

First observation on the mating behaviour of the marbled ray, *Taeniurops meyeri*, in the tropical Eastern Pacific

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Abstract Elasmobranch reproductive behaviour remains understudied, particularly for batoids (rays). Most of the information available originates from opportunistic observations of mating scars in the wild and/or from individuals held in captivity. Here we describe the first complete mating sequence of the marbled ray (*Taeniurops meyeri*) in the wild. The event was filmed at Isla del Coco National Park in Costa Rica, in the Tropical Eastern Pacific. The complete sequence lasted approximately 3 hrs and is defined by the following behaviours: (1) close following or chasing: a group of

males swim in a close formation chasing an individual female; (2) pre-copulatory biting: oral grasping of the female's posterior pectoral fin by the males, with anterior bending of one clasper and rotation of the pelvic region towards the female's cloaca; (3) copulation/ insertion of the male's clasper followed by 'ventral to ventral' position and energetic thrusting of the male's pelvic region; (4) post-copulatory behaviour: the male removes its clasper from the female's cloaca while releasing her posterior pectoral fin and (5) separation: the male sets the female free and separates himself from the group. The mating behaviour described here shares some similarities with the few other studies of batoids in the wild and highlights the need to further understand their mating system to guide conservation plans for this vulnerable species.

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Introduction

Mating sequences in elasmobranchs (sharks and rays) have been rarely documented in the wild. Most available information on the reproductive behaviour of this group of species has been obtained from opportunistic observations of mating scars in females in the wild or from individuals held in captivity (Henningsen 2000; Kajiura et al. 2000; Chapman et al. 2003; Henningsen et al. 2004; Whitney et al. 2004) with limited direct observations of courtship and mating recorded for wild populations (but see Tricas 1980; Nordell 1994;

Chapman et al. 2003; Yano et al. 1999; Pierce et al. 2009; Salinas-de-León et al. 2017b).

Most of the research describing elasmobranch reproduction has been conducted on sharks, and very little on rays (batoids). Only eight species of batoids, out of the approximately 600 recorded, have been observed copulating in the wild (Chapman et al. 2003; Mull et al. 2010). Despite this lack of data on their reproductive behaviour, large numbers of batoid species are highly exploited by target and non-target fisheries around the world (Worm et al. 2013; Oliver et al. 2015). In the Tropical Eastern Pacific (TEP) marine ecoregion (Spalding et al. 2007) batoids are frequently caught as by-catch in commercial fisheries, mainly shrimp trawling, making up for a significant proportion (> 40%) of fishing landings (Gómez and Mejía-Falla 2008; Smith et al. 2009; Mejía-Falla et al. 2012). Additionally, these species commonly occur in marine coastal habitats where they are permanently exposed to anthropogenic stressors like artisanal and recreational fishing, habitat destruction, and pollution (Gómez and Mejía-Falla 2008; Mull et al. 2010). Thus, understanding their reproductive strategies and life-history becomes critical for population management and conservation.

The marbled ray or blotched fantail ray, *Taeniurops meyeri* (Müller & Henle 1841), is a large batoid species reaching up to 1.8 m in disc width and 3.3 m in total length (Last et al. 2016). Marbled rays are widely distributed across the Indo-Pacific Ocean. However, in the TEP they are only known at two oceanic islands: Isla del Coco in Costa Rica and the Galapagos Islands in Ecuador, both considered elasmobranch hotspots (McCosker and Rosenblatt 2010; Friedlander et al. 2012; Salinas-de-León et al. 2016). The mating sequence described here was documented at Isla del Coco located approximately 550 km off the Pacific Coast of Costa Rica. Isla del Coco was designated a National Park in 1978 and recognized as a UNESCO World Heritage Site in 1997 (Cortés-Núñez 2008). Even though batoid populations are protected from fisheries in this marine protected area (MPA), the marbled ray is still targeted by unregulated fisheries in many parts of the world for the consumption of its meat (Stobutzki et al. 2002; Smith et al. 2009; Kyne and White 2015). Considering that this species is highly affected by overfishing (White et al. 2015; Kyne and White 2015) the International Union for Conservation of Nature (IUCN) Red List has the marbled ray listed as

“Vulnerable”. However, despite its significant population reduction and evident vulnerability (White et al. 2015), little is known about its biology and no specific information on its reproduction has been produced in the TEP. In this study, we provide the first detailed description of a complete mating event sequence for the marbled ray in the wild.

Observations

The mating event was recorded at Manuelita Coral Garden, Isla del Coco, Costa Rica, in June 2016 (Fig. 1). A group of approximately 26 marbled rays were initially seen swimming in a compact formation close to the sandy bottom at 30 m depth (Fig. 2a). The group was significantly male-biased, with just one female being chased by all the males. This group chase concluded with three males closing in on the single female high up in the water column at a depth of 12 m (Fig. 2b). At midwater, two males successfully bit and grasped the female on the posterior margins of its pectoral disc, with one male on each pectoral fin (Fig. 2c). Soon after, a third male also grasped the female by the rear edge of its left pectoral fin (Fig. 2c). Male 1 positioned itself at the right side of the female and flexed one of its claspers forward (Fig. 2d), managing to insert the right clasper into the female’s cloaca (Fig. 2e). Clasper insertion occurred at a shallower depth range from 5 to 10 m.

After successfully achieving clasper insertion, male 1 flipped over and adopted a ‘ventral to ventral’ position (Yano et al. 1999; Chapman et al. 2003) with the female, while maintaining a grip of its pectoral fin (Fig. 2f). Male 1 actively thrust its pelvic region for approximately one minute while maintaining ‘ventral to ventral’ position. During this rapid motion, sperm is being transferred from the urogenital papilla to the clasper groove of the male into the female’s genital tract (Luer and Gilbert 1985; Pratt and Tanaka 1994). Subsequently, male 1 removed its right clasper from the female’s cloaca and stopped biting its pectoral fin. After separating from the female, a cloud of sperm was clearly visible in the water column (Fig. 2g).

After separating from the female, male 1 shook its claspers and these appeared to return to their natural relaxed position (Fig. 2h). Throughout the entire copulation event that lasted approximately 2 min, from the time male 1 inserted its clasper, both male 2 and male 3 continued to hold on to the female by oral grip. After

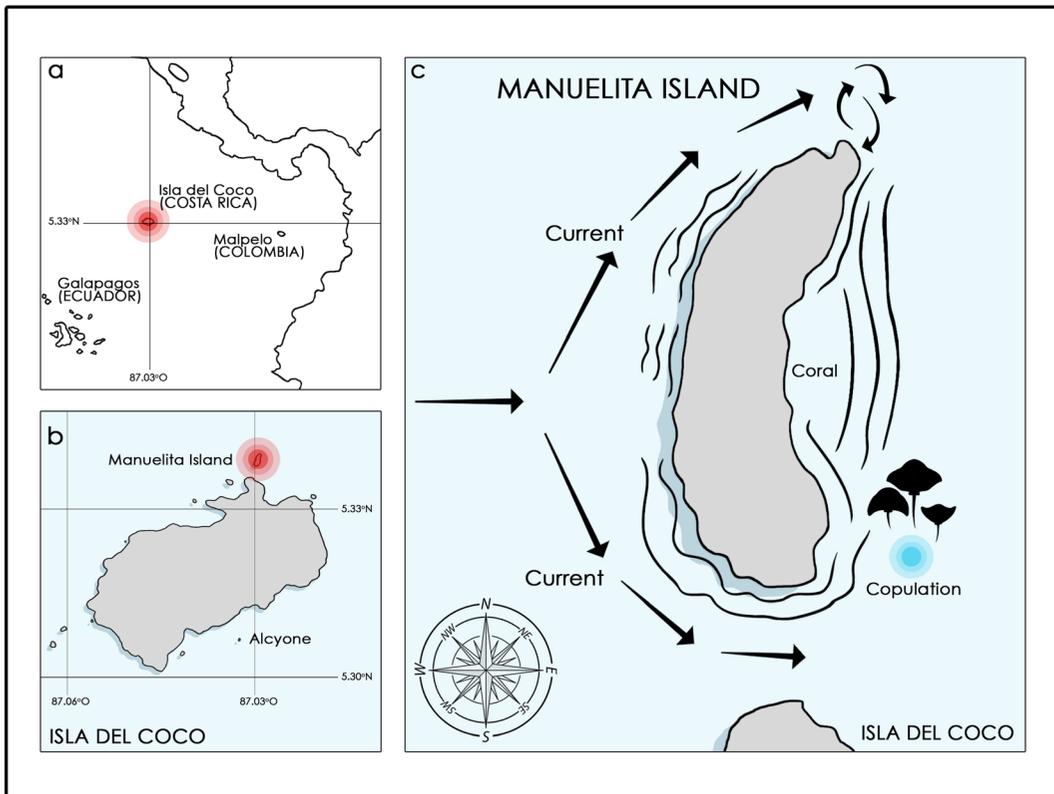


Fig. 1 Isla del Coco Island, Costa Rica, detailing the location of Manuelita Coral Garden (blue dot) around Manuelita Islet, where the copulation event was recorded

male 1 swam away, the rest of the group started to sink to the bottom (at approximately 30 m) and observations of other males successfully achieving clasper insertion with the same female were not witnessed. The female remained passive and did not engage in any avoidance behaviour during the entire sequence. The complete mating event described here, from swimming as a group, the chase, matting, and final separation, lasted approximately three hours observed over consecutive SCUBA dives (Supplementary material 1).

Discussion

In this study, we provide the first detailed description of the mating behaviour of the marbled ray *T. meyeri*. Behavioural patterns observed here can be summarized as follows: (1) Close following or chasing: males chase a female from the sandy bottom into the water column by swimming in a close parallel position; (2) Pre-copulatory biting: consisting in oral grasping of the female's posterior pectoral fin by the male(s), with

anterior bending of one of the claspers and rotation of the pelvic region towards the female's cloaca; (3) Copulation: the insertion of the male's clasper followed by ventral to ventral position and energetic thrusting of the male's pelvic region; (4) Post-copulatory behaviour: the male removes its clasper from the female's cloaca while releasing his posterior pectoral fin; (5) Separation: the male separates from the group (Fig. 2a-h). During step 5, a cloud of sperm was clearly visible in the water column. The mating sequence described for *T. meyeri* follows a similar sequence reported for other batoids in the wild, such as, the white spotted eagle ray, *Aetobatus narinari* (Tricas 1980), the yellow stingray, *Urobatis jamaicensis* (Young 1993), the round stingray, *Urobatis halleri* (Nordell 1994), the giant manta ray, *Mobula birostris* (Yano et al. 1999) and the southern stingray, *Hypanus americanus* (Chapman et al. 2003).

Based on current knowledge, we cannot determine a specific mating aggregation site for marbled rays around Isla del Coco. However, the sequence of the mating event described here at Manuelita Coral Garden, have

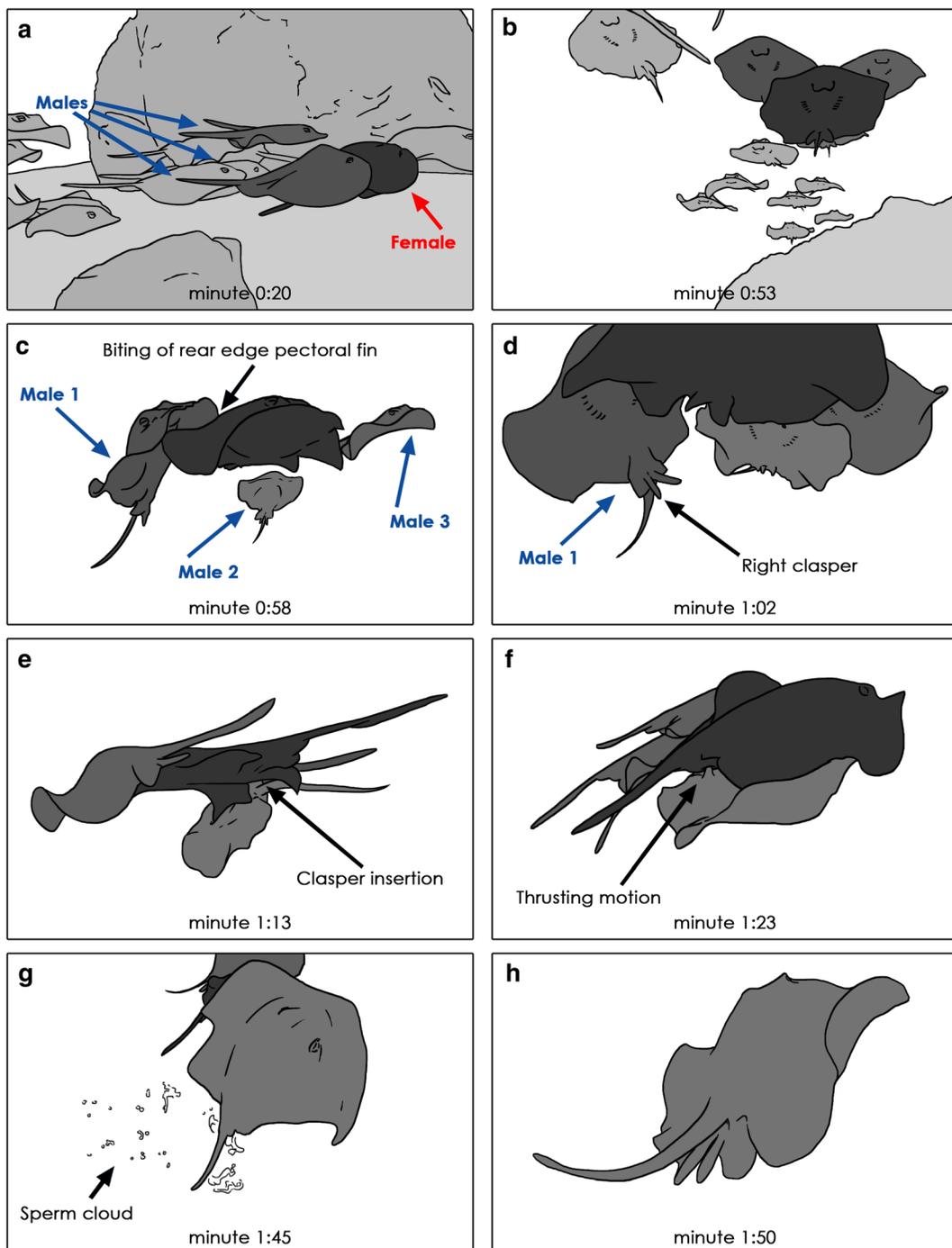


Fig. 2 Mating sequence of the marbled ray, *Taeniurops meyeni* at Isla del Coco. Timestamps indicate video time after editing, not actual sequence time

been also witnessed at other dive sites around the island (Pochet, personal observations), which suggests that reproductive behaviour is not site-specific for this species.

This study, and few others on batoids reproduction, showed that males engage females from behind prior to copulating (Nordell 1994; Yano et al. 1999; Chapman et al. 2003), suggesting the presence of sex-attractant

chemicals being released through the female's cloaca that act as olfactory cues (Gordon 1993; Tricas et al. 2000). Nevertheless, how male elasmobranchs discriminate between receptive and non-receptive females remains unclear. Based on nurse sharks (*Ginglymostoma cirratum*) swimming behaviour, Carrier et al. (1994) suggested that males use olfaction and vision as main sensory cues to find receptive females. They observed sharks approaching non-receptive females and immediately swimming away in search of another female to engage. A similar study by Johnson and Nelson (1978) suggested that a specific pheromone released by the female could signal sexual maturity and lead to pair formation in the blacktip reef shark, *Carcharhinus melanopterus*. Moreover, Kajiura et al. (2000) studied mating scars on the Atlantic stingray, *Hypanus sabinus* (formerly known as *Dasyatis sabinus*) and found that most of the scars were located on the posterior half of the female body close to the trailing edge of the pectoral fins.

Aggressiveness during male-male competition and mate choice are the main driving forces that affect sexual selection and influence the use of different reproductive strategies (Henningsen et al. 2004; Barbosa and Magurran 2006; Fitzpatrick et al. 2012). Some male elasmobranchs, such as the sand tiger shark (*Carcharias taurus*), have exhibit a dominance hierarchy in captivity demonstrating strong male competition (Gordon 1993; Lucifora et al. 2002; Henningsen et al. 2004). Moreover, mating wounds have also been recorded in wild males, possibly indicating competition for access to females (Kajiura et al. 2000). In this event, the only male-male competitive behaviour recorded was males hitting each other with their snouts to gain position next to the female's pectoral fins.

Conversely, recent studies have focused on female mate choice by using genetic tools and direct observations to determine the reproductive strategies involve in this decision-making (Feldheim et al. 2001; Pratt and Carrier 2001; Daly-Engel et al. 2006; Daly-Engel et al. 2007; Byrne and Avise 2012; Fitzpatrick et al. 2012; Lyons et al. 2017). Female elasmobranchs have shown to display 'avoidance' and 'cooperative' behaviours as pre-copulatory mate choice. These behaviours involve arching their body to actively keep their cloaca away from the males' claspers or seeking refuge to prevent male access (Pratt and Carrier 2001; Whitney et al. 2004; Jacoby et al. 2010). In our observation, it was

clear that the female was displaying a 'cooperative' behaviour with male 1. However, we also observed female marbled rays seeking refuge from males in rocky caves around Isla del Coco, which indicates active male avoidance. Future studies using a combination of genetics and direct observation of multiple mating events (i.e. behavioural polyandry) should be conducted to further understand mating system for this species. This could reveal multiple paternity for the marbled ray, as documented in other elasmobranchs (Byrne and Avise 2012; Fitzpatrick et al. 2012; Lyons et al. 2017).

As observed in previous studies, pectoral grip was maintained by the three males during the entire sequence of the mating event. Biting is considered a common behaviour within elasmobranchs (Tricas 1980; Tricas and Le Feuvre 1985; Kajiura et al. 2000; Pratt and Carrier 2001). It has been hypothesized that biting stimulates the female to mate by inducing her into a submissive state or by acting as a cue for ovulation and receptiveness (Tricas 1980; Gordon 1993). However, there is no clear evidence to support that biting acts as a sensory cue that stimulates reproduction behaviours in female elasmobranchs (Carrier et al. 1994; Kajiura et al. 2000). Another reason for biting behaviour is to simply help maintain contact during copulation (Klimley 1980). There is evidence suggesting that without a secure pectoral grip the male would not be able maintain a proper alignment with the female and would fail to achieve clasper insertion (Pratt and Carrier 2001). Additionally, it enables the maneuvering of the female by the male during copulation (Nordell 1994; Whitney et al. 2004).

Despite the total protection from fishing provided by the Isla del Coco National Park, marbled ray relative abundance has declined by 73% over the past 20 years (White et al. 2015). This reduction has been linked to an increase of top predators' abundance, such as the tiger shark (*Galeocerdo cuvier*) and Galapagos shark (*Carcharhinus galapagensis*), as well as, an increase in El Niño events and higher water temperatures (Sibaja-Cordero 2008; White et al. 2015). Anecdotal evidence, from ten years of observation by dive guides, suggest that mating of marbled rays usually happens when the temperature of the water remains stable at approximately 24 °C (Pochet, personal observation), which typically occurs during the wet season from June to November (White et al. 2015). Change in water temperature is widely recognized as an important environmental factor triggering elasmobranch reproduction

globally (Wearmouth and Sims 2008; Le Port et al. 2012; White et al. 2015). In the TEP numerous studies have linked reproductive events in reef fishes to changes in water temperature (Usseglio et al. 2015; Salinas-de-León et al. 2017a). Considering that marbled ray mating behaviour might only occur during stable warm temperatures (approximately 24 °C), and that climate change is predicted to result in more dramatic and frequent El Niño events (Wang et al. 2017), this phenomenon could alter the reproduction of this species. The oceanic islands of the TEP could represent an ideal scenario to conduct further research to understand elasmobranch complex social behaviours and reproduction under climate change scenarios.

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