Two's company: first record of two free-swimming megamouth sharks, Megachasma pelagios (Lamniformes: Megachasmidae), off the California coast

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Two's company: first record of two free-swimming megamouth sharks, *Megachasma pelagios* (Lamniformes: Megachasmidae), off the California coast

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Abstract On September 11, 2022, two megamouth sharks (*Megachasma pelagios*), estimated at 3.7–4.6 m TL, were observed swimming together near the surface about 39 km off the coast of San Diego, CA, USA. Megamouth sharks are rarely observed pelagic sharks, and the film from this encounter provided new insight into the social behavior of this species. We attempt to put the behavior of these two individuals into the context of past sightings, known megamouth shark biology, and with analogous behavior observed in other shark and pelagic fish species.

Keywords Megachasmidae · Lamniformes · Megamouth shark · Behavior

Despite being one of the largest extant fishes, the megamouth shark *Megachasma pelagios* Taylor et al. 1983 (Lamniformes: Megachasmidae) is an elusive pelagic and primarily oceanic shark with little known about its biology (Ebert et al. 2021). Since the first known encounter in 1976 (Taylor et al. 1983), there have been 273 total confirmed megamouth sightings (Florida Museum of Natural History; Yu et al. 2021; Diez et al. 2022). Megamouth sharks are usually found in epi- and meso-pelagic waters, and most often encountered individually as bycatch in commercial fishing nets (~89% of encounters; $n = 243$), are most often encountered in the Western Pacific Ocean (~83% of encounters; $n = 227$), and most of these encounters have occurred in recent years (~82% from 2010 onward; $n = 225$). Here, we report the first record of two individual megamouth sharks swimming together

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and comment on previously unseen megamouth shark behavior.

At 11:26 a.m. on September 11, 2022, recreational fishermen in a 6.4-m boat encountered two megamouth sharks (estimated 3.7–4.6-m total length, TL based on size comparison to the boat) at the surface around 39 km off the coast of San Diego, CA, USA (32.75220 N 117.71890 W; bottom depth ~ 1000 m). Prior to this encounter, only five free-swimming individuals (< 2% of previous encounters) have been scientifically recorded, and all were solitary individuals (free-swimming defined as an alive individual that was opportunistically observed swimming on its own and not captured by fishing equipment or stranded). The value of this encounter was understandably not immediate to the fishermen and therefore was kept brief before the fishermen moved on. However, rapid transmission of the sighting through social networks and communication with Birch Aquarium at the Scripps Institution of Oceanography allowed scientists to quickly get in contact and analyze the media. Using the compiled photos and video recordings (04:07 *mm:ss*), and subsequent interview of the fishermen, we describe previously unknown megamouth shark social behavior and we attempt to contextualize this with known megamouth shark biology and analogous behavior of other shark and pelagic fish species.

The sharks were first spotted from a distance when the dorsal and caudal fins of the larger shark (estimated 4.6 m TL) broke the surface about 45–60 m from the boat. Upon approach, the sharks were noted to be circling near each other (0–5 m) creating a disturbance in the surface water. The larger shark was at the surface making a tight circle nearly 360°, able to bend its body so much that it almost appeared to be turning on a stall (Supplemental V-1). As the boat neared the sharks, the smaller of the two (estimated 3.7 m TL) dove to about 5-m depth where it continued to circle under the larger shark. The larger shark remained at the surface and approached the boat, while the smaller shark, still at depth, tailed the larger shark towards the boat (Fig. 1a; Supplemental V-1 and V-4). The larger shark approached the idling motor and then made a near 180° turn away

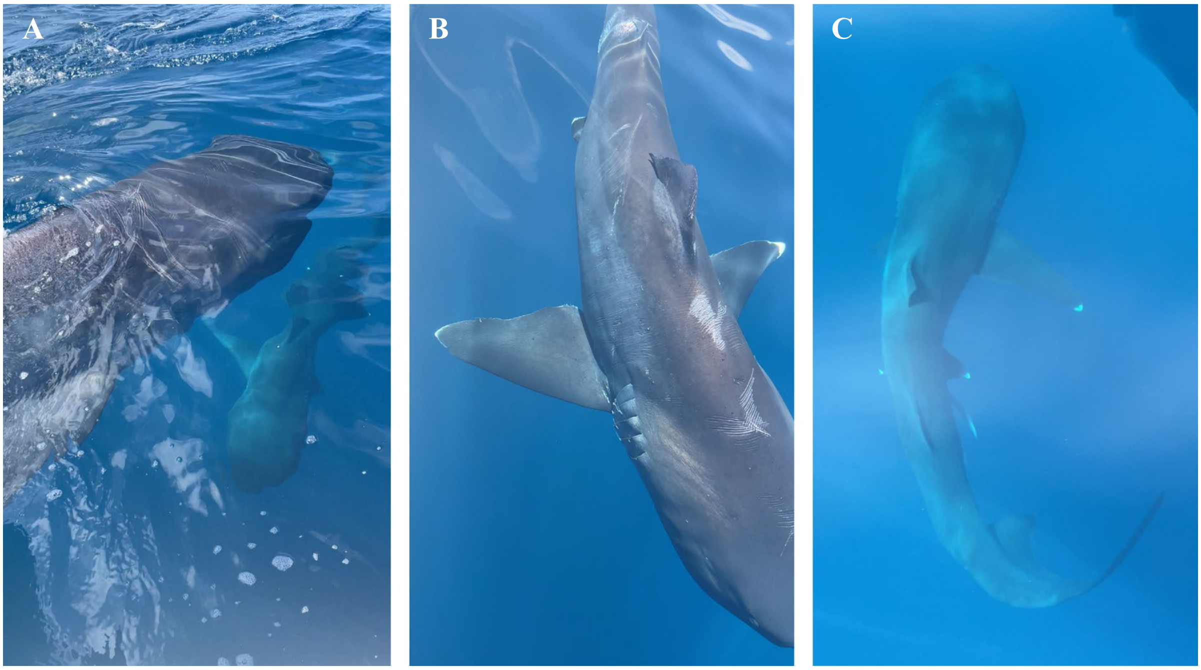

Fig. 1 Images captured from videos of two free-swimming megamouth sharks (*Megachasma pelagios*) off of San Diego, CA, USA around 11:30 a.m. on September 11, 2022. **a** Still of the larger megamouth (estimated 4.7 m) turning away from the boat with the smaller shark (estimated 3.7 m; identified male) following at depth. **b** Still of the larger shark with visible scars (i.e., potential mating scars) all along the dorsolateral surface. **c** A clasper visible on the smaller shark confirming it is male. All videos were captured by David Stabile and Andrew Chang on an iPhone 14 and Galaxy s9

from the boat (Supplemental V-1 and V-4). During this approach, it was clear the individual had scarring along its dorsal surface (Fig. 1b; scarring also noticeable in Supplemental V-1, V-2, V-4, V-5, V-8, V-9, V-11). The larger shark made two other identified passes towards the motor (Supplemental V-2, and V-5, V-9). The larger shark remained at or near the surface for the duration of the encounter (~10 min) while the smaller shark circled deeper (estimated 3–10 m down; Supplemental V-7) for the entire encounter except for one instance where it made a slow approach to the surface towards the side of the boat before descending again (Supplemental V-3, V-6, V-10). During this pass, the claspers were clearly visible and extended past the pelvic fin on the smaller individual as the shark's tail oscillated. The claspers, based on their sturdiness and thickness, may have been calcified indicating possible maturity in this individual (Fig. 1c; Supplemental V-3, V-6, V-7, V-10. Both sharks were curious of the boat for a few minutes but then appeared to lose interest and continued to swim in circles in no apparent pattern or course. Neither shark had their mouths wide open nor appeared to be exhibiting any feeding behavior during the encounter, and both appeared to have healthy body conditions. As the boat left, the smaller shark remained deep yet close to the larger shark, while the larger shark remained at the surface and continued to swim with no apparent heading.

There are many possible reasons for why two megamouth sharks were observed together. While this could be a chance encounter between the two individuals, there are other plausible explanations. One such explanation is that the sharks were there to forage. The feeding biology of megamouths is largely a mystery, although they are believed to be filter feeders and consume namely euphausiids (Yano et al. 1997; Nakaya et al. 2008; Tomita et al. 2011; Sawamoto and Matsumoto 2012), as well as copepods, and gelatinous organisms (Berra and Hutchins 1990). While the sharks did not exhibit any feeding-like behavior, this could have been altered due to the boat disturbance as seen in other filter-feeders (Quiros 2007; Montero-Quintana et al. 2020; Legaspi et al. 2020). Both sharks exhibited interest in the boat, and the larger shark approached the motor multiple times, yet it is unclear if the larger shark exhibited curiosity in the motor itself as observed in white sharks (*Carcharodon carcharias*; Dudley et al. 2000; Dicken 2008) or if it was just because it was at a close angle of approach. The fishermen did note there was an abnormal number of molas (*Mola sp.*; 20–25 estimated total) in the region that day which is intriguing as molas and megamouths are often caught together (Ebert unpublished data; Yu et al. 2021). Molas are the largest bycatch of the California swordfish drift net fishery (Cartamil and Lowe 2004), and this fishery has led to 81% of the megamouth encounters within California waters (13 of 16 total reported encounters including one unconfirmed encounter; Supplemental Table 1). In Taiwan, the drift net fishery that specifically targets two mola species and a species of sailfish is also the leading source for all known megamouth encounters worldwide (~54%; 148 total; Yu et al. 2021). The fishermen noted many gelatinous organisms that are known prey of both molas (Hooper et al. 1973; Pope et al. 2010; Nakamura and Sato 2014) and megamouth sharks (Berra and Hutchins 1990), but they did not observe any schools of baitfish nor feeding activity from other species. Although, there were some kelp rafts and some small yellowfin tuna (*Thunnus albacares*) spotted later that day within the general region. Further, the water was notably clear at the site of the encounter, and thus, the encounter could have occurred during a state of rest or movement between patches.

It is possible the conditions that drive mola abundance are linked to the drivers of megamouth shark abundance. Molas are known to move and aggregate along oceanographic fronts driven by upwelling (Thys et al. 2015; Hahlbeck et al. 2017), a behavior also exhibited by the filter-feeding whale shark (*Rhincodon typus;* Ryan et al. 2017) and basking shark (*Cetorhinus maximus*; Miller et al. 2015; McInturf et al. 2022), the former of which was also uncharacteristically sighted multiple times from September 1–16, 2022 off the coast of San Diego (videos made public by Captain Bryan McGrory from San Diego Whale Watch and Carl S. via @airpilikia on Instagram). However, data on the movement of megamouth sharks is limited to two individuals and only so much can be inferred from their tracks. Nelson et al. (1997) tracked a male (4.9 m TL) for a 50.5-h tag deployment in 1990, where the shark dove deep (120–166 m) during the day and stayed shallow at night (12–25 m) likely to follow the diel vertical migration of their prey much like basking sharks (Dewar et al. 2018) and whale sharks (Hsu et al. 2007). Similarly, vertical movement was also exhibited by a 3.5-m shark tracked by the Taiwan Ocean Conservation Administration (OCA) in June 2022, and information from the track was released to the public in a news article (not published data). According to the article, the shark was tracked for 210 h and exhibited diel migrations deeper than 400 m during the day and shallower than 200 m at night, although never quite reaching the surface during the shallow ascents (OCA data presented in Mengyu 2022). This is somewhat corroborated by Taiwanese bycatch data ($n=23$) where nets deployed at dusk mostly caught megamouth sharks in 0–200 m of water and nets at dawn mostly caught sharks at 200–1200-m depth (Yu et al. 2021). However, if megamouth sharks are at depth during the day, what would cause these two sharks to be at the surface during this encounter? It is possible that the diel vertical migration of megamouths change with region and season as seen in basking sharks (Sims et al. 2003, 2005; Dewar et al. 2018) and whale sharks (Wilson et al. 2006; Sequeira et al. 2012). It is also possible that acute changes in the vertical plankton distribution led to this break in pattern. Hurricane Kay began in the coastal waters off Baja California in early September and made its way northward ending in a post-Tropical Cyclone with its center 196 km southwest (31.3N 118.9W) of the megamouth sighting just 40 h prior to this encounter. With the predicted windfall 165 km from the center of the storm, it is possible storm-induced upwelling, as seen with other hurricanes (Babin et al. 2004), leads to ideal surface conditions for megamouths at the time of the encounter. Bycatch data from the California drift net fishery also shows that molas exhibit increased seasonal abundance in the fall with low interannual variability (Hahlbeck et al. 2017), and seasonal changes in abundance at foraging sites are also observed in the other filter-feeding shark species (Ryan et al. 2017; McInturf et al. 2022). In this regard, it is possible that megamouth abundance off Southern California is seasonal and linked to regional upwelling. Of the 21 megamouth sightings along the eastern North Pacific Ocean (Morro Bay, CA, USA to the State of Nayarit, Mexico), including the two individuals described here and one unconfirmed sighting, 19 occurred between the months of September to December (~90% of encounters; Supplemental Table 1). This is also not the first time a megamouth shark has been spotted at the surface during the day either. In 2019, a free-swimming megamouth (estimated 4.6 m) was spotted at the surface 39 km west of San Diego about 15–30 km south of the latest sighting at 12:50 p.m. (videoed observation by Ryan Brandeberg; Supplemental V-9). Megamouth shark seasonal abundance has also previously been reported from a known hotspot off of Taiwan (Yu et al. 2021). However, drivers of megamouth fine-scale and broad movement, abundance, and seasonality are not well understood and represent areas that need to be studied further.

The social behavior exhibited by the two sharks may also be associated with mating. Opportunistic mating at feeding aggregations has been witnessed in both basking sharks (Gore et al. 2019) and whale sharks (Macena and Hazin 2016; Clingham et al. 2016). The close following of the identified male (smaller shark) to the larger shark of (of unidentified sex) and the trailing of the male underneath the larger shark are similar to pre-copulatory behavior seen in other species (Tricas and Le Feuvre 1985; Gordon 1993; Pratt and Carrier 2011; Whitney and Crow 2007; McCauley et al. 2010). Although proximity following can also be related to hydrodynamics in filter-feeders (Gore et al. 2019), that is unlikely in this case due to the lack of active feeding during the encounter. During the observation, the male did not exhibit other possible pre-copulatory behaviors such as nosing the underside of the larger shark nor did it try to copulate with the other shark. Observations of actual copulation in sharks, particularly filter-feeders and large mobile sharks, is extremely rare. Close following in other species may also last for over an hour (Sims et al. 2000), and therefore, the encounter may have only been a brief glimpse into the potential courtship behavior of megamouth sharks.

Intriguingly, the larger shark had noticeable scars along the dorsal surface anterior to the dorsal fin, on the lateral surface between the gills and pectoral fin, as well as the dorsolateral surface between the caudal peduncle and the second dorsal fin (Fig. 1b). The tip of the first dorsal fin and edge of the pectoral fin also appeared to have slight scrape marks. The dorsal surface exhibited clear tooth-like scratch marks with parallel lines and in a cross-hatch pattern. The shark also had curved scar marks indicative of biting—one on the dorsal surface and one on the lateral surface that were in the shape of a jaw with tooth-like scratch marks. The tail scars were harder to make out but also appeared to have curved jaw-like patterns and deeper injury than other sites. Many of the scars appear fresh with loose dermis still dangling and apparent redness (Supplemental V-1, V-2, V-4, V-5, V-8, V-9, V-11). The pattern, shape, and placement of the scars were similar to suspected mating scars found on a mature female megamouth shark (see Fig. 6 from Yano et al.

1997 for reference). These scars also resembled and were in similar positions to mating scars described in other shark species (Ritter and Amin 2019; Calich and Campana 2015). While we cannot confirm whether the larger individual was female, the lack of obvious claspers when presented with a similar view to the smaller shark (which had obvious claspers) and the presence of what appeared to be mating scars suggest it was female. Of note, dorsal scarring was also evident on the individual spotted in the same region in 2019 (Supplemental V-12). There also appeared to be a fresh injury on the left lateral side of the male shark around the pelvic fin (Supplemental V-6, V-10) which could be abrasion from an attempted copulation or may not be related.

Male megamouths are thought to mature at around 4.0–4.3 m and females around 4.8–5.2 m (Nakaya 2010; Watanabe and Papastamatiou 2019). Although both sharks were estimated to be smaller than their respective presumed maturity lengths, there is such limited data on maturation that it is possible that megamouths mature at a smaller size than previously thought or size at maturity could vary regionally. It is also possible that the size estimates may be off as diffraction can often distort the size of objects underneath the water (Ross and Nawaz 2003). We could not use video analysis to corroborate the size of the sharks due to lack of scale. Regardless, the general size of the sharks and the presence of large, likely calcified, claspers on the smaller shark indicate that it was either a mature or adolescent male. Even if the larger shark was not a mature female, male sharks are sometimes documented mating with immature or adolescent/subadult females (Stevens 1976; Pratt 1979; Calich and Campana 2015) and sometimes other males (Brunnschweiler and Pratt 2008) and could still have been pre-copulatory behavior exhibited by the identified male.

Since there was no witnessed contact between the two sharks, the scars on the larger shark could have occurred by other means. There have been well-documented cases of boat strikes on megafauna including whale sharks (Speed et al. 2008; Penketh et al. 2021), basking sharks (Speedie et al. 2009), and white sharks (Towner et al. 2012). While a propeller strike is possible, the superficial nature of the scarring and the pattern of the scars indicate that this is likely not the cause, especially given the softness of megamouth shark skin (Compagno 1990). It is also possible that the scarring was a form of social hierarchical behavior as seen in other species of sharks (Ebert 1986; Pratt and Carrier 2011; Brunnschweiler and Pratt 2008). However, it would be rather peculiar for a smaller shark (estimated 1 m difference) to try and exhibit dominance over a larger shark so it is also possible that the scars were inflicted by another shark. Megamouth shark sociality has never been seen prior to this encounter, and whether they exhibit social hierarchy like other sharks remains to be seen. Further, the scars could have come from another species. There is a documented instance of sperm whales (*Physeter macrocephalus*) either playing with or preying on a megamouth shark near the surface at midday in Indonesia (White et al. 2004). However, there were no whales sighted in the vicinity of the sharks or boat and the scars did not seem consistent with large, conical sperm whale teeth.

Based on the information provided, past sightings, known megamouth biology, and insights from other species, it is our assumption that the coastal waters off San Diego may present as a foraging and potential aggregation site that could allow for opportunistic mating to occur. We believe that the most cogent explanation for the social interaction may have been pre-copulatory behavior, although this remains inconclusive. Regardless, this rare and incredible encounter is an important addition to our understanding of megamouth behavior, and it appears that San Diego is a site for further megamouth exploration.

In addition, several megamouth shark sightings have come from the public, and with increased ocean traffic (Tournadre 2014; Sardain et al. 2019) and shark-human interactions (McPhee 2014; Lagabrielle et al. 2018), increased marine stewardship (Dammannagoda 2018; Leithäuser and Holzhacker 2020), and the near instantaneous interconnectedness of social media, it is likely that reports of megamouth sharks will become more common. Citizen science and social media have become a more frequent tool for biological reports, and conservation efforts in various fields including shark biology (Camacho 2016; Taklis et al. 2020; Boldrocchi and Storai 2021) and in cases like the megamouth shark where any type of encounter is rare, it is of great benefit to have more open communication with the public.

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Data availability The datasets generated during and/or analyzed during the current study are available in the figshare repository: https://figshare.com/s/b2f03ccac354963b18ea.

Declarations

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study.

Conflict of interest The authors declare no competing interests.

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