



INSTITUTO POLITÉCNICO NACIONAL



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CENTRO INTERDISCIPLINARIO DE CIENCIAS MARINAS

Munk's devil ray ecology and fisheries vulnerability in the Gulf of California and Mexican Pacific.

TESIS
QUE PARA OBTENER EL GRADO DE
DOCTORADO EN CIENCIAS EN MARINAS

PRESENTA
MARTA LAURA DÍAZ PALACIOS
DIRECTOR Y CO-DIRECTOR DE TESIS
DR. FELIPE GALVÁN MAGAÑA Y DONALD ANGUS CROLL
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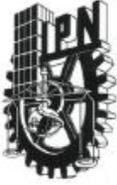
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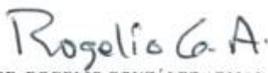
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ABSTRACT

Manta and devil rays (mobulids) are filter feeding elasmobranchs with extreme K-selective life histories found circumglobally from temperate to tropical waters. Their vulnerability to fisheries exploitation, bycatch, boat collisions, entanglement and unregulated tourism is exacerbated by their aggregative behavior. Studies have identified aggregation sites around the world for all nine mobulid species, with these groupings varying from a few individuals to thousands. However, the terminology used to define these aggregations and the drivers underpinning them remain unclear, hindering the development of effective management and conservation strategies. Here, we analyze aggregation behavior for mobulid species, providing consistent definitions for grouping events and summarizing the existing research on drivers and environmental factors triggering these events. We find that aggregation behaviors facilitate key life history functions in mobulids, including feeding, courtship and mating, predation avoidance, cleaning, and thermoregulation. Conservation threats and management mitigation opportunities associated with aggregations sites include fisheries, tourism, spatial protection, and climate change. Finally, we highlight knowledge gaps for future research prioritization and developments in the field for the identification of aggregation sites, the study of aggregation size and demographics and the functions and timing of aggregations.

On the other hand, Munk's pygmy devil rays (*Mobula munkiana*) are medium-size, zooplanktivorous filter feeding, elasmobranchs characterized by aggregative behavior, low fecundity and delayed reproduction. These traits make them susceptible to targeted and by-catch fisheries and are listed as Vulnerable on the IUCN Red List. Multiple studies have examined fisheries impacts, but nursery areas or foraging neonate and juvenile concentrations have not been examined. This study describes the first nursery area for *M. munkiana* at Espiritu Santo Archipelago, Mexico. We examined spatial use of a shallow bay during 22 consecutive months in relation to environmental patterns using traditional tagging (n = 95) and acoustic telemetry (n = 7). Neonates and juveniles comprised 84% of tagged individuals and their residency index was significantly greater inside than outside the bay; spending a maximum of 145 consecutive days within the bay. Observations of near-term pregnant females, mating behavior, and neonates indicate an April to June pupping period. Anecdotal photograph review indicated that the nursery area is used by neonates and juveniles across years. These findings confirm, for the first time, the existence of nursery areas for Munk's pygmy devil rays and the potential importance of shallow bays during early life stages for the conservation of this species.

Finally, we examined the reproductive behavior (courtship and mating) and its seasonality in three *Mobula* species, spintail, bentfin, and Munk's devil rays (*M. mobular*, *M. thurstoni*, and *M. munkiana*) in the southwestern Gulf of California, Mexico, using boat surveys (with drone and in-water observations) (n=69 survey days), spotter planes (n= 428 flights) and citizen science observations (n=31). We examined whether (1) reproductive grounds existed within the area for any of these

species, (2) whether reproductive behavior followed seasonal patterns, and (3) if this behavior was similar among all mobula rays. We observed reproductive behavior in 221 events in 2017 and 2021–2022, for *M. mobular* (n=10), *M. thurstoni* (n=3), and *M. munkiana* (n=208) dispersed along 312 km of the eastern Baja California Peninsula between 4 m to 6.3 km away from the coast. Most events (n=209) occurred in the La Ventana and Ensenada de Muertos areas. Courtship was observed for *M. mobular* and *M. thurstoni* and a copulation attempt for *M. munkiana*, with reproductive behavior following a seasonal pattern occurring from March to August, with a peak during May (81.9 % of the events). *Mobula munkiana* displayed previously undescribed behaviors, such as the “piggyback leaps” as a precopulatory position and the “courtship vortex”, where 122 individuals were observed circling in a clockwise direction for five hours with courtship groups joining and leaving the main vortex formation. This study highlights the areas of La Ventana and Ensenada de Muertos as critical habitats for reproductive behavior of two endangered and one vulnerable devil ray species.

RESUMEN

Las rayas mobulas (mobúlidos) son elasmobranquios filtradores con historias de vida extremadamente conservadoras del tipo K-selectivas que se encuentran globalmente distribuidas, desde aguas templadas a tropicales. Su vulnerabilidad a la explotación pesquera, la captura incidental, las colisiones con embarcaciones, el enredo y el turismo no regulado se ve exacerbada por su comportamiento de agregación. Estudios han identificado sitios de agregación en todo el mundo para las nueve especies de mobúlidos, con estos grupos variando desde unos pocos individuos hasta miles. Sin embargo, la terminología utilizada para definir estas agregaciones y los impulsores que las sustentan siguen siendo poco claros, dificultando el desarrollo de estrategias efectivas de gestión y conservación. Aquí analizamos el comportamiento de agregación de las especies de mobúlidos, proporcionando definiciones consistentes para eventos de agrupación y resumiendo la investigación existente sobre los impulsores y factores ambientales que desencadenan estos eventos. Descubrimos que los comportamientos de agregación facilitan funciones clave en la historia de vida de los mobúlidos, incluyendo la alimentación, el cortejo y el apareamiento, la evasión de la depredación, la limpieza y la termorregulación. Las amenazas de conservación y las oportunidades de mitigación de la gestión asociadas con los sitios de agregación incluyen la pesca, el turismo, la protección espacial y el cambio climático. Finalmente, destacamos lagunas de conocimiento para la priorización de investigaciones futuras y desarrollos en el campo para la identificación de sitios de agregación, el estudio del tamaño y la demografía de las agregaciones, y las funciones y el momento de las agregaciones.

Por otro lado, las rayas mobulas pigmeas de Munk (*Mobula munkiana*) son elasmobranquios filtradores de tamaño mediano, zooplánctívoros, con comportamiento de agregación, baja fecundidad y reproducción tardía. Estas características los hacen susceptibles a la pesca dirigida y la captura incidental, y están clasificados como Vulnerables en la Lista Roja de la UICN. Varios estudios han examinado los impactos de la pesca, pero no se han examinado áreas de cría o agregaciones de neonatos y juveniles. Este estudio describe la primera área de crianza para *M. munkiana* en el Archipiélago Espíritu Santo, México. Examinamos el uso espacial de una bahía poco profunda durante 22 meses consecutivos en relación con patrones ambientales utilizando marcaje tradicional ($n = 95$) y telemetría acústica ($n = 7$). Los neonatos y juveniles comprendieron el 84% de los individuos marcados y su índice de residencia fue significativamente mayor dentro que fuera de la bahía, pasando un máximo de 145 días consecutivos dentro de la bahía. Observaciones de hembras preñadas a término, comportamiento de apareamiento y neonatos indican un período de alumbramiento de abril a junio. La revisión anecdótica de fotografías indicó que el área de cría es utilizada por neonatos y juveniles a lo largo de los años. Estos hallazgos confirman, por primera vez,

la existencia de áreas de crianza para las rayas mobulas pigmeas de Munk y la importancia potencial de las bahías poco profundas durante las primeras etapas de vida para la conservación de esta especie.

Finalmente, examinamos el comportamiento reproductivo (cortejo y apareamiento) y su estacionalidad en tres especies de rayas mobula (*M. mobular*, *M. thurstoni* y *M. munkiana*) en el suroeste del Golfo de California, México, utilizando muestreos desde embarcación (con observaciones de drones y bajo el agua) (n = 69 días de muestreo), avioneta ultraligera (n = 428 vuelos) y observaciones de ciencia ciudadana (n = 31). Examinamos si (1) existían áreas de reproducción dentro del área para cualquiera de estas especies, (2) si el comportamiento reproductivo seguía patrones estacionales y (3) si este comportamiento era similar entre todas las rayas mobula. Observamos comportamiento reproductivo en 221 eventos en 2017 y 2021–2022, para *M. mobular* (n = 10), *M. thurstoni* (n = 3) y *M. munkiana* (n = 208) dispersas a lo largo de 312 km de la península de Baja California, entre 4 m y 6.3 km de distancia de la costa. La mayoría de los eventos (n = 209) ocurrieron en las áreas de La Ventana y Ensenada de Muertos. Se observó cortejo para *M. mobular* y *M. thurstoni* y un intento de cópula para *M. munkiana*, con un patrón estacional que ocurrió de marzo a agosto, con un pico durante mayo (81.9% de los eventos). *Mobula munkiana* mostró comportamientos previamente no descritos, como los "saltos a cuevas" como posición precopulatoria y el "vórtice de cortejo", donde se observó a 122 individuos dando vueltas en sentido horario durante cinco horas, con grupos de cortejo uniéndose y saliendo de la formación principal del vórtice. Este estudio destaca las áreas de La Ventana y Ensenada de Muertos como hábitats críticos para el comportamiento reproductivo de dos especies de rayas mobula en peligro de extinción y una vulnerable.

CHAPTER 1.

Manta and devil ray aggregations: Conservation challenges and developments in the field

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Introduction

It is well documented that many elasmobranchs form large aggregations, varying from temporary groups to structured, long-term associations (e.g., hammerhead sharks, basking sharks, blacktip sharks, and common stingrays) (Klimley 1987; Ward et al., 2004; Croft et al., 2006; Ward et al., 2007; Croft et al., 2011; Crowe et al., 2018; Chaikin et al., 2020; Ayres et al., 2021; Sims et al., 2022). The functions of such aggregation behaviors have been hypothesized to include reproduction (Klimley 1987; Chaikin et al., 2020; Sims et al. 2022), feeding (De la Parra Venegas et al., 2011), energy conservation, (Klimley and Nelson 1984; Economakis and Lobel, 1998; Hight and Lowe 2007), refuge from predators (Heupel et al., 2007; McAllister et al., 2017) and social learning (Sih et al., 2009; Brown and Laland 2011). The formation of these aggregations can be seasonal and is often linked to environmental factors and life history stages (Rohner et al., 2013; Kajiura and Tellman 2016), food abundance (Clua et al., 2013; Hacothen-Domené et al., 2015), critical habitats (Oh et al., 2017, Chiriboga-Paredes et al., 2022) and reproduction (Heupel and Simpfendorfer 2005; Reyier et al., 2008). The seasonality of these aggregation events, along with the large number of individuals at specific areas (i.e., coastal areas, productive systems) can also increase the likelihood and intensity of exposure to anthropogenic threats such as targeted fishing (Litvinov 2006, Croll et al., 2016), bycatch (Watson et al., 2009; Hall and Roman 2013), habitat degradation (Cattano et al., 2021), irresponsible tourism (Venables et al., 2016; Zemah-Shamir et al., 2019), boat strikes (Lester et al.,

2020; Allen et al., 2021; Womersley et al., 2022) or climate change (particularly if mismatches in the timing of migration, reproduction or foraging interactions occur) (Lezama-Ochoa et al., 2023, *in prep*).

Among elasmobranchs, the nine manta and devil ray species (collectively referred to as mobulids) inhabit tropical to temperate waters circumglobally (Couturier et al., 2012; Stevens et al., 2018a; Stewart et al., 2018a). Mobulids seasonally form aggregations ranging from a few to thousands of individuals (Anderson et al., 2011; Couturier et al., 2012; Stevens 2016; Harris and Stevens 2021; Palacios et al., 2021). These aggregations often occur in habitats or locations associated with concentrated food resources (Couturier et al., 2011; Armstrong et al., 2016; Harris et al., 2020; Harris and Stevens 2021), parasite removal (O’Shea et al., 2010; Jaine et al. 2012; Perryman et al., 2019), thermal refugia (Stevens 2016; Palacios et al., 2021), reproductive behavior (Mendonça et al., 2020), and predator avoidance (Germanov et al., 2019; Pate and Marshall 2020). Mobulids are also highly vulnerable to overexploitation due to their low fecundity (one pup per pregnancy, low birth rate, and delayed reproduction), leading to slow population growth rates (Stevens et al., 2000; Dulvy et al., 2014). The primary anthropogenic threat to mobulids is fisheries exploitation from both targeted fisheries and bycatch (Croll et al., 2016). Mobulid rays' tendency to aggregate in productive pelagic areas, where commercially valuable species are targeted by both artisanal and industrial fisheries using a variety of gears (e.g. gillnets, purse-seines, and longlines) results in bycatch being a primary impact for most species of mobulid rays (Hall and Roman 2013; Rohner et al., 2013; Croll et al., 2016; Lezama-Ochoa et al., 2019a) and contributes to declines in mobulid populations globally (Couturier et al. 2013; Lawson et al., 2017; Rohner et al., 2017). As a result, all mobulid species are listed as Endangered or Vulnerable on the IUCN’s Red List of Threatened Species (IUCN, 2022). Furthermore, mobulid aggregations in coastal areas can lead to exposure to boat collisions (Germanov et al., 2019; Pate and Marshall 2020; Strike et al., 2022), habitat degradation (Stewart et al., 2018a) and unregulated tourism impacts (Venables 2013; Murray et al., 2020; Gómez-García et al., 2021). The identification of aggregation sites for some species has led to the creation of Marine Protected Areas (MPAs) (e.g., UNESCO World Heritage Sites Revillagigedo Archipelago in Mexico, and Hanifaru Bay MPA in Maldives) and the establishment of management measures, such as best practices to reduce the mortality of mobulids caught incidentally by tuna purse seiners, or codes of conducts to ensure responsible tourism practices (Poisson et al., 2012; Lezama-Ochoa et al., 2019b; Murray et al., 2020, Cronin et al., 2022).

The aim of this review is to: 1) provide consistent definitions and terminology for mobulid aggregation and grouping events; 2) summarize existing research on the drivers and environmental factors underpinning aggregation events in mobulids; 3) identify conservation threats, management strategies, and mitigation opportunities associated with aggregation sites; and 4) identify knowledge gaps for future research prioritization.

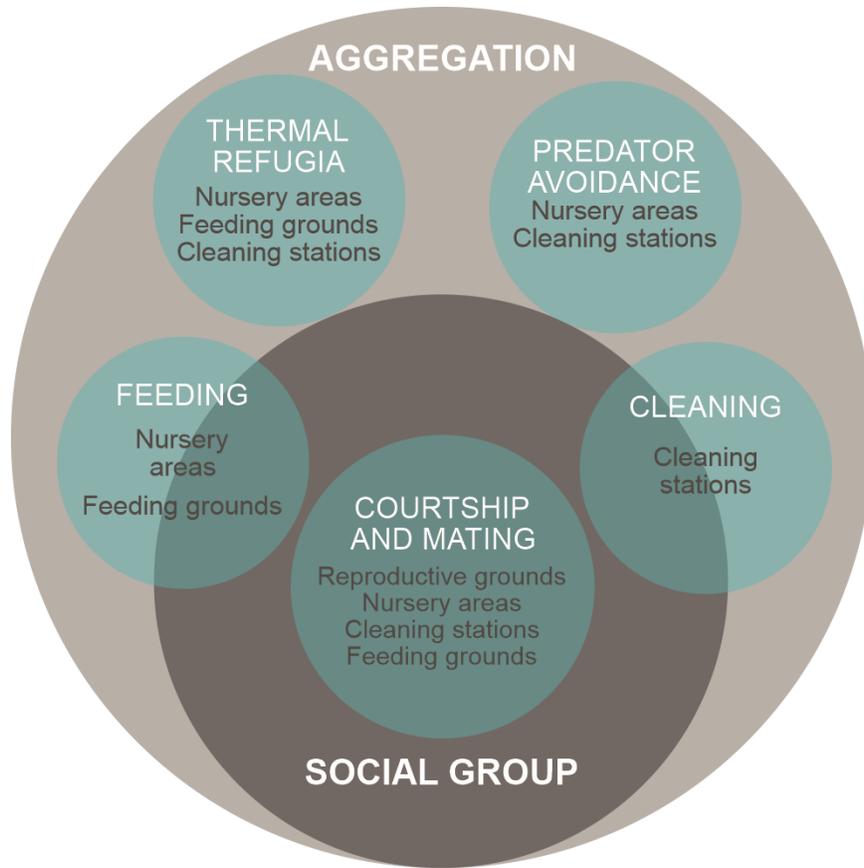


Figure 1. Conceptual framework of grouping behaviors in elasmobranchs. Aggregation (individuals are passively drawn together) is the general term to describe any group and the first prerequisite for the formation of social groups (individuals are drawn to one another). Life history functions (in white italics) acting as drivers of manta and devil ray aggregations. In grey are the key aggregation sites where these life history functions occur.

2. Aggregation and social grouping in mobulids

The terminology used in describing aggregation behavior in elasmobranchs is often inconsistent and confusing (McInturf et al. *in review*). Here we present a conceptual framework (**Figure 1**) to classify the different types of aggregation behaviors that have been described in the elasmobranch literature. We propose **aggregation** as the most general term, which can be used to describe any group of individuals that forms for any purpose (Johnson et al., 2002; Guttridge et al., 2009; Guttal and Couzin 2010; Jacoby et al., 2012). Some aggregations can be **social groups**, within which individuals exhibit interactive behaviors such as courtship, mating (Sims et al., 2022), or cooperative feeding (Mourier et al., 2012), and dynamic associative relationships among individuals may be present (Guttridge et al., 2009; Jacoby et al., 2012). In several marine species including elasmobranchs, these associations

have been described as fission-fusion dynamics, where groups merge (fusion) or split (fission) depending on various factors including the costs and benefits of the size of the group (e.g., increased competition for food versus reduced predation risk) (Haulsee et al., 2016).

Social grouping can facilitate collective behaviors like cooperative or optimal feeding (Sih et al., 2009, Villegas-Ríos et al., 2022), predator avoidance (Chivers et al., 1995; Ward et al., 2011), and social learning (Lachlan et al., 1998; Brown et al., 2011). Aggregations are likely the first prerequisite for the establishment of social grouping because they facilitate the establishment of social interactions among aggregating individuals (Sims et al., 2000; Jacoby et al., 2012).

Aggregation behavior has been documented in all mobulid species (**Table 1**) (Childs 2001; Weeks et al., 2015; Stevens 2016; Couturier et al., 2018; Lezama-Ochoa et al., 2019a; Solleliet-Ferreira et al., 2020; Palacios et al., 2021; Harris and Stevens 2021, McCann et al., 2021). However, less attention has been paid to the social interactions within aggregations that may be indicative of more complex social grouping (Marshall and Bennett 2010a; Stewart et al., 2017a; Stevens et al., 2018b; Perryman et al., 2019; Murray 2019). Nonetheless, some mobulid aggregations have been described as social groups (Marshall and Bennett 2010a; Stevens 2016; Stevens et al., 2018b; Perryman et al., 2019). Within aggregations and social groups, segregation by size and sex has been observed (Notarbartolo di Sciara 1988; Cerutti 2005; Stewart et al., 2018a; Stevens 2016; Germanov et al., 2019; Perryman et al., 2019; Palacios et al., 2021) (**Table 1 Supplementary material**).

Mobulids possess the highest brain: body weight ratios of all fishes, with enlarged telencephalon regions (Ari 2011). The telencephalon region drives complex social behaviors in other animals, including for the establishment of dominance hierarchies and social bonds (Dunbar and Shultz 2007; Ari 2011). However, the few studies analyzing the social structure of mobulids have focused only on reef manta rays (*Mobula alfredi*) and have found social groups that last for only short durations (weeks) where interactions are open with fluid hierarchical social structures among females and juveniles (Perryman et al., 2019) or unstructured aggregations with associations based on spatiotemporal overlap among individuals driven by food availability (Murray 2019).

2.1. Drivers of mobulid aggregations

Aggregation behaviors facilitate key life history functions in mobulids, including feeding, courtship and mating, predation avoidance, cleaning, and thermoregulation (**Figure 1**). Locations where one or more aggregation drivers are present and predictable can become key aggregation sites that are used repeatedly by mobulids, such as cleaning stations and feeding sites, or sites that facilitate long-term stable aggregations such as nurseries (**Figure 2**). Below, we describe the importance of aggregation behavior in each of these life history functions and at these key sites.

2.1.1 Feeding aggregations

Large aggregations are often driven by feeding behavior associated with mobulids' reliance on dense prey assemblages that may correspond to seasons and locations with higher productivity and prey

abundance (Notarbartolo-di-Sciara, 1988; Jaine et al., 2012; Anderson et al., 2011; Stevens 2016; Hacothen-Domene et al., 2017; Stewart et al., 2017b; Lezama-Ochoa et al., 2019b, 2020; Harris and Stevens 2021). In the most closely studied example of large feeding aggregations (*M. alfredi*), no cooperative grouping behavior was observed, indicating that these feeding aggregations are likely site-specific behaviors in which prey availability and site characteristics lead to local enhancement of prey (Silverman et al., 2004; Jourdaina and Vongraven 2017) and the co-occurrence of multiple individuals, with prey availability likely also determining the group size (Murray 2019).

Table 1. Grouping behavior for mantas and devil rays. * Maximum aggregation size from tuna purse seine fisheries data and is the number of individuals in one single set. References refer to the maximum aggregation size.

Species (Latin/ common name)	IUCN status	Distribution	Min-Max DW Size (cm)	Max aggregation size	Drivers of aggregations	Threats at aggregation sites	References
<i>M. birostris</i> / Oceanic manta ray	EN	Circumtropical, warm, and temperate waters	200 - 700	50	Feeding/Predator avoidance/ Cleaning/Courtship and mating/Thermal refugia	Bycatch/Unsustainable tourism/Boat traffic/ Entanglements	Notarbartolo-di-Sciara and Hillyer, 1989
<i>M. alfredi</i> /Reef manta ray	VU	Indo-West Pacific Oceans in tropical and warm waters	130 - 450	250	Feeding/Predator avoidance/ Cleaning/Courtship and mating/Thermal refugia	Bycatch/Unsustainable tourism/Boat traffic/ Entanglements	Harris et al., 2020
<i>M. tarapacana</i> / Sicklefins devil ray	EN	Circumtropical, warm, and temperate waters	105 - 370	50	Feeding/Courtship and mating	Bycatch/Target fisheries	Solleliet-Ferreira et al., 2020
<i>M. mobular</i> / Spinetail devil ray	EN	Circumtropical, warm, and temperate waters	92-320	162*	Feeding/Courtship and mating	Bycatch/Target fisheries	Lezama-Ochoa et al., 2019a
<i>M. thurstoni</i> / Bentfin devil ray	EN	Circumtropical, warm, and temperate waters	65-183	220*	Feeding/Courtship and mating	Bycatch/Target fisheries	Lezama-Ochoa et al., 2019a
<i>M. eregoodoo</i> / Longhorned pygmy devil ray	EN	Indo-West Pacific Oceans in tropical and warm waters	34 - 130	30	Feeding	Bycatch/Bather-protection gillnets	Notarbartolo-di-Sciara et al., 2019
<i>M. munkiana</i> / Munk's pygmy devil ray	VU	Eastern Tropical Pacific in tropical and warm waters	35 - 130	>1000	Feeding/Predator avoidance/ Courtship and mating/ Thermal refugia	Bycatch/Unsustainable tourism	Palacios et al., 2021
<i>M. hypostoma</i> / Atlantic pygmy devil ray	EN	Atlantic Ocean in tropical and warm waters	31 - 125	50	Feeding/Courtship and mating	Bycatch	Childs, 2001
<i>M. kuhlii</i> / Shorthorned pygmy devil ray	EN	Indo-West Pacific Oceans in tropical and warm waters	31-122	100	Feeding/Cleaning	Bycatch	McCann et al., 2021

* Maximum aggregation size from tuna purse seine fisheries data and the number of individuals in one single set. References refer to the maximum aggregation size.

These aggregations in areas of local enhancement may also be easier to find because of the presence of conspecifics feeding on them, further increasing aggregation size and improving foraging efficiency by reducing search time (Thorpe 1963; Galef 2013). In some cases, the coordination of several feeding individuals may also facilitate prey concentration, enhance prey capture, and increase foraging efficiency (Lett et al., 2014). In mobulids, this coordinated behavior occurs during several feeding strategies, such as piggyback, chain, lunge, or cyclone feeding (Stevens 2016; Stevens et al., 2018b; Bucair et al., 2021) described below.

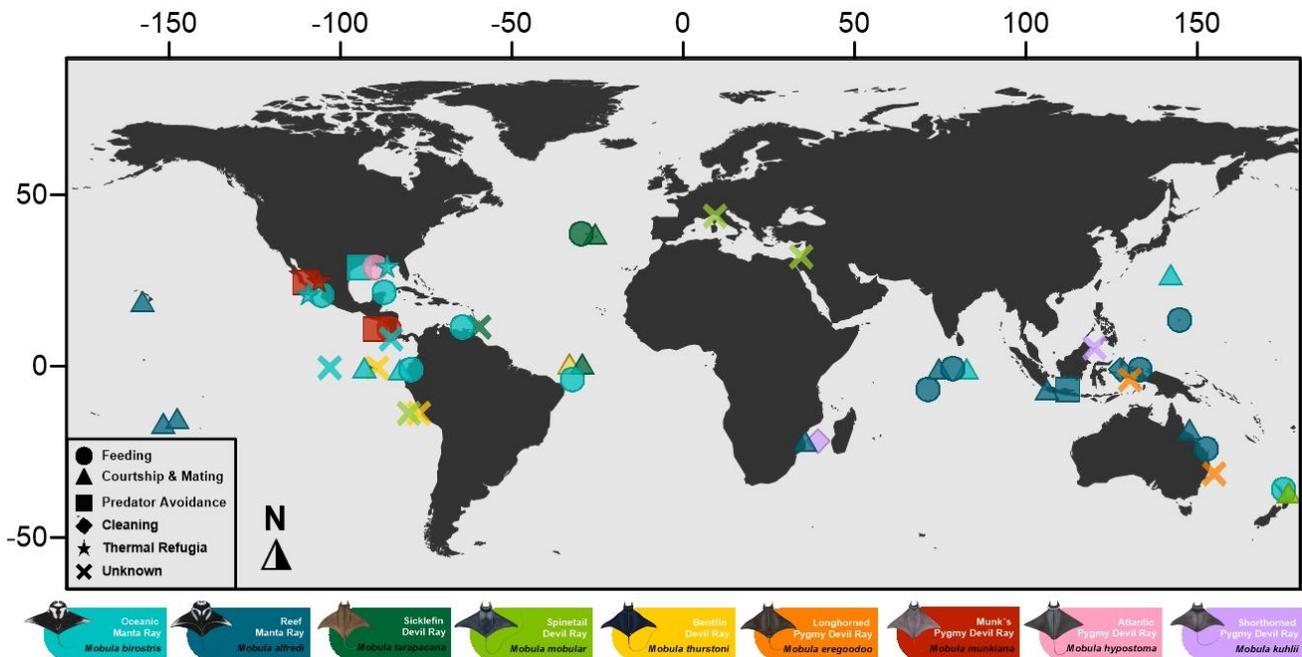


Figure 2. Manta and devil rays aggregation sites worldwide by species (colors) and drivers of the aggregation or social group (geometric figure). Aggregations illustrated with an X have no information related to the purpose of the group.

Large-scale oceanographic processes and regimes such as seasonal upwelling systems (La Niña in the Eastern Tropical Pacific, and the South Asian Monsoon in the Indian Ocean) have a strong influence on the occurrence of mobulid aggregations (Anderson et al., 2011; Stevens 2016; Burgess 2017; Beale et al., 2019; Lezama-Ochoa et al., 2019a, b; Harris et al., 2020; Harty et al., 2022; Fonseca-Ponce et al., 2022). At fine scales, the bathymetry of aggregation sites, combined with tidal cycles and tidal currents, helps accumulate and condense zooplankton at densities up to 40 times higher than in surrounding waters (Armstrong et al., 2016), triggering feeding aggregations such as

those described in the Maldives (Stevens 2016; Harris and Stevens 2021), eastern Australia (Armstrong et al., 2016), and the Chagos Archipelago (Harris et al., 2021). In conjunction with these environmental factors, moon phases have also been shown to influence the presence of *M. alfredi* at several aggregation sites (Dewar et al., 2008; Anderson et al., 2011; Jaine et al., 2012; Harris and Stevens 2021). These mobulid feeding aggregations can be influenced by zooplankton size, species, and concentration. For example, in Hanifaru Bay, Maldives, Armstrong et al. (2021) found that *M. alfredi* formed feeding aggregations when the zooplankton community was dominated by large crustaceans (copepods) and total biomass was greater than a theoretical prey density threshold for net energy gain (25.2 mg m^{-3}). At this feeding aggregation site, the foraging opportunities appeared to occur when strong lunar tides overcame the force of the prevailing monsoonal current, drawing plankton-rich water from deep waters outside the atoll into the shallow reef inlet (Harris and Stevens 2021) attracting up to 250 *M. alfredi* individuals (Stevens 2016; Harris et al., 2020) (**Table 2**). Interactions between lunar tides and bathymetry may be a coherent explanation for why moon phase and tidal range have been identified as important predictors of mobulid presence at many aggregation sites (Dewar et al., 2008; Anderson et al., 2011; Jaine et al., 2012; Harris and Stevens 2021; Fonseca-Ponce et al., 2022). At Lady Elliot Island, Australia, however, *M. alfredi* began feeding in aggregations at lower prey densities than this theoretical density threshold (Armstrong et al., 2016). Here, river outflow, dynamic eddy activity, convergent fronts and ebb tides triggered large *M. alfredi* feeding aggregations of more than 150 individuals (Weeks et al., 2015).

During feeding aggregations, social groups can be formed as coordinated feeding strategies emerge (e.g., chain, piggyback and lunge feeding). Here, mobulids use the position of a conspecific to improve their chances of successful feeding, enhancing prey capture, hydrodynamic efficiency, and collision avoidance between individuals (Stevens 2016; Stevens et al., 2018a; Solleliet-Ferreira et al., 2020; Armstrong et al., 2021; Harris and Stevens 2021). Such coordinated feeding has been described in *M. alfredi*, *M. birostris*, *M. kuhlii*, *M. munkiana*, *M. hypostoma*, *M. eregoodoo* and *M. tarapacana* while feeding on zooplankton and shoals of anchovies or mesopelagic lanternfish (Stevens 2016; Stevens et al., 2018a; Stewart et al., 2018c; Solleliet-Ferreira et al., 2020; Bucair et al., 2021) (**Figure 3B, G**). An additional type of coordinated feeding, cyclone feeding, has been described for *M. alfredi* in the Maldives (Stevens 2016; Stevens et al., 2018a) involving up to 150 individuals circling in an anticlockwise direction in the water column, resembling a 15 m diameter cyclone, for as long as 60 minutes (Stevens 2016). This behavior presumably creates hydrodynamic conditions favorable to foraging success and is correlated with high zooplankton biomass values over 200 mg m^{-3} (Armstrong et al., 2021) (**Figure 3E**).

2.1.2 Courtship and mating aggregations

Courtship and mating in elasmobranchs are often complex and variable across species (Carrier et al., 1994; Pratt and Carrier 2001). Under our conceptual framework, all reproductive aggregations would be considered social groups. Some elasmobranch species form reproductive social groups via active partner preferences that can be sporadic and short (Jacoby et al., 2012). In mobulids, reproductive social groups seem to be initiated by males (Stevens et al., 2018b).

Table 2. Types of aggregations and social groups based on drivers of the groups for manta and devil rays. Only studies with >10 individuals aggregating at the same time were considered in this table. (NS) Not stated in the study. Grey highlight cells are aggregations not protected or not fully protected by Marine Protected Areas.

Drivers of aggregations	Species	Aggregation region	Max aggregation size	Conservation threats	References
Feeding	<i>M. birostris</i>	Ecuador (Isla de La Plata)	60	Entanglement, bycatch	Harty et al., 2022
		Mexico (Bahía de Banderas)	20	Entanglement and boat strikes	Fonseca-Ponce et al., 2022
		Venezuela (Caribbean)	50	NS	Notarbartolo-di-Sciara and Hillyer, 1989
		Mexico (Caribbean)	10	NS	Hacohen-Domené et al., 2017
	<i>M. alfredi</i>	Australia (Lady Elliot Island)	150	Climate change	Jaine et al., 2012; Weeks et al., 2015
		Indonesia (Raja Ampat)	67	Unregulated tourism and increased boating	Perryman et al., 2019
		Chagos Archipelago (Egmont Atoll)	40	NS	Harris et al., 2021
		Maldives (Hanifaru Bay)	250	Unregulated tourism, dredging and climate change	Stevens, 2016; Armstrong et al., 2021
		Guam (Tumon Bay)	12	NS	Hartup et al., 2013
	<i>M. tarapacana</i>	Portugal (Azores)	21	Entanglement, unregulated tourism, bycatch	Solleliet-Ferreira et al., 2020
<i>M. hypostoma</i>	USA (Flower Garden Banks)	50	NS	Childs, 2001	
<i>M. munkiana</i>	Costa Rica (Punta Descartes)	10	Coastal development	Porsiel et al., 2021	
Courtship and mating	<i>M. alfredi</i>	Maldives	27	Entanglement, unregulated tourism	Stevens et al., 2018b
		Mozambique	14	NS	Marshall and Bennett, 2010a
		Indonesia (Nusa Penida)	14	Entanglement, unregulated tourism	Germanov et al., 2019

(Continued)

Drivers of aggregations	Species	Aggregation region	Max aggregation size	Conservation threats	References
		USA (Maui)	22	Entanglement, unregulated tourism	Deakos, 2012; Stevens et al., 2018b
	<i>M. tarapacana</i>	Portugal (Azores)	16	Entanglement, unregulated tourism, bycatch	Sobral, 2013
		Brazil (Saint Peter and Saint Paul Archipelago)	24	NS	Mendonça et al., 2020
Predator Avoidance	<i>M. munkiana</i>	Costa Rica (Punta Descartes)	10	Coastal development	Porsiel et al., 2021
		Mexico (Espiritu Santo Archipelago)	19	Bycatch and unregulated tourism	Palacios et al., 2021
Cleaning	<i>M. alfredi</i>	Indonesia (Raja Ampat)	55	Unregulated tourism and increased boating	Perryman et al., 2019
Thermal refugia	<i>M. birostris</i>	Mexico (Bahia de Banderas)	20	Entanglement and boat strikes	Fonseca-Ponce et al., 2022
	<i>M. munkiana</i>	Mexico (Espiritu Santo Archipelago)	19	Bycatch and unregulated tourism	Palacios et al., 2021

The duration of reproductive social groups may be related to the number of males involved in the courtship of the female, with more extended periods when more males are involved (Marshall and Bennett 2010a). This reproductive behavior has been described for five mobulid species (**Table 2**) at oceanic islands, seamounts, ridge systems, coral reefs, feeding aggregation sites, cleaning stations, and within the thermocline at depths between 50 to 80 m (Yano et al., 1999; Marshall and Bennett 2010a; Sobral 2013; Stevens et al., 2018b; Germanov et al., 2019; Stewart et al., 2019; Mendonça et al., 2020). During courtship events, several individuals are generally involved, with one or two females chased by as many as 26 males (Stevens et al., 2018b).

Reproductive social groups are often seasonal. In *M. alfredi* in Mozambique, fresh mating wounds and mating events were observed during the austral summers from October to January (Marshall and Bennett 2010a). While *M. tarapacana* (Saint Peter and Saint Paul Archipelago, Brazil) and *M. munkiana* (Gulf of California, Mexico) are present year-round, social groups displaying courtship and mating behaviors occur only during spring and summer months. Mobulids are believed to give birth shortly before mating (Uchida et al., 2008; Stevens et al., 2018a) and the seasonality of courtship and mating groups may therefore be linked to seasonal food availability and higher temperatures that would benefit the development of neonates (Notarbartolo-di-Sciara, 1988; Mendonça et al., 2020; Palacios et al., 2021). The reported aggregations of *M. mobular* in the southeast corner of the Mediterranean Sea (off the coasts of Palestine and Israel) during the coldest time of year could be related to the rays accessing the portion of the Mediterranean where sea temperatures are mildest. Evidence of mating was reported in this region based on the presence of oozing sperm in males caught in the fishery (Abudaya et al., 2017).



Figure 3. Mobulid aggregations. **(A)** *M. hypostoma* in the Mexican Caribbean. Photo © Guy Stevens. **(B)** A feeding aggregation of *M. eregoodoo* at Raja Ampat, Indonesia. Photo © Jeff Lemelin. **(C)** *M. kuhlii* aggregation in the Maldives. Photo © Guy Stevens. **(D)** *M. munkiana* aggregating in the Gulf of California, Mexico. Photo © Siddharta Velázquez Hernández, Ocean Life Flights. **(E)** *M. alfredi* during a cooperative feeding aggregation in Hanifaru Bay, Maldives. Photo © Guy Stevens. **(F)** Aggregation of *M. mobular* in the Gulf of California, Mexico. Photo © Siddharta Velázquez Hernández, Ocean Life Flights. **(G)** *M. tarapacana* at Princess Alice Banks, Azores. Photo © Tane Sinclair-Taylor.

2.2.3 Predator avoidance aggregations

Forming aggregations may help diminish the risk of predation in elasmobranchs (Heupel and Simpfendorfer 2005). Mobulids have several known predators, mainly sharks and killer whales (Alava and Merlen 2009; Marshall and Bennet, 2010a; Stevens et al., 2018a). Larger species of mobulids (*M. birostris* and *M. alfredi*) tend to form smaller aggregations than smaller species, such as the pygmy devil rays (*M. munkiana*, *M. eregoodoo*, *M. hypostoma*, and *M. kuhlii*; **Table 1**) and are more likely to survive attacks with different degrees of sublethal injuries (Marshall and Bennett, 2010b; Deakos et al., 2011; Strike et al., 2022). However, survival from predation on pygmy devil rays is less likely to occur, although no studies have formally addressed sub-lethal injuries or natural mortality of pygmy devil rays. The larger aggregations formed by pygmy devil rays may have evolved as a predator-avoidance strategy for these smaller species (Broadhurst et al., 2018; Notarbartolo-di-Sciara et al., 2019).

Aggregating at protected or sheltered habitats during vulnerable periods, such as early life stages, to reduce predation risk has been observed in several elasmobranch species (Heupel et al., 2007; Heupel and Simpfendorfer 2011). Aggregations at cleaning stations may also help reduce predation

risk because of the shallow bottom habitats that helps protect mobulids (*M. alfredi*) from shark attacks from below (Stevens 2016; Stewart et al., 2018b).

Mobulids exhibit substantial maternal investment in a single offspring, and individuals may take 5-15 years to reach sexual maturity, depending on the species (Couturier et al., 2012; Stevens 2016; Stewart et al., 2018a). Mobulids appear to utilize nursery areas, where neonates or juveniles aggregate in a similar manner to many other elasmobranchs (Heupel et al., 2007; Martins et al., 2018). This aggregation behavior results in higher residency in habitats that appear to enhance the survival of neonates and juveniles (Heupel and Simpfendorfer 2011). During early life stages, social behaviors (Reyier et al., 2008), active association with conspecifics (Guttridge et al., 2009), and even individual personalities (Finger et al., 2017) have been described for some shark species (e.g., lemon sharks). To date, there is no evidence of similar social behaviors in mobulid nurseries. However, aggregating in nursery areas at vulnerable life history stages may be critical to reduce predation in early life stage mobulids. Mobulid nurseries have been identified at reef lagoons (Setyawan et al., 2022a), along the coast (Pate and Marshall 2020; Knochel et al., 2022), estuarine systems (Medeiros et al., 2015), and at shallow bays (Germanov et al., 2019; Palacios et al., 2021). These nearshore areas likely provide refuge from predators (Stevens 2006; Stewart et al., 2018a, b; Palacios et al., 2021; Setyawan et al., 2022a) as well as foraging opportunities (Setyawan et al., 2022a). Nursery areas have been described for juvenile *M. birostris*, (Childs 2001; Medeiros et al., 2015; Stewart et al., 2018b; Pate and Marshall 2020; Knochel et al., 2022), *M. alfredi* (Germanov et al., 2019; Setyawan et al., 2022a), and *M. munkiana* (Palacios et al., 2021). Neonates and juveniles have been shown to use and aggregate in these nursery areas with the occasional presence of adult individuals (Germanov et al., 2019; Palacios et al., 2021). Group sizes within mobulid nurseries tend to be smaller than adult aggregations (e.g., maximum of 19 juvenile individuals in *M. munkiana* compared with adult aggregations of thousands of individuals) (Palacios et al., 2021). In some of these nursery areas there is segregation by size (Palacios et al., 2021), similar to descriptions in other juvenile elasmobranchs (Guttridge et al., 2011), which could be the result of differences in swimming capabilities or habitat preferences at different size/age stages (Jacoby et al., 2012).

2.2.4 Cleaning aggregations

Cleaning stations play a vital role in the ecology and health of several mobulid species by providing an opportunity for them to rid themselves of harmful parasites by being cleaned by small fishes (O'Shea et al., 2010). Cleaning stations are well-defined areas, typically on inshore reefs or around seamounts (Jaine et al., 2012) where small 'cleaner' fishes (primarily Labridae) feed on the ectoparasites, mucus, dead or diseased tissue and scales of their larger 'clients' (Grutter 1996,

O'Shea et al., 2010) creating a mutually symbiotic interaction (Hay et al., 2004). Aggregations at cleaning stations have been documented in *M. kuhlii* (Murie and Marshall 2016), *M. birostris* and *M. alfredi* (which in many cases exhibit strong site fidelity to the station) (**Table 2**) (Dewar et al., 2008; O'Shea et al., 2010; Marshall and Bennett 2010b; Stewart et al., 2016a; Setyawan et al., 2018).

In addition to providing health benefits, these sites also provide opportunities where social interactions among individuals can occur (Stevens 2016; Stevens et al., 2018a, b; O'Shea et al., 2010; Perryman et al., 2019). The aggregation of mobulids at cleaning stations also has the potential to facilitate reproductive social behaviors, acting as lek sites for these species (Stevens 2016). For example, courtship and mating behavior in *M. alfredi* are frequently observed at cleaning stations in the Maldives (Stevens 2016; Stevens et al., 2018b) and Indonesia (Dewar et al., 2008; Germanov et al., 2019; Perryman et al., 2019). In Australia, *M. alfredi* visits at cleaning stations last for an average of 30 minutes per visit and up to five hours at the same site, facilitating frequent social interactions among individuals before, during, or after cleaning (O'Shea et al., 2010). In Raja Ampat, Indonesia, cleaning sites with as many as of 55 mobulids present at the same time have been described (Perryman et al., 2019). At the Revillagigedo Archipelago, Mexico, *M. birostris* have been observed socializing at different cleaning stations, including repetitive movements of the cephalic lobes and half-somersault maneuvers between individuals (Stewart et al., 2017a; Stewart et al., 2019).

2.2.5 Thermal refugia aggregations

Water temperature is a major driver of changes in movement and habitat use in elasmobranchs (Schlaff et al., 2014), and may affect metabolic and physiological functions such as digestion, reproduction, and somatic growth (Wallman and Bennett 2006; Hight and Lowe 2007; Tenzing 2014). Mobulids are found in tropical and temperate seas with an optimal thermal range from 20 to 26°C in the case of *M. alfredi* (Couturier et al., 2012; Lassauce et al., 2022). However, several species (*M. birostris*, *M. alfredi*, *M. tarapacana*, *M. mobular* and *M. munkiana*) perform deep dives, possibly to feed on zooplankton and other prey concentrated in the mesopelagic and bathypelagic zones (Stewart et al., 2016b; Lassauce et al., 2022; Andrzejczek et al., 2022) where water temperatures can reach < 4°C (Thorrold et al., 2014). After deep dives in cold water, mobulids bask at the surface as a behavioral thermoregulation mechanism to warm up their body temperatures (Canese et al., 2011; Thorrold et al., 2014; Stewart et al., 2016b; Lassauce et al., 2022). Aggregations during basking behavior at shallow coastal waters have been observed in *M. birostris* in Bahia de Banderas (Mexico), presumably after mesopelagic and thermocline associated foraging (Fonseca-Ponce et al., 2022). Coastal nursery areas for *M. birostris* in the Gulf of Mexico and enclosure estuaries in Brazil and for *M. munkiana* in the Gulf of California (where higher residency occurred during warmer temperatures) could also provide thermal refugia that accelerate the metabolic rates and growth of juveniles and

thereby reduce the duration of these vulnerable life history stages (Tenzing 2014; Stewart et al., 2018b; Palacios et al., 2021) (**Table 2**). In Maldives, individuals aggregating at warmer inshore reefs around cleaning stations and staying for longer periods than the cleaning activity, may be augmenting metabolic and physiological functions after deep water feeding forays (Stevens 2016). Surface aggregations of *M. mobular* and *M. tarapacana* in the Mediterranean Sea and the Azores, respectively, have been repeatedly observed (Celona 2004; Sobral 2013; Notarbartolo-di-Sciara et al., 2015; Solleliet-Ferreira et al., 2020), coinciding with diving data in the area, suggesting that basking behavior could be a thermal recovery strategy after deep dives (Canese et al. 2011; Thorrold et al. 2014) (**Figure 3F**). Aggregations at the surface during basking behavior may exacerbate the vulnerability of these species to anthropogenic threats, such as boat strikes (Stevens 2016; Fonseca-Ponce et al., 2022; Strike et al., 2022) and bycatch (Canese et al., 2011).

3. Conservation threats and management mitigation opportunities

As a group with extreme K-selective life history strategies, mobulids are vulnerable to overexploitation, and as a result are suffering from large population declines worldwide (Dulvy et al., 2014; Pardo et al., 2016; Rohner et al., 2017; Dulvy et al., 2021; Fernando and Stewart 2021). Mobulid aggregations occur at sites that serve important functions (e.g., feeding, reproduction) for the survival and recovery of threatened populations (Stevens et al., 2018b; Germanov et al., 2019; Setyawan et al., 2022a). The tendency of mobulids to aggregate in these areas can increase their vulnerability to anthropogenic activities by increasing the likelihood that multiple individuals will be impacted by any single threat (e.g., a single gill net or purse seine) (Croll et al., 2016; Rohner et al., 2017; Stewart et al., 2018a). Effective conservation and management for mobulids will benefit from the identification of mobulid aggregation sites, knowledge of the geographical extent from which the aggregation sites draw individuals, their seasonality, and the various environmental components influencing them to develop effective threat mitigation strategies through conservation measures at aggregations sites.

3.1 Fisheries

Targeted fishery exploitation and bycatch of mobulid aggregations is leading to major populations declines (e.g., *M. mobular*, *M. tarapacana*, *M. birostris* and *M. thurstoni* in Sri Lanka; Fernando and Stewart 2021) and even local extinctions (e.g., *M. birostris* in the Gulf of California and *Mobula* spp. in several regions in Indonesia; Lewis et al., 2015; Stewart et al., 2016a). Fisheries targeting mobulids still occur throughout the ranges of most species, including areas where aggregations and social groups occur (e.g., Sri Lanka, Indonesia, India, Peru, Philippines, Palestine, West Africa; Couturier et al., 2013; Acebes and Tull 2016; Setyawan et al., 2020; Fernando and Stewart 2021; Guirkingner et al., 2021). In industrial fisheries, tuna purse seine vessels in all tropical oceans of the world have relatively high bycatch of mobulids due to the overlap between tuna and mobulid species distributions within productive regions (Croll et al., 2012; Lezama-Ochoa et al., 2019a, b, 2020; Grande et al., 2020;

Guirhem et al., 2021). Captures of up to 220 individuals (*M. thurstoni*) from a single purse seine set have been reported (Lezama-Ochoa et al., 2019a), indicating the potential for incidental captures of aggregations to have a major impact on mobulid populations. Records of >50 bycaught mobulids within a single purse seine set normally occur at productive oceanographic fronts (e.g., off Peru in March for *M. mobular*; the Galapagos islands in December for *M. thurstoni*) (Lezama-Ochoa et al., 2019a) (**Table 3**). The spatial and temporal distribution data of mobulid bycatch collected by scientific observer programs is a powerful tool for identifying where and when large mobulid aggregations may occur and where they overlap with tuna purse seine fisheries. These datasets have been used in the creation of species distribution models for several mobulid species (Lezama-Ochoa et al., 2019b, 2020). The use of tracking data to validate or complete fisheries datasets are essential to support the effective development of spatially restricted seasonal areas as management strategies (Lezama-Ochoa et al., 2019a). Understanding the oceanographic preferences of these species may help to reduce their interactions with fisheries if dynamic spatial management approaches are implemented, as has already successful applied to other fisheries to reduce bycatch (Hazen et al., 2018).

Mobulid bycatch in artisanal fisheries is poorly documented worldwide, but it exists in at least 21 small scale fisheries (Lewis et al., 2015; Croll et al., 2016; Alfaro-Cordova et al., 2017). In a coastal stingray fishery in the Gulf of California, up to 84 *M. munkiana* have been bycaught in a single net at an aggregation area described as a nursery ground for this species (Del-Valle-González-González 2018; Palacios et al., 2021) (**Table 3**). In coastal Peru, an artisanal pelagic gillnet fishery using surface driftnet to target pelagic sharks and yellowfin tuna, reported several sets with more than 60 mobulid individuals per set in the coastal area in front of the Zorritos locality (Alfaro-Cordova et al., 2017). Furthermore, bather-protection nets in Australia have also shown to affect a pygmy devil ray species, *M. eregoodoo* (Broadhurst et al., 2018). There is an urgent need for regulations in artisanal fisheries to monitor and mitigate the bycatch rates of mobulids, as well as the quantification of post-release survival of bycaught mobulid species in these fisheries. Mitigation of bycatch at aggregation sites could be achieved with spatio-temporal closures for gillnets at critical habitats, such as nursery areas or feeding aggregations. Fishing bans of mobulids should also be considered throughout their range, while identifying mobulid aggregations at specific times and locations can offer important management and conservation opportunities (Clark et al., 2014) such as the designation of spatial protection areas. Such an approach is being included in the identification of Important Shark and Ray Areas (ISRAs) for mobulids (Hyde et al. 2022). However, socio-economic surveys among fishermen communities and associated stakeholders should also be implemented to understand the economic and social impacts that can arise from such management designations (e.g., Peru; Guirkingner et al., 2021).

Table 3. Manta and devil ray aggregations obtained from artisanal fisheries, industrial fisheries, and bather protection nets* data. Max aggregation size corresponds to the number of individuals within a single set (commercial tuna purse seiners) or a single net (artisanal fisheries or bather protection net).

Species	Aggregation region	Max aggregation size	Seasonality	References
<i>M. birostris</i>	Eastern Tropical Pacific (Equatorial Area)	200	June	Lezama-Ochoa et al., 2019a
	(Costa Rica Dome)	167	August	
<i>M. mobular</i>	Palestine (Gaza strip)	35	February	Abudaya et al., 2017
	Peru	162	March	Lezama-Ochoa et al., 2019a
<i>M. thurstoni</i>	Peru	97	April	
<i>M. eregoodoo*</i>	Australia (Eastern coast)	6	April	Broadhurst et al., 2018
<i>M. munkiana</i>	Mexico (Espiritu Santo Archipelago)	84	March-September	Del-Valle-González-González 2018
Mobulid spp.	Peru (Zorritos)	>60	October-January	Alfaro-Cordova et al., 2017

3.2 Tourism

Predictable aggregations of mobulids at specific locations offer opportunities to develop non-consumptive uses such as ecotourism focused on observing and swimming with mobulids. Tourist activities with mobulids at aggregation sites have been reported for several species worldwide: *M. alfredi* in Australia, Indonesia, and Maldives (Venables 2013; Germanov et al., 2019; Murray et al., 2020), *M. birostris* in Mexico and Ecuador (Kumli and Rubin, 2010; Burgess 2017; Gómez-García et al., 2021; Harty et al., 2022), *M. tarapacana* in the Azores (Sobral 2013, Solleliet-Ferreira et al., 2020), and *M. munkiana* in the Gulf of California (Palacios et al., 2021). Manta and devil ray tourism not associated with aggregation sites is also widespread globally (O'Malley et al., 2013). Mobulid tourism can contribute significantly to local economies (Gallagher et al., 2011; O' Malley et al., 2013), with direct economic benefits of manta ray tourism to the global economy estimated to be at least \$140 USD million annually (O' Malley et al., 2013). While ecotourism is a potential economic opportunity, the large number of individuals present at mobulid aggregations can increase their vulnerability to unregulated or poorly implemented tourism activities (Harris et al., 2020).

Tourist disruption at feeding aggregation sites, where mobulids benefit from temporally high-density prey patches, can reduce food intake, potentially diminishing fitness (Venables 2013; Murray et al., 2020). Similarly, tourism at mobulid cleaning aggregation sites can result in anthropogenic impacts from SCUBA divers with poor buoyancy generating physical damage to the cleaning site substrate, which is often coral and may also impact the cleaner fish community (Toyoshima and Nadaoka 2015). Mobulids may be disrupted during their cleaning activities or when engaging in social behaviors such as courtship or mating (Murray et al. 2020).

Anthropogenic disturbance to *M. alfredi* by boats accessing nursery and courtship areas for tourism was observed in Indonesia (Germanov et al., 2019). In Ningaloo Reef, Australia, feeding *M. alfredi* were disturbed or showed a behavioral response in 34 % of tourism interactions (Venables 2013). In the Maldives, Hanifaru Bay is considered the most important feeding site for *M. alfredi* in terms of the number of individuals aggregating at the same time (Harris et al. 2020; Armstrong et al., 2021). Due to the predictability and size of the groups at this site, a large tourist industry around manta rays has been established at the site. In a recent study, avoidance responses by *M. alfredi* at Hanifaru were reported in 37% of the observations, and the animals' natural behavior was stopped or changed during in-water interactions with humans (Murray et al., 2020). In Mexico, *M. birostris* at aggregation sites showed higher probabilities of evasive behavior when interacting with divers actively chasing individuals (Gómez-García et al., 2021). While several studies have described anthropogenic disturbances for manta rays at aggregation sites (Venables 2013; Germanov et al., 2019; Murray et al., 2020; Gómez-García et al., 2021), and addressed potentially problematic human-manta interactions by developing science-based best practices guidelines or codes of conduct (e.g. [How to Swim with Manta Rays; swimwithmantas.org](#)), these types of studies and guidelines are largely non-existent for the smaller devil rays. Finally, increased tourism at mobulid aggregations may increase the risk of other lethal and sublethal impacts such as boat strikes and entanglements in mooring lines (Lester et al., 2020; Allen et al., 2021; Womersley et al., 2022; Strike et al., 2022).

To address these problems, greater effort in educating guides, boat captains, and tourists should be put in place at local communities and businesses that benefit from tourist activities with mobulids. This can be achieved by guides who give educational briefings before in-water activities and then enforce these recommendations throughout the encounter (Murray et al., 2020). MPAs can be established to provide regulations and enforcement of boat traffic limits, boat speeds, and snorkeler or diver capacities in such critical aggregation sites, helping to reduce anthropogenic threats to mobulids.

3.3 Spatial Protection and Important Shark and Ray Areas (ISRAs)

Spatial protection, particularly if based on ISRAs, can play an important role in protecting populations from anthropogenic impacts at aggregation sites (Murray et al., 2020; Germanov et al., 2019; Setyawan et al., 2022b). ISRAs provide refereed, actionable information on sites that are critical to mobulid survival, such as aggregations (Hyde et al., 2022). While it is likely not feasible to protect the entire home ranges of most mobulid species, aggregation sites for mobulids may encompass important areas for critical life history stages (Marshall and Bennett 2010a; Stevens 2016; Germanov et al., 2019; Setyawan et al., 2022b). Indeed, the establishment of spatial protections for megafauna at aggregation sites has proven to be extremely successful when paired with adequate enforcement and surveillance and when local communities directly benefit from the protection of their surrounding

areas (e.g., Cabo Pulmo, El Vizcaíno Biosphere Reserve and Bahía de Loreto National Park; Aburto-Oropeza et al., 2011; Urbán and Vilorio-Gómora 2021).

Many mobulid aggregation sites with established spatial protection are primarily focused on the larger-bodied mobulid species, especially manta rays (Weeks et al., 2015; Germanov et al., 2019; Armstrong et al., 2021; Harris et al., 2021). Important aggregation areas are largely unknown for pygmy devil rays, which are smaller in size but with a greater tendency for aggregation behavior and a more coastal distribution (Stevens et al., 2018a; Murie and Marshall 2016; Notarbartolo-di-Sciara et al., 2019; Palacios et al., 2021). These species are likely to be threatened by coastal and artisanal fisheries (Smith et al., 2009; Rojas-Perea 2016; Del-Valle-González-González 2018), where very little information exists on bycatch rates (Fernando and Stewart 2021; Mustika et al., 2021) making it challenging to use fishery reports to identify aggregation areas or to establish bycatch mitigation strategies.

Despite protection of mobulid species in most of their distributional range and their inclusion in international trade management measures such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS), targeted fisheries and opportunistic bycatch retention persists in some countries (Akyol et al., 2005; Acebes and Tull, 2016; Alfaro-Cordova et al., 2017; Fernando and Stewart 2021; Guirkingner et al., 2021). Without specific action to understand the occurrence of mobulid aggregations and their overlap with and susceptibility to human impacts, a major biological and ecological vulnerability for these species will remain unaddressed.

3.4 Climate change

Climate change is one of the most important anthropogenic threats to vulnerable marine megafauna such as mobulid rays and is predicted to increase the intensity and frequency of changes in environmental conditions (Cheung et al., 2009; Stewart et al., 2018a). These environmental changes may cause mobulid aggregation sites to shift to new locations in search of more favorable conditions or to follow new prey distributions. As a result, predator and prey shifts may occur at different magnitudes and directions (Hazen et al., 2013), potentially impacting specialized predators like mobulid rays (e.g., *M. mobular* in the Gulf of California, Mexico) (Lezama-Ochoa et al., 2023, *in prep*). Phenological changes, including changes to reproductive periodicity, foraging, or migration may affect their populations. Current protected areas at aggregation sites may not be efficient if mobulids' new distributions do not match previously established boundaries. In these cases, more dynamic management approaches may be preferential (Lewison et al., 2015; Dunn et al., 2016). Understanding long-term changes in the distribution of mobulid rays is essential to identify species most at risk and anticipate management options. Species distribution model outputs combined with global climate models are an important tool for projecting species' shifts and future habitat (Lezama-Ochoa et al., 2023, *in prep*).

4. Key knowledge gaps and developments in the field

4.1 Identification of aggregation sites

Most mobulid aggregation sites have been identified by opportunistic observations from divers or fishermen using Traditional Ecological Knowledge surveys (Anderson et al., 2011; Sobral 2013; Burgess 2017; Palacios et al., 2021). Once aggregation sites are proposed or identified through initial observations, they can be further studied using tracking technology (such as active and passive acoustic telemetry, as well as satellite tagging studies) to determine when and how often mobulid aggregations occur in these locations in the absence of active observation effort (**Figure 4**) (Dewar et al., 2008; Setyawan et al., 2020; Peel et al., 2020; Andrzejaczek et al., 2020; Harris and Stevens 2021; Palacios et al., 2021). For the identification of aggregation sites in pelagic habitats, fishery-dependent data offer a unique opportunity to obtain large-scale information on species distribution, group sizes, and seasonality over long periods of time and with wide spatiotemporal coverage (Notarbartolo-di-Sciara, 1988; White et al., 2006; Croll et al., 2016; Abudaya et al., 2017; Lezama-Ochoa et al., 2019a; Fernando and Stewart 2021). Scientific observer programs implemented in some industrial fisheries can facilitate the collection of information on environmental parameters from remote sensing databases, bycatch species, abundance, and bycatch size frequencies (Lezama-Ochoa et al., 2019a, b; 2020). Remote aggregation sites can also be identified by sporadic or standardized aerial surveys, as demonstrated through the identification of aggregation sites of *M. mobular* in the Mediterranean and *M. birostris* in the Caribbean Seas (Notarbartolo-di-Sciara and Hillyer 1989; Notarbartolo di Sciara et al., 2015). Further, the use of aerial surveys from seaplanes or helicopters assisting industrial fisheries to locate their target catch could potentially aid real-time identification and bycatch avoidance of mobulid grouping events (Cronin et al., 2022).

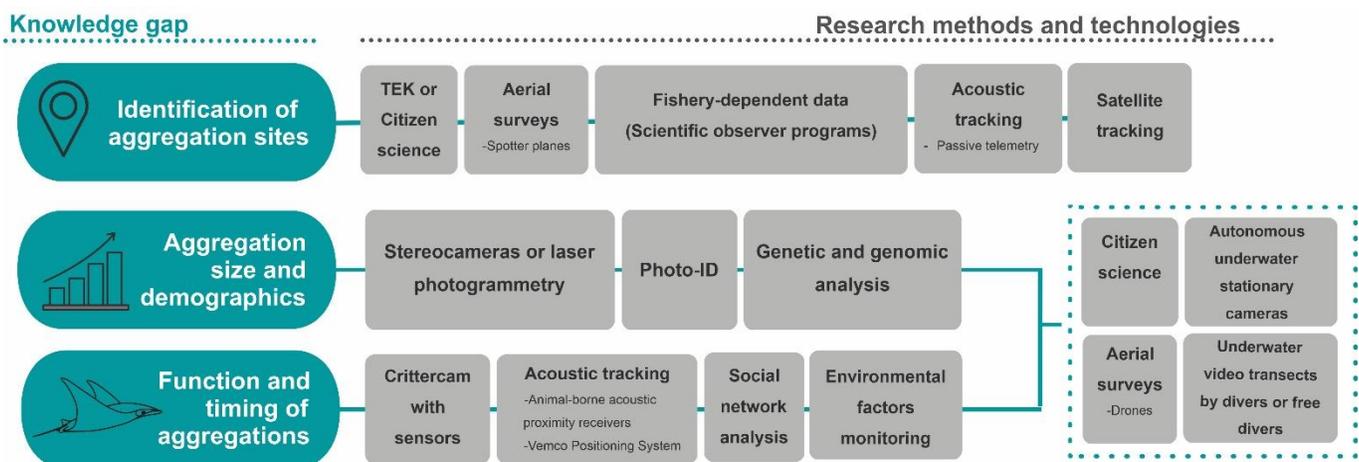


Figure 4. Illustration of key knowledge gaps in manta and devil ray aggregation research, and proposed methods and technologies for developments in the field.

4.2 Aggregation size and demographics

Sorting of aggregations by size and sex have been observed for several species of mobulids (Stevens 2016; Perryman et al., 2019; Germanov et al., 2019; Mendonça et al., 2020; Palacios et al., 2021). For manta rays, photo identification using distinctive ventral markings has been used for decades to produce comprehensive databases of dozens of manta ray populations globally and estimate their population size and structure (Germanov et al., 2014; Marshall et al., 2011; Stevens et al., 2018b; Harty et al., 2022; Cabral et al., 2023). However, information on the demographic composition of aggregations and how it relates to aggregation size and function is lacking for most species, especially the smaller devil rays.

Emerging technologies can facilitate the collection of more detailed demographic data in aggregations. To investigate individual size distributions in aggregations, the use of photogrammetry (both in-water and via aerial drones) is an affordable and non-invasive option for the analysis of the size and sex structures of aggregations (Deakos 2010; Setyawan et al., 2020; Setyawan et al., 2022c). Body size of individuals, which is a proxy for maturity stage in mobulids (Stevens 2016; Rambahiniarison et al., 2018), can be measured using calibrated underwater stereo camera systems and paired-laser photogrammetry, enabling accurate estimates of ray disc width and other body measures (Deakos 2010; Langlois et al., 2012). Furthermore, the use of calibrated stereo camera systems and R software packages such as StereoMorph (Olsen and Westneat 2015) allow for accurate measurement of several individuals in the same frame. The use of drones for mobulid research has not been widely applied; however, the few studies using this technology have shown that they can be a useful tool to determine morphometric measurements, such as disc length, width, and cranial width using the known length of a floating object as a reference scale (Setyawan et al., 2022c). Furthermore, photo identification of somersaulting manta rays, determination of female maturity based on the presence of mating scars, and male maturity by the extension and calcification of claspers is also possible to collect at aggregation and social grouping sites using drones (Pate and Marshall 2020; Setyawan et al., 2020; 2022c). Autonomous underwater cameras placed in strategic sites such as cleaning stations can provide continuous coverage, allowing presence/absence analysis and eliminating the potential deterrent effect of diver presence (Barr and Abelson 2019). From underwater video transects operated by SCUBA divers or free divers, to stationary underwater video stations at grouping sites, these methods have proven valuable in collecting data on abundance, body size, sex ratios, maturity status and even behavior of mobulids at grouping sites (O'Shea et al., 2010; Deakos 2012; Stevens et al., 2018b; Stewart et al., 2018a; Barr and Abelson 2019). Beyond observational technology, emerging population genetic and genomic techniques (e.g., RAD sequencing and/or full genome sequencing) can allow for assessments of relatedness within aggregations, as well as calculations of population size estimates that can be used to contextualize aggregations within the larger population (Sigsgaard et al., 2017; Lieber et al., 2020). Additionally, genetic studies could test whether kin aggregation occurs

in mobulids, whether aggregating individuals originate from shared or differing original populations, and broadly the extent to which genetic factors shape aggregation behavior (Selwyn et al., 2022). Recent research using population genomic methods for mobulids (e.g., Hosegood et al., 2020; Lassauce et al., 2022; López et al., 2022) has laid the foundation for more fine-scale investigations of genomics within and between aggregating groups.

4.3 Function and timing of aggregations

Understanding function, structure, timing, frequency, and size of mobulids aggregations is critical for mobulid conservation, as it will improve predictions of where and when large aggregations are most vulnerable to human impacts, and what life stages or demographic units are represented. To address these gaps, habitat use and behaviors at aggregation sites can be studied using technologies such as drones (Setyawan et al., 2020; 2022c), acoustic telemetry (Dewar et al., 2008; Harris and Stevens 2021; Palacios et al., 2021), crittercams with sensors (Stewart et al., 2019), in-person observations from citizen science (Sobral 2013; Germanov et al., 2019) and underwater visual census with fixed cameras or operated by divers or snorkelers (Germanov et al., 2019) (**Figure 4**). Drones can also collect high-resolution aerial images of marine megafauna, documenting grouping behavior, abundance, and distribution, in a replicable manner over time and space (Johnston et al., 2019; Schofield et al., 2019) with low disturbance towards wildlife and habitats when appropriately used (Kiszka et al., 2016; Colefax et al., 2018). Detectability issues can be challenging for submerged fauna like sharks and rays (Brack et al., 2018). However, mobulids often have dark dorsal coloration, large body sizes (Stevens et al., 2018a), a tendency to form aggregations or social groups (Stevens 2016; Lezama-Ochoa et al., 2019a; Perryman et al., 2019) and a preference to swim near the surface in the water column (Croll et al., 2012; Thorrold et al., 2014; Stevens et al., 2018a; Lezama-Ochoa et al., 2019a) making them good candidates for study using drone technology. Using fixed transects with drones can be an efficient strategy to monitor seasonal changes in abundance, behavior, and population demographics, while also providing quantitative data on habitat use that can be replicated over years (Perryman et al., 2019; Setyawan et al., 2020). In addition to aerial observation, visitation patterns obtained through acoustic telemetry or visual data collected from underwater surveys can inform habitat use and aggregation behavior, especially when correlated with environmental factors such as temperature, conductivity, chlorophyll-a concentrations, zooplankton abundance and tides (Dewar et al., 2008; Jaine et al., 2012; Barr & Abelson 2019; Setyawan et al., 2020; Harris et al., 2020; Armstrong et al., 2021; Harris and Stevens 2021; Palacios et al., 2021). These data can help conservation and management efforts to correctly identify habitat drivers of aggregations and therefore implement more informed spatial-temporal measures for conservation.

Social dynamics can also be studied with acoustic telemetry (e.g., Vemco Positioning System), allowing for the calculation of near-continuous fine-scale animal locations with overlapping receiver

arrays (Espinoza et al., 2011) to elucidate association patterns among tagged individuals (Armansin et al., 2016). Crittercams with sensors (Stewart et al., 2019) or animal-borne acoustic proximity receivers, where the individual tagged can transmit their own code and store signals from other tagged animals (Holland et al., 2009) are other options to quantify interactions between individuals. However, this method is limited by the need to recover the instruments from animal (Stewart et al., 2019) via passive release or the recapture of the tagged animal to retrieve the data (Guttridge et al., 2010).

5. Conclusions

Aggregative behavior facilitates multiple life history functions, providing benefits for the intake of food as well as for the survival of the species through mating and protection of early life stages. However, aggregations may also exacerbate the risk of major impacts to mobulid populations if threats occur at key aggregations sites. Similar to fisheries targeting spawning aggregations of bony fishes, targeted fisheries or bycatch at mobulid courtship and mating aggregation sites can affect the viability of the next cohort.

With emerging technologies, the study of aggregations and social behaviors are becoming more accessible and affordable. However, the nature and location of mobulid aggregation sites are sometimes difficult to identify because of a lack of consistency in which the term 'aggregation' is used. Often, aggregation sites are described without giving information on the details of the behavior and the number of individuals present rather, they are described loosely as 'an area where mobulids are frequently sighted.' This terminology makes it difficult to assess the importance of the site for aggregation behavior.

While aggregative behavior is a characteristic of all mobulid species, smaller species often form larger aggregations, potentially leading to higher vulnerability given heightened exposure to anthropogenic risks associated with aggregations. Paradoxically, these smaller devil rays are less studied and enjoy less legal protection in comparison to the larger manta rays. Therefore, it is important than in future research and studies the pygmy devil rays are prioritized. Otherwise, the partial disappearance of pygmy devil rays from some of their range is likely to occur, as has already occurred in the eastern Atlantic for *M. hypostoma cf. rochebrunei*. Furthermore, many of the pygmy devil rays are still not protected from fisheries in most parts of their range, which exacerbates the urgency to study their aggregation sites and behaviors.

Supplementary material

Table 1 (Supplementary material). Summary of published literature on mobulid aggregations, where the numbers of individuals of manta or devil rays aggregating at a given time were stated. (NS) Not stated in the study.

Species	Region	Drivers of aggregations	Maturity Stage	Seasonality	Influential Environmental factors	Max aggregation size	Research methods and technologies	Reference
<i>M. birostris</i>	Venezuela (Caribbean)	Feeding	NS	May, August-September	Upwellings systems and trade winds	50	Aerial survey	Notarbartolo-di-Sciara and Hillyer 1989
	Japan (Ogasawara Islands)	Courtship and mating	Adults	July-August	NS	4	Underwater video with SCUBA	Yano et al., 1999
	New Zealand (Mokohinau Island)	Feeding	Adults	April	NS	2	Aerial survey	Duffy and Abbott 2003
	Suriname	Unknown	Adults	May	NS	2	Sightings from boat	De-Boer et al., 2015
	Brazil (Paranaguá estuary)	Predator avoidance	NS	October-May	High water temperatures	3	TEK/ Land surveys	Medeiros et al., 2015
	USA (Flower Garden Bank)	Feeding, predator avoidance and thermal refugia	Juveniles/ Subadults/ Adults	Year-round	NS	5	Underwater video and scuba sightings	Childs 2001, Stewart et al., 2018b
	Mexico (Caribbean)	Feeding	NS	July-September	High productivity	10	Underwater video transects by free divers/ Environmental factors monitoring	Hacohen-Domené et al., 2017
	Maldives	Courtship and mating	Adults	NS	NS	9	Photo-ID/ Underwater video transects by divers	Stevens et al., 2018b
	Ecuador (Galapagos)	Courtship and mating	Adults	NS	NS	2	Underwater video with SCUBA	
Brasil (Fernando de Noronha Archipelago)	Feeding	Juveniles	Year-round	NS	3	Photo-ID/ Citizen science	Bucair et al., 2021	

	Ecuador (Isla de La Plata)	Feeding and courtship and mating	Adults	May-October	Low water temperature and high chl a concentration	60	Photo-ID/ Underwater video with SCUBA	Stevens et al., 2018b; Harty et al., 2022
	Mexico (Bahía de Banderas)	Feeding and thermal refugia	NS	April, September-December	La Niña phase, upwelling systems, low water temperature, high densities zooplankton and intermediate moon phases	20	Photo-ID/ Underwater video transects by free divers/ Environmental factors monitoring	Fonseca-Ponce et al., 2022
<i>M. alfredi</i>	Mozambique	Courtship and mating	Adults	October-January	NS	14	Photo-ID/ Underwater video transects by divers	Marshall and Bennett 2010
	Maldives	Feeding and cleaning	NS	December-April (Western side); May-November (Eastern side)	Monsoon currents and upwelling systems	100	TEK/ Environmental factors monitoring	Anderson et al., 2011
	USA (Maui, Hawaii)	Courtship and mating	Adults	Year-round	NS	18	Photo-ID/ Laser photogrammetry	Deakos 2012
	Australia (Lady Elliot Island)	Feeding and cleaning	NS	May-August	Slower wind speeds, high productivity, and new and full moon	80	Underwater video transects by divers/ Environmental factors monitoring	Jaine et al., 2012
	Guam (Tumon Bay)	Feeding	NS	January-June	Spawning aggregations of <i>Acanthurus</i>	12	Underwater video transects by divers	Hartup et al., 2013

	Australia (Lady Elliot Island)	Feeding	NS	January-February	River outflow, eddy activity, upwelling, convergent fronts and tides	150	Aerial survey/ Environmental factors monitoring	Weeks et al., 2015
	Indonesia (Alor and Pantar Islands)	Unknown	Adults	NS	NS	15	TEK	Lewis et al., 2015
	Maldives (Hanifaru Bay)	Feeding	NS	June-November	Monsoon winds and chlorophyll-a concentration	150	Photo-ID/ Underwater video transects by divers	Stevens 2016
	Australia (Coral Sea)	Courtship and mating	Adults	August	NS	4	Underwater video with SCUBA	Stevens et al., 2018b
	French Polynesia (Rangiroa)	Courtship and mating	Adults	NS	NS	3	Underwater video with SCUBA	
	French Polynesia (Bora Bora)	Courtship and mating	Adults	NS	NS	2	Underwater video with SCUBA	
	Indonesia (Nusa Penida)	Courtship and mating	Adults	September	NS	7	Underwater video with SCUBA	
	USA (Hawaii, Hawaii)	Courtship and mating	Adults	March	NS	2	Underwater video with SCUBA	
	USA (Maui)	Courtship and mating	Adults	NS	NS	22	Underwater video with SCUBA	
	Maldives	Courtship and mating	Adults	NS	NS	27	Photo-ID/ Underwater video transects by divers	
	Indonesia (Raja Ampat)	Feeding and cleaning	NS	NS	NS	67	Photo-ID/ Underwater video transects by divers	

	Indonesia (Nusa Penida, Manta Bay)	Feeding and predator avoidance	Juveniles/ Subadults/ Adults	Year-round	High productivity	8	Photo-ID/ Citizen science	Germanov et al., 2019
	Indonesia (Nusa Penida, Manta Point)	Courtship and mating	Adults	Year-round	High productivity	14		
	Chagos Archipelago (Egmont Atoll)	Feeding	Juveniles/ Subadults/ Adults	March	Cold water bores, tide and high zooplankton biomass.	40	Acoustic tracking/ Underwater video transects by divers/ Environmental factors monitoring	Harris et al., 2021
	Maldives (Hanifaru Bay)	Feeding	NS	August	High zooplankton biomass and tide.	250	Underwater video transects by divers/ Environmental factors monitoring	Armstrong et al., 2021
<i>M. tarapacana</i>	Venezuela (Caribbean)	Unknown	NS	July	Upwellings systems and trade winds	9	Aerial survey	Notarbartolo-di-Sciara and Hillyer 1989
	Portugal (Azores)	Feeding and courtship and mating	Adults/ Pregnant	June-September	Temperature range 22.5 - 24.5°C	16	Photo-ID/ Citizen science	Sobral 2013
	Brazil (Saint Peter and Saint Paul Archipelago)	Courtship and mating	Subadults/ Adults	January-June	High productivity and high-water temperatures	24	Photo-ID/ Underwater video transects by free divers	Mendonça et al., 2020
	Portugal (Azores)	Feeding	Adults	June-August	NA	50	Underwater video transects by divers	Solleliet-Ferreira et al., 2020
<i>M. mobular</i>	Italy (Strait of Messina)	Feeding	Adults	May-August	NS	6	Citizen science/ Fishery-dependent data	Celona 2004

	Palestine (Gaza strip)	Unknown	Adult Males	February-April	NS	35	TEK/ Fishery-dependent data	Abudaya et al., 2017
	Italy	Unknown	NS	April-August	High productivity	18	Aerial survey	Notarbartolo-di-Sciara et al., 2015
	New Zealand (Southwest Pacific Ocean)	Courtship and mating	Adults	March	NS	5	Underwater video transects by free divers	Duffy and Tindale, 2018
	Peru	Unknown	NS	December-January and March	Upwelling systems	162	Fishery-dependent data/ Environmental factors monitoring	Lezama-Ochoa et al., 2019a
<i>M. thurstoni</i>	Ecuador (Galapagos)	Unknown	NS	December - January	Upwelling systems	220	Fishery-dependent data/ Environmental factors monitoring	
	Brazil (Archipelago of Saint Peter and Saint Paul)	Courtship and mating	Adult	May	NS	4	Aerial survey (Drone)	McCallister et al., 2020
<i>M. eregoodoo</i>	Australia (Eastern coast)	Unknown	Adults	April	High water temperatures	6	Fishery-dependent data	Broadhurst et al., 2018
	Indo-Pacific	Unknown	NS	NS	NS	30	Fishery-dependent data / Underwater video transects by divers	Notarbartolo-di-Sciara et al., 2019
<i>M. munkiana</i>	Mexico (Espiritu Santo Archipelago)	Unknown	Juveniles/ Adults	March-September	NS	84	Fishery-dependent data	Del-Valle-González-González 2018
	Mexico (Espiritu Santo Archipelago)	Predator avoidance and thermal refugia	Neonate/ Juveniles	August-May	High water temperatures and high zooplankton biomass	19	Acoustic tracking/ Environmental factors monitoring	Palacios et al., 2021

	Costa Rica (Punta Descartes)	Feeding/ Predator avoidance	Juveniles	June- September	High mysid biomass and breaking zone of the low tide waves	10	Land surveys/ Aerial surveys/ Environmental factors monitoring	Porsiel et al., 2021
<i>M. hypostoma</i>	USA (Flower Garden Bank)	Feeding/ Courtship and mating	Subadults/ Adults	June-August	NS	50	Video and scuba sightings	Childs 2001
<i>M. kuhlii</i>	Mozambique (Bazaruto Archipelago National Park)	Cleaning	NS	NS	Abundance of the cleaner fish, topography, and substrate cover	6	Underwater video transects by divers	Murie and Marshall 2016
	Malaysia (Pulau Si Amil, Sabah)	Unknown	NS	May-July	NS	100	Underwater video transects by divers	McCann et al., 2021
Mobulid spp.	Peru (Zorritos)	Unknown	NS	October- January	High productivity and high-water temperatures	>60	Fishery- dependent data	Alfaro-Cordova et al., 2017

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CHAPTER 2.

Description of first nursery area for a pygmy devil ray species (*Mobula munkiana*) in the Gulf of California, Mexico.

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1. Introduction

Nursery areas have been shown to be important for many elasmobranch species^{1,2}. These discrete areas have biotic and abiotic features that can be important for pupping and for enhancing the survival of neonates, and juveniles². For an area to be considered an elasmobranch nursery, it must follow at least three criteria: 1) neonates, and juveniles are more commonly encountered within the area compared to adjacent areas, 2) individuals tend to remain or return to the area over weeks or months, and 3) the area is used in a similar manner repeatedly across years^{3,4}.

While many studies have identified the importance of nursery areas for sharks^{3,5,6} little is known about nursery areas for batoids^{7,8,9}. Indeed, only three important juvenile habitats for manta rays have been identified in the Gulf of Mexico^{9,10}, in Florida¹¹ (*Mobula birostris* and *Mobula. cf. birostris* for both areas), and in Indonesia¹² (*Mobula alfredi*). In addition, a potential pupping ground for *Mobula mobular* in the Northern Gulf of California¹³, has been suggested, but more research is needed to confirm.

Mobulids (manta and devil rays) are planktivorous filter feeders with vulnerable life histories^{14,15}, that include the lowest fecundity of all elasmobranchs (one pup per litter)^{16,17}, and delayed, aplacental viviparous matrotrophic reproduction cycles of 1–3 years^{18,19,20,21}. Such low reproductive rates make mobulids extremely vulnerable to anthropogenic impacts including targeted small-scale fisheries^{18,22,23} and bycatch in small- and large-scale fisheries^{22,24}. As a result, all mobulid species are IUCN Red list, Endangered or Vulnerable²⁵, with all species experiencing population declines^{26,27}.

Pygmy devil rays (5 of the 10 mobulid species)²⁸, include the smaller species reaching < 1.3 m disc width as adults with more restricted distribution than the larger mobulid species¹⁵. Munk's pygmy devil ray (*Mobula munkiana*) is endemic to the Eastern Pacific, found in neritic and coastal habitats that

extend from the Gulf of California, Mexico to Peru²⁹. In the Gulf of California, *M. munkiana* feed predominantly upon Mysidacea spp. with the euphausiid, *Nyctiphanes simplex*, as a second prey item^{18,30}.

While size at birth remains unknown, estimations and comparisons with other pygmy devils rays indicate that disc width could range from 35 cm¹⁸ to 42.3 cm³¹, and reach up to 112 cm as an adult³². *Mobula munkiana* is particularly known for its social behavior¹⁸, often congregating in large aggregations of thousands of individuals, presumedly for mating purposes¹⁵. *M. munkiana* is currently classified as “Vulnerable” on the IUCN Red List of Threatened Species²⁹. While the species is nationally protected in Mexican waters under the NOM-029-PESC-2006 and NOM-059-SEMARNAT-2010 regulations, illegal targeted fishing still exists in several areas in the Gulf of California³³.

When *M. munkiana* was first described in the Southern Gulf of California, segregation by size was described^{18,34,35}, leading to the potential for differential habitat use between juvenile and adult stages. Since 2013, local fishermen and tour operators in the Southern Gulf of California, have known of a well-established aggregation of *M. munkiana* in Ensenada Grande, a shallow bay with sandy bottom seafloor, located on the northwest side of the Espiritu Santo Archipelago (Fig. 1). These anecdotal observations prompted us to examine whether pygmy mobulid rays utilize nursery areas for mating, pupping, and foraging of juveniles.

Here we report the reproductive seasons (mating and parturition) for adults, and residency linked to environmental factors of early life stages of *M. munkiana* in a shallow bay at the Espiritu Santo Archipelago, Mexico. We used a combination of nonlethal methodologies including traditional tagging, passive acoustic telemetry, and environmental monitoring (zooplankton biovolume and water temperature) to examine the spatial use and foraging ecology of early life history stages of *M. munkiana* and to determine if *M. munkiana* utilize the shallow bay as a nursery area.

2.Methods

2.1 Study Area

The Espiritu Santo Archipelago is located in the south west region of the Gulf of California and is the eastern limit of La Paz Bay (Fig.1). The Archipelago was declared a Marine National Park in 2007, only allowing artisanal fisheries and ecotourism activities in some restricted areas. The bathymetry of the eastern Espiritu Santo Archipelago is characterized by steep terracing, with water over 100 m occurring just a few meters from the shore, particularly off the eastern side of the archipelago. Our main study area at Ensenada Grande is located on the western coast of the Espiritu Santo Archipelago and is comprised of several sandy bottom embayment's (<40 m depth) (Fig. 1c). Productivity of the Espiritu Santo Archipelago is influenced by the monsoonal wind pattern of the Gulf of California with northwesterly winds that cause strong upwelling events during the cold season (December to May), with primary production rates ranging between 1.16–1.91 g Cm² d⁻¹⁵¹. Strong thermal stratification

occurs during the warm season (June to November), when upwelling is weak along the east coast of Baja California peninsula⁵² with low primary production rates (0.39 to 0.49 g C m² d⁻¹)⁵¹.

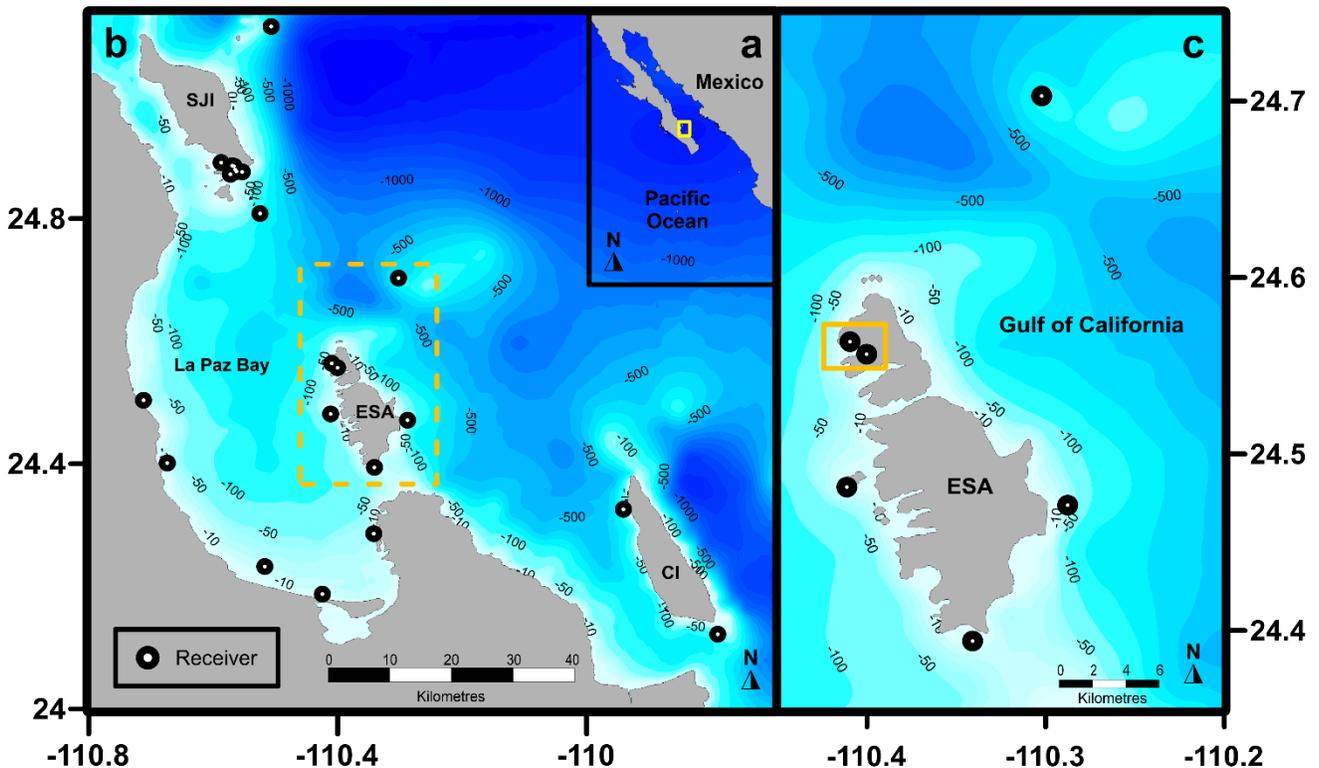


Figure 1. (a) Mexican Pacific and Baja California Peninsula. The yellow square located on the southwestern portion of Gulf of California outlines the location of (b) La Paz Bay and the surrounding islands of San Jose (SJI), Cerralvo (CI), and the Espiritu Santo Archipelago (ESA) outlined in yellow dashed square. The receiver locations (n = 21) are indicated with black–white dots. (c) *Mobula munkiana* early life stage individuals aggregate in the shallow bay of Ensenada Grande outlined with a yellow square. The map was created using Surface Mapping System (Golden Software, Inc., 1993–2012, <https://www.goldensoftware.com/products/surfer>) and the coastline data was extracted from GEODAS-NG (National Geophysical Data Center, 2000).

2.2 Ethics statement

The methods were approved under the research permit PPF/DGOPA-133/17 issued by Comisión Nacional de Acuacultura y Pesca with authorization of Comisión Nacional de Áreas Naturales Protegidas. The tagging and surgical procedures followed the Institutional Animal Care and Use Committee of the University of California, Davis (IACUC, Protocol No. 16022).

2.3 Data Collection

Mobula munkiana, were caught between August 2017 and June 2018 at Ensenada Grande during 5 capture trips. Individuals were captured with encircling surface cotton twine nets 150 m long, 15 m deep, with 25 cm mesh. Captured individuals were maintained in the water, allowing water to pass over their gills to reduce stress levels before transferring them into a holding tank onboard the boat.

Individuals were sexed, measured (total length and disc width), and evaluated for mating scars on pectoral fins, cloacal state (females) and development state of claspers (males). Release was typically completed < 5 min after capture and all devil rays were released in good condition.

2.4 Life stages description

Mobula munkiana maturity was classified in four states, according to estimates of their disc width size at maturity as either neonate (< 97 cm female or 98 cm male disc width with umbilical scars present), juvenile (< 97 cm female or 98 cm male disc width with no umbilical scar) and adult (> 97 cm female or 98 cm male disc width)³². Adult females with a noticeably distended abdominal region on both the dorsal and ventral surfaces were classified as likely pregnant females²⁰.

2.5 Conventional Tagging

Individuals were tagged with conventional fish tags (FLOY TAG & Mfg., Inc.) in the dorsal part of the pectoral fin with a special applier for future identification purposes.

The data collected from captures and conventional tagging were used to characterize the overall size and demographic composition of the population captured in Ensenada Grande. A χ^2 test was used to test for skewed sex ratios in captured juveniles and neonates in Ensenada Grande.

Size data set did not meet the normality assumptions according to the Shapiro-Wilk test ($n = 95$, $W = 0.92567$, $P = 4.446e-05$), therefore a nonparametric Wilcoxon test was performed to compare disc width and sex distribution. Capture locations were plotted using Surface Mapping System (Golden Software, Inc., 1993-2012, <https://www.goldensoftware.com/products/surfer>) and the coastline data was extracted from GEODAS-NG (National Geophysical Data Center, 2000).

2.6 Acoustic Telemetry

Mobula munkiana were fitted with internal acoustic transmitters (Vemco Ltd. V13; $n = 7$) with an expected battery life of 991 days in August 2017 at Ensenada Grande. Transmitters were coated with a beeswax/paraffin wax mixture and internally placed by surgically inserting them into a 3 cm incision in the abdominal cavity. The incision was closed with synthetic surgical sutures. Transmitters operated at 69 kHz and were coded to pulse randomly once every 40–80 s allowing the simultaneous monitoring of multiple individuals without continuous signal overlap. Acoustic receivers (model VR2w and VR2Tx Vemco Ltd; $n = 6$) were moored at depths between 5–26 m at locations previously known to be frequented by Munk's pygmy devil rays within the Espiritu Santo Archipelago as part of a larger receiver array ($n = 21$ receivers) installed within La Paz Bay Cerralvo Island and San Jose Island, providing a much greater coverage of our main Ensenada Grande study site and adjacent areas (Fig. 1). We tested acoustic array range and found a maximum detection range of 350 m for the receivers at the Espiritu Santo Archipelago. Receivers recorded the transmitter code, time, and date of tagged *M. munkiana* that swam within the detection range of the receivers. Movements of neonates and juveniles *M. munkiana* were monitored on the array between August 2017–May 2019.

Receiver data in this network were downloaded and batteries are changed at least annually, and data were processed using the VUE Software (Vemco Inc., <https://support.vemco.com/s/downloads>). We filtered the data to include only detections with two or more consecutive detections as a means to avoid false positive detections that could arise from background noise⁵¹.

The distribution and residency of detections throughout the receiver array were visualized and analyzed using the package “VTrack” (<https://CRAN.R-project.org/package=VTrack>) in R (<https://www.r-project.org/>). A residency index⁵⁴ for each individual captured in the Espiritu Santo Archipelago was calculated with the formula (1).

$$(1) \text{ Residency Index (\%)} = \frac{\text{No. of days detected}}{\text{No. of days between first and last detection}}$$

The sequential series of detections over time throughout the receiver array from the first detection to the last is referred to as the “track” for each individual.

Daily presence data were analyzed to determine the number of consecutive days that an individual was resident (continuous presence) at a location. Since the acoustic data set did not meet the normality assumptions according to the Shapiro-Wilk test ($n = 7$; $W = 0.78852$, $P = 0.03148$) a nonparametric Spearman correlation and Wilcoxon tests were carried out to determine whether residency indices differed significantly with disc width, sex, and maturity stage of tagged *M. munkiana*. Habitat preference was studied by grouping the acoustic receivers of Ensenada Grande ($n = 2$) as inside-bay receivers and the rest of the Espiritu Santo Archipelago acoustic array ($n = 4$) as offshore receivers. A Wilcoxon test was used to compare the residency index found inside-bay receivers vs. offshore. Differences in residency between seasons was examined by comparing monthly residences of warm months (June to November) against cold months (December to May) using a Wilcoxon test. To quantify diel changes in the *M. munkiana* presence of Ensenada Grande we produced circular plots of the number of detections during daytime (0600–1900 h) vs. nighttime (1900–0600 h); limits of diel times were determined using defined cutoffs for dawn and dusk for the Ensenada Grande location. We used Rao’s test to analyze the uniformity of the detections for the receivers inside Ensenada Grande. We calculated the minimum linear dispersal distance for each individual defined as the distance between the two furthest receivers at which an individual was ever detected using Surface Mapping System (Golden Software, Inc., 1993–2012, <https://www.goldensoftware.com/products/surfer>)

2.7 Environmental factors

Water temperature data was collected every 2 hours by a temperature logger (Onset HOB0 Water Temperature, Pendant 64k) deployed at Ensenada Grande at 13 m depth during 9 months from August 2017 to April 2018. Temperature records were averaged over each day of the study period and aligned with the acoustic detection data to examine temperature effects on mobulid presence/absence.

Zooplankton was sampled during day and night at three locations inside Ensenada Grande (Fig. 5a). A total of 125 zooplankton samples were collected from August 2017 to June 2018 (25 samples per monitored month). Zooplankton was collected during a three minute oblique tow with a 60 cm mouth diameter zooplankton net (300 μm mesh), equipped with a calibrated flow meter (G.O. 2030R) mounted in the mouth of the net to estimate the filtered seawater volume⁵⁵. Samples were preserved with 4% formalin. Zooplankton biovolume ($\text{mL } 100 \text{ m}^{-3}$) was estimated for each sample using the displacement volume method⁵⁶.

Temperature ($n = 3466$ $W = 0.91839$, $P = 1.848\text{e-}05$) and zooplankton biovolume ($n=128$, $W = 0.75869$, $P = 3.424\text{e-}11$) data sets did not meet the normality assumptions according to the Shapiro-Wilk test respectively, therefore nonparametric Wilcoxon tests were used to compare seawater temperatures among seasons and zooplankton biovolume between day/night and between warm/cold seasons. We tested the correlation between the seawater temperature and zooplankton biovolume with the mean monthly residency index at Ensenada Grande using Spearman correlations. Kruskal Wallis non-parametric tests were used to compare the zooplankton biovolume among months and sampling stations and post-hoc Dunn test were used to determine which months and sampling stations significantly differed.

3. Results

3.1 Conventional Tagging

A total of 95 Munk's pygmy devil rays were captured at Ensenada Grande from August 2017 to June 2018 during five capture periods (Supplementary Information Table S1). *Mobula munkiana* catches and life stage varied seasonally, with greater captures occurring during late summer and fall than during winter, spring, and early summer (Fig. 2). Disc width was not normally distributed ($W_{94} = 0.925$, $P = 0.0004$), and we found no significant difference in size by sex ($W_{93} = 905$, $p = 0.18$). Juveniles (65 %, $n = 62$) and neonates (19 %, $n = 18$) dominated the sampled population with a 1:1 sex ratio ($X^2 = 0.05$, $P = 0.8$) with 39 females and 41 males.

Neonates ($n = 18$) were identified by the presence of the umbilical scar on the ventral side below the gills (Supplementary Information Figure S1). Neonate size ranged from 49.5–56 cm disc width and were only captured inside Ensenada Grande during August, at depths between 2–5 m. Juveniles ($n = 62$) ranged from 49–85 cm disc width and were captured during all sampling months at Ensenada Grande. Neonates and juveniles were only caught with individuals of the same life stage, indicating size segregation of the schools. All neonate and juvenile males had undeveloped claspers without calcification or rotation (Supplementary Information Figure S1), while neonate and juvenile females showed no evidence of mating scars and the state of the cloaca was not distended.

Adults (15%, $n = 14$) and pregnant females (1%, $n = 1$) were only captured during spring and early summer (April and June) at >15 m depth in Ensenada Grande. The adults ($n = 4$) captured in April

2018 were females with swollen distended cloaca evidenced with a reddish coloration indicating possible recent mating or parturition (Supplementary Information Figure S1) as it has been interpreted in other elasmobranch species^{36,37}.

During June 2018, we captured a group of adults composed of one female and four males displaying courtship behavior at the surface (initiation and endurance) as described for *Mobula alfredi* and *M. birostris*³⁸. All four males had developed claspers with sperm. Courtship behavior was also observed during April 2018, but those animals were not captured. A female in an advanced state of pregnancy was captured at Ensenada Grande during June 2018 showing distended abdominal region on both the dorsal and ventral surface (Supplementary Information Figure S1). Pregnancy was confirmed on another individual with the same characteristics captured at Espiritu Santo Archipelago in April 2018 using ultrasound techniques, with a single and well-developed term-embryo present (Ramírez-Macías unpub. data). This corroborated the estimation of the litter size of a single pup for *M. munkiana*³⁹ and other mobulid species^{14,40}.

During this study we had seven recaptures (6.23%) of six individuals, four juveniles and two neonates. The straight-line capture/recapture distance for all recaptured devil rays was between 0.1 to 0.5 km, with recapture durations ranging from one day to eight months from initial capture.

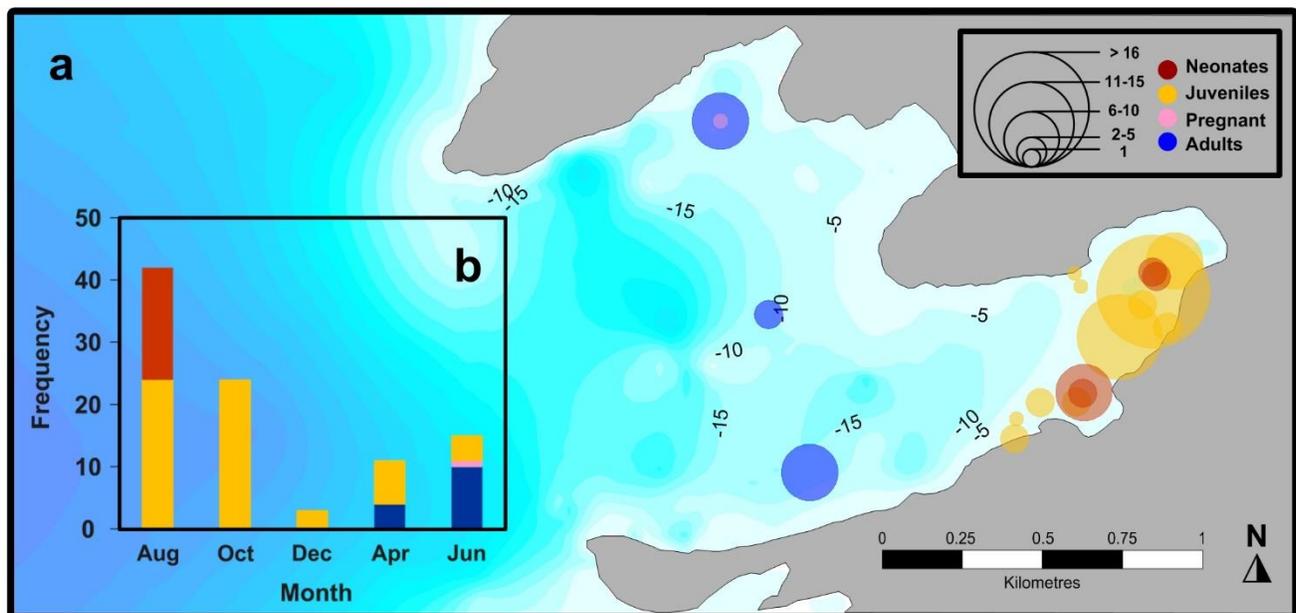


Figure 2. (a) Capture locations of *M. munkiana* between August 2017 and June 2018 at Ensenada Grande. Circle size indicates the number of individuals captured at each location by life stage. Numbers indicate the bathymetric lines. (b) Number of *M. munkiana* captured at Ensenada Grande per month and life stage following the same color code.

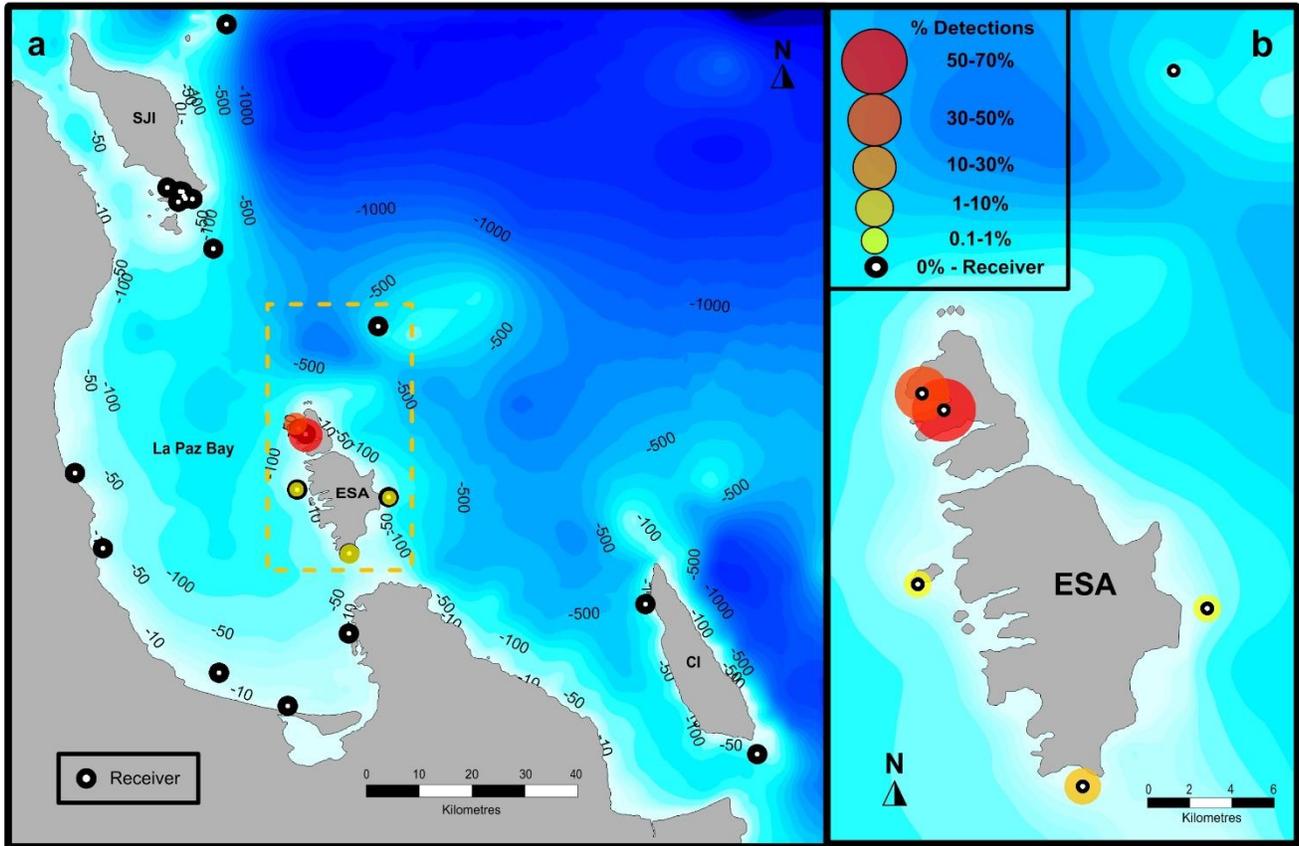


Figure 3. (a) *Mobula munkiana* detection map between August 2017 and May 2019 at La Paz Bay and the surrounding islands of San Jose (SJI), Cerralvo (CI), and (b) the Espiritu Santo Archipelago (ESA). The proportion (%) is indicated by circle size and color for each receiver described in the legend.

3.2 Acoustic Telemetry

3.2.1 Detection summary

All seven acoustic tags deployed on *M. munkiana* (four neonates and three juveniles) (Table 1) were recorded by at least two receivers around the Espiritu Santo Archipelago. We recorded 38,275 detections for all individuals at five of the six receivers placed around Espiritu Santo Archipelago during the monitoring period (643 days) and no other detections were recorded on the rest of the acoustic array ($n = 15$) (La Paz Bay, Isla San Jose and Isla Cerralvo) (Fig. 3a).

Females accounted for 64.5% of detections (two neonates with 63.9% and two juveniles with 0.6% of total detections), while males accounted for 35.5% of detections (two neonates with 27% and one juvenile with 8.5% of total detections).

3.2.2 Residency

Overall residency indices for Espiritu Santo Archipelago-tagged individuals ranged from 1% to 99% ($27 \pm 33\%$, mean \pm SD). The tracking duration for individual *M. munkiana* ranged from 151 to 631

days (435 ± 195 days, mean \pm SD). Detections on consecutive days were found in receivers both within (maximum 145 consecutive days) and outside Ensenada Grande (maximum of three consecutive days). Neonates were present at Ensenada Grande during 26 to 145 successive days while juveniles were present from 1 to 17 successive days. There were no significant differences in the residency index between sexes ($W_6 = 4$, $P = 0.63$), maturity stages ($W_6 = 2$, $P = 0.23$) or sizes ($S = 88.59$, $P = 0.17$).

3.2.3 Habitat preference and spatial movements

Areas of high activity as determined by the number of detections of tagged Munk's pygmy devil rays were in coastal waters inside Ensenada Grande where 98.6 % of the validated receiver detections were registered (Fig. 3b). The other receivers around the Espiritu Santo Archipelago were categorized as offshore and accounted for just 1.4% of the detections, while no detections were registered in the remainder of the receiver array (Fig. 3a).

Table 1. Summary of acoustic tag deployments on 4 neonates (1–4 ID) and 3 juveniles (5–7 ID) of *M. munkiana* at Ensenada Grande (EG), Espiritu Santo Archipelago in 2017. Dates are given as d/mo/yr. DW: disc width; no. det: number of detections; det: detections.

Mobula ID	Sex	DW (cm)	Deployment date	Last detection	Total no. det	Total track days	Total det. days	Residency index EG (%)	Max no. of consecutive days det at EG
1	F	50	02/08/17	08/01/18	15432	151	150	99	145
2	M	50	02/08/17	21/10/18	4777	437	50	11	46
3	M	52	02/08/17	09/01/19	5582	498	139	26	26
4	F	55	02/08/17	16/04/19	9011	614	129	20	70
5	F	72	01/08/17	22/03/19	208	537	16	1	1
6	M	72	01/08/17	29/04/19	3248	631	173	26	17
7	F	75	02/08/17	01/03/18	27	183	9	4	3

As a result, the Ensenada Grande receivers had a statistically greater residency index compared to other receivers placed around the Espiritu Santo Archipelago ($W_{13} = 44$, $P = 0.01$). Individuals moved throughout the Espiritu Santo Archipelago with a travelling minimum linear dispersal distance of 18.5 ± 7.6 km (mean \pm SD) and a maximum of 21.4 km based on detections around the archipelago. One single individual (neonate, 50 cm disc width) was never detected outside of Ensenada Grande, and had a minimum linear dispersal distance of only 1.22 km.

3.2.4 Seasonality

Acoustic detections occurred at the Espiritu Santo Archipelago throughout the year for most devil rays, with no statistically significant differences in residency index between warm and cold seasons ($W_{53} = 249$, $P = 0.07$). The largest residency indices included September, October, November (warm season), and December (start of cold season) 2017 (Fig. 4). Detection rates for all tagged neonates and juveniles decreased during March and April when adults tend to be more frequent at Ensenada Grande and Espiritu Santo Archipelago. Larger juveniles also appear to recruit into the adult population sometime between April and June, supported by our field observation of a tagged (conventional tag) juvenile (≈ 85 cm disc width) swimming in the deeper part of Ensenada Grande (>20 m) as part of a large school of *M. munkiana* adults.

3.2.5 Diel change

All detections at Ensenada Grande showed that the spatial distribution of Munk's pygmy devil rays varied by time of the day (Fig. 5a). Tagged *M. munkiana* were detected by the shallow receiver, RS1 (5 m depth) during all hours, but detections were significantly more frequent during daytime ($U = 359.6$, $P < 0.05$). We found three peaks in detections: between 0400–0500 h (nighttime), 0700–0800 h (daytime) and 1600–1700 h (daytime). We also found significantly greater detections during the daytime at the receiver placed in a deeper area within Ensenada Grande, RS2 (26 m depth) ($U = 359.39$, $P < 0.05$) with almost no detections during nighttime when *M. munkiana* appear to move to shallower areas.

3.3 Environmental Factors

3.3.1 Temperature

Sea water temperature from Ensenada Grande was recorded from August 2017 until April 2018. Temperature values followed seasonal patterns previously described⁴¹ with maximum temperatures from June to November (24.1–29.6 °C) and minimum values from December to May (18.1–26.5 °C). We found a statistically significant correlation between water temperature and the mean monthly residency index of tagged *M. munkiana* at Ensenada Grande ($S = 2.496^{e+09}$, $P < 0.0001$, $\rho = 0.643$). Detections of tagged individuals were consistently greater (up to 145 days of consecutive detections) between August to April of the first year of the study (2017–2018) when water temperature ranged from 18.8–29.6°C, suggesting that they may range less widely during those months of the year. About 77 % of the detections in Ensenada Grande occurred when water temperature ranged 25.5–29.6 °C (total range 18.1 to 29.6 °C) (Fig. 4).

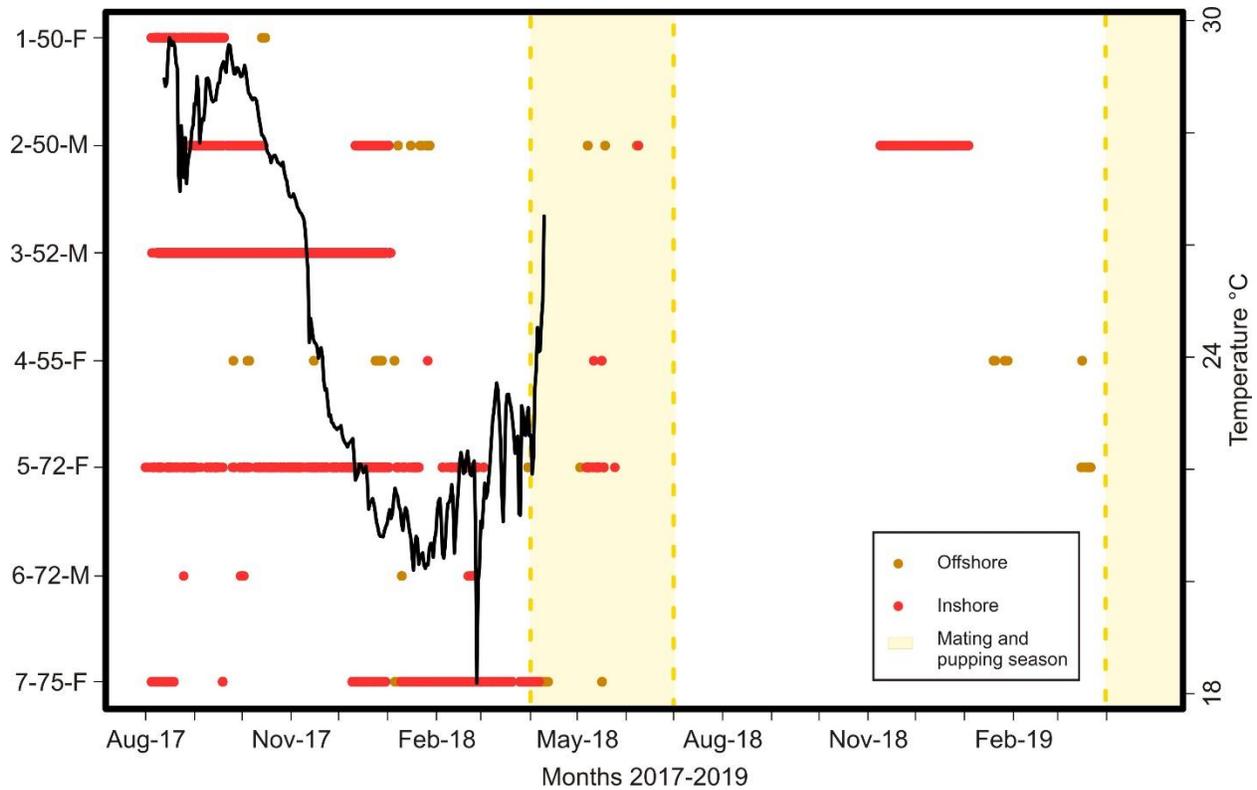


Figure 4. *Mobula munkiana* (n = 7) detections recorded at Espiritu Santo Archipelago between August 2017 and May 2019. Left axis specified code of the animal tag–disc width in centimeters–Sex (F: female; M: male). Ensenada Grande receivers are indicated in red (Inshore) and the rest of the Espiritu Santo Archipelago array is in orange (Offshore). Black line represents the temperature at Ensenada Grande from August 2017 to April 2018. Months of mating and pupping season are indicated in yellow.

3.3.2 Zooplankton

Zooplankton was primarily composed of major taxonomic groups of holoplankton (Copepoda, Cladocera, Euphausiids, Chaetognatha, Mysidacea and Decapoda).

Zooplankton biovolume was significantly greater during the night compared to day ($W_{126} = 1175$, $P = 0.0001549$) (Fig. 5b) across all sampling months, with a peak value of 36.27 ± 8.25 mL 100 m^{-3} (mean \pm SEM) during nighttime samples in December. We found a significantly greater mean zooplankton biovolume during the cold season (December to May) ($W_{126} = 2454.5$, $P = 0.027$) as well as between months (Kruskal-Wallis $X^2 = 23.1$, $df = 5$, $p = 0.0003$), with maximum zooplankton biovolume values observed during December (31.12 ± 4.98 mL 100 m^{-3} , mean \pm SEM) and lowest values in June (10.91 ± 1.64 mL 100 m^{-3} , mean \pm SEM). We also found significant differences of zooplankton biovolume across our three sampling stations inside Ensenada Grande (Kruskal-Wallis $X^2 = 13.478$, $df = 2$, $P = 0.00118$; Dunn test, $P < 0.05$). The deeper station had significantly greater nighttime zooplankton biovolume (29.13 ± 4.89 mL 100 m^{-3} , mean \pm SEM) even though we mainly detected devil rays during night hours at the shallower station where mean zooplankton biovolume values were lower ($19.55 \pm$

5.08 mL 100 m⁻³, mean ± SEM). Nevertheless, mean monthly residency index and the zooplankton biovolume within Ensenada Grande were significantly positively correlated ($S = 221340$, $P = 5.046 \times 10^{-5}$, $\rho = 0.3516104$).

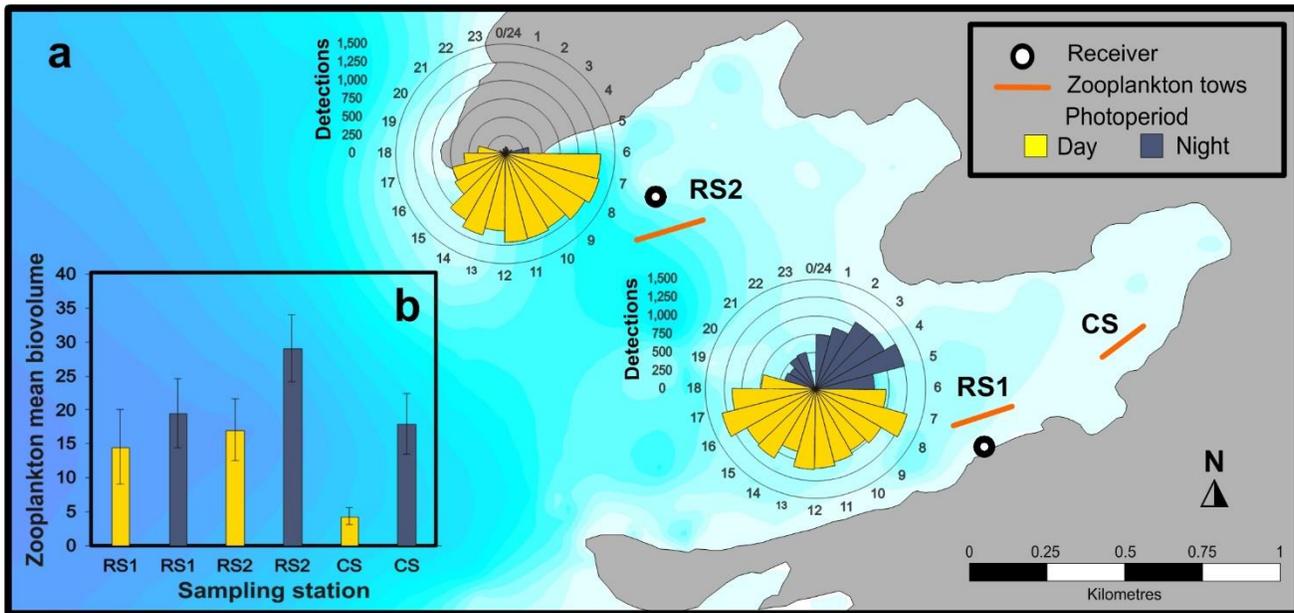


Figure 5. (a) Receiver locations (black–white dots: RS1 at 5 m depth and RS2 at 26 m depth) and zooplankton sampling stations (orange lines) locations at Ensenada Grande. Circular plots of detections per hour of acoustic tagged *M. munkiana* ($n = 7$) at each receiver. (b) Zooplankton mean biovolume (mL 100 m⁻³) and standard error at the three sampling stations collected at day and night during the study period.

4. Discussion and conclusions

Our results indicate that *M. munkiana* utilize nursery areas following the definition proposed for elasmobranch nursery areas. The Ensenada Grande bay of the Espiritu Santo Archipelago can be considered a nursery area for *M. munkiana* following the three criteria:

1. Neonate and juvenile rays are more commonly encountered in Ensenada Grande than in other areas due to their high relative abundance, 84 % ($n = 80$) compared with other studies^{18,32} where proportions for neonates (8.3 %, $n = 2$) and juveniles (15 %, $n = 22$) captured were much lower in adjacent areas.
2. Neonates and juveniles exhibited greater residency indices in Ensenada Grande, being detected almost daily for up to 7 of the 22 months monitoring period in the bay. Individuals resided inside this inshore area from 1 to 145 consecutive days. Moreover, recapture data from traditional tagging demonstrated a site fidelity of 2 to 8 months inside Ensenada Grande for neonates and juveniles.
3. *Mobula munkiana* neonates and juveniles use Ensenada Grande as a nursery area across multiple years. Using anecdotal professional photographs from 2013-2016 (Fig. 6), there is evidence that since

ecotourism activities started, sightings of *M. munkiana*, including juveniles and neonates, are common each year from September to December.

Furthermore, our results provide compelling evidence that *M. munkiana* use Ensenada Grande as a primary nursery area⁴² due to the presence of neonates and near-term pregnant females, and as a secondary nursery area⁴² due to the presence of juveniles (non-newborn). Therefore, overlapping primary and secondary nursery areas for pygmy devil ray species occurs, similar to that observed for other elasmobranch species³.

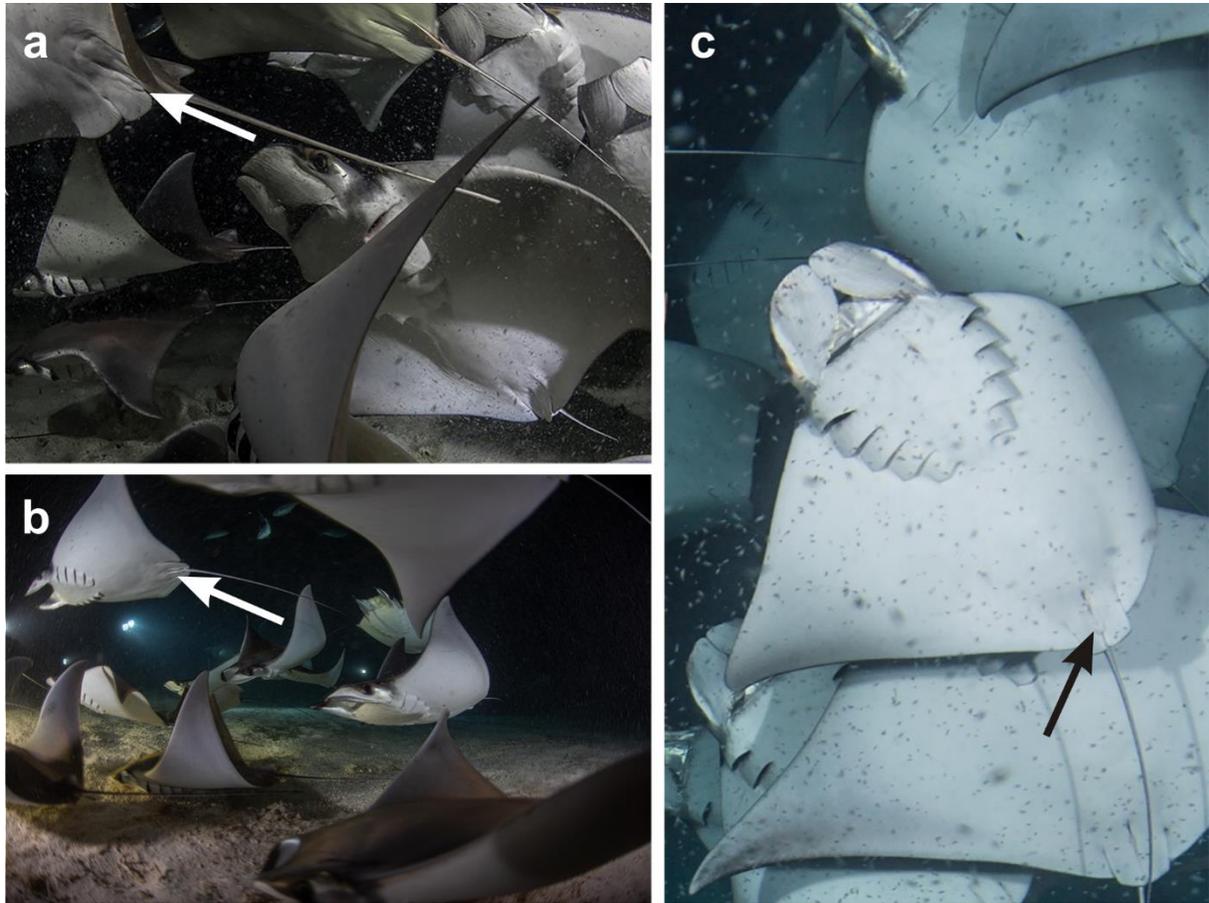


Figure 6. Juvenile males *M. munkiana* with undeveloped claspers (indicated by arrows) at Ensenada Grande during recreational dives in (a) November 2013, (b) October 2014 and (c) October 2016. Images copyright: (a),(b) Erick Higuera and (c) Luke Inman.

The Southern Gulf of California was previously thought to be a wintering ground for *M. munkiana*, with them disappearing from the region during the warmer season for mating and pupping¹⁸. However, we instead propose the use of shallow bays adjacent to high secondary production, such as Ensenada Grande, as a nursery area where neonates and juveniles likely remain throughout the year. We suggest that there are likely other similar, yet undiscovered, nursery areas elsewhere in the Gulf of California and Eastern Pacific for this species. We found that early life stage *M. munkiana* exhibited a

higher residency index during warmer water temperatures. This warm temperature residency may provide an ecological advantage by accelerating the metabolic rates and thus growth of juveniles and thereby reducing the duration of these vulnerable life-history stages^{3,43}. The habitat preference of one of its main prey Mysidacea spp., in shallower parts of the neritic zone,⁴⁴ combined with protection of *M. munkiana* early life stages from large predators, could partially explain the higher detection rate recorded at shallower receivers. As a result, there appears to be an advantage for *M. munkiana* neonates and juveniles to behave as residents with a high fidelity to shallow-coastal habitats in contrast to adults which range widely in oceanic waters.

We observed a clear ontogenetic spatio-temporal segregation among neonates, juveniles, and adults since these different life stages were all caught during different seasons and areas within Ensenada Grande. Size segregation appears to be a common feature for this and other species of mobulids^{18,45}. Although sex segregation has been reported in the southern part of the Gulf of California across different years for primarily adult *M. munkiana*^{18,32,39}, we found a 1:1 sex ratio for neonates and juveniles, a typical feature in elasmobranch nursery areas^{1,46}. This suggests that *M. munkiana* does not segregate by sex during early stages but perhaps may initiate sex segregation when they reach sexual maturity.

Reproductive seasonality has been documented for several mobulid species^{38,40}. Based on our information we suggest that the mating and pupping season for *M. munkiana* begins in April and ends in June when water temperatures range between 18–29 °C. Parturition for *M. munkiana* in La Paz Bay has been previously reported between May and June³⁹, however based on our observations of near term pregnant females in April and June, females with signs of possible parturition in April, and the neonate sizes in August we believe that an extended pupping season is feasible.

This time frame coincides with a transition around June from the cold season when the euphausiid, *N. simplex*, one of the two main *M. munkiana* prey items³⁰, attains its maximum abundance and reproductive period in the Gulf of California^{47,48,49}. A gestation period of 10 to 12 months has been reported for another pygmy devil ray, *Mobula eregoodootenkee*³¹ (originally cited as *M. kuhlii* cf. *eregoodootenkee*) with very similar body size^{15,22}, therefore is very likely that Munk's pygmy devil ray gestation period is the same. Indeed, we observed courtship and pregnancy in the same area and time period in La Paz Bay. The timing of parturition and mating are further supported by observations of *M. alfredi* in captivity⁵⁰ and wild individuals³⁸.

This is the first description of a pygmy devil ray nursery area and the habitat used by neonates and juveniles within it. Individuals of early life stages displayed a high level of residency to the area, more correlated to warmer temperatures than to zooplankton abundance. Nursery and mating grounds for devil rays are highly likely to overlap in temporal and geographic space. Ultimately, since devil rays have the lowest fecundity of all elasmobranchs¹⁷, this information may be useful in the design of spatial and temporal management strategies to mitigate bycatch in artisanal fishing and to regulate

ecotourism activities not only within the Southern Gulf of California, but elsewhere throughout their range. In addition, the information presented here will be useful in identifying nursery areas for other devil ray species world-wide.

Supplementary material

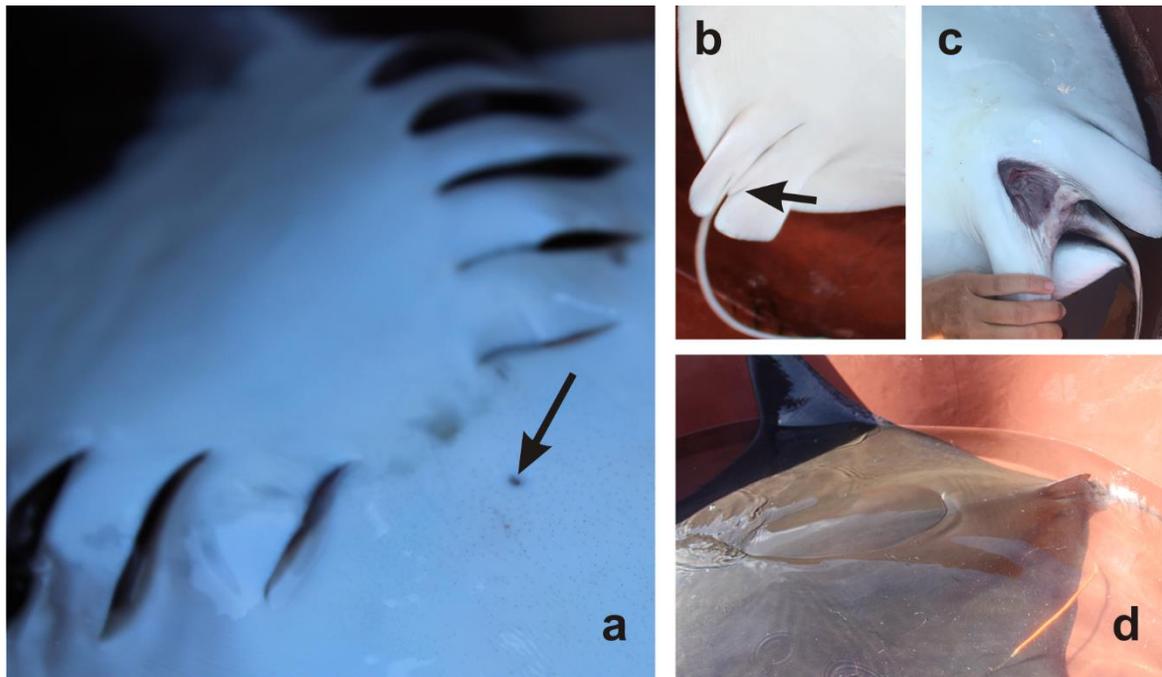


Figure 1 (Supplementary material). (a) Neonate Munk's devil ray with the umbilical cord scar and (b) juvenile male with undeveloped claspers (indicated by arrows) captured at Ensenada Grande in August 2017. (c) Adult female with swollen distended cloaca evidenced with a reddish coloration at Ensenada Grande in April 2018. (d) Pregnant female showing distended abdominal region at Ensenada Grande in June 2018.

Table 1 (Supplementary material). Summary of traditional tagged individuals (n= 95) at Ensenada Grande from August 2017 to June 2018. Capture Date is d/mo/yr; C/R: Capture / Recapture; Sex: M (Male) / F (Female); DW: disc width; TL: Total length. Acoustically tagged individuals are shown in yellow.

Latitude	Longitude	Capture Date	Mobula ID	C/R	Sex	Maturity Stage	DW (cm)	TL (cm)	Observations
24.5616	-110.398	01/08/2017	426	C	M	Juvenile	81.0	47.5	
24.56	-110.395	01/08/2017	437	C	F	Juvenile	76.0	45.0	
24.56	-110.395	01/08/2017	355	C	M	Juvenile	75.0	40.0	
24.56	-110.395	01/08/2017	1	C	M	Juvenile	72.0	40.0	
24.56	-110.395	01/08/2017	2	C	F	Juvenile	72.0	40.0	
24.5581	-110.397	02/08/2017	356	C	M	Neonate	56.0	31.0	Umbilical scars
24.5581	-110.397	02/08/2017	3	C	M	Neonate	52.0	29.0	Umbilical scars
24.5581	-110.397	02/08/2017	408	C	F	Neonate	52.0	30.0	Umbilical scars

24.5581	-110.397	02/08/2017	446	C	M	Neonate	52.0	30.0	Umbilical scars
24.5581	-110.397	02/08/2017	445	C	M	Neonate	51.0	29.0	Umbilical scars
24.5581	-110.397	02/08/2017	4	C	F	Neonate	50.0	29.0	Umbilical scars
24.5581	-110.397	02/08/2017	5	C	M	Neonate	50.0	31.0	Umbilical scars
24.5581	-110.397	02/08/2017	6	C	F	Neonate	55.0	33.0	Umbilical scars
24.5581	-110.397	02/08/2017	350	C	F	Neonate	54.0	32.0	Umbilical scars
24.5581	-110.397	02/08/2017	429	C	F	Neonate	51.0	29.0	Umbilical scars
24.561	-110.395	02/08/2017	438	C	M	Juvenile	79.0	45.0	
24.561	-110.395	02/08/2017	436	C	F	Juvenile	78.0	44.0	
24.561	-110.395	02/08/2017	358	C	M	Juvenile	78.0	46.0	
24.561	-110.395	02/08/2017	435	C	M	Juvenile	77.5	45.0	
24.561	-110.395	02/08/2017	373	C	M	Juvenile	77.0	43.0	
24.561	-110.395	02/08/2017	434	C	M	Juvenile	76.0	43.0	
24.561	-110.395	02/08/2017	7	C	F	Juvenile	75.0	42.0	
24.561	-110.395	02/08/2017	363	C	M	Juvenile	75.0	42.0	
24.561	-110.395	02/08/2017	369	C	F	Juvenile	75.0	41.0	
24.561	-110.395	02/08/2017	449	C	F	Juvenile	75.0	43.5	
24.561	-110.395	02/08/2017	425	C	M	Juvenile	74.0	41.0	
24.561	-110.395	02/08/2017	444	C	M	Juvenile	74.0	38.0	
24.561	-110.395	02/08/2017	443	C	M	Juvenile	73.0	41.0	
24.561	-110.395	02/08/2017	431	C	F	Juvenile	72.0	44.0	
24.561	-110.395	02/08/2017	353	C	F	Juvenile	72.0	43.0	
24.561	-110.395	02/08/2017	428	C	M	Juvenile	71.5	42.0	
24.561	-110.395	02/08/2017	346	C	M	Juvenile	70.5	41.0	
24.561	-110.395	02/08/2017	448	C	F	Juvenile	70.0	40.0	
24.561	-110.395	02/08/2017	370	C	F	Juvenile	69.0	42.0	
24.5615	-110.395	03/08/2017	366	C	F	Neonate	55.0	31.0	Umbilical scars
24.5615	-110.395	03/08/2017	397	C	F	Neonate	54.0	31.0	Umbilical scars
24.5615	-110.395	03/08/2017	8	C	F	Neonate	53.0	29.5	Umbilical scars
24.5615	-110.395	03/08/2017	439	C	F	Neonate	50.5	28.5	Umbilical scars
24.5616	-110.395	03/08/2017	441	C	M	Neonate	55.0	32.5	Umbilical scars
24.5616	-110.395	03/08/2017	354	C	F	Neonate	51.0	28.5	Umbilical scars
24.5616	-110.395	03/08/2017	351	C	F	Neonate	50.0	29.5	Umbilical scars
24.5616	-110.395	03/08/2017	440	C	F	Neonate	49.5	28.0	Umbilical scars
24.5619	-110.395	07/10/2017	344	C	M	Juvenile	82.0	43.0	
24.5619	-110.395	07/10/2017	363	R	M	Juvenile	78.5	43.0	
24.5619	-110.395	07/10/2017	372	C	F	Juvenile	78.0	45.0	
24.5619	-110.395	07/10/2017	380	C	F	Juvenile	77.0	46.0	
24.5619	-110.395	07/10/2017	340	C	M	Juvenile	74.0	42.0	
24.5619	-110.395	07/10/2017	346	R	M	Juvenile	74.0	42.0	
24.5619	-110.395	07/10/2017	341	C	F	Juvenile	70.0	43.0	
24.5619	-110.395	07/10/2017	365	C	F	Juvenile	57.0	31.5	
24.5619	-110.395	07/10/2017	361	C	F	Juvenile	51.0	28.0	

24.5597	-110.396	08/10/2017	393	C	F	Juvenile	82.0	43.0	
24.5597	-110.396	08/10/2017	387	C	M	Juvenile	82.0	41.0	
24.5597	-110.396	08/10/2017	377	C	M	Juvenile	80.0	42.0	
24.5597	-110.396	08/10/2017	378	C	M	Juvenile	80.0	39.0	
24.5597	-110.396	08/10/2017	399	C	M	Juvenile	78.0	42.0	
24.5597	-110.396	08/10/2017	367	C	M	Juvenile	78.0	40.5	
24.5597	-110.396	08/10/2017	359	C	M	Juvenile	74.0	43.0	
24.5597	-110.396	08/10/2017	391	C	F	Juvenile	74.0	40.0	
24.5597	-110.396	08/10/2017	385	C	M	Juvenile	71.0	40.5	
24.5597	-110.396	08/10/2017	364	C	F	Juvenile	68.0	42.5	
24.5597	-110.396	08/10/2017	371	C	M	Juvenile	65.0	33.0	
24.5597	-110.396	08/10/2017	422	C	M	Juvenile	60.0	32.0	
24.5597	-110.396	08/10/2017	441	R	M	Juvenile	60.0	32.5	
24.5597	-110.396	08/10/2017	361	R	F	Juvenile	51.0	28.0	
24.5597	-110.396	08/10/2017	392	C	M	Juvenile	49.0	27.5	
24.5607	-110.396	03/12/2017	392	R	M	Juvenile	52.5	32.5	
24.5607	-110.396	03/12/2017	441	R	M	Juvenile	64.0	38.0	
24.5607	-110.396	03/12/2017	405	C	M	Juvenile	56.0	34.0	
24.5612	-110.397	05/04/2018	403	C	F	Juvenile	64.0	37.5	
24.5604	-110.406	05/04/2018	33580	C	F	Adult	110.0	70.0	Distended cloaca and mating scars
24.5604	-110.406	05/04/2018	33581	C	F	Adult	110.0	66.5	Distended cloaca and mating scars
24.5604	-110.406	05/04/2018	33588	C	F	Adult	103.5	65.0	Distended cloaca and mating scars
24.5604	-110.406	05/04/2018	33831	C	F	Adult	102.0	63.0	Distended cloaca and mating scars
24.5579	-110.397	06/04/2018	421	C	F	Juvenile	65.0	37.0	
24.5579	-110.397	06/04/2018	351	R	F	Juvenile	65.0	38.0	
24.5579	-110.399	07/04/2018	430	C	F	Juvenile	75.0	42.0	
24.5579	-110.399	07/04/2018	396	C	M	Juvenile	64.0	37.0	
24.5578	-110.399	07/04/2018	410	C	F	Juvenile	72.0	41.0	
24.5574	-110.399	07/04/2018	337	C	F	Juvenile	67.0	39.5	
24.5558	-110.405	04/06/2018	33593	C	F	Adult	102.0	66.0	
24.5558	-110.405	04/06/2018	33838	C	M	Adult	101.0	58.0	Sperm on claspers
24.5558	-110.405	04/06/2018	33835	C	M	Adult	101.0	61.0	Sperm on claspers
24.5558	-110.405	04/06/2018	33834	C	M	Adult	101.0	65.0	Sperm on claspers
24.5558	-110.405	04/06/2018	33844	C	M	Adult	98.0	58.5	Sperm on claspers
24.5659	-110.408	05/06/2018	33586	C	M	Adult	108.0	64.0	
24.5659	-110.408	05/06/2018	10	C	F	Adult	100.0	68.0	Heavily pregnant
24.5659	-110.408	05/06/2018	33525	C	M	Adult	102.0	62.0	
24.5659	-110.408	05/06/2018	33837	C	M	Adult	105.0	61.0	
24.5659	-110.408	05/06/2018	33836	C	M	Adult	98.0	58.0	
24.5659	-110.408	05/06/2018	33833	C	M	Adult	98.0	61.0	
24.5568	-110.399	06/06/2018	400	C	M	Juvenile	73.0	39.0	
24.5568	-110.399	06/06/2018	412	C	F	Juvenile	87.0	52.5	

24.5568	-110.399	06/06/2018	406	C	F	Juvenile	80.0	47.5	
24.5568	-110.399	06/06/2018	401	C	M	Juvenile	69.0	39.0	

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CHAPTER 3.

Reproductive behavior, seasonality, and distribution of three devil ray species (*Mobula mobular*, *M. thurstoni*, and *M. munkiana*) in the Southern Gulf of California, Mexico

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1. Introduction

The reproductive behavior of many species of sharks and rays (elasmobranchs) is poorly understood due to the difficulties associated with observing courtship and mating events in the wild (Pratt and Carrier 2001). Much of the research on elasmobranch reproductive behavior has been conducted using fresh fisheries carcasses (Serrano–Lopez et al. 2021) where reproductive behavior is inferred from mating scars on females or the state of male claspers (Marshall and Bennett 2010; Rangel et al. 2022; Whitehead et al. 2022), or from sporadic observations in the wild (Whitney et al. 2010; Arnés–Urgellés et al. 2018) or captivity (Uchida et al. 1990, Smith et al. 2004). Few studies report specific reproductive grounds based on direct and repeated observations of courtship and mating behavior in the field with exceptions including whitetip reef shark *Triaenodon obesus*, reef manta rays *M. Alfredi* and basking sharks *Cetorhinus maximus* (Whitney et al. 2004; Marshall and Bennett 2010; Deakos 2011; Stevens et al. 2018a; Sims et al. 2022). It is particularly important to identify the timing and location of elasmobranch reproductive behavior as such areas may be critical in providing specific conditions that support reproductive success. These areas may be important for elasmobranch conservation and management measures to ensure the viability of future elasmobranch populations (Hyde et al. 2022; Palacios et al. 2023).

Mobulid rays (manta and devil rays) are filter feeding batoids distributed in all oceans from temperate to tropical waters (Couturier et al. 2012; Stevens et al. 2018b). The Mobulidae family has the lowest fecundity of all elasmobranchs (Stevens et al. 2000; Dulvy et al. 2014), giving birth to just one pup per gestation period that lasts up to 13 months (Deakos 2011; Marshall and Bennett 2010; Stevens 2016; Broadhurst et al., 2019). Their reproductive cycles normally involve resting periods, with a two to seven year interval between pregnancies (Deakos 2011; Marshall and Bennett 2010; Stevens 2016). The reproductive strategy of mobulids is aplacental viviparity with histotrophy (Serrano–Lopez et al. 2021) and mate through internal fertilization (Conrath and Musick, 2012) occurring after courtship behaviors that can last from several minutes to days (Marshall and Bennett 2010; Stevens et al., 2018a). Studies of the reproductive behavior (courtship and mating) of mobulids have focused on a limited number of species such as the oceanic manta ray *M. birostris*, *M. alfredi* and sicklefin devil ray *M. tarapacana* (Marshall and Bennett 2010; Deakos 2011; Stevens et al. 2018a, b; Mendonça et al. 2020) with anecdotal observations of other mobulid species (spinetail devil ray *M. mobular*, bentfin devil ray *M. thurstoni*, Atlantic pygmy devil ray *M. hypostoma* and shorthorned pygmy devil ray *M. kuhlii*) (Coles 1910; Duffy and Tindale 2018; McCallister et al. 2020; Carpenter and Griffiths 2023). These studies examined all or some of the seven stages described for mobulid courtship and mating (Stevens 2016; Stevens et al. 2018a). Courtship behavior includes the first four stages: initiation, endurance, evasion, pre–copulatory positioning, while mating behavior refers to the three stages when copulation, post–copulation holding, and separation occurs (Stevens et al. 2018a). During courtship events, several individuals are involved, with one or two females are chased by males, in a formation described as a courtship train, numbering from just a few to up to 26 males (Marshall and Bennett 2010; Stevens et al. 2018a). Mobulid courtship aggregations have been described at: oceanic islands, seamounts, ridge systems, coral reefs, feeding aggregation sites and cleaning stations (Yano et al. 1999; Marshall and Bennett 2010; Sobral 2013; Stevens et al. 2018a; Germanov et al. 2019; Mendonça et al. 2020; Palacios et al. 2023). While reproductive behavior has been described for the larger mobulids (e.g., *M. birostris*, *M. alfredi*), there is only two observational description of courtship behaviors for the pygmy devil ray (*M. hypostoma* and *M. kuhlii*) (Coles 1910; Carpenter and Griffiths 2023) with only one mating event described (*M. hypostoma*) (Coles 1910). Lack of information currently exists on how or where these devil ray species mate or whether they follow the same courtship behaviors described for the better–studied species (Childs 2001, Notarbartolo–di–Sciara et al. 2019). In this study we use direct field observations to examine the courtship and mating behavior of three lesser-known devil ray species: *M. mobular*, *M. thurstoni*, and *M. munkiana*.

Due to their conservative life history traits (Dulvy et al. 2014) and anthropogenic threats, including target fisheries and bycatch (Croll et al. 2016; Lezama–Ochoa et al. 2019), all mobulids species are listed as Endangered or Vulnerable on the IUCN’s Red List of Threatened Species (IUCN, 2023). In the Mexican Pacific, the most abundant devil ray species are *M. mobular*, *M. thurstoni*, and *M.*

munkiana (Notarbartolo–di–Sciara 1988; Serrano–Lopez et al. 2021). Mobulids have been protected in Mexico since 2006 by NOM–029–PESC–2006, and since 2019 by NOM–059–SEMARNAT–2010 regulations, with their primary threats including incidental capture in artisanal fisheries using gillnets (Del–Valle–González–González 2018) as well as bycatch in industrial fisheries, especially in the tuna purse seine fishery (Croll et al. 2012; Croll et al. 2016; Lezama–Ochoa et al. 2019). In recent years, emerging nonregulated ecotourism activities based on snorkeling with mobulid aggregations have brought new economic opportunities to the local communities in the southern Gulf of California, Mexico. However, increasing ecotourism, particularly during critical life history stages and at key aggregation sites (e.g., mating, nursery), could potentially become a problematic source of disturbance (Murray et al. 2020).

Mobula mobular and *M. thurstoni* are found globally in tropical and subtropical oceans, and can reach up to 3.20 m and 1.83 m disc width (DW), respectively (Stevens et al. 2018b, Stewart et al., 2018). Courtship for these species has been reported from direct observations at offshore areas of New Zealand (*M. mobular*, Duffy and Tindale 2018) and in Brazil (*M. thurstoni*, McCallister et al. 2020). In the southern Gulf of California, Mexico, *M. thurstoni* is present year–round (Notarbartolo–di–Sciara 1988; Serrano–Lopez et al. 2021), while *M. mobular* is present April–August and October–December (Notarbartolo–di–Sciara 1988; Croll et al. 2012; Serrano–Lopez et al. 2021). The reproductive season for these species occurs during June and July, inferred from morphometry and histology studies of fisheries caught individuals in this region (Notarbartolo–di–Sciara 1988; Serrano–Lopez et al. 2021). *Mobula munkiana* is distributed in the eastern tropical Pacific, is present year–round in the southern Gulf of California and reaches a maximum DW of 1.30 m (Stewart et al. 2018; Serrano–Lopez et al. 2021; Palacios et al. 2021). No direct observations of *M. munkiana* reproductive behavior have been reported for this species; however, Palacios et al. (2021) speculated that they mate in the southern Gulf of California from April to June, based on courtship observations and the presence of sperm in the developed claspers of males captured at the Espiritu Santo Archipelago.

Diver avoidance behavior by devil rays and a lack of survey effort focused on these three devil ray species has resulted in significant knowledge gaps in important life history parameters and behaviors, particularly reproduction. However, recent citizen science efforts, collaborations with tourism companies using spotter seaplanes, and the use of scientific drones has facilitated field observations in remote or inaccessible areas (Stevens et al. 2018a; Ehemann et al. 2022; Rambahiniarison et al. 2022) and the collection of important behavioral and demographic data on mobulid species (Setyawan et al. 2020, 2022).

Here, we examined the behavior, distribution and seasonality of reproductive events for *M. mobular*, *M. thurstoni*, and *M. munkiana* in the southern region of the Gulf of California, Mexico, to determinate (1) if reproductive grounds exist within the Gulf of California area for any of these species, (2) if

reproductive behavior of the three species follows a seasonal pattern and (3) if courtship and mating behavior is similar among mobulid species.

2. Methods

2.1 Study area

All reproductive behavior observations described in this study occurred in the southern region of the Gulf of California, along the east coast of the Baja California Peninsula, Mexico (**Fig. 1, a, b**). The area is characterized by sandy and rocky coastlines with deep depths (>3700 m), small tidal ranges (annual maximum range of 2.3 m), and sea surface temperatures ranging between 20–30° C (Brusca et al. 2005). The ocean productivity in the area is influenced by a monsoonal wind pattern, with northwesterly winds causing upwelling events during the cold season (December to May), with an average primary production of 10–mg. m⁻³ of sea surface chlorophyll a (Santamaría-del-Ángel et al. 1999, Lavín and Marinone 2003). During the warm season (June to November), strong thermal stratification occurs, with warm water from the Pacific entering the southern Gulf of California, and southeast winds create weak upwelling on the peninsula east coast with an average primary production of 0.1–mg. m⁻³ (Santamaría-del-Ángel et al. 1999, Lavín and Marinone 2003).

2.2 Data Collection

2.2.1 Behavioral data

Reproductive behavior refers to courtship and mating events and was distinguished from other behaviors such as feeding and cruising following the criteria proposed by Stevens et al. (2018a) for mobulids. We define breaching behavior as an arial behavior where individual mobulids accelerate rapidly towards the surface, propelling themselves clear of the water (Medeiros et al. 2021).

Near-term pregnancy was identified by the distended abdominal area on the dorsal and ventral surfaces in females (Marshall and Bennett 2010, Stevens et al. 2018a). We confirmed the external evidence of late-term pregnancy using ultrasound on *M. munkiana* individuals (Palacios unpubl data). Maturity was established based on visual estimation of body size or elongated claspers beyond their pelvic fins (males) and presence of mating scars or wounds (females). Mating scars and wounds were identified as the parallel wounds scratches and abrasions healed (mating scars) or fresh (mating wounds) on females' left pectoral fins (dorsal or ventral) resulting from the teeth of conspecific males to hold her fin during copulation (Stevens 2016; Stevens et al., 2018a). Mating scars are evidence of past mating events (months or years) while mating wounds are evidence of recent mating events (days or weeks) (Stevens 2016; Stevens et al., 2018a).

2.2.2 Boat surveys

Between May 2021 and June 2022, a total of 69 survey-days (between 2 to 24 surveyed days per month) were conducted in La Ventana and Ensenada de Muertos area (**Fig. 1, b**). Each survey consisted of a non-systematic transect of at least five hours (7am–12pm) of observations from a small boat (panga) covering a fixed study area (**Fig. 1, b**) during conditions of Beaufort sea state ≤ 2. Once

an individual or mobulid group were located by sight (by their breaching behavior and/or swimming activity at or near the surface), the research boat remained ~20–m distant from the animals with the motor switched off or in neutral to record group information. A drone (DJI Mavic Pro 2) was launched from the boat and aerial observations were conducted flying at an altitude between 20 to 50 meters above ocean surface for 10–20 minutes. Finally, when possible, in–water observations were conducted by free divers taking video and/or still images using a GoPro7. For each sighting, we recorded date, time, location, species observed and estimated number of individuals, behavior, and when possible, pregnancy status and maturity stage.

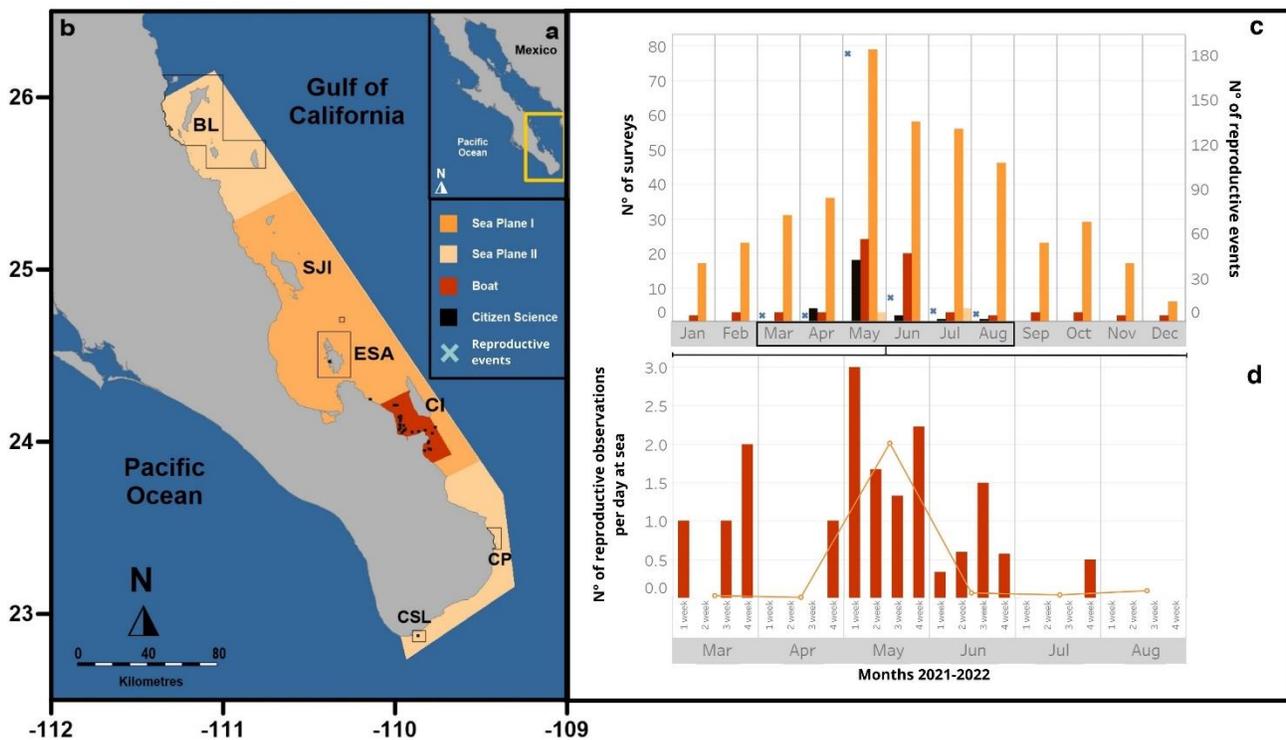


Figure 1. (a) Location of Baja California Peninsula in Mexico **(b)** Study area in the southwestern region of the Gulf of California. Black polygons indicate MPAs in the region: Cabo San Lucas (CSL), Cabo Pulmo (CP), Espiritu Santo Archipelago (ESA) and Bahía de Loreto (BL). Orange and yellow polygons are the areas surveyed by seaplanes, the red polygon is the area covered by boat surveys near Cerralvo Island (CI) and the black points are sightings reported by citizen scientists. **(c)** Survey effort (number of surveys, left axis) during 2021–2022 for two seaplanes, boat surveys, and sightings days from citizen scientists (colors correspond to the legend in panel b), and the number of reproductive events (right axis) observed (blue cross x). **(d)** Effort–corrected reproductive events by two seaplanes (orange line) and boat surveys (red bars) from March to August.

2.2.3 Citizen science data

Photographs and video files of mobulid reproductive events were collected from ecotourism guides and ecotourism boat captains in Baja California Sur (from La Paz to Cabo San Lucas, along the western Gulf of California coast) during 2017, 2021, and 2022. Images were elicited during public educational talks with local communities and submitted via email with information on the sighting date

and location. All reported sightings of *M. mobular* and *M. thurstoni* were accompanied by photographic material to verify the accuracy of the data. *Mobula munkiana* sightings from citizen scientists that did not have associated photographic evidence were only considered if provided by guides trained (n=5) in the collection of this data. These guides were trained on species identification and behavior recognition with the lead author of this study. All video and photographic materials are used with permission and include owner credit.

2.2.4 Seaplane data

During 2021–2022, spotter flights operated by private tourism companies were conducted on the southeastern portion of the Gulf of California, originating from La Paz, Baja California Sur. Although these flights did not follow a standardized transect, they were designed to spot megafauna in the area and all sightings of marine animals were recorded during the flight by trained observers with location, date, species, number of individuals or size of the group and, behavior. A total of 428 flights were conducted, each flight lasted between two to four hours for a total of 858.3 flight hours between January 2021 and December 2022. The total study area covered by these flights was 8,317 km², and flights were conducted during all months of the year (**Fig. 1, b Seaplane I**). During May–August 2022 seven flights covered an additional area of 8,547 km² along the coast from Cabo San Lucas to Loreto (**Fig. 1, b Seaplane II**). The weather conditions during surveys were Beaufort sea state ≤ 3, no clouds, with light and gentle breeze. The aircraft used for these flights were an SLA Seaplane or a Citabria flying at an altitude of ~500–1,000 feet (152–305 m) at a ground speed between ~45–69 knots (83–128 km⁻¹). During these surveys maturity and sex of mobula individuals was assumed based on ongoing behavior (courtship trains).

2.2.5 Analisis

Individuals observed in videos and photographs were counted using the software ImageJ (ImageJ) using the multipoint tool. To estimate the number of reproductive events observations per effort, we divided the number of observations per week (from boat surveys) and per month (from seaplane observations) between the days at sea for each method. Maps were created using Surface Mapping System (Golden Software, Inc., <https://www.goldensoftware.com/products/surfer>) and the coastline data was extracted from GEODASNG (National Geophysical Data Center, 2000).

3. Results

A total of 221 direct observations of reproductive behavior were recorded between March and August in 2017 (n=1, 0.5%), 2021 (n=13, 6%), and 2022 (n=207, 93.5%) (**Supplementary material Table 1**). We recorded 126 (57%) courtship events by seaplane, 64 (29%) by boat surveys, and 31 (14%) by citizen science images (**Table 1**). The single copulation attempt event we observed for *M. munkiana* was recorded during boat surveys using the drone. All reproductive events were observed between the surface and ~5 m depth.

Table 1. Number of reproductive events for each species and type of data collection method.

Species	Data collection method	Number of reproductive behavior events
<i>Mobula mobular</i>	Citizen science	3
	Seaplane	7
<i>Mobula thurstoni</i>	Citizen science	3
<i>Mobula munkiana</i>	Boat surveys	64
	Citizen science	25
	Seaplane	119
Total Events		221

3.1. Distribution and seasonality of reproductive behaviors

All reproductive behaviors events occurred during spring and summer months (**Fig. 2**), coinciding with the transition between the cold season (December to May) and warm season (June to November) in the southern Gulf of California. The peak of reproductive events occurred during the month of May. Sightings were dispersed along 312 km of the east coast of the Baja California Peninsula, from Cabo San Lucas to Ensenada de Cortes at the entrance of San Jose Island channel between the peninsula coast and San Jose Island (SJI); however, the majority (n=209, 95%) occurred within La Ventana (LV) and Ensenada de Muertos (EM) areas (**Fig. 3**). Observations occurred between 4 m and 6.3 km of the coast, while the plane flew from 0 to 60 km offshore.

Mobula mobular

Courtship behavior was observed for *M. mobular* on ten events (**Table 1**) during the months of May (n=5) in 2017, 2021, 2022, July (n=4) in 2022, and August (n=1) in 2022. Sightings were dispersed more than 312 km along the east coast of Baja California Peninsula, from Cabo San Lucas to Ensenada de Cortes at the northern entrance of San Jose Island channel (**Fig. 3, a**). During a courtship event observed in May 2021, one of the females was pregnant in the last stages of gestation (evidenced by a highly distended abdomen).

Mobula thurstoni

Courtship behavior was observed for *M. thurstoni* on three events (**Table 1**) during the months of June (n=1) in 2021, July (n=1) in 2022, and August (n=1) in 2022. Sightings were dispersed more than 43– km along the east coast of Baja California Peninsula, from El Saltito to Punta Arenas (**Fig. 3, b**).

Mobula munkiana

Reproductive behavior was observed for *M. munkiana* on 208 events (**Table 1**) during the months of March (n=4) in 2022, April (n=5) in 2022, May (n=177), June (n=16) and July (n=3) during 2021–2022, and finally in August (n=3) in 2022. The peak of sightings was during the month of May in both years. During this peak, increased courtship activity was observed for the last 10 days of the month. Sightings were dispersed more than 184 km along the east coast of Baja California Peninsula, from El Saladito in the Bay of La Paz to Cabo Pulmo (**Fig. 3**). A copulation attempt was observed (n=1) during a boat survey (28 May 2022) and filmed with the drone. In addition, the following day during a boat survey (29 May 2022) a large number of courtships trains were observed in La Ventana over an extended area. A seaplane flight flying in a straight transect of 8.06 km (**Supplementary material Fig. 1**) in the area counted 102 courtship trains on 29 May 2022.

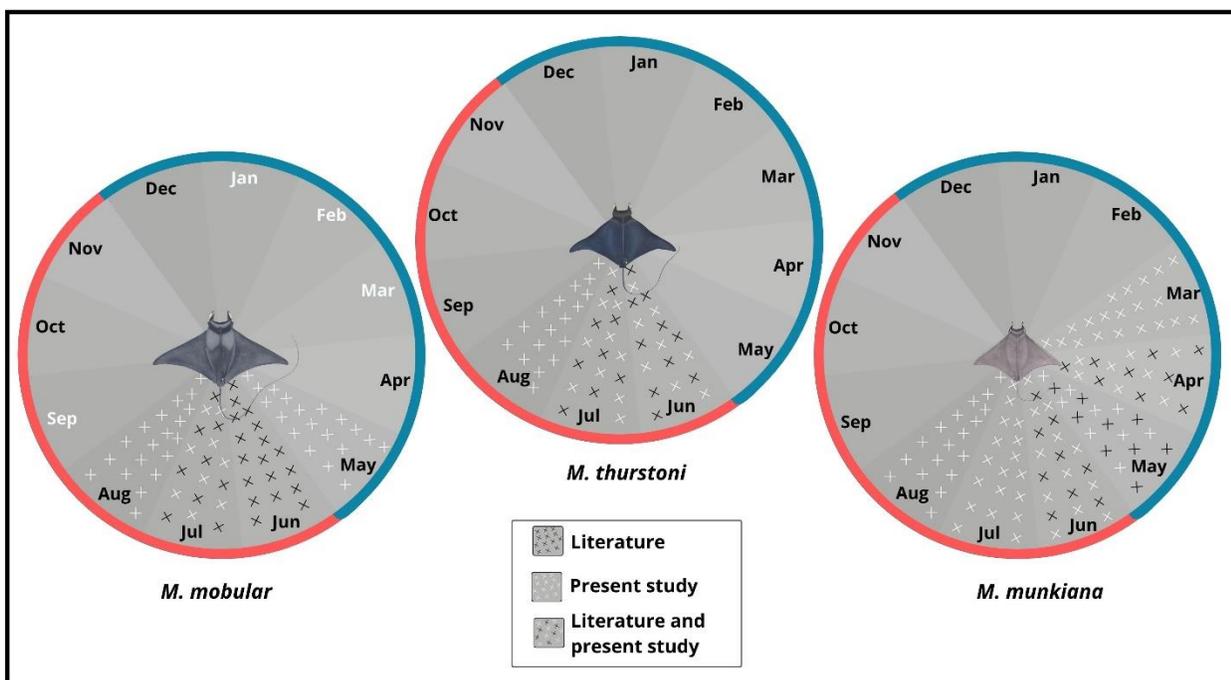


Figure. 2 Seasonality of *M. mobular*, *M. thurstoni* and *M. munkiana* reproductive behavior in the southern Gulf of California based on fisheries information from previous research (Notarbartolo–di–Sciara 1988; Guerrero–Maldonado 2002; Serrano–Lopez et al. 2021) and from direct observations reported on this study. Red indicates warm water months, while blue indicates cold water months. White colored months indicate absence of the species in the study area (Notarbartolo–di–Sciara 1988; Serrano–Lopez et al. 2021). Black crosses (x) indicate courtship and mating from the literature, and white crosses (x) indicate courtship and mating observations in the present study. Devil ray species illustrations by Julie Johnson, Life Science Studio.

3.2 Reproductive Behavior Description

Here we provide detailed descriptions of the reproductive behaviors of these species.

Mobula mobular

The number of individuals involved in the documented *M. mobular* courtship events (n=10) ranged from two to nine, with the sex of individuals determined for three of these events (recorded by citizen

science observations) (**Fig. 4**). Three of the seven stages of courtship and mating behavior (Stevens et al. 2018a) were recorded. Detailed descriptions of events are provided below.

Event 1: On 5 May 2017 at Cabo San Lucas (**Fig. 4, a–d**) a group of nine individuals (two females and seven males) were observed engaging in courtship behavior. One of the females was chased by seven males at high-speed close to the surface (endurance) (**Fig. 4, a**), with one of the males approaching the female by the ventral side (**Fig. 4, b**). The female performed one forward somersault, copied by two males (evasion) (**Fig. 4, c**) and one minute and 10 seconds later reduced speed, and stopped at the surface (pre-copulation positioning), while one of the males approached her from underneath (**Fig. 4, d**). Right after the female swam down followed by one male and the observations stopped.

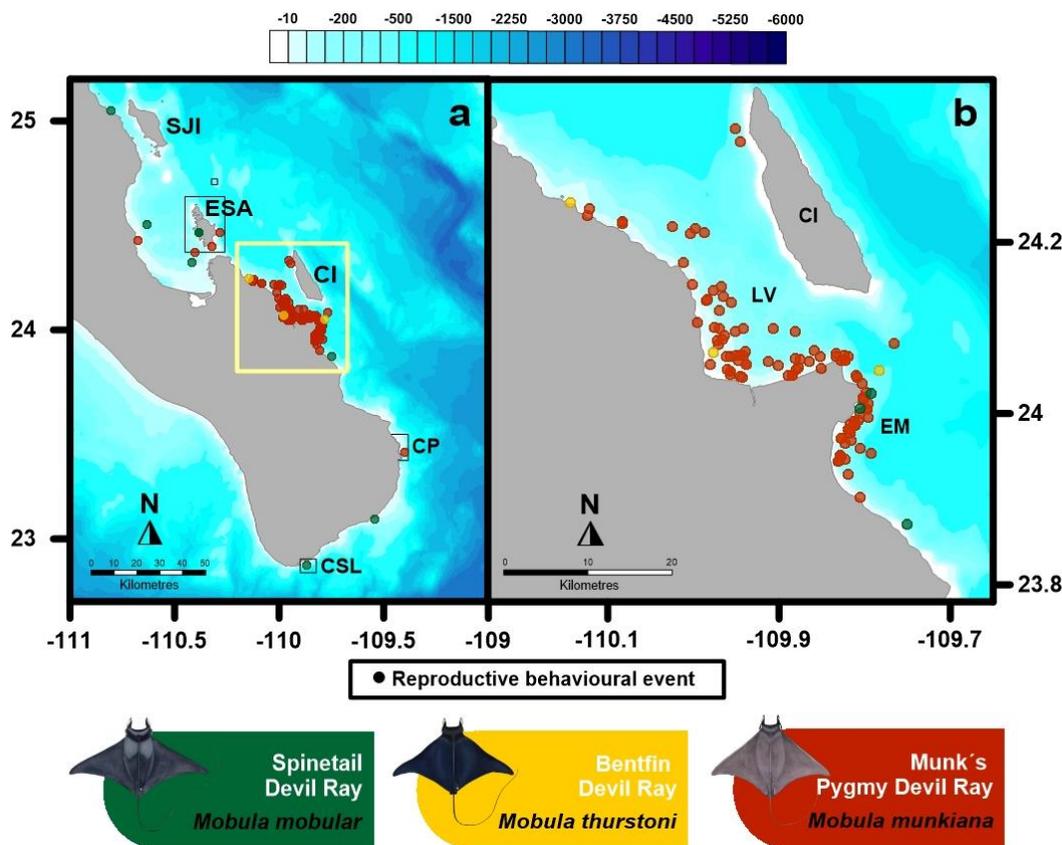


Fig. 3 (a) Southern portion of Baja California Peninsula, with reproductive behavioural events (colored dots) observed between 2017–2022 for *M. mobular* (green), *M. thurstoni* (yellow), *M. munkiana* (red). Black polygons indicate MPAs in the region: CSL, CP, ESA **(b)** Expanded detail in the area of La Ventana (LV), Ensenada de Muertos (EM), and Cerralvo Island (CI) as indicated by the yellow polygon in (a).

Event 7: On 20 May 2021 at the Espiritu Santo Archipelago (**Fig. 4, e–h**), one near-term pregnant individual, was chased by three males (endurance) (**Fig. 4, e**), one of the males subsequently positioned himself on top of the female's dorsal surface attempting to reach and bite the left pectoral fin of the female (pre-copulation positioning) (**Fig. 4, f–g**). After two failed attempts the female performed four forward somersaults copied by the same male (evasion) (**Fig. 4, h**)

Event 8: Another event was observed in proximity and on the same day (**Fig. 4, i–j**). It involved one female and one male performing erratic movements and forward somersaults (evasion) (**Fig. 4, i**) and the positioning of the male on top of the female, trying to reach the female’s left pectoral fin (pre-copulation positioning) (**Fig. 4, j**).

Mobula thurstoni

The number of individuals in *M. thurstoni* courtship groups ranged between three to five, although courtship occurred within bigger groups (>10) that included individuals not engaging in reproductive behavior. Three of the seven stages of courtship and mating behavior (Stevens et al. 2018a) were recorded for *M. thurstoni*. Detailed descriptions of events are provided below.

Event 209: On 28 June 2021 at El Saltito Beach (**Fig. 5, a–d**) a group of five individuals (one female and four males) were engaged in courtship behavior at the surface. A female with mating scars on her left pectoral fin was chased at speeds elevated above average swimming speed by three males (endurance) (**Fig. 5, a–b**). The female performed erratic movements; changes of direction, and somersaults (evasion) (**Fig. 5, c**). During these movements, the female was copied by a male directly behind her during the entire observation period. This male approached the female from underneath, and then positioned himself on top of the female (pre-copulation positioning) (**Fig. 5, d**).

Event 210: On the 1 July 2022 at Punta Arenas (**Fig. 5, e–h**) a female with fresh mating wounds on her left pectoral fin was chased by three males in a courtship train (endurance) (**Fig. 5, e**), while performing turns (evasion) (**Fig. 5, f**). The third male in the train advanced position and speed to a position on top of the female’s dorsal surface (pre-copulation positioning) (**Fig. 5, g–h**).

Event 217: On the 5 August 2022 in La Ventana (**Fig. 5, i–j**) within a group of *M. thurstoni* (>10), a courtship train of two males was recorded chasing a female (endurance) (**Fig. 5, i**) and performing backward somersaults (evasion) (**Fig. 5, j**).

Mobula munkiana

We observed a maximum of 29 *M. munkiana* individuals in a single reproductive group. We recorded five of the seven stages of reproductive behavior (Stevens et al. 2018a) in *M. munkiana*. Below, we present descriptions of two previously undocumented reproductive behaviors for mobulids, the courtship vortex and the piggyback leaping (pre-copulatory behavior) enhancing and broadening our comprehension of pygmy devil ray reproductive behaviors.

Event 6: On 19 May 2021 at Ensenada de Muertos (**Fig. 6, a–c**) a vortex formation at the surface between 2 to 5 m wide was observed during a five-hour period starting the observation at 9: 40 am (**Supplementary material, Video 1**). During this event, females and males (n = 122) were swimming at a consistent average swimming speed, circling in a clockwise direction, collectively swimming up and down to a maximum of 5 m depth in the water column. No feeding was observed, yet numerous small courtship trains (approximately 20) where a female was chased by one to three males regularly occurred (**Fig. 6, a**). The individuals in courtship trains did not separate more than 5–10m from the

main formation (**Fig. 6, b–c**), returning to the courtship vortex after a few seconds of chase (endurance). Sexually mature males engaged in these courtship trains. No visible pregnant females were observed within the group. Some females presented abrasions on the lower area of their dorsal surface probably produced by the pre–copulatory positioning of the male on top of them (**Fig.7, a–d**). Breaching behavior was not observed in the vortex during the five–hour observation period.

Events 87–188: On 29 May 2022 at La Ventana (**Fig. 6, d–e**), 102 courtship groups were observed at the surface between 7:24 and 9:10 am. Reproductive behavior consisted of courtship trains (initiation, endurance, and evasion) dispersed within La Ventana area in a straight transect of 8.06 km (**Supplementary material, Fig. 1**). Courtship groups occurred at the surface, while larger groups (>100 individuals) of *M. munkiana* remained cruising a few meters below. On many occasions several courtship events occurred in proximity. Courtship trains were dynamic with males switching chasing one female to another nearby female.

Event 84: On 28 May 2022 at La Ventana (**Fig. 6, f–i**) a group of 29 individuals (one female and 28 males) were engaging in courtship behavior (**Supplementary material, Video 2**). The group was observed for 45 minutes and included one female swimming at below average cruising speed at the surface with her pectoral fins often lifting out of the water. The males (28) were circling, chasing her, and swimming from behind positioning themselves on top of her (piggyback leaping) as a pre–copulatory behavior (**Fig.7**), approximately 135 times during the observation period. The female swim speed increased when a male positioned himself directly behind or onto her dorsal surface, turning her swim angle acutely or flipping forwards (evasion). After successfully evading the male, the female returns to the surface and resumes below average swim speeds, slowly moving around within a small area (approx. 50 m²).

Although individual males could not be identified, preventing from an assessment of the number of different males which chased the female, some male individuals chased each other away when in proximity to the female (**Supplementary material, Video 3**). On one occasion one male approached the female from underneath while up to three males rushed from behind and swam on top of her (piggyback leaping) (**Fig. 6, g**). However, the most common behavior was when males, one at a time, approached the female from the ventral part and then slid along one of the female's pectoral fins and swam on top of her (piggyback leaping). When on top of the female, males erected their tail dorsally at 90° (**Fig. 7 b, c**), bending their pelvic area and making rapid pelvic thrusts (**Supplementary material, Video 4**). On one occasion, we observed a clear copulation attempt where the male swam on top of the female and started to make rapid pelvic thrusts, they both subsequently sank towards the bottom while spinning around (copulation attempt) for 14 seconds. The pair then separated, and the female swam off to the surface (**Supplementary material, Video 2**). Immediately after, courtship behavior continued with this female and other males in the group.



Figure 4. *Mobula mobular* courtship events. Event 1: **(a, b)** endurance, **(c)** evasion, **(d)** pre-copulation positioning. Photo © Marta D. Palacios. Event 7: **(e)** endurance, **(f, g)** pre-copulation positioning, and **(h)** evasion. Event 8: **(i)** evasion and **(j)** pre-copulation positioning. Photo © Paulo Gómez Aldana



Figure 5. *Mobula thurstoni* courtship events. Event 209: **(a, b)** endurance, **(c)** evasion, **(d)** pre-copulation positioning. Photo © Adriá Bosch-Soler. Event 210: **(e)** endurance, **(f, g, h)** evasion and **(g)** pre-copulation positioning. Photo © Maru Brito. Event 217: **(i)** evasion and **(j)** pre-copulation positioning. Photo © Afelandra González-Cibrián.

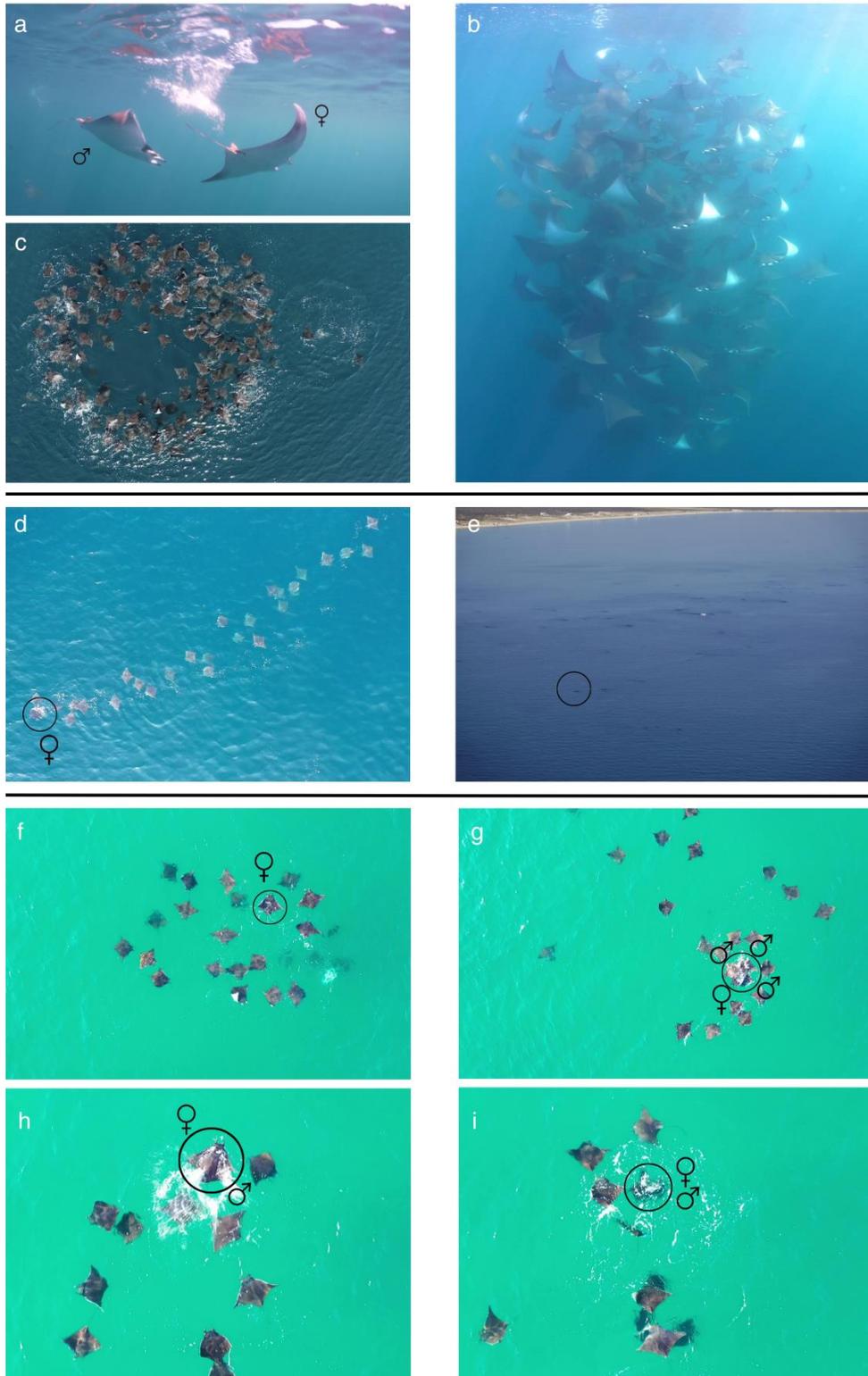


Figure. 6 *Mobula munkiana* courtship and mating event. Event 6: **(a)** endurance and **(b, c)** courtship vortex. Photo © Shawn Hendrich and Jay Clue. Event 111: **(d)** endurance. Photo © Marta D. Palacios. Events 85–186: **(e)** view of courtship trains from the seaplane in a circle. Photo © Sidharta Velázquez–Hernández. Event 84: **(f)** Evasion, **(g, h)** pre–copulation positioning and **(i)** copulation attempt. Photo © Marta D. Palacios

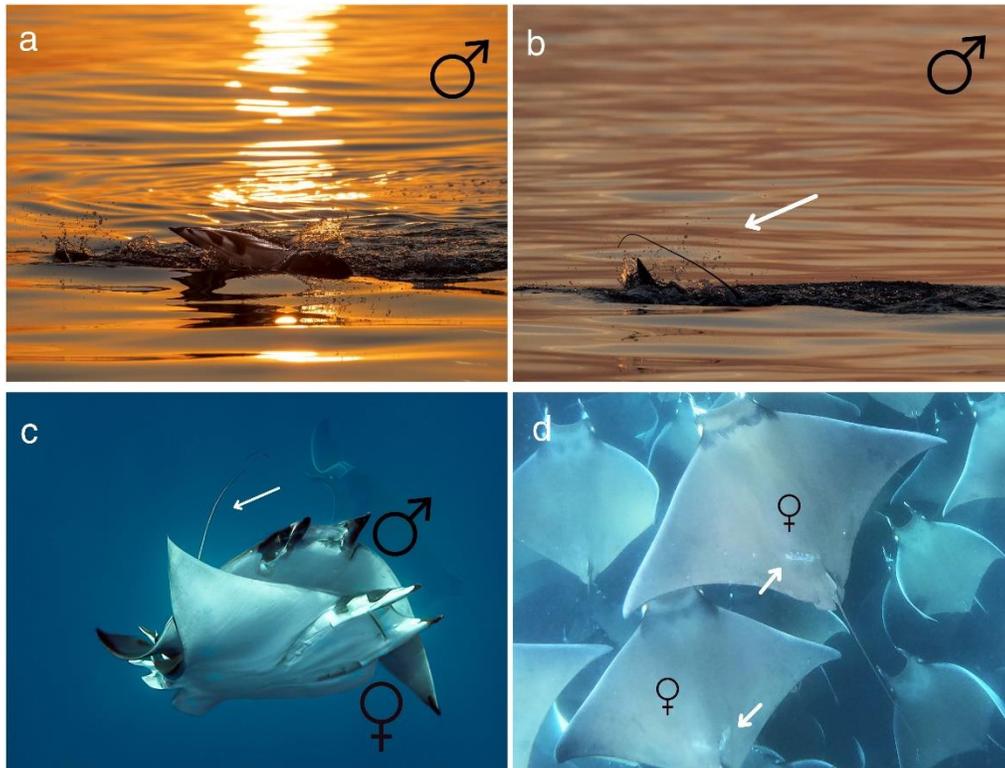


Figure 7. Reproductive behavior of *M. munkiana*: piggyback leaping. **(a)** Male positioning himself onto the female dorsal surface (event 82). **(b, c)** Examples of males erecting their tails when on top of the female (events 82 and 72). Photos © Laurent Ballesta. **(d)** Courtship abrasions on the posterior half of the disc on female's dorsal side indicated by white arrows (May 2022). Photo © Marta D. Palacios.

3.3 Associated observations

Pregnancies

Mobula mobular (n=1) (event 7) (**Fig. 7, a**) and *M. munkiana* (n=10) (events 5, 11, 12, 27, 28, 50, 62, 73, 205, 206) females showing evidence of later-term were observed engaging in courtship behaviors during the months of May and June 2021–2022.

Mating scars, fresh mating wounds and courtship abrasions

Parallel fresh mating wounds scratches and abrasion on females' left pectoral fins (dorsal or ventral) resulting from the teeth of conspecific males were observed only on the left side in *M. thurstoni* during courtship (**Fig. 8, b, c**). We recorded mating scars on a female on the ventral part of the left pectoral fin at El Saltito Beach (event 209) (**Fig. 5, a–d**), and fresh mating wounds on a female engaging in courtship train at Punta Arenas (event 210) (**Fig. 5, e–h**).



Figure 8. (a) Near-term *M. mobular* engaging in a courtship (event 7). Photo © Paulo Gómez–Aldana (b, c) Females *M. thurstoni* with fresh mating wounds indicated by white arrows (event 210 and June 2019). Photos © Maru Brito and Cecilia Mar–Ruiz (d) *M. munkiana* female with courtship abrasions (posterior dorsal area) and scars on her left pectoral fin resulting from the male's biting hold of her fin during copulation indicated by white arrows (May 2022). Photo © Marta D. Palacios. (e) Female *M. munkiana* with fresh mating wound indicated by white arrows (May 2022). Photo © Marine Bruges (f) *M. munkiana* females with courtship abrasions (posterior dorsal area) indicated by white arrows (May 2023). Photo © Karissa Nanetta.

We recorded mating scars and mating fresh wounds in *M. munkiana* on the left pectoral fins (**Fig. 8, d, e**). We also recorded a new indicator of courtship activity for this species, the courtship abrasions, which are visible on the posterior half on *M. munkiana* dorsal side (**Fig. 7, d and Fig. 8, d, f**). These abrasions appear as a result of the repeated back-leaps from males onto the female's dorsal surface during courtship, when performing the pre-copulatory behavior "piggyback leaping". Although we did not record the number of individuals presenting these courtship abrasions due to the large size of groups and the high frequency of these abrasions, we observed the courtship abrasions on near-term pregnant females, mature females and males. Pregnant females showing courtship abrasions on their lower dorsal area didn't always have pectoral fin mating scars or wounds. These courtship abrasions were also visible on female individuals outside of the reported reproductive period (November) (**Supplementary material, Fig. 2**).



Figure 9. *Mobula munkiana* breaching behavior **(a)** Adult male. Photo © Blanca Idalia González–Garza **(b)** Juveniles. Photo © Juan Camilo Mora–Parra **(c)** non–pregnant female. Photo © Antoni Murcia **(d, e)** Pregnant females with fetal bulge on their dorsal side indicated by white arrows. Photos © Jay Clue **(f)** Pregnant female with fetal bulge and courtship abrasions on its dorsal side indicated by white arrows. Photo © Antoni Murcia.

Breaching behavior

We only recorded breaching groups in *M. munkiana*, although single individuals of *M. thurstoni* were also frequently sighted breaching out of the water during all surveyed months in 2021–2022. During boat surveys (n= 64), *M. munkiana* breaching groups were recorded (n=58 of a total 118 groups, 49%) between 2021–2022. We observed breaching behavior in individuals of all maturity stages (juveniles and adults) and sexes (male and female), and in pregnant females (**Fig. 9, a–f**). During some of the breaches, the individuals shook their pectoral fins when they had a remora attached to their bodies. During courtship, breaching was not observed among individuals that were engaging in reproductive behavior, whereas breaching was observed among individuals within the larger groups who were not actively participating in the courtship. Near–term pregnant females breaching were common sights during the months of May and June (**Fig. 9, d–f**). Different kinds of breaches were observed for this species, breaching forward to land on the ventral surface or slapping the surface of the water with their pectoral fins, breaching and landing on one side, as well as breaching to land on the dorsal surface.

4. Discussion

Distribution and seasonality

This study extends the reproductive season described for three (*M. mobular*, *M. thurstoni*, *M. munkiana*) of the five mobulid species present in the Gulf of California. Previously, *M. mobular* and *M. thurstoni* were reported to reproduce during June and July, inferred from dead specimens from artisanal fisheries (Notarbartolo–di–Sciara 1988; Guerrero–Maldonado 2002; Serrano–Lopez et al. 2021). However, based on direct observations of living animals in this study, reproductive behavior occurs from May to August for *M. mobular*; two months longer than previously reported. We found that the reproductive season for *M. thurstoni* occurs from June to August; one month longer than previously reported (Serrano–Lopez et al. 2021). *Mobula munkiana* was observed displaying reproductive behavior from March until August; an extension of three months (Palacios et al. 2021). In the south–west Gulf of California, these three species are found in greatest abundance during the spring and summer (March–July) (Notarbartolo–di–Sciara 1988; Palacios et al. 2021; Serrano–Lopez et al. 2021), likely correlated to the abundance peak of their main prey in the region, the euphausiid *Nyctiphanes simplex* (Gendron 1992; Sampson et al. 2010). This time frame also coincides with the transition from the cold season (December–May), when northwest winds lead to lower sea surface temperature (SST) between 21–24 °C, to the warm season (June–November), when weaker winds from the southeast bring warm tropical water from the Pacific and SST are between 27–31 °C (Herguera et al. 2001; Lluch–Cota et al. 2007).

The extension of these reproductive seasons could be the result of the combination of our larger study area throughout the year than previous studies (Notarbartolo–di–Sciara 1988; Guerrero–Maldonado 2002; Serrano–Lopez et al. 2021; Palacios et al. 2021) and the different observational methodologies used (drone, in–water observation, citizen science, and seaplanes) which have proven to be useful in the collection of behavioral data (Fiori et al. 2017; Stewart et al. 2018; Oleksyn et al. 2021; Palacios et al. 2023). Direct observations of courtship events for *M. mobular* and *M. thurstoni* have been previously reported at offshore areas and remote archipelagos (Duffy and Tindale 2018; McCallister et al. 2020). In our study, reproductive events occurred between 4 m to 6.3 km from the Baja California Peninsula coastline or adjacent islands. The southern Gulf of California is characterized by steep slopes, with a narrow shelf and deep basins where enriched waters contribute to a high primary production close to the coast (Lavín and Marinone 2003; Lluch–Cota et al. 2007). The greatest number of reproductive events occurred at La Ventana, a channel with a maximum width of 17 km and 293 m depth between the peninsula coast and the island of Cerralvo (Nava–Sanchez et al., 1995), and at Ensenada de Muertos, where the ocean floor falls to 300 m within the first 2 km from the coast. These bathymetric features, in conjunction with high seasonal productivity during spring (Lluch–Cota et al. 2007), may favor high abundance of food and optimal conditions for the aggregation of large numbers

of devil rays, facilitating the encounter of potential mating partners; similar to other reproductive aggregations in other elasmobranchs (Sims et al. 2022; Palacios et al. 2023).

Reproductive behavior

Reproductive behavior for manta ray species is well established in seven stages (Stevens et al. 2018a) of which we observed five during this study; endurance, evasion, and pre-copulation positioning were the most common.

For *M. munkiana*, we describe two new courtship behaviors: the courtship vortex and the piggyback leaping. Vortex formations are regularly performed by *M. munkiana* in the La Ventana area, probably for predator avoidance and as a coordinated feeding strategy (Palacios et al. in prep), similar to the cyclone feeding of *M. alfredi* in Maldives (Stevens 2016; Armstrong et al. 2021). However, we hypothesize that the courtship vortex observed in this study has a reproductive function based on the absence of feeding behavior or visible predators in the area (Higuera-Rivas et al. 2023) throughout the five hours of the encounter. Further, the presence of sexually mature individuals of both sexes (males with elongated claspers and females with mating scars) and the observation of courtship trains entering in and out of the main formation indicates that this may represent a social and reproductive aggregation where adults assess and chose potential mates before engaging in individual courtship trains and copulation. The structure and speed of the vortex allowed physical contact among most of the individuals within the vortex, especially those situated in the center. Similar behaviors have been studied for basking sharks (*Cetorhinus maximus*) (Sims et al. 2022) but have never been reported for mobulid species (Yano et al. 1999; Pratt and Carrier 2001; Marshall and Bennett 2010; Deakos 2011; Stevens 2016; Stevens et al. 2018a; Mendonça et al. 2020).

In addition, a new courtship behavior was observed on *M. munkiana* mature males, the piggyback leaping. This courtship strategy consists of back-leaps performed by mature males onto the females back. To achieve this, males actively pursue the female, positioning themselves directly behind or beneath her to execute these leaps. This behavior occurs while the female is right at the surface, likely to prevent the males from getting onto her dorsal surface. Since we did not observe males rubbing the backs of the females with their cephalic fins at any time (Stevens et al. 2018a), it is likely that these dorsal abrasions could be the result of the leaping on top of the female from behind as the males attempt to copulate (**Fig. 7, a-d**). These repeated leaps create “courtship abrasions” visible several months after the end of the reproductive season (up to 3 months) for this species (**Supplementary material, Fig. 2**). The presence of these courtship abrasion on some adult males, were probably the result of the simultaneous back leaps, where several males leaped onto the female at the same time. Therefore, the presence of these courtship abrasions could be used as an indicator of sexual maturity on *M. munkiana*.

Male biting of the pectoral fins of the female during reproductive events is a reproductive behavior in elasmobranchs (Klimley 1980; Uchida et al. 1990; Pratt and Carrier 2001; Marshall and Bennett 2010),

and in mobulids is included in the pre-copulation positioning phase (Stevens et al. 2018a). This behavior enables the proper positioning of the male for the insertion of the claspers in the female cloaca, while the female remains motionless during copulation (Kajiura et al. 2000) and results in female pectoral fin abrasions, wounds, and permanent scars (Yano et al. 1999; Marshall and Bennett 2010; Stevens et al. 2018a). Devil ray species have teeth on both jaws (Notarbartolo-di-Sciara 1987; Stevens et al. 2018b), leaving mating scars on both sides of the females' pectoral fins when biting occurs. Wounds or mating scars (Marshall and Bennett 2010; Stevens et al. 2018a) (**Fig. 8, b–d**) were present on the dorsal and ventral sides of *M. thurstoni* individual's pectoral fins, while *M. munkiana* individuals also presented courtship abrasions on the posterior half of the disc.

During copulation attempts, *M. munkiana* males did not always wait until pre-copulation positioning (e.g., biting the female's pectoral fin) before erecting their tail, bending their pelvic area, and making rapid pelvic thrusts for copulation (**Fig. 7, b, c**) (**Supplementary material, Video 4**).

Breaching behavior

Breaching behavior, or leaping, is a commonly observed behavior in elasmobranchs, with several species (thresher shark, basking shark, white shark, eagle rays, and blacktip sharks) breaching for various hypothesized reasons including feeding, courtship, parasite removal, and predator avoidance (Curtis and Macesic, 2011, Berthe et al. 2018; Gore et al. 2019). Breaching behavior for the mobulids has been hypothesized as a form of signaling mechanism to aggregate for reproduction (Marshall and Bennett 2010; Medeiros et al. 2021; Stevens et al. 2018a). The males breach to attract more potential mates and demonstrate their fitness by creating as loud a splash as possible, while the females breach to attract more potential mates from which to select a partner from during courtship (Stevens 2016). While breaching behavior may be related to reproductive behavior in *M. munkiana*, it is important to note that we observed all maturity stages (juveniles, adults, and pregnant females) and sexes breaching. Additionally, we found that breaching occurred year-round in the Gulf of California, including outside of the reproductive season, suggesting that it is highly likely this behavior is also driven by other biological functions as well. Based on this evidence we hypothesize that most breaching events for *M. munkiana* may be a form of communication meant to attract other groups or individuals to a certain area to feed, perhaps cooperatively, or as a predator avoidance mechanism. These functions have been suggested for *M. alfredi* during coordinated feeding events (e.g., cyclone or chain feeding) in Maldives (Stevens 2016; Armstrong et al. 2021) and for *M. birostris* in estuarine environments in Brazil (Medeiros et al. 2021). Breaching behavior may also be related to parasite removal: during some of the breaching events, we observed *M. munkiana* actively shake pectoral fins where remoras were attached, and similar behavior has been observed for other elasmobranchs (Ritter and Brunnschweiler 2003; Brunnschweiler 2006).

5. Conservation implications

The southwestern Gulf of California is a reproductive area for *M. mobular*, *M. thurstoni*, and *M. munkiana*, based on our observations and on histological and morphological studies previously conducted in the area (Notarbartolo–di–Sciara 1988; Serrano–Lopez et al. 2021). Reproductive behavior for these three species has been observed in this area from March to August. This period extends three months outside of the currently established elasmobranch fishing ban in the Mexican Pacific, which extends from the first of May to the first of August. Although mobulids have been protected from target fisheries in Mexico since 2006 (NOM–029–PESC–2006), gillnets, longlines and simpleras (bottom–fixed lines with baited hooks) are used in the Gulf of California by artisanal and industrial fisheries to legally fish for stingrays and sharks during the other nine months of the year (Bizzarro et al. 2009; Del–Valle–González–González 2018). The main threats to mobulids in the study area includes commercial fisheries, such as industrial purse seiners targeting tuna (Croll et al. 2016; Lezama–Ochoa et al. 2019), shrimp boats, artisanal gillnets and illegal fishing activities that specifically target devil rays (Palacios unpubl data). *Mobula mobular* and *M. thurstoni* are the dominant species captured as bycatch in industrial fisheries in the region (Lezama–Ochoa et al. 2019). While the extent of the impact of bycatch and target fisheries on *M. munkiana* is unknown across its range (Alfaro–Cordova et al. 2017, Lezama–Ochoa et al. 2019), high rates of mobulid bycatch in artisanal gillnets have been observed within the study area (Del–Valle–González–González 2018; Palacios unpubl data). The lack of spatial management for shark and ray fisheries (Bizzarro et al. 2007) and the use of non–selective gear (gillnets) in Mexico, coupled with the limited enforcement of existing regulations potentially puts critical habitats at risk, even for protected species like mobulids (Salomón–Aguilar 2015; Jabado et al. 2023). Establishing greater spatial and temporal restrictions on the use of gillnets along the coast and islands in the southwestern Gulf of California, especially around critical habitats such as reproductive grounds (La Ventana and Ensenada de Muertos area) and nursery areas (Espiritu Santo Archipelago) (Palacios et al. 2021) may help reduce the impact of bycatch of these species during key life periods.

The results of this study indicate reproductive areas are within 6.3 km of the coast, where we observed surface aggregations of the three devil ray species. This distribution makes them vulnerable not only to bycatch, but to other anthropogenic threats such as an increasing coastal development in the region and the associated sound and chemical pollution, habitat loss, and boat traffic. During our surveys we observed reproductive behavior at the surface, creating the potential for individuals engaging in reproduction to be exposed to boat strikes potentially resulting in lethal or sublethal injuries (Womersley et al. 2022; Strike et al. 2022). Furthermore, currently unregulated tourist activities offering free diving and snorkeling with devil rays, especially *M. munkiana*, is growing in the area with more than 80 tourism companies (Bruges et al. in prep) providing new economic opportunities to local communities. Currently, little is known about the extent to which these activities affect the reproductive

behavior and movement patterns of these species. However, unregulated tourism has negatively impacted manta rays in the Maldives, Australia (Venables 2013; Venables et al. 2016) and Mexico (Gómez–García et al. 2021), showing to disrupt or stop natural behaviors during 37% of the observations (Murray et al. 2020). The establishment of management measures, including studies of the optimal carrying capacity for mobulid tourism (Zekan et al. 2022), and codes of conduct to observe and interact with these species may help mitigate the negative impacts of tourism activities (Murray et al. 2020) at reproductive grounds while offering economic benefits to local communities (O' Malley et al. 2013).

Only four of the 221 reproductive behavior events occurred inside a marine protected area (MPA) (Espiritu Santo Archipelago and Cabo Pulmo), with only Cabo Pulmo being a strict no–take MPA. This is of potential concern because near–term mobulids are routinely thought to mate within hours or days of giving birth (Stevens et al. 2018a). This is supported by our observations of heavily pregnant *M. mobular* and *M. munkiana* females engaging in courtship behavior indicating it is likely that birthing areas are located adjacent to these nursery areas, as previously described for *M. munkiana* (Palacios et al. 2021). This suggests that further spatial protection of reproductive areas could be useful to simultaneously protect both nursery, courtship, and mating areas. Recently, several Important Shark and Ray Areas (ISRA) (Hyde et al. 2022) have been established in the Mexican Pacific and Gulf of California (Jabado et al. 2023), however, some of the critical habitats for reproductive behavior reported in this study such as the Ensenada de Muertos area are not covered inside the designated polygons of ISRA. The existing MPAs in the region prove inadequate for mobulids, needing immediate action to improve spatial protection against gillnets, industrial fisheries, and other anthropogenic threats.

Supplementary material

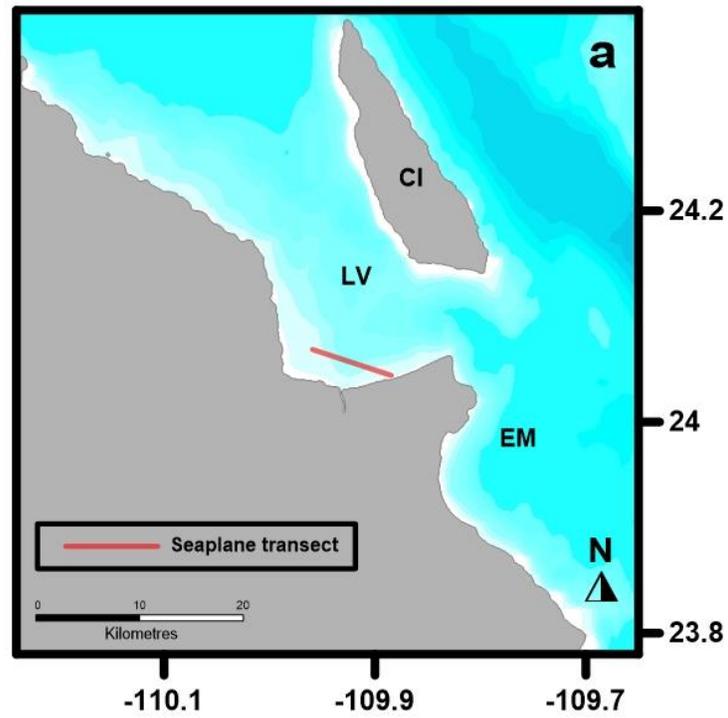


Figure 1 (Supplementary material). Straight seaplane transect (8.06 km distance) in La Ventana Bay on 29 May 2022. LV (La Ventana), EM (Ensenada de Muertos) and CI (Cerralvo Island).

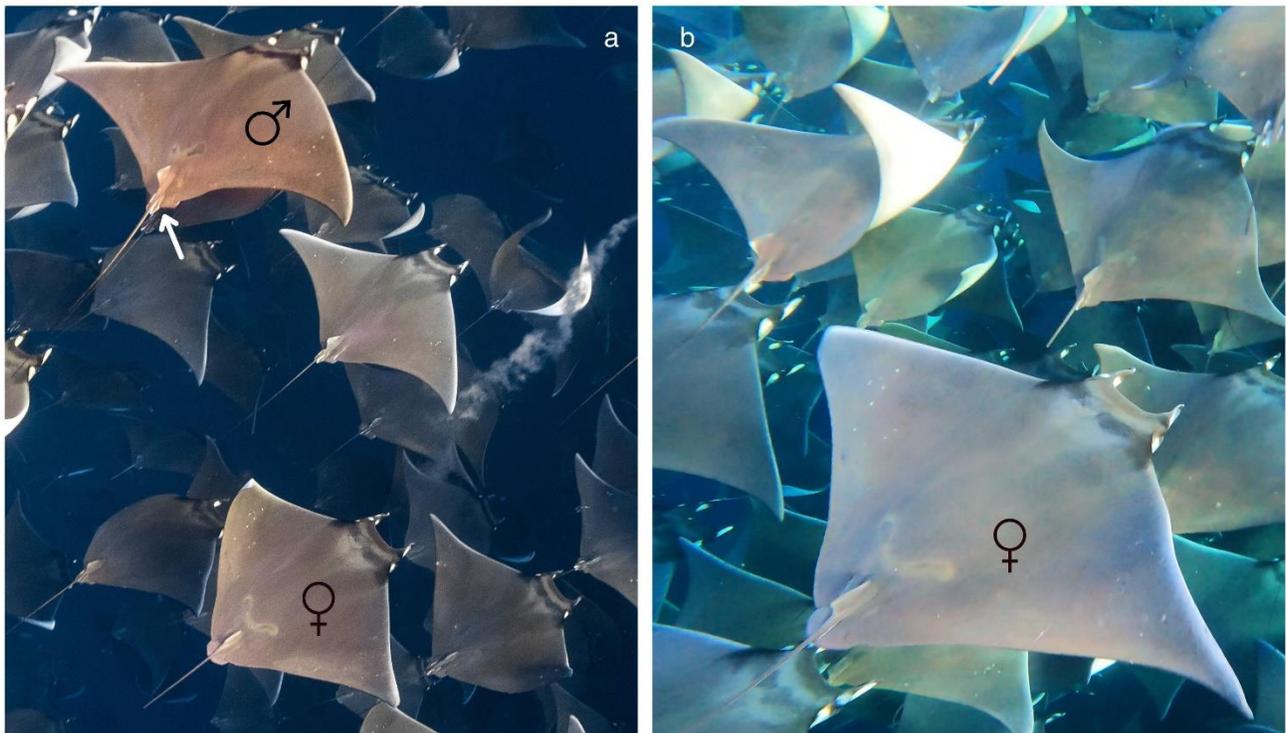


Figure 2 (Supplementary material). Courtship abrasions on mature female and males outside of the reported reproductive season (November 2022). **(b)** White arrows indicate elongated claspers on mature male. Photos **(a)** Wojciech Dopierala **(b)** © Sara Jaramillo.

Table 1 (Supplementary material). Reproductive behavior events in the southern Gulf of California 2017, 2021-2022. Courtship trains refer to initiation, endurance, evasion and piggyback leaping behavior. Events in yellow have graphic evidence provided in this work. LINK: [HERE](#)

Video 1. Courtship vortex of *M. munkiana* on 19 May 2021 at Ensenada de Muertos. LINK: [HERE](#)

Video 2. Copulation attempt of *M. munkiana* on 28 May 2022 at La Ventana (event 84). The female individual in the group can be identified by a darker coloration and by a small white dot on top of her head. Copulation attempt occurs at minute 1:10. LINK: [HERE](#)

Video 3. Piggyback leaping behavior of *M. munkiana* (fragment of event 84). LINK: [HERE](#)

Video 4. Example of copulation behavior (male erect his tail, bend his pelvic area, and makes 1 rapid pelvic thrusts). LINK: [HERE](#)

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GENERAL CONCLUSION.

With all mobulids species categorized as either Endangered or Vulnerable by the IUCN and presenting the lowest fecundity among all elasmobranchs, immediate attention and concerted efforts on a global scale are needed. The identified threats, ranging from fisheries and unregulated tourism to habitat loss, boat strikes, entanglements, and climate change, collectively pose an existential threat to the devil rays.

In conclusion, the findings presented in this thesis underscore the urgent need for comprehensive conservation measures to safeguard the world's devil ray populations and their critical habitats. The lack of comprehensive information on critical aspects of their biology, such as key life history traits, critical habitats, and migratory routes, further exacerbates the challenges in formulating effective conservation strategies.

This research highlights the importance of fostering collaborative efforts among scientists, policymakers, fishermen, and local communities to fill the existing information gaps and implement conservation measures that can ensure the survival and recovery of devil ray species in Mexican waters.

Additionally, the thesis advocates for the regulation of tourism activities, and the mitigation of irregular practices to secure a future for devil rays in the Gulf of California and Mexican Pacific and the local communities that can benefit from their protection and conservation. The insights derived from this research contributed significantly to the foundation of knowledge necessary for the formulation of evidence-based conservation strategies. This included the formulation of management plans for Marine Protected Areas in Baja California Sur.