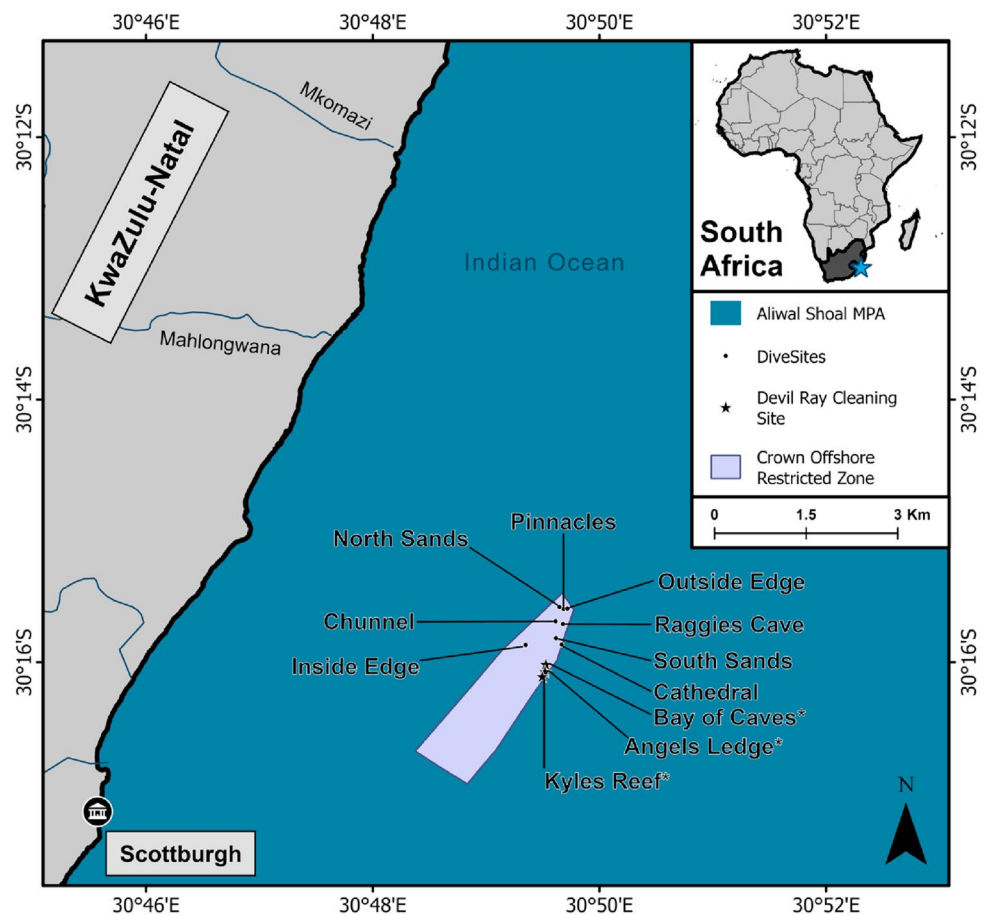
Data collection

Sightings logbook

Data were collected from opportunistic recreational SCUBA or snorkeling trips between September 2020 and March 2022. Eleven sites varying in depth (6–26 m) and in exposure to swell and wave action within the Crown Area Restricted Zone in Aliwal Shoal (Fig. 1; Table S2) were surveyed for *M. kuhlii* cleaning stations. Due to the close proximity of the sites to one another and the frequent currents that occur at Aliwal Shoal, multiple named sites were often visited during a single survey.

A single recreational 'dive', or a recreational snorkel 'drift', was defined as a single drift over the reef from one location to another, going with the current. The names of the sites and the times spent at each were recorded in situ using an underwater slate and underwater dive computer. The time spent at each location was measured as effort, with minute (min) being the unit of effort. The maximum number of individuals of *M. kuhlii* (Max N) present at the same time, and their behaviors, were recorded during

Fig. 1 Map showing dive sites where *Mobula kuhlii* were encountered during recreational snorkeling or SCUBA diving at the Crown Restricted Zone of Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa between 2020–2022



each dive. Sightings per unit effort (SPUE) were then calculated for each site. Environmental conditions recorded were current direction (N, S, E, W, or 'none'), wind speed (km/h), wind direction ($^{\circ}$), sea surface temperature (SST; 1°C intervals), bottom sea temperature (BST; 1°C intervals), and estimated horizontal visibility (m). Temperature was measured using an underwater dive computer. Daily moon phase data were sourced from the 'suncalc' package (Thieurmel and Elmarhraoui 2019) in R Studio (R Core Team 2021).

'Cleaning' behavior was defined as observation of a cleaner fish making obvious contact with the body of one or more *M. kuhlii*. The observation of cleaning behavior at a specific location in at least two survey days resulted in the location being designated a cleaning station. A surface marker buoy signaled the skipper on the surface to mark the precise coordinates of such sites on a Lowrance Elite 5 GPS system.

Collecting footage of *Mobula kuhlii* cleaning behavior

Due to frequent observations of cleaning behavior during preliminary surveys, one cleaning station (Angels Ledge (AL), Figure S1), at a depth of 22 m, was selected for more

detailed observation of *M. kuhlii* cleaning behavior. Remote underwater video (RUV) was obtained by placing a GoPro Hero 5 or Hero 9 attached to two 1 kg dive weights in the sand facing the ledge by freediving or during recreational SCUBA dives. Two RUVs were placed for one hour at a time, back-to-back to ensure no overlap in field of view, et al. (Figure S1). These then gathered video data of *M. kuhlii* cleaning behavior in the absence of humans.

Evaluating/processing data

Coding behavior and cleaning interactions

Videos were processed using frame by frame analysis in BORIS Software (Friard and Gamba 2016), whereby user-defined behaviors could be permanently logged, as point or continuous observations, showing their frequencies and durations. When *M. kuhlii* were present in the video the maximum number (Max N) of individuals present in one frame was recorded. Behavior data could not be collected on separate *M. kuhlii* individuals due to the inability to identify them by unique spot patterning as it is currently unknown how to distinguish individuals of this species. The sex of each individual, maturity status, and present and type of

injuries were recorded, where possible. Sex was determined by presence or absence of claspers, with fully extended claspers signifying a mature male, and the presence of mating scars or pregnancy indicating mature females (Notarbartolo di Sciara 1987; Marshall and Bennett 2010a; White et al. 2006). Injuries were identified by crescent-shaped scars, which were attributed to predation (Marshall and Bennett 2010b), or triangular scars and/or truncated tail injuries, which were attributed to either predation or entanglement in monofilament (Deakos et al. 2011; Germanov et al. 2019). Sex ratio and injury prevalence were calculated based only on individuals that were close enough to the camera during video recording to describe these.

Cleaning interactions were defined as any cleaner fish making contact with ('biting') a *M. kuhlii*, indicating attempted parasite removal (Oliver et al. 2011; Murie et al. 2020). Cleaning time was defined as periods of time where cleaner fish were surrounding *M. kuhlii* individuals, or within 1 m of them, but not necessarily biting the whole time. This allowed for determination of the cleaning effort (average bites per second of cleaning time). Several aspects of cleaning behavior were recorded, including 'hovering or

swimming slow' (Fig. 2a), 'jolting' (Fig. 2b), when a client suddenly jerks part or all of its body, possibly in response to 'cheating' cleaner fish (Soares et al. 2008) or uncomfortable interactions, 'posing' (Fig. 2c) which involves terminating pectoral fin beats and opening the mouth and gills (O'Shea et al. 2010), and 'following' (Fig. 2d) which involves mobulid individuals following each other around a cleaning station (Perryman et al. 2021).

'Cruising' behavior was recorded when *M. kuhlii* were swimming in one direction, either singly or in a group, with the cephalic lobes furled and clearly not engaged in cleaning (Table 1). If individuals were observed in the area and exhibiting aspects of cleaning behavior, but were too far away to detect cleaner fish bites, this was recorded as 'cleaning out of sight'.

As different areas of a client's body are known to host different parasites (Bshary and Grutter 2002; Caira and Healy 2004; Marshall 2008; Oliver et al. 2011; Murie et al. 2020), both the number of bites and the region of the body being cleaned were recorded. The same eight body patches outlined by Murie et al. (2020) were used to evaluate the specific areas of *M. kuhlii* cleaned by a

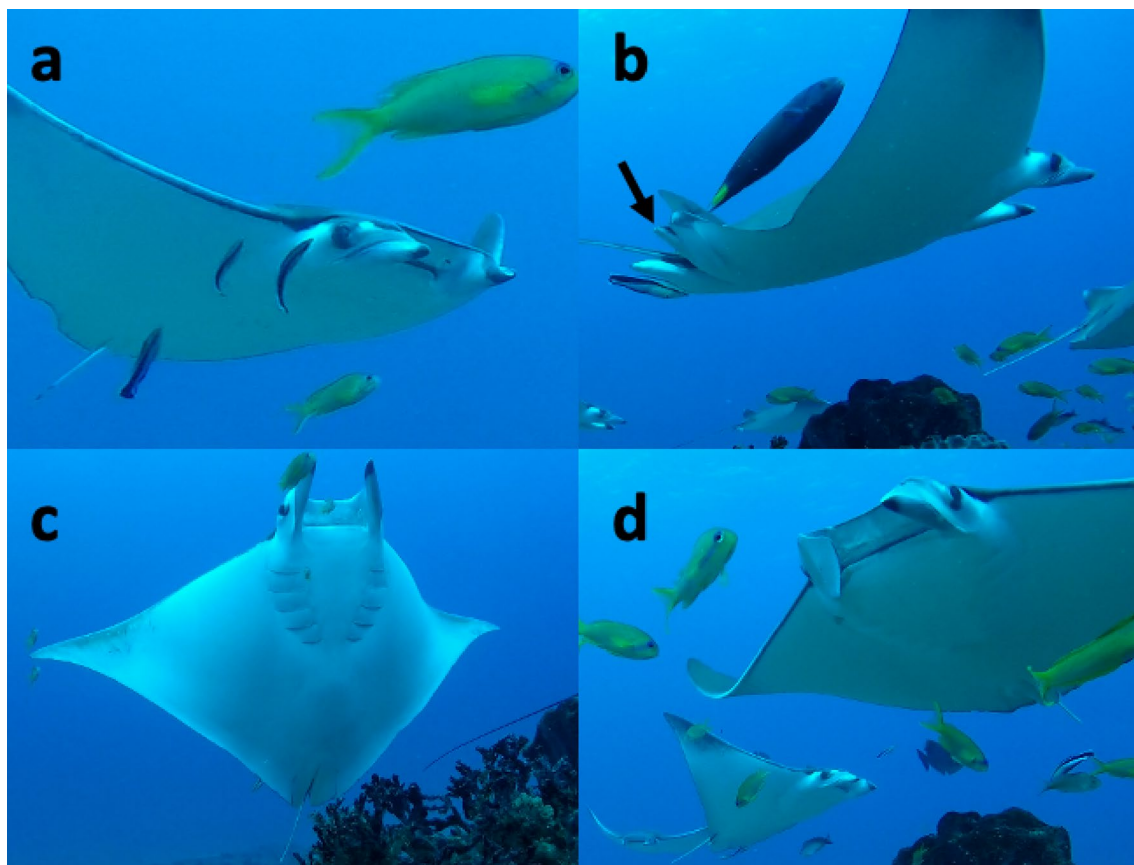


Fig. 2 Types of *Mobula kuhlii* cleaning behavior including (a) 'hovering/swimming slow', (b) 'jolting', (c) 'posing', and (d) 'following' photographed at Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa

Table 1 Ethogram of shortfin devil ray, *Mobula kuhlii*, behaviors opportunistically observed on Angels Ledge, KwaZulu-Natal, South Africa and recorded in BORIS software, between January 2021 and March 2022

Behavior	Type	Description	Modifiers
Cleaning	State	One or more <i>L. dimidiatus</i> individuals being within 1 m of one or more <i>M. kuhlii</i> Sex, cephalic lobe position, and injuries recorded each time, when possible	Hovering/swimming slow: swimming slowly in and around the cleaning station during cleaning Posing: Terminating the pectoral fin beats, opening the mouth and gills, and vertical positioning Jolting: body shutters in response to a cleaner fish bite Following: Two or more <i>M. kuhlii</i> individuals following one in and around the cleaning station during cleaning
Cleaner fish bite	Point	The mouth of <i>L. dimidiatus</i> making contact with a <i>M. kuhlii</i> individual	Dorsal head, dorsal body, ventral head, gills, ventral body, pectorals ventral, pelvic ventral, tail
Cleaning out of sight	State	Cleaning behavior that was observed but too far away to detect <i>L. dimidiatus</i> bites	None
Cruising	State	One or more <i>M. kuhlii</i> swimming in a direction, either solitary or in a group, with the cephalic lobes furled and clearly not engaged in cleaning	None
Courtship	State	One or more <i>M. kuhlii</i> actively engaged in courtship behavior as per the description by Stevens et al. 2018	Initiation: Male(s) mimic the female's movements, following behind her; both the male and female maintain cruising speed. A male may attempt to position his body on top of the female's back facing in the same direction. This action may involve the male unfurling cephalic cephalic lobes and positions them so they are in contact with the dorsal head region of the female
Other species cleaning	State	Other species greater than 1 m in total length or disc width cleaning on Angels Ledge	Spotted eagle ray, <i>Aetobatus ocellatus</i> Pickhandle barracuda, <i>Sphyrna jello</i> Round ribbontail ray, <i>Taeniurops meyeri</i> Bull ray, <i>Aetomylaeus bovinus</i> Giant trevally, <i>Caranx ignobilis</i>

cleaner fish, these being: tail, gills, pelvic fins (ventral), ventral body cavity, ventral pectoral fins, ventral head, dorsal head, and dorsal body (Figure S2). Cleaner interactions were recorded in BORIS software using a point-event function named 'Cleaner fish bite', with body part selected as a modifier. Cephalic lobe positions were also recorded when they changed during a cleaning interaction (both unfurled, both furled, one unfurled and one furled) to compare with manta ray cephalic lobe use at cleaning stations (Perryman et al. 2021).

Cleaning species have been suggested to compete with one another and to prefer larger over smaller clients (Kitchen-Wheeler 2013). Therefore, the presence of other species that had a total length or disc width of 1 m or greater simultaneously cleaning on AL, such as spotted eagle rays *Aetobatus ocellatus*, pickhandle barracuda *Sphyrna jello*, round ribbontail rays *Taeniurops meyeri*, potato groupers *Epinephelus tukula*, bull rays *Aetomylaeus bovinus*, or giant trevally *Caranx ignobilis*, were also recorded as observations in BORIS. Interactions with these species were then compared with *M. kuhlii* cleaning durations and cleaner fish bite numbers to determine effects of multiple species using the same cleaning station.

Statistical analysis

Mobula kuhlii presence on aliwal shoal

Generalized additive models (GAMs) fitted with binomial error distributions were used to investigate the effects of environmental conditions on the presence or absence ('probability of encounter') of *M. kuhlii* on the Aliwal Shoal MPA. We fitted GAMs using the packages 'mgcv' and 'nlme' (Wood 2006) in R software (R Core Team 2021). Data were used from one snorkel drift or dive in a single day, to avoid double counting of encountered *M. kuhlii*. A stepwise analysis was used to test effects of all variables recorded during a recreational dive or snorkel drift. Moon phase was included with a cyclical smoother and current direction as a categorical variable (Wood 2006). Sequential F-tests were used to determine the covariates that were significant ($p < 0.05$) to the deviance explained, with non-contributing variables removed from the final model. A Chi square analysis comparison of all models was used to select the best fitted model. The model used to predict *M. kuhlii* presence on Aliwal Shoal MPA was as follows:

$$\text{logit}(p) = \alpha + s1(\text{SST})$$

where logit denotes the binomial link function, p is the likelihood of encountering at least one individual, α is the intercept, and $s1$ signifies a standard smoothing function for SST (Wood 2006).

Cleaning interactions

From the remote underwater video (RUV) cameras, basic statistics on behavior were produced and exported using the ‘synthetic time budget’ code in BORIS software (Friard and Gamba 2016). From this, mean durations of behaviors were calculated (\pm Standard Deviation). To test the effects of the same environmental parameters tested for *M. kuhlii* presence, as well as the presence of other megafauna cleaning at the same cleaning station, on mean *M. kuhlii* cleaning duration (s), a mixed model with gamma distribution was used, with day as a random effect, to account for the lack of independence of many of the remote videos. Mean cleaning duration (s) and number of bites per second (bites / s) were both included in the model sets. These were used instead of total cleaning duration (s), to avoid bias in the abundance or total amount of rays present on the cleaning station. The videos collected by RUVs, were placed at 22 m and were consistently in waters at least 1 degree less than the surface temperature, as displayed by the underwater dive computer. Therefore, Bottom Sea Temperature (BST; °C), instead of SST, was used to account for thermoclines that may affect cleaning visitation. Current direction was treated as a categorical variable. Sequential F-tests were used to determine the covariates that were significant ($p < 0.05$) to the deviance explained, with non-contributing variables removed from the final model list. Due to a lower sample size from the RUVs, the predictors were assessed individually. The final selected model for testing environmental predictors on mean *M. kuhlii* cleaning behavior duration on AL was:

$$Y_{\text{Mean Cleaning Duration}} = (\beta_0 + \beta_{0j}) + \text{BST} + \text{Current} + \text{Visibility}$$

The final model for testing environmental predictors and mean cleaning duration (s) on mean *L. dimidiatus* bites per second on *M. kuhlii* during cleaning was:

$$Y_{\text{Mean Bites Per Second}} = (\beta_0 + \beta_{0j}) + \text{BST} + \text{Current} + \text{Visibility}.$$

Gamma regression models were fit using `stat_smooth` function in package `ggplot2` (Wickham 2016).

We compared the average number of bites per body patch by *L. dimidiatus* during cleaning behavior and plotted this. To further elucidate the specific body patches preferred by *L. dimidiatus* of cleaner fish preferences, pairwise comparisons between different body parts were conducted with a Kruskal–Wallis test and Dunn test with Bonferroni

correction for multiple comparisons (Dunn 1961), in R software which was used in all statistics (R Core Team 2021). The z-test was used to describe the relationship to the mean group of values in order to confirm *L. dimidiatus* preference of one *M. kuhlii* body patch over another.

Results

Mobula kuhlii visitation to Aliwal Shoal

A total of 329 recreational dives/snorkeling drifts by a single diver were made across 144 days between September 2020–March 2022. From these, *Mobula kuhlii* were observed to be present 81 times. Sea surface temperature was the only significant predictor of *M. kuhlii* presence, with probability of occurrence peaking between 24–25 °C (Fig. 3). This model was chosen based on highest significance when compared to other models that included the other predictor variables (edf = 2.346; Ref.df = 2.718; Chi.sq = 10.670; $p = 0.007$).

Cleaning stations were observed on all dive sites on Aliwal Shoal, with clients including teleost fish, sea turtles, and shark and ray species. *M. kuhlii* were only observed cleaning in the area of Angels Ledge (Figure S1), Bay of Caves, and Kyles Reef (Fig. 1; Table S2). The only cleaner fish identified cleaning *M. kuhlii* on these stations was the blue streak cleaner wrasse, *Labroides dimidiatus* (Figure S3). During cleaning an individual *M. kuhlii* would swim slowly, terminate pectoral fin beats by hovering over the cleaning station, or exhibit posing behavior, with pelvic fins angled towards the reef, exposing more of the ventral surface. The number of *M. kuhlii* per minute of diving (mean = 6 ± 10) was highest at Angels Ledge and Kyles Reef (Fig. 4; Table S2), which are adjacent to one another (roughly 30 m apart).

When observed, a group of *M. kuhlii* consisted of an average of 12 (± 10) individuals. The largest group observed

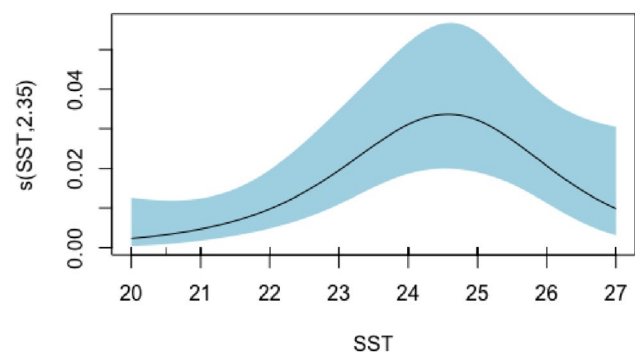
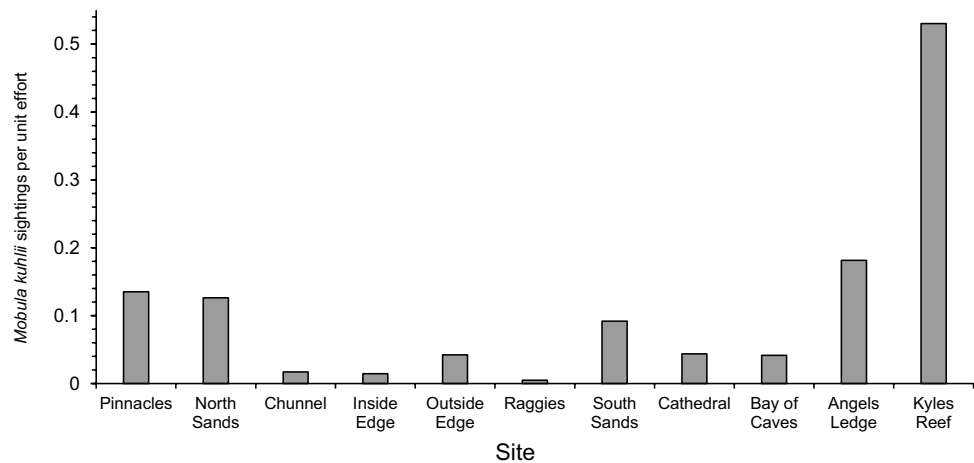


Fig. 3 Significant predictor, Sea Surface Temperature (SST), of *Mobula kuhlii* visitation to the Aliwal Shoal Marine Protected Area, KwaZulu–Natal, South Africa, recorded on recreational snorkeling or diving, between September 2020–March 2022

Fig. 4 Number of *Mobula kuhlii* encounters per minute at various dive sites visited during recreational SCUBA dives and snorkel drifts on Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa between September 2020–March 2022



was > 150 individuals, including at least 10–20 individuals RAM feeding, seen on North Sands on 11 December 2021. Other large groups (between 50–75 *M. kuhlii*) were encountered at Pinnacles, South Sands, AL, and Kyles Reef. When *M. kuhlii* were encountered during recreational dives or drifts, the most common behavior was cruising ($n=36$), followed by cleaning ($n=25$), courtship ($n=6$), feeding ($n=6$), and following spotted eagle rays *Aetobatus ocellatus* ($n=2$), with unknown behavior recorded 7% of the time ($n=6$). Breaching behavior was also observed ($n=5$). *Mobula kuhlii* were present across all temperatures recorded, ranging from 19–27 °C, and in all types of current direction, including the absence of current. However, East or West currents were uncommon (1%). During the study, the estimated horizontal visibility ranged from 6–30 m, cloud cover from 5–100%, wind speed between 0–33 km/hr, and moon phase between 0.005–0.993.

Cleaning behavior

Mobula kuhlii cleaning behavior was described in detail for the first time (Table 1). Remote GoPro mounts were placed in the same spot in the sand in the Angels Ledge cleaning station area during 41 recreational dives between January 2021–March 2022. *Mobula kuhlii* were recorded in 46% ($n=19$) of the videos. Between one and 23 (± 7) individuals were observed cleaning at the same time. Up to five *L. dimidiatus* individuals surrounded a single *M. kuhlii* simultaneously (Figure S3).

A total of 4.04 h (14,571 secs) of *M. kuhlii* cleaning behavior was recorded at Angels Ledge. From this, 1.40 h (5,041 secs) of video was of sufficient quality to analyze specific *L. dimidiatus* bites on specific body parts, types of cleaning behaviors and cephalic lobe positions. A total of 1.18 h (4311 secs) of cruising behavior were recorded. Cleaning behavior had a mean duration of 53.06 secs (± 73.81 s SD) with *M. kuhlii* receiving direct cleaning

bites from *L. dimidiatus* an average of 31.16 (± 47.71 SD) times, with an overall cleaning rate of 0.59 bites/s while cleaning. The most common type of cleaning behavior was ‘hovering’, with a mean duration of 32.04 s (± 46.54 SD), followed by ‘following’ (20.46 s ± 40.41 SD), ‘posing’ (4.61 s ± 12.61 SD), and ‘jolting’ (3.15 s ± 5.14 SD). *Mobula kuhlii* was more likely to clean together with other individuals (total = 4,395 s) than alone (total = 645.99 s).

Mobula kuhlii used a variety of cephalic lobe positions (Figure S4). While cleaning, the cephalic lobes were most commonly both in a furled position (61%; mean = 5.11 times ± 7.40 SD), followed by both being unfurled (20%; mean = 1.63 times ± 2.97 SD), and one unfurled and one furled (19%; mean = 1.56 times ± 2.60). Cephalic lobe positions were changed at a mean of 0.16 times/s (± 0.15 SD position changes/s). *Mobula kuhlii* cephalic lobes were often unfurled simultaneously as one or more *L. dimidiatus* approached their face.

Sex could not be determined for most of the *M. kuhlii* individuals in the video footage, but of those successfully sexed ($n=30$), more were males ($n=22$) than females ($n=8$), with all males being mature ($n=22$), and most females of undetermined maturity and only two confirmed as mature (Figure S5). The most prevalent injuries observed were truncated tails (42), scarred pectoral fin (16), complete loss of tail (4), and bent tail (1) (Figure S6). Individuals with no signs of scarring or injury were observed 17 times, but most *M. kuhlii* observed were too far from the GoPro camera to confidently describe injuries, so 70 individuals were assigned with unknown injuries. *Mobula kuhlii* was found to clean simultaneously alongside one or more spotted eagle rays, *Aetobatus ocellatus* (total time = 207.47 s) (Figure S7), followed by pickhandle barracuda, *Sphyrna jello* (127.73 s), potato groupers, *Epinephelus tukula* (22.76 s), and loggerhead turtle, *Caretta caretta* (3.00 s).

Table 2 Effects of environmental parameters on the mean cleaning duration (s) of *Mobula kuhlii* at the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa. Mixed model with gamma error structure, with mean cleaning duration (s) as dependent variable.

Predictors	Estimates	Std. beta	STD. ci	Std. P
(Intercept)	1.88	1.91	1.31 to 2.50	< 0.001
Bottom sea temperature	-0.00	-0.00	-0.22 to 0.21	0.966
Current (none vs. north)	-0.39	-0.39	-1.14 to 0.37	0.316
Current (South vs. north)	-0.68	-0.68	-1.08 to -0.29	0.001
Current (South vs. none)	-0.30	-0.30	-1.09 to 0.49	0.461
Other animal cleaning	0.00	0.10	-0.09 to 0.28	0.295
Visibility	0.07	0.11	-0.12 to 0.33	0.348
Random effects				
σ^2	0.34			
$\tau_{00 \text{ Day}}$	0.00			
N_{Day}	15			
Observations	52			
Marginal r^2	0.274			

Estimates=Effect size (based on units of variable); Std. Beta=Standardized beta effect size (comparable between variables); Std. CI=Confidence interval (95%) for Std. Beta; Std. P=P-value for Std. Beta. σ^2 =Residual variance; $\tau_{00 \text{ Day}}$ =Random intercept variance (between groups); N_{Day} =Number of groups for random intercept (Day); Marginal R^2 =variance explained by fixed effect predictors relative to the total variance

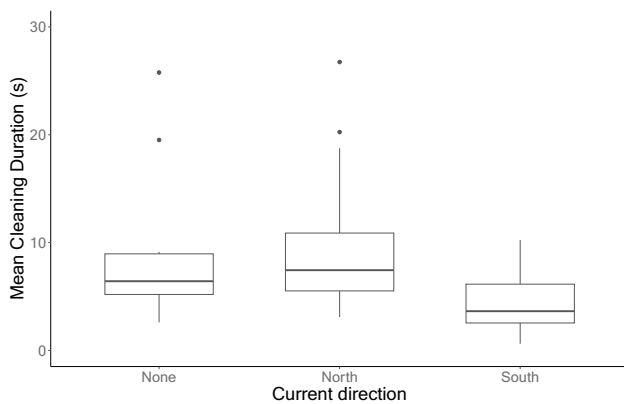


Fig. 5 Mean cleaning duration (s) of *Mobula kuhlii* at Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa, under different current conditions (lack of current, or 'none', current flowing from the north, 'north', and current flowing from the south, 'south'). The thick black lines represent medians, boxes encompass the inter-quartile ranges, whiskers extend to the most extreme data points within 1.5×the interquartile range outside the box, and the dots show data points beyond the whiskers

Cleaning duration

Mean cleaning duration (s) of *M. kuhlii* was significantly correlated with current direction et al. cleaning station (Table 2), with longer cleaning times during currents flowing from north to south (Fig. 5). No other predictors significantly affected mean cleaning duration (Table 2).

The number of *L. dimidiatus* bites per second on *M. kuhlii* while cleaning was significantly correlated with current, bottom sea temperature (BST), and mean cleaning duration (Table 3). Currents flowing south to north

Table 3 Effects of environmental parameters on the number of *Labroides dimidiatus* bites per second of *Mobula kuhlii* at the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa. Mixed model with gamma error structure, with bites per second as dependent variable.

Predictors	Estimates	Std. beta	Std. ci	Std. P
(Intercept)	2.88	-0.52	-0.83 to -0.21	0.001
Bottom temperature	-0.15	-0.28	-0.49 to -0.08	0.007
Current (none vs. north)	0.01	0.01	-0.79 to 0.80	0.984
Current (South vs. north)	0.48	0.48	0.04 to 0.92	0.032
Current (South vs. none)	0.47	0.47	-0.28 to 1.22	0.220
Mean cleaning duration	-0.03	-0.18	-0.35 to -0.01	0.038
Visibility	0.11	0.16	-0.06 to 0.38	0.159
Random effects				
σ^2	0.36			
$\tau_{00 \text{ Day}}$	0.00			
N_{Day}	15			
Observations	52			
Marginal r^2	0.299			

Estimates=Effect size (based on units of variable); Std. Beta=Standardized beta effect size (comparable between variables); Std. CI=Confidence interval (95%) for Std. Beta; Std. P=P-value for Std. Beta. σ^2 =Residual variance; $\tau_{00 \text{ Day}}$ =Random intercept variance (between groups); N_{Day} =Number of groups for random intercept (Day); Marginal R^2 =variance explained by fixed effect predictors relative to the total variance

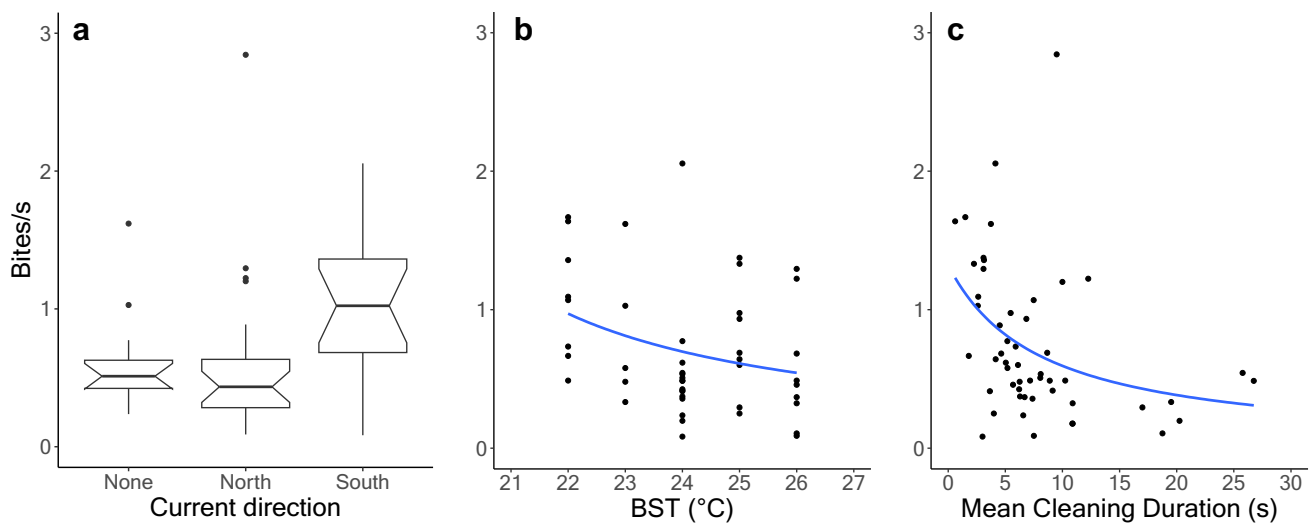


Fig. 6 Cleaner fish bites/s under different environmental conditions, showing variables found to be significant in Table 3: (a) Current direction; (b) Bottom temperature; (c) Mean cleaning duration. Panels (b) and (c) show gamma regression models fit using `stat_smooth` function in `ggplot2`

(South current) resulted in higher bite rates compared to north to south (North current) (Fig. 6), the opposite of the results of mean cleaning duration. This is because higher bites per second rates were significantly correlated with shorter cleaning durations (Fig. 6). Lower bottom temperatures had significantly higher bites per second, with the highest rates generally occurring at 22 °C (Fig. 6).

Mobula kuhlii body patch preference by Labroides dimidiatus

There was a significant difference in *M. kuhlii* body patch foraging preference by *L. dimidiatus* (Kruskal–Wallis, $p < 0.05$). The Bonferroni multiple comparison further supported significant associations or differences among body patch groups (Table 4). More *L. dimidiatus* bites occurred on the dorsal body (significantly higher than dorsal head, gills and tail), and ventral head (significantly more than tail

Table 4 Results (top number, Z-statistic) and adjusted

	Dorsal body	Dorsal head	Gills	PELVIC fins	TAIL	Ventral body	Ventral HEAD
Dorsal head	3.399724 0.0094*						
Gills	4.544579 0.0001*	1.144855 1.0000					
Pelvic fins	-0.083530 1.0000	-3.483254 0.0069*	-4.628110 0.0001*				
Tail	3.859364 0.0016*	0.459639 1.0000	-0.685215 1.0000	3.942894 0.0011*			
Ventral body	1.942189 0.7296	-1.457535 1.0000	-2.602390 0.1296	2.025719 0.5991	-1.917174 0.7730		
Ventral head	0.320720 1.0000	-3.079004 0.0291	-4.223859 0.0003*	0.404250 1.0000	-3.538643 0.0056*	-1.621468 1.0000	
Ventral pectoral	1.725993 1.0000	-1.673731 1.0000	-2.818586 0.0675	1.809523 0.9852	-2.133370 0.4605	-0.216195 1.0000	1.405273 1.0000

p-values (bottom number, with significance *) from Kruskal Wallis and Dunn tests (with Bonferroni correction) for multiple comparisons of *Labroides dimidiatus* preferences across different *Mobula kuhlii* body patches during cleaning behavior at Angels Ledge, Aliwal Shoal, Kwa-Zulu-Natal, between 2020–2022. Positive Z-statistic value correlates to the top row having significant preference over the first column, while negative value corresponds to the first column of body patches having significant preference over the first row of body patches

and gills) of *M. kuhlii* (Table 4). The pelvic fins of *M. kuhlii* received significantly more *L. dimidiatus* bites than the tail, gills, and dorsal head (Table 4). The ventral surface of the head, the dorsal surface of the body, and the pelvic fins body patches of *M. kuhlii* received the most *L. dimidiatus* bites on average in a given observation (Fig. 7).

Discussion

This study describes the cleaning behavior of *Mobula kuhlii* for the first time in South Africa. Our results support the initial findings of Murie and Marshall (2016) in the Bazaruto Archipelago of southern Mozambique, confirming that this species actively cleans on shallow, inshore reefs in a similar manner to manta ray species. This is only the second aggregation site scientifically documented where individual *M. kuhlii* receive cleaning services discovered after Two Mile Reef, Mozambique. Both mature male and pregnant female *M. kuhlii* were observed cleaning at Aliwal Shoal MPA, and this site was consistently utilized over several years. These results indicate that the Aliwal Shoal MPA to be important habitat for *M. kuhlii* due to their repeated use of the specific cleaning station

and for the occurrence of mating at this area (Carpenter and Griffiths 2023). This easily-accessible site also presents an excellent opportunity to continually monitor this species, which is Endangered and currently unprotected in South Africa.

Mobula kuhlii were significantly more likely to be encountered at sea surface temperatures of 24–26 °C, which is normal for summer (December–January) in KZN (Smit et al. 2013), agreeing with other studies on mobulids (manta rays, *M. alfredi*, *M. birostris*) in this area (Carpenter et al. 2023). Summer in KZN is known for increased productivity and subsequent abundance of zooplankton (Lamont and Barlow 2015). A group of > 150 *M. kuhlii* was encountered in December 2021, with many of these individuals exhibiting feeding behavior, confirming that the reef within the MPA supports both feeding and cleaning sites. While *M. kuhlii* were encountered at all recreationally-visited dive sites, individuals predominantly cleaned at Angel's Ledge and nearby locations, including Bay of Caves and Kyles Reef. The majority of cleaning activity took place along a very specific section of the reef, supporting findings of other mobulid studies, which found that individuals were highly selective and showed affinity to specific sites for cleaning (Couturier et al. 2012; Murie and Marshall 2016).

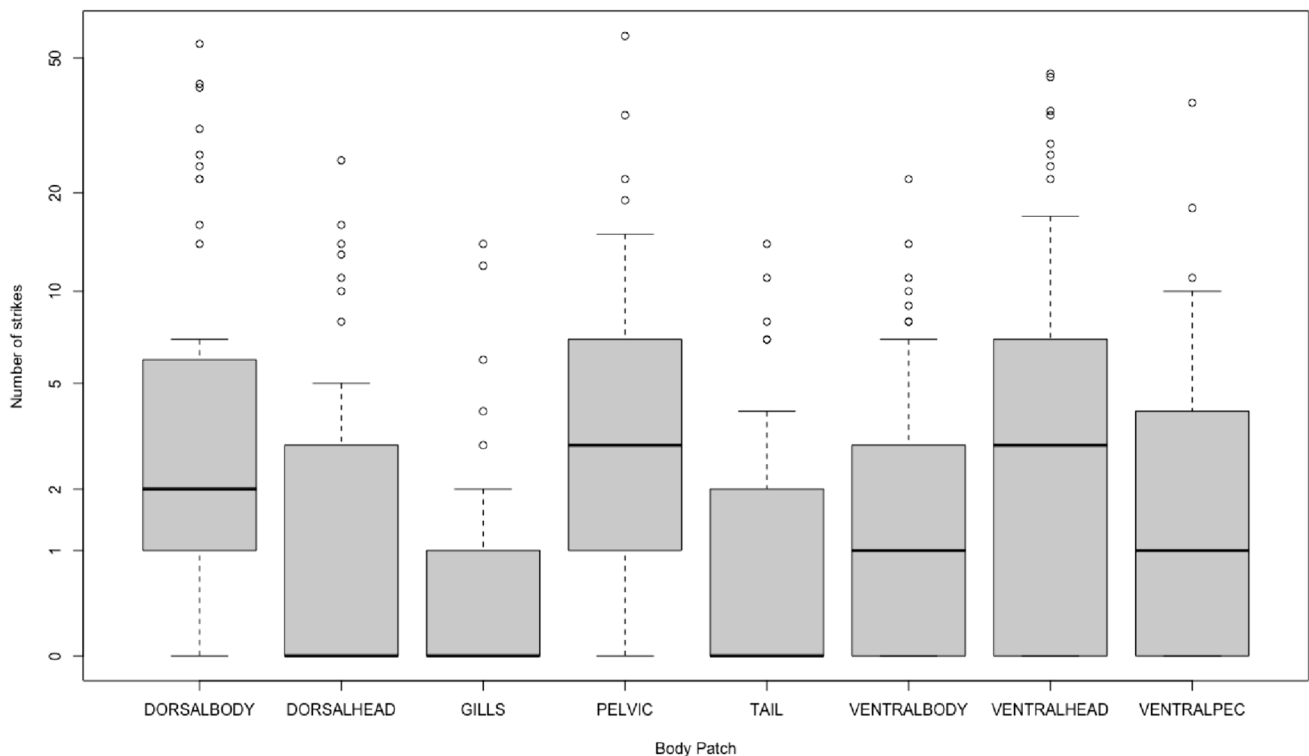


Fig. 7 Boxplot with logscale of cleaner fish bites by *Labroides dimidiatus* (y-axis) across the different body patches of *Mobula kuhlii* (x-axis) during cleaning behaviour at the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa between 2020–2022. The

thick black lines represent medians, boxes encompass the inter-quartile ranges, whiskers extend to the most extreme data points within 1.5×the interquartile range outside the box, and the dots show data points beyond the whiskers

Unlike manta rays, which support cleaning from a variety of cleaner species (Marshall 2008), only *L. dimidiatus* were recorded cleaning *M. kuhlii*, with all body patches being cleaned, and a significant preference for the pelvic fins, dorsal body, and ventral head surfaces. Our results on pelvic fin preference partially agree (pelvic fins) with a study on *Mobula birostris* which was selectively foraged by *L. dimidiatus* on the gills, pelvic fins, and pectoral fins (Murie et al. 2020). Different cleaner fish have been documented to clean different parts of large-bodied clients, with certain fish species targeting specific parasites (Marshall 2008; Murie et al. 2020). *Labroides dimidiatus* is known to preferentially target caligid copepods (*Pupulina cliffi*) (Grutter 1997) and in KZN, *M. kuhlii* has been found to have high density loads of this ectoparasite (Lebepe and Dippenaar 2013). Parasitic copepods can impact the growth, fecundity, and survival of their wild hosts by feeding on mucous, tissues, and blood (Neilson et al. 1987; Johnson et al. 1996; Clague et al. 2011). The attachment and feeding activities by parasitic copepods lead to primary diseases, skin lesions, and secondary infections in host species (Neilson et al. 1987; Johnson et al. 1996, 2004; Ho et al. 2000). Thus, visiting cleaning stations, such as those found on Aliwal Shoal MPA may be important for *M. kuhlii* health.

Our findings support other studies on mobulids that show individuals feeding, cleaning and exhibiting courtship in close proximity (Stewart et al. 2016; Stevens et al. 2018; Germanov et al. 2019). Often, environmental conditions correspond with each activity (Rohner et al. 2013). In this study, *M. kuhlii* cleaned for significantly longer periods during North currents, which is often associated with the presence of the warmer, nutrient-poor Agulhas current (Hutchings et al. 2002). Contrastingly, South currents are associated with colder water and green, more turbid visibility, which may be more productive. These collective findings may be indicative of the tendency of *M. kuhlii* to engage in cleaning activities when it is suboptimal for them to feed (Barr and Abelson 2019). Notably, Aliwal Shoal is influenced by various water bodies that affect zooplankton abundance (Pretorius et al. 2016). As such, *M. kuhlii* might exhibit a trade-off between cleaning and feeding, foraging when conditions are favorable with high abundances of plankton and cleaning when food densities are low (Barr and Abelson 2019; Murie et al. 2020).

Our findings suggest that *M. kuhlii* cleaning behavior is similar to that of other mobulids, including *M. alfredi*. *M. kuhlii* rarely cleaned alone, being in close proximity (1 m or less) to at least one conspecific individual 87% of the time recorded (n = 4,395 s). Mobulids are known to be social elasmobranchs (Notarbartolo di Sciara 1987; Perryman et al. 2019, 2022b) and Kitchen-Wheeler (2013) hypothesized that the presence of an established *M. alfredi* individual at a cleaning station may bring in other individuals, who then

imitate their behavior. *Mobula alfredi* are well-studied for their sociality, and are thought to use cleaning stations as ‘social meeting points’ where they interact with preferred social partners (Perryman et al. 2019, 2022b). They also exhibit ‘following’ behavior (Perryman et al. 2021), reflecting a possible learned ritual. Further, the distinct contrasting dark and light colouration on the cephalic lobes of *Mobula* spp. has been suggested to aid in social signaling (Notarbartolo di Sciara 1987), which may occur at *M. alfredi* cleaning stations (Perryman et al. 2021). *Mobula kuhlii* recorded in this study displayed similar cephalic lobe positions to *M. alfredi* (Perryman et al. 2021), as well as similar ‘posing’ positions while cleaning (Marshall 2008). However, more research on *M. kuhlii* cleaning behavior is needed to determine the detailed social behavior patterns associated with these areas.

Mobula kuhlii occasionally visited cleaning stations at the same time as other megafauna species (7% of the time), but never with another mobulid species. Manta rays (*M. alfredi*, *M. birostris*) have been seen cleaning at the Pinnacles dive site on the Aliwal Shoal MPA and spotted ragged tooth sharks, *Carcharias taurus*, have been seen cleaning at the dive sites Cathedral and Chunnel (Carpenter, pers. obs.). Manta rays and ragged tooth sharks all have a larger total length or disc width than *M. kuhlii*. Many cleaning studies have reported on larger individuals being preferred by cleaner fish, and this is attributed to them likely having more parasites on a greater surface area (Grutter et al. 2005; Oliver et al. 2011; Kitchen-Wheeler 2013). Likewise, in Vilanculos, Mozambique, there is no observed instance of *M. alfredi* engaging in cleaning activities at Two Mile Reef, which is the originally-discovered *M. kuhlii* cleaning station (Murie and Marshall 2016). Moreover, no sightings of *M. kuhlii* have been recorded at a well-documented *M. alfredi* cleaning station in southern Mozambique, despite more than two decades of research efforts in the region (Marshall, pers. comm.). A total of 57% of the time that *M. kuhlii* cleaned with another megafauna species, this was with one or more *A. ocellatus*, the first description of these species simultaneously cleaning at the same cleaning station. It is possible that the cleaning station habitat was partitioned by *M. kuhlii* to avoid competition with larger, more dominant species, with adult *A. ocellatus* being only slightly larger or the same size (White et al. 2010) as adult *M. kuhlii*.

Mobula kuhlii is currently unprotected in South Africa. In KZN, gill netting as a means of subsistence is not prolific, but bather protective nets are gill nets that sometimes catch mobulids (Young 2001). As Aliwal Shoal MPA is a heavily-used recreational area, it is crucial that unregulated scuba and snorkeling tourism does not further impact *M. kuhlii* cleaning behavior, as it has been shown to affect *M. alfredi* (Kitchen-Wheeler 2013; Venables et al. 2016). All *M. kuhlii* seen on Aliwal Shoal MPA were of adult size,

and included mature males and pregnant females, supporting the importance of this area for reproduction (Carpenter and Griffiths 2023). Reproductive behavior may also be negatively impacted by recreational diving if divers interrupt the behavior (Venables 2013; Murray et al. 2020). Therefore, we recommend a strict code of conduct procedure at the Aliwal Shoal MPA, which has already been implemented at the local dive centers by the authors. We also recommend this species to be awarded national protection due to its conservation status and the potential importance to the ecotourism economy (Russel 2022, Dive Magazine).

In this study, we emphasize the importance of understanding fine-scale habitat use in the southernmost range of *M. kuhlii* distribution. Our findings support the role of cleaning stations in mobulids for social and reproductive purposes. The aggregation site's location offers unique opportunities for ecotourism and long-term monitoring of Endangered *M. kuhlii*. To improve future studies at this site, employing high-definition video recording devices could capture and analyze complex interactions more effectively through slow-motion reviews, or even 360° camera systems for broader fields of view. Additionally, future investigations should focus on delineating juvenile habitats for *M. kuhlii*, incorporating acoustic and/or satellite telemetry to verify their movements within and outside the MPA. A precise understanding of movement patterns and the use of critical inshore habitats is crucial for effectively safeguarding this endangered species. Considering their vulnerability and the potential for ecotourism, prioritizing national protection measures and management plans for *M. kuhlii* in South Africa is imperative.

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Author contributions MC and AM conceived the idea of the study. Data was collected by MC. Data analysis was conducted by MC and RP. MC wrote the manuscript with input from all authors.

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Data availability The datasets generated and/or analyzed during the study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethical approval No ethical approval was required.

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