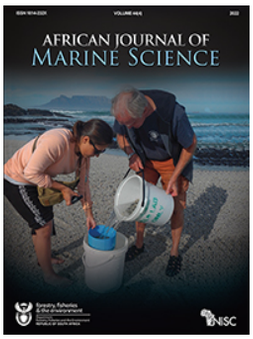

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'Flash *Mobula*': first observations of courtship behaviour of the shortfin devil ray *Mobula kuhlii*

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First-time observations of courtship behaviour of the Endangered shortfin devil ray *Mobula kuhlii* are described from the Aliwal Shoal Marine Protected Area (MPA), KwaZulu-Natal, South Africa. Three events of *M. kuhlii* courtship, called 'mating trains', were recorded on video during the months of November 2020 and January 2021. These included a near-term pregnant female, and two lead females followed by up to four males. The common behaviours associated with courtship were documented: multiple males following a single female, rapid speed bursts, avoidance of the female, and swerving. This study confirms that *M. kuhlii* mating occurs in KwaZulu-Natal waters and that courtship is similar across mobulids. The findings demonstrate the importance of the habitat provided by the Aliwal Shoal MPA for this currently unprotected species.

Keywords: aggregation site, Aliwal Shoal Marine Protected Area, elasmobranch reproduction, KwaZulu-Natal, Mobulidae, pre-mating behaviour, South Africa, underwater video

Online supplementary material: The Supplementary Information, available at https://doi.org/10.2989/1814232X.2022.2158131, includes raw video footage of the encounters of *Mobula kuhlii* courtship. Videos S1 and S2 are from 17 November 2020, Video S3 from 27 November 2020, and Video S4 from 3 January 2021.

Introduction

The family Mobulidae is composed of nine recognised zooplanktivorous species which are pelagic/epipelagic, migratory, and found circumglobally in tropical, subtropical and temperate seas (Couturier et al. 2012; White et al. 2017; Notarbartolo di Sciara et al. 2020). Of these species only *Mobula kuhlii* (Valenciennes, 1841), *Mobula birostris* (Walbaum, 1792), and *Mobula alfredi* (Krefft, 1868) are regularly observed in inshore waters off KwaZulu-Natal Province (KZN), South Africa (Compagno 1999; G Cliff, KwaZulu-Natal Sharks Board, pers. comm.; MC unpublished data).

Mobulids have *K*-selected life histories, including aplacental vivipary, late maturation, long gestation periods of between 10 and 12 months, and as few as one pup per litter (Couturier et al. 2012). Their life histories render them easily overexploited both by directed fisheries for their meat and gill plates and by other fisheries as incidental bycatch (Croll et al. 2016; O'Malley et al. 2017; Pacoureau et al. 2021). All species of Mobulidae are thus listed as threatened by the International Union for the Conservation of Nature Red List (Marshall et al. 2018a, 2018b, 2018c, 2018d, 2018e, 2018f, 2018g; Rigby et al. 2022a). *Mobula kuhlii* is listed as Endangered (Rigby et al. 2022b).

Elasmobranch mating behaviour in the wild is seldom documented owing to the innate challenges of studying mobile marine species. Thus far, only 14 reports on reproductive behaviour of free-living batoids exist, including five reports for mobulids: *M. thurstoni* (McCallister et al. 2020), *M. alfredi* (Marshall and Bennett 2010; Stevens et al. 2018), *M. birostris* (Yano et al. 1999; Stevens et al. 2018), *M. tarapacana* (Sobral 2013; Mendonça et al. 2020) and *M. mobular* (Duffy and Tindale 2018). Mating behaviour appears to be consistent across batoids, with the general sequence of events being: (i) the prolonged following of a female by one or more males; (ii) pre-copulatory biting by the male onto one of the female's pectoral fins; (iii) copulation/insertion of one of the male's claspers into the female's cloaca, flapping his pectorals to stay in place; (iv) resting; and (v) separation (Chapman et al. 2003). In mobulids, courtship in *M. birostris* was first described by Yano et al. (1999) who noted the 20–30-min pursuit of one female by multiple males (a 'mating train'), whereas the 'prolonged following' by southern stingray *Hypanus americanus* males included additional behaviours within the 'following' stage (Chapman et al. (2003). Mating trains have variable numbers of up to 40 males and observed durations of up to 48 h for *M. alfredi* (Clark 2010) and up to 147 min for *M. mobular* (Duffy and Tindale 2018). This behaviour appears to be similar across mobulid species, but there is a lack of observations of mating in *M. eregoodoo*, *M. hypostoma*, *M. munkiana* and *M. kuhlii*. Here, we provide the first scientifically documented events of *M. kuhlii* courtship, a description of the environmental conditions that prevailed during these events, and a description of pre-mating behaviour.

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Materials and methods

Sightings and behaviours of *M. kuhlii* were encountered opportunistically while snorkelling or SCUBA diving recreationally in the Crown Offshore Restricted Zone of the Aliwal Shoal Marine Protected Area (MPA), South Africa, between November 2020 and March 2022 (Figure 1). We identified *M. kuhlii* by the distinct grey to black colouring on the ventral surface of the pectoral-fin apex which fades into white on the remainder of the pectoral fin and on the abdomen (Notarbartolo di Sciara et al. 2016; White et al. 2017). Sex was determined by the presence or absence of claspers, with maturity in males signified by fully extended claspers, and in females by the presence of mating scars or pregnancy (Notarbartolo di Sciara 1987). Pregnancy was determined by an obvious protrusion of the abdominal cavity (Marshall and Bennett 2010). Size at maturity of *Mobula kuhlii* is estimated to be 1.03–1.12 m disc width (DW) for males and at least 1.16 m DW for females, with a maximum recorded size of 1.22 m DW (White et al. 2006; Notarbartolo di Sciara et al. 2016; Rigby et al. 2022b). Each mating train consistently included some or all of the following behaviour patterns: (i) males closely chasing a female; (ii) fast swimming; (iii) males performing similar movements following after the female and one another; and (iv) many instances of swerving and lunging (Yano et al. 1999; Marshall and Bennett 2010; Stevens et al. 2018).

The total number of *Mobula kuhlii* in each group was recorded *in situ*, as well as the number of individuals involved in each mating train, segregated by sex. Size of individuals was estimated visually. Subsequently, photographs and video data of the behaviours were recorded with an underwater camera. The time of day, duration of the behaviour observed, estimated horizontal visibility, water colour, current direction and estimated strength, and a description of plankton were also documented. Plankton composition and abundance was categorised according to Rohner et al. (2013) as either: (i) 'suspended sediment', representing mostly detritus; (ii) 'zooplankton', representing zooplankton scattered throughout the water column; (iii) 'phytoplankton', representing thick phytoplankton clouds; (iv) 'surface slick', representing dense zooplankton communities concentrated

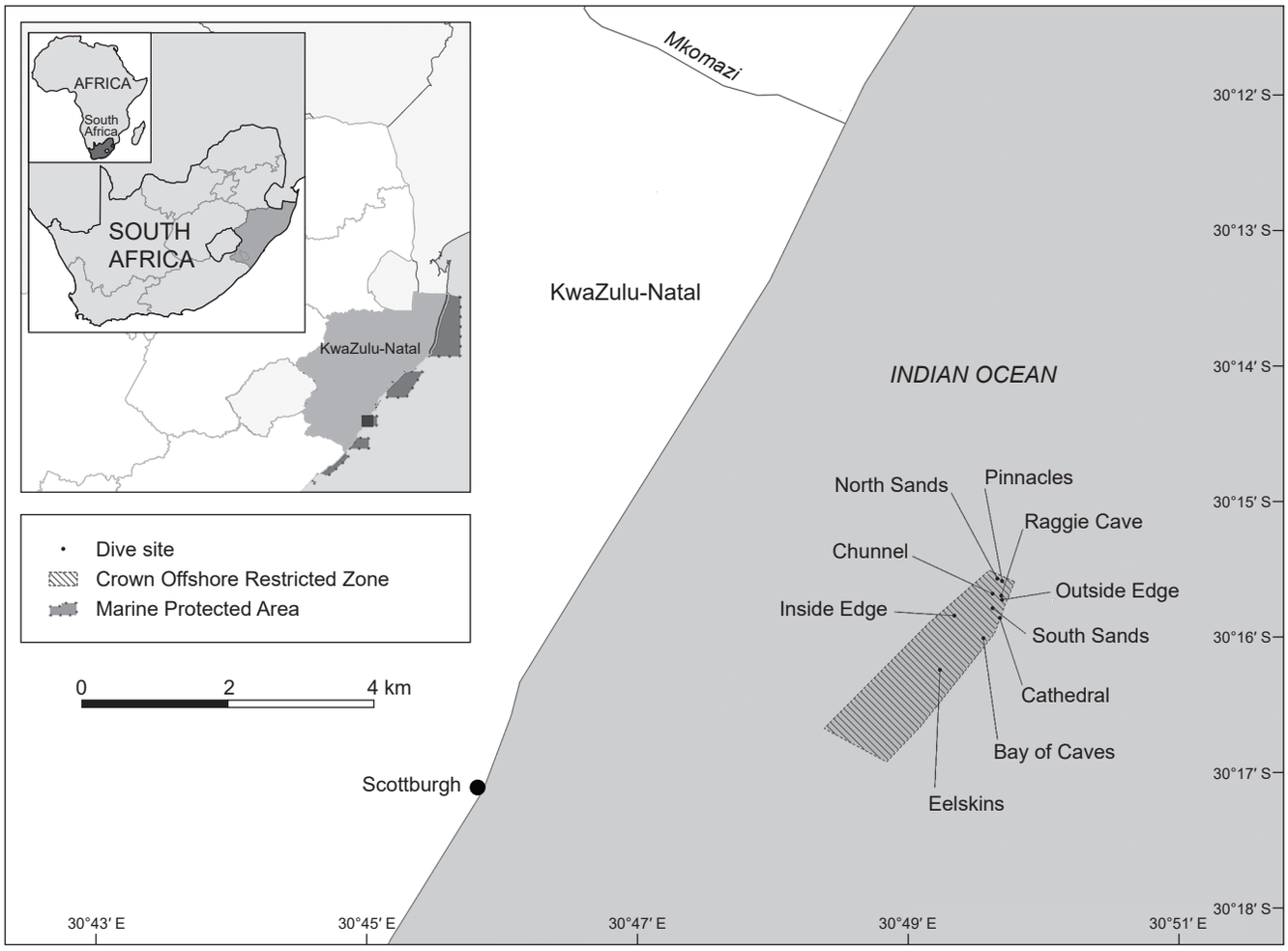

Figure 1: Map of the dive sites visited at the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa, at some of which *Mobula kuhlii* courtship was observed, between November 2020 and March 2022

on the water surface; or (v) 'no visible plankton'. Depth and sea surface temperature (SST) were recorded using a Mares Puck Pro underwater dive computer. Videos were analysed and screenshots taken in QuickTime 10.5.

Ethics statement

The novel behaviours in this study were encountered while diving recreationally or snorkelling. As these observations were made opportunistically and did not involve the capture, use, care or manipulation of any live or dead species, no permits or ethics approvals were required.

Results

A total of 192 recreational snorkel/dive trips were conducted at the Aliwal Shoal MPA between November 2020 and June 2021, with an additional 66 snorkel/dive trips between September 2021 and March 2022. Ten named dive sites within the Crown Restricted Area were visited (Figure 1). Natural (COVID-19, major flooding) and political (KZN riots) disasters within the country prevented diving before November 2020, between July and August 2021, and after March 2022. Although *M. kuhlii* was present during 76 trips, no courtship behaviour was observed outside of the months of November and January. Three courtship events were photographed (Figure 2; Supplementary Figures S1 and S2) and recorded on video (Supplementary Videos S1–S4). Of these, one event involved a lead female that was pregnant and near-term. We observed six components of *M. kuhlii* courtship (Figure 2). All events occurred in shallow waters of less than 30 m depth, during daylight between 08:40 and 15:34, in sea surface temperatures (SST) of between 22 and 25 °C, in water with an estimated horizontal visibility of between 15 and 25 m, and during times of dense slicks of zooplankton on the surface (Table 1). All *M. kuhlii* observed in mating trains were estimated to be between 1.0 and 1.2 m DW. Courtship behaviour was observed at three sites: Bay of Caves, North Sands and Outside Edge (Figure 1).

Discussion

This study provides the first information on courtship in *Mobula kuhlii*. We documented six behavioural components of *M. kuhlii* courtship that are common to the six mobulid species that have been observed thus far. These behaviours included mating trains of multiple males following one female, close pursuit with faster-than-average swimming speeds, female avoidance, rapid direction change ('veering' or 'swerving'), female–male contact, and male grasp attempt (Yano et al. 1999; Sobral 2013; Duffy and Tindale 2018; McCallister et al. 2020). The behaviours observed in this study are consistent with the observations of Stevens et al. (2018), specifically the categories described as 'Initiation', 'Endurance' and 'Evasion'. In *M. alfredi*, these categories involve males following the movements of a single female, rapid chase by 1–26 males in single file, and the female making abrupt turns at an increased swimming speed (Stevens et al. 2018). Copulation in mobulids entails the closest male biting on the left pectoral fin of the female and subsequently positioning himself abdomen-to-abdomen with the female (Yano et al. 1999; Marshall and Bennett 2010). Prior to biting, the male will position close to the female's dorsal surface while in pursuit (Stevens et al. 2018). We observed several attempts by the males to grasp the female's pectoral fin on the dorsal surface but copulation itself was not observed.

On one occasion a pregnant female was observed engaged in a courtship event, representing 33% of observations. Despite the small sample size, this is consistent with reports from the Maldives where 12% of *M. alfredi* mating trains included a near-term pregnant female (Stevens et al. 2018). Mating in elasmobranchs may be facilitated by olfaction (Johnson and Nelson 1978; Chapman et al. 2003). This has been reported across several mobulid species, indicating that pregnancy signals a reproductively receptive female who likely secretes chemical cues (Marshall and Bennett 2010; Deakos 2012; Duffy and Tindale 2018). Our observations suggest that mating in *M. kuhlii* occurs immediately following birth, which agrees with studies on *M. mobular* and other batoids (Chapman et al. 2003; Duffy and Tindale 2018).

In this study *M. kuhlii* courtship events were observed during summer (November–February), which is associated with increased primary productivity within KZN waters (Woodson et al. 2012; Guastella and Roberts 2016). Thus, summer conditions likely provide the food availability ideal for *M. kuhlii* reproduction. *Mobula alfredi* sometimes engage in courtship while on surface-feeding grounds (Armstrong et al. 2016), whereas *M. birostris* have been observed courting within a deep (50–80 m) thermocline layer where zooplankton was trapped (Stewart et al. 2019). Reproductive activity appears to be seasonal in mobulids (Marshall and Bennett 2010; Duffy and Tindale 2018; Stevens et al. 2018). In southern Mozambique, *M. alfredi* reproductive activity peaks in austral summer (October–January) at Tofo (Marshall and Bennett 2010), yet 90 km farther south, at Závora, it occurs during winter and austral summer (July–November) (Carpenter et al. 2022). *Mobula tarapacana* courtship was observed in April–May at the Saint Peter and Saint Paul Archipelago, Brazil (Mendonça et al. 2020), and in autumn (March) for *M. mobular* in New Zealand (Duffy and Tindale 2018). Hence the seasonality of mobulid reproduction evidently varies by species and location. Despite some sampling in KZN in 2021–2022, *M. kuhlii* courtship was rarely encountered. When mating trains were encountered, observation times were short, and the high swimming speeds of *M. kuhlii* individuals inhibited the distinguishing of mating scars on lead females. More research is needed, therefore, to capture the full cycle of *M. kuhlii* mating in KZN and to determine how widely South African waters are used for reproduction.

This study provides insights on the reproductive ecology of *M. kuhlii* and confirms the presence of a mating area for this species within KZN waters. It further highlights the importance of the Aliwal Shoal MPA and increases knowledge on the use of this habitat by *M. kuhlii*. The identification of critical sites for this Endangered species, which is not yet protected in South Africa, is urgently required to improve management strategies for its long-term conservation. Global abundance of *M. kuhlii* has declined by 50–79% in the past 38 years (Rigby et al. 2022b). In

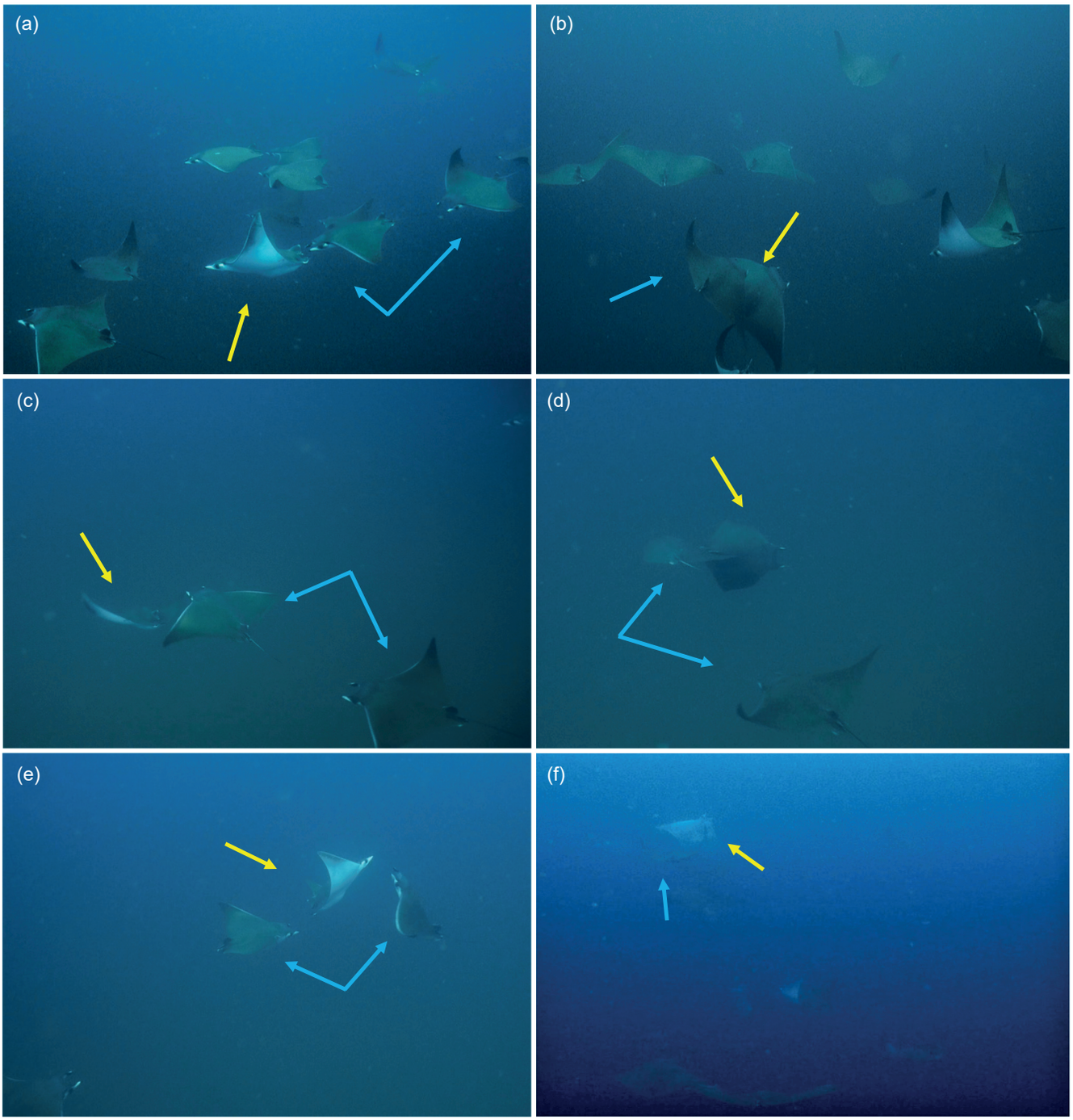

Figure 2: Courtship behaviour of shortfin devil rays *Mobula kuhlii*, observed at Bay of Caves within the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa, on 17 November 2020. Blue arrows point to males and yellow arrows to the lead female who (a) is heavily pregnant and (b) avoids attempts by males to bite her pectoral fin by (c) rapid speed bursts, (d) swerving sharply, and (e) when encountered by males on the ventral side, and (f) swimming vertically towards the surface. Photograph: Michelle Carpenter

Tofo, southern Mozambique, the closest known aggregation site of *M. kuhlii* to KZN, sightings declined by 99% between 2003 and 2017 (Rohner et al. 2017). Mobulid populations in the Indian Ocean are impacted by directed fisheries (Kiszka 2012; Croll et al. 2016; Rigby et al. 2022b) and as bycatch from the use of gillnets (Temple et al. 2018), purse-seine nets (Guirham et al. 2021) and longlines (Ward-Paige et al. 2013; Lezama-Ochoa et al. 2015). In KZN, *Mobula* spp. are commonly caught in the bather protection nets, including an installation within the Aliwal Shoal MPA (Dudley and Cliff 1993). Recent research has demonstrated the Aliwal Shoal MPA to be a hotspot for *M. kuhlii*

Table 1: Environmental parameters during the times when a *Mobula kuhlii* courtship event was observed at the Aliwal Shoal Marine Protected Area, KwaZulu-Natal, South Africa, in November 2020 and January 2021. The maximum number of rays in each overall group (Max N) was recorded, as well as the number of individuals participating in the 'mating train' (also see Figure 2; Supplementary Figures S1 and S2). GPS locations were recorded in decimal degrees. The time of the initial observation was recorded on video, as well as the duration that the mating train was visible to the observer *in situ*. A dive computer and visual references were used to record the depth, sea surface temperature (SST), current, horizontal visibility, water colour and plankton description *in situ*

Date	Dive site	Max. depth (m)	Coordinates	Max N	Max. no. of rays in mating train	Depth of mating train (m)	Time	Total observation time (min)	SST (°C)	Current	Horizontal visibility (m)	Water colour	Plankton description	Observed courtship behaviour
17 Nov 2020	Bay of Caves	26	30.27111° S, 30.96833° E	19	4	8–10	10:46	15	22	Light, N to S	15	Blue, green	Surface slick	Train formation, close pursuit, veering, female–male contact, male grasp attempt, female avoidance
27 Nov 2020	North Sands	15	30.41056° S, 30.99667° E	5	5	Surface	15:34	1	23	Light, SE to NW	20	Blue	Surface slick	Train formation, close pursuit, veering, female avoidance
3 Jan 2021	Outside Edge	18	30.48667° S, 31.00222° E	4	4	Surface	08:40	2	24	Medium, N to S	15	Blue, green	Surface slick	Train formation, close pursuit, veering, female avoidance

(Carpenter et al. 2021). Considering the findings of this study it is essential to mitigate impacts on *M. kuhlii* in South Africa by, for instance, declaring the species nationally protected and establishing fine-scale management plans.

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