Whale shark (*Rhincodon typus*) predatory flexible feeding behaviors on schooling fish

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Abstract

Whale sharks are known to feed primarily on zooplankton all over the world; however, recent findings suggest that they also prey on fish using behaviors that have not been fully described. Here, we provide detailed evidence of whale sharks interacting with schools of anchovy on four occasions in Bahía de Los Angeles, Baja California, Mexico. Three of these were predatory interactions in multi-species feeding frenzies, and one was a non-predatory interaction. In predatory interactions, whale sharks exhibited two types of feeding behaviors: (1) stationary suction-feeding, a previously described behavior for whale sharks, and (2) lunge-feeding, which has not been previously described in whale sharks, but has been observed among other large filter feeders, such as rorqual whales. The whale sharks moved simultaneously around the school of anchovy, lunging simultaneously or one after another into the school, with 66% ($N=17$) of these lunges occurring in the same direction. In the non-predatory interaction, whale sharks exhibited “sit-and-wait” behavior. The evidence presented here, along with previous observations, suggests that whale sharks may change their feeding strategy from suction to lunge-feeding when other predators corner schooling fish.

Keywords *Rhincodon typus* · Feeding strategies · Predation · Multi-species feeding frenzy · Lunge-feeding · Sit-and-wait · Anchovies · Bahía de Los Angeles

Introduction

The whale shark (*Rhincodon typus*, Smith 1828) is the largest fish on earth (McClain et al. 2015). It inhabits tropical and warm temperate seas (Compagno 2002) and forms seasonal feeding aggregations in different sites around the world (Rowat et al. 2011). The predictability of these aggregations has allowed the development of a tourism industry (Colman 1997) and, thus, frequent observation of the whale shark's behavior. In most aggregations, studies have demonstrated that whale sharks preferentially feed on high concentrations

of zooplanktonic prey, such as copepods (Boldrocchi et al. 2020; Ketchum et al. 2013), sergestid shrimps (Rohner et al. 2015), mysids (Rohner et al. 2013), crab larvae (Meekan et al. 2009; Sampaio et al. 2018), and fish spawn (De la Parra-Venegas et al. 2011; Robinson et al. 2013). Some of these investigations have described whale sharks aggregating in abundant numbers, in some cases reaching hundreds of individuals (De la Parra-Venegas et al. 2011).

To date, the most common behaviors described among whale sharks have been forward locomotion without feeding, known as “cruising,” and three zooplankton “filter-feeding” techniques (Nelson and Eckert 2007). The first one is a continuous ram filter-feeding (or passive feeding), in which water enters the animal's mouth by its slow forward movement, keeping the mouth open without interruption (Heyman et al. 2001; Nelson and Eckert 2007; Rowat and Brooks 2012; Sims et al. 2000). The second is surface ram filter-feeding (or active feeding), in which the whale shark moves forward or in a circular path, but keeps its upper jaw above the water surface and sometimes moves against the waves, which drives zooplankton into its mouth (Graham

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2003; Heyman et al. 2001; Motta et al. 2010; Nelson and Eckert 2007; Rowat and Brooks 2012). The third behavior is called stationary suction-feeding (or vertical feeding), in which the animal stays still and feeds by gulping water (Heyman et al. 2001; Motta et al. 2010; Nelson and Eckert 2007; Rowat and Brooks 2012).

Some reports have indicated that the whale shark can feed on fast-swimming prey, such as fish and invertebrates (see Table 1 for further descriptions), using stationary suction-feeding strategy in most occasions (Bigelow and Schroeder 1948; Duffy 2002; Fox et al. 2013; Gudger 1941; Harterink and Stijn 2010; Springer 1957).

In this context, Andrewartha (1993) reported that whale sharks were attacking schools of fish, apparently feeding on them, in Ningaloo, Australia. Moreover, Boldrocchi and Bettinetti (2019) recently reported the same feeding behavior in Djibouti. To our knowledge, these are the only reports of whale sharks exhibiting lunging behaviors, presumably to feed on schools of fish. The ecological factors influencing the shift in prey and feeding technique are still poorly

known. In this study, we described and presented evidence of whale sharks interacting with anchovies in Bahía de Los Angeles, Mexico. Specifically, we described the whale shark's lunge-feeding and two behaviors not previously reported in this species before: "sit-and-wait" behavior and coordinated swimming.

Materials and methods

Observations

We recorded whale sharks interacting with schools of anchovies (*Anchoa sp.*) on four occasions during the 2014 and the 2015 whale shark seasons at Bahia de Los Angeles, Baja California, Mexico. These interactions were observed by the whale shark community-monitoring group, Pejesapo. This group annually monitors whale shark individuals arriving to Bahia de Los Angeles and maintains a long-term record for research and management. Observations

Table 1 Previous reports of whale sharks' feeding behavior on non-planktonic prey

Prey type	Type of observation	Feeding behavior	Location	Reference study
Cuttlefish	Stomach content and anecdotal observations	N/A	Batavia Bay, Java	Gudger (1941)
Squid	Fed directly by humans	Does not specify	Okinawa Expo Aquarium in Japan	Clark and Nelson (1997)
Krill	Fed directly by humans	Does not specify	Okinawa Expo Aquarium in Japan	Clark and Nelson (1997)
Unidentified fish remains Sardines and anchovies	Stomach content	N/A	Tuticorin, India	Sillas and Rajagopalan (1963)
	Stomach content	N/A	Bombay, India	Karbhari and Josekutty (1986)
	Anecdotal observations	Does not specify	Seychelles	Gudger (1941)
	Anecdotal observations	Stationary suction-feeding	Cuba	Bigelow and Schroeder (1948), Gudger (1941)
	Anecdotal observations	Surface ram filter-feeding	The Bahamas	Gudger (1941)
	Anecdotal observations	Stationary suction-feeding	Gulf of California	Gudger (1941)
	Direct observation	Stationary suction-feeding	Coast of Mississippi (Gulf of Mexico)	Springer (1957)
	Stomach content	N/A	Kaup, India	Rao (1986)
	Direct observation	Lunge-feeding	Ningaloo, Australia	Andrewartha (1993)
	Direct observation	Stationary suction-feeding	Bay of Plenty, New Zealand	Duffy (2002)
Other fish	Direct observation	Stationary suction-feeding	Cenderawasih Bay, Indonesia	Harterink and Stijn (2010)
	Direct observation	Surface ram filter-feeding	Angola	Weir (2010)
	Direct observation	Stationary suction-feeding and surface ram filter-feeding	Utila, Honduras	Fox et al. (2013)
	Direct observation	Lunge-feeding	Djibouti	Boldrocchi and Bettinetti (2019)
	Stomach content	N/A	Batavia Bay, Java	Gudger (1941)
	Direct feed	Does not specify	Okinawa Expo Aquarium in Japan	Clark and Nelson (1997)

N/A not applicable

were made during trips to monitor the whale shark population from a 7 m-long skiff and underwater. An experienced free-diver swam alongside and underneath whale sharks to capture underwater footage of the spot patterns and the animals' sex (by presence or absence of claspers) for individual identification during the first three events (see Brooks et al. 2010). The distance between the swimmer and the focal animals varied from less than 1 m to more than 10 m. For the above-water observations, we used a Canon 70D digital SLR camera during interactions one and two and a Canon EOS T3i for interactions three and four. For underwater observations, we used a Go Pro Hero 3 camera. Above water, we began filming when a whale shark began lunge-feeding, and we stopped the video several seconds after the lunge. We also filmed when other predators were active on the surface and stopped the video when the activity was apparently over.

Interactions with anchovies and multi-species feeding frenzies

The term “feeding frenzy” was used to refer to the increase in a predator's feeding frequency along with a decrease of its responses to intruders (Clua and Grosvalet 2001; Hobson 1963; Motta and Wilga 2001; Staddon 2010). We used the term “multi-species feeding frenzy” to refer to events that include predators of two or more species, and “whale shark feeding frenzy” for events at which only whale sharks were present.

Event 1 was recorded on November 29 of 2014, when a dense school of anchovies was found at 1030 h at the surface at the following coordinates: 28°56'58.02" N, 113°32'17.30" W. The sea surface temperature was 22 °C. During the event, the presence of people in three kayaks as well as on a skiff were also recorded. Observations lasted from 1030 to 1351 h (3 h 21 min), when the feeding frenzy ended. Event 2 was recorded on December 9, 2014, when a school of anchovies was detected at 28°57'3.852" N, 113°32'31.02" W. Conditions were similar to event 1, with a sea surface temperature of 21 °C. Sea lions were the only other predator apparently present. Observations lasted from 0936 to 1039 h (1 h 3 min). Event 3 was recorded on October 20 of 2015, when a multi-species feeding frenzy was found at the following coordinates: 28°57'41.66" N, 113°31'44.09" W. The sea surface temperature was 26.5 °C. Observations lasted from 1709 to 1822 h (1 h 13 min), and two other skiffs were observing the feeding frenzy. Event 4 was recorded on October 22 of 2015, however no coordinates are available for this occasion. Other predatory fishes (species not identified) were also present. The observations lasted from 0907 to 0913 (0 h 6 min).

Analysis of feeding behavior

For the analysis, the term “lunge” was defined as when the whale shark accelerated in the direction of the anchovies with its mouth open and with intense movements of the caudal fin. Lunging sessions were grouped into three categories: (a) individual lunging sessions, when only one whale shark carried out lunging behaviors toward the anchovy school; (b) simultaneous lunging sessions, when more than one whale shark charged against the anchovies at the same time; and (c) sequential lunging sessions, during which more than one whale shark charged at the anchovies consecutively.

We also analyzed whether lunges were in the same direction. Furthermore, we recorded whether sharks responded to the vessels present in the area by changing direction, diving, accelerating, inspecting, banking, or vigilance (for definitions see Cubero-Pardo et al. 2011; Montero-Quintana et al. 2020, 2021; Pierce et al. 2010; Quiros 2007). Individuals were identified by extracting frames from the videos where the post-gill area of whale sharks is clearly visible and comparing the dot spot pattern using the Interactive Individual Identification System software, I3S (Brooks et al. 2010; Meekan et al. 2006; Speed et al. 2007). Whale shark size was estimated by comparing total body length to the lengths of the vessel and swimmer (Ketchum et al. 2013; Nelson and Eckert 2007).

Results

A total of 182 video clips were analyzed to describe the whale shark behavior during feeding events. From the videos of event 1 ($N=58$ from the boat, $N=62$ underwater), we obtained 117 observations of whale sharks and other marine predators feeding on the school of anchovies (Table 2). The marine predators recorded in this feeding frenzy besides whale sharks were barracudas (*Sphyrna argentea*, Girard 1854), common dolphins (*Delphinus capensis*, Gray 1828), California sea lions (*Zalophus californianus*, Lesson 1828), and seabirds (*Larus heermanni*, Cassin 1852; *L. livens*,

Table 2 The number of observations of predators interacting with the school of anchovies during the first event, on November 29, 2014

Observations			
	Interactions with the school	No interactions with the school	Total
Seabirds	7	110	117
Dolphins	43	74	117
Sea Lions	83	34	117
Whale sharks	108	9	117

The total number of observations was 117

Dwight 1919; and *Pelecanus occidentalis*, Linnaeus 1766). From this event, we identified nine whale sharks actively feeding on a school of anchovies. Four of these were identified as males and one as female; the sexes of the remaining four sharks could not be identified. Sharks were estimated to range from 4.5 to 7.3 m. The response to vessels we recorded was a change of direction. Although the kayaks and boats did not pursue the sharks, six slight collisions with the tourist kayaks and our boat were recorded when sharks moved to encircle the anchovy school. These collisions did not injure the whale sharks and did not stop the feeding frenzy.

The swimmer's presence in the water caused changes of direction when the animal moved outside the anchovy school, although the animals continued feeding. The swimmer never interfered between the focal animals and the anchovy school. When feeding on the school of fish, whale sharks moved faster and more frenetically, contrary to their common behaviors of cruising or filter-feeding (see supplementary videos). They moved continuously around the anchovy school and lunged using two different techniques: (a) horizontal lunge, a movement from outside the anchovy

school toward the surface of the school with their mouth open (Fig. 1A and supplementary video 1; and (b) vertical lunge, a movement from below the school toward the surface, closing their mouth once they broke the water surface (Fig. 1B and supplementary video 2). The second technique is similar to the lunge-feeding of whales, in that whale sharks also accelerate, which is different from stationary suction-feeding when the animals are not moving. During event 1, suction-feeding behavior was not recorded.

During the event 1, from 117 observations, we recorded 108 whale shark lunges into the school of anchovies during the feeding frenzy, and in 9, we recorded other predators feeding (Table 2). The total lunges were divided into 67 lunge sessions: 41 (61%) were individual sessions, 7 (11%) were simultaneous sessions with up to three sharks (Fig. 2A and supplementary video 3), and 19 (28%) were sequential sessions with up to five sharks (Fig. 2B and supplementary video 4). Of the 108 lunges, 27 (25%) were vertical lunges, and 81 (75%) were horizontal lunges. Of the 81 horizontal lunges, 20 (25%) were high-intensity horizontal lunges, which caused anchovies to be slapped

Fig. 1 **A** Horizontal lunge. This frame, extracted from supplementary video 1, shows a whale shark lunging toward a school of anchovies. “A1” shows the original image, and “A2” shows the image cropped and magnified by 2×. “D” indicates a common dolphin (*Delphinus delphis*). **B** Vertical lunge. This frame, extracted from supplementary video 2, shows a whale shark lunging the school of anchovies from below. “B1” and “B2” show the sequence of the lunge. “B1” shows

anchovies jumping in the middle of the school (white spot). “B2” shows the whale shark’s mouth breaking the water surface. “B3” shows the image “B2” cropped and magnified by 3× to show the anchovies entering the whale shark’s mouth before suddenly closing it. A dead brown pelican (*Pelecanus occidentalis*) was found floating on the school of anchovies (P); the cause of its death is unknown

Fig. 2 Image “A” shows two whale sharks (S) lunging simultaneously into the school of anchovies, extracted from supplementary video 3 (“K” indicates a tourist kayak). Image “B” shows two whale sharks

lunging in sequence, extracted from supplementary video 4 (cropped and increased by 2.5×). The first shark (S1) did a horizontal lunge, and the second shark (S2) did a vertical lunge

by the shark’s caudal fin during the lunge (Fig. 3, and supplementary videos 4 and 5). The remaining lunges (61, 75%) were of lower intensity, and the anchovies were not observed to be slapped by the sharks’ caudal fin.

Of the 26 sequential and simultaneous lunging sessions, the sharks lunged in the same direction each one, in 17 (66%) of them (Figs. 2, 3), in different directions in 5 (19%), and in opposite directions in 4 (15%). In addition, we recorded whale sharks apparently swimming in coordination around the anchovy school in two cases (supplementary video 6).

We also investigated whether lunges occurred in the presence of other marine predators, such as sea lions, dolphins, and seabirds. Of the total lunges, 81 (75%) occurred in the presence of sea lions, but 27 (25%) occurred when these predators were absent. A total of 39 (36%) occurred in the presence of dolphins, but these were absent in 69 (63%)

lunges. Finally, 4 (4%) occurred in the presence of seabirds, but these were absent in 104 (96%) lunges (Fig. 4).

Underwater videos of this interaction revealed that dolphins, sea lions, and barracudas were feeding on the anchovy school. These videos also revealed that whale sharks swam around the anchovy school with their mouths closed (supplementary video 7) and only occasionally opened their mouths, likely to let water pass through their gills (supplementary video 8) until they lunged into the anchovy school. Furthermore, anchovies did enter and were trapped inside the whale sharks’ mouths during the lunges (Fig. 5). One collision occurred between two lunging whale sharks, but it did not lead to apparent injuries.

From the video of event 2 ($N=1$ from the boat), we recorded four male whale sharks positioning themselves toward a school of anchovies with their mouths closed (Fig. 6 and supplementary video 9). The whale sharks slowly

Fig. 3 Two whale sharks lunging into the school of anchovies in the same direction. “S” indicates anchovies being hit by a strong move of the whale shark tail. “A” “B” “C”, and “D” show the sequence of the lunge. “A2” shows image “A” magnified by 3× (supplementary videos 4 and 5)

followed the school as it moved away but stopped swimming when the school stopped moving away. The longest recorded period of a stationary whale shark was 1 min 21 s. However, the scene was cut off, so the stationary behavior may have lasted longer. When the whale sharks approached the school, the anchovies apparently reacted at a greater distance compared to event 1, when the anchovies were compact on the surface. No predator attacked the anchovy school, and

the anchovies did not adopt a tight school formation. Additionally, the whale sharks did not circle the anchovy school as they did in event 1. A sea lion was observed near the anchovy school and the whale sharks, but no other predators were observed on this day. The presence of the swimmer in the water caused changes of direction by the whale sharks, but no other evasive response (such as diving, accelerating, or banking) was observed.

Fig. 4 Presence and absence of whale shark lunges related to the interaction of other predators with the anchovy school during the first event, November 29 of 2014 (percentage inside the bars is rounded)

From the videos of event 3 ($N=55$ from the boat, $N=1$ underwater), we did not identify individuals, but we observed five whale sharks, feeding by stationary suction, horizontal lunge, and vertical lunge on a school of anchovies. Skipjack tuna (*Katsuwonus pelamis*, Linnaeus 1758) and cormorants (*Phalacrocorax* sp., Brisson 1760) were herding the school. Seabirds (*L. heermanni*, *L. livens* and *Sula neboxii*, Milne-Edwards 1882) were also feeding on the anchovies (supplementary videos 10 and 11). In this feeding frenzy, we recorded a total of 8 (15%) stationary suction-feeding events, 21 (38%) vertical lunges, and 26 (47%) horizontal lunges. We also recorded a slight collision between a whale shark and our boat. The whale shark swam past, while our boat was stationary. Also, whale sharks collided with each other on two occasions. On one occasion, we

Fig. 5 Frame extracted from an underwater video showing a whale shark immediately after a lunge. “A” shows a whale shark with anchovies trapped in its mouth. “A2” shows the image “A” magnified by 3×. “V” indicates anchovies

Fig. 6 Frame extracted from an underwater video showing a two whale sharks (S)

recorded a whale shark feeding on anchovies that escaped from the tunas. The whale shark was in a vertical position with its mouth closed, and the anchovies avoided getting close to the whale shark's mouth. When the tunas attacked, the anchovies swam in the opposite direction but headed for the whale shark's mouth. Then, the whale shark opened its mouth and suctioned them (supplementary video 10).

From the video of event 4 ($N=1$ from the boat), we observed three whale sharks feeding by stationary suction on a small school of anchovies that was being attacked by predatory fishes (unknown species) and cormorants (supplementary video 12). From this video, there was no identification of the individuals during this feeding event.

Discussion

Lunge-feeding

Underwater videos of event 1 showed that whale sharks swam with their mouths closed around the school of anchovies, confirming that they were not filter-feeding zooplankton. This behavior was different from the feeding behaviors commonly exhibited in aggregations (Heyman et al. 2001; Nelson and Eckert 2007; Motta et al. 2010; Rowat and Brooks 2012). They were more active, encircling the anchovy school and accelerating toward the school with

their mouths open while performing strong tail movements. Although the speed and acceleration of the lunges could not be quantified, the supporting video materials clearly show a qualitative difference in the behavior pattern between whale sharks targeting zooplankton and baitfish. Following the definition for feeding behaviors by Motta and Wilga (2001) as well as Werth (2000), the behavior would be referred to as accelerated ram filter-feeding. However, a nearly identical behavior carried out by rorqual whales (attacking a school of prey by accelerating and engulfing a large amount of water and prey) is already known as lunge-feeding (Goldbogen et al. 2006; Werth 2000). Accelerating and charging open-mouthed at their prey are a frequent behavior among sharks. For instance, white sharks (*Carcharodon carcharias*, Linnaeus 1758) perform vertical and horizontal predatory lunges against surface prey (Bromilow and Webb 2014; Martin et al. 2005; Tricas and McCosker 1984), and blue sharks (*Prionace glauca*, Linnaeus 1758) also accelerate to catch as many preys as possible (Tricas 1976). However, this behavior is quite rare for the whale shark and has been reported only in multi-species feeding frenzies.

Sit-and-wait and facilitation

In the second event, the only marine predators observed were whale sharks and a sea lion. The anchovies did not

form a tightly packed bait ball formation at the surface as in the first event when we observed whale sharks lunging. Instead, we observed whale sharks remaining stationary near the anchovy school. This behavior was different from the stationary feeding previously observed in this area, because whale sharks were not feeding in this case. Therefore, this is likely a behavior known as "sit-and-wait". In this feeding strategy, the animal waits for the prey to cross the boundary of its strike by remaining immobile during long periods of time (O'Brien et al. 1990). Animals that cannot remain stationary, like the white shark, continue moving but in a restricted area (Towner et al. 2016). This type of sit-and-wait was recorded before for whale sharks in the Belize Barrier Reef by remaining up to 10 h in an area less than 500 m in diameter, waiting for cubera (*Lutjanus cyanopterus*, Cuvier 1828) and dog snapper (*L. jocu*, Bloch and Schneider 1801) to spawn (Graham 2003). However, to our knowledge, no previous reports have shown whale sharks remaining stationary near their prey without feeding. If the association with other predators allows whale sharks to access this type of prey, whale sharks could be waiting for other predators to encircle and compact the anchovies (Fontes et al. 2020). Facilitation is commonly observed with other marine predators in these feeding events, and several studies have indicated that multi-species feeding frenzies often occur when predators' initial attacks round up prey into a tight group. For example, cetaceans (*Lagenorhynchus albirostris*, Gray 1846 and *Phocoena* sp., Linnaeus 1758) and pursuit-diving seabirds (*Uria aalge*, Pontoppidan 1763 and *Alca torda*, Linnaeus 1758) encircle schools of fish and drive them to the surface, cutting off escape routes for the fish and making them accessible to non-diving seabirds (*Morus bassanus*, Linnaeus 1758 and *Rissa tridactyla*, Stephens 1826; Camphuysen and Webb 1999). Tunas (*Thunnus thynnus*, Linnaeus 1758 and *T. albacares*, Bonnaterre 1788) do benefit feeding in association with common dolphins (*Delphinus delphis*, 1758), as this mammals, encircling and concentrate preys making easy to capture (Clua and Grosvalet 2001). Minke whales (*Balaenoptera acutorostrata*, Lacépède 1804) exploit prey patches herded by pursuit-diving seabirds, such as *U. aalge*, *A. torda*, and *Fratercula arctica*, Linnaeus 1758 (Anderwald et al. 2011). Camphuysen and Webb (1999) termed "beaters" the predators that round up their prey and make them available to other predators that cannot initially access the resource. It seems likely that whale sharks' lunge-feeding on anchovies is due to this type of facilitation. Whale sharks are not as fast as dolphins, tunas, pursuit-diving seabirds, barracudas, or sea lions. Therefore, the ability of these predators to encircle the anchovies and force them into a compact formation could facilitate the whale shark to access the anchovies.

Association of whale sharks and other marine predators

Cape gannets (*Morus capensis*, Lichtenstein 1823) have been reported to change their feeding technique on a school of fish (*Sardinops sagax*, Jenyns 1842) when the frequency of attack by other predators increases (Thiebault et al. 2016). When the frequency of predator attacks against a school of fish increases (occurring every 2.7 s) and the time between attacks decreases, the school does not have time to return to its synchronized state (Thiebault et al. 2016). This disorganization in the school's coordination may increase the feeding success of each predator involved (Thiebault et al. 2016). Our underwater videos showed that barracudas were constantly attacking anchovies from below the school, pushing them toward the surface; this is likely to benefit whale sharks and other predators by cutting off anchovies' escape routes and keeping them surrounded. This behavior has been observed in the Azores (Portugal) before (Barreiros et al. 2002). Fishermen there and in Kuwait have reported seeing barracudas swimming near whale sharks (Bishop and Abdul-Ghaffar 1993). It was not possible to record barracuda attacks in this study to know if they were related to whale shark lunges. However, the other events in which whale sharks were seen lunging occurred in the presence of other predatory fish: golden trevally (*Gnathanodon speciosus*, Forsskål 1775) and rainbow runners (*Elagatis bipinnulata*, Quoy and Gaimard 1825) in Ningaloo (Andrewartha 1993), trevallies (possible *Caranx ignobilis*, Forsskål 1775) in Djibouti (Boldrocchi, personal communication; see Boldrocchi and Bettinetti 2019), and skipjack tuna in event 3 of this study. These records may support the hypothesis that the whale shark takes advantage of the disturbance caused by predatory fishes.

Do whale sharks take turns to feed?

Feeding events on schooling fish might represent important nutritional opportunities for whale sharks, because lunge-feeding is likely to consume more energy compared to zooplankton feeding techniques. Therefore, the frequency of simultaneous and sequential attacks should be high due to the competition among predators to access the temporarily available resource. Yet, of all lunging sessions, just 11% were simultaneous lunges and 28% sequential lunges. The low frequency of simultaneous lunging sessions suggests that whale sharks may be avoiding lunging at the same time or taking turns to feed. Considering their massive bodies, if they lunge at the same time, they may collide with each other. It is known that other species of elasmobranchs, such as the white shark, establish temporary social ranks to feed (Compagno 2002; Martin et al. 2005). Furthermore, 66% of simultaneous and sequential sessions occurred in the

same direction, and we observed whale sharks moving in an apparently coordinated manner around the anchovy school. This tendency could be to avoid collisions, or it could mean that lunging in the same direction increases feeding success. When whale sharks performed horizontal lunges in the first event, they struck anchovies with their caudal fins. Their strong movements appeared to be a consequence of the whale shark's acceleration across the water surface. However, this can cause the anchovies to be stunned, affecting the number of anchovies caught by whale sharks and other predators. This may be similar to the way the thresher shark (*Alopias vulpinus*, Bonnaterre 1788) uses its tail to stun its prey (Bernal and Sepulveda 2010; Oliver et al. 2013), but with an overall benefit to all involved predators. Thiebault et al. (2016) found that cape gannets' feeding success increased when other predators (various species) attacked in the previous seconds. If the frenetic entry of a whale shark into the school could disturb or stun the anchovies, this may explain the tendency to carry out consecutive attacks in the same direction, but more observations will be needed to test this hypothesis.

Conclusions

We detail or documented several separate events of lunge-feeding in whale sharks, which has only been reported a handful of times in the scientific literature, including behaviors such as simultaneous lunges, sequential lunges, coordinated swimming, and sit-and-wait, which have never before been reported in whale sharks. Although interactions between whale sharks and anchovies had not been reported before in Bahia de Los Angeles, we observed these events in 2 consecutive years, suggesting that whale sharks may commonly prey on baitfish in this area. These observations, along with previous reports, show that whale sharks change their feeding strategy to lunge-feeding when predatory fish round up baitfish. This would explain why in other reports of whale sharks preying on fish, lunge-feeding was not reported. Although further studies should be conducted on the whale shark's feeding behavior on schooling fish, these preliminary observations, suggest that whale sharks exhibit flexible feeding behavior strategies to possibly maximize their energy gains. In this context, fish consumption could be more important than previously thought for this species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10164-021-00717-y>.

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Author contributions Conceived the work: MOB, ANMQ, and CFOV. Recorded the videos: ANMQ, CFOV, JAVH, and OSN. Recorded the data: ANMQ and CFOV. Analysis of videos: ANMQ and CFOV. Wrote the text: MOB and ANMQ. Revised the text: all the authors.

Declarations

Conflict of interest Authors declared no conflict of interests.

Ethical approval This research was carried out in accordance with Mexican laws and guidelines for the ethical treatment of animals in general (Animal Behavior Society 2012).

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