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Could convulsive body shuddering of a white shark near a shark cage be an element of a threat display?

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Abstract

In this short note, we describe the convulsive body shuddering of a white shark as it approached two large metallic shark cages, each with multiple divers standing within them. When animals feel threatened, they experience conflicting instincts — one is to escape and another is to fight. In this situation, they do not always fight but often perform an agonistic, or aggressive display. Having arrived at the source of an olfactory corridor, this white shark was confronted with highly visible cages made with aluminium bars. The divers use hookah air hoses to breathe, and were therefore releasing bubbles, which reflect light and generate sounds as they oscillate toward the surface. The photographers may also have been taking pictures of the shark with their flash-bulb equipped cameras, which produce a sudden disruptive flash of irradiance. The shark's behaviour is illustrated with a series of video frames as he approaches the cage. The body of the shark shutters convulsively and he opens his mouth, keeping it open for a prolonged period of 2.8 s as he passes close to the cage, while (1) depressing his pectoral fins, (2) hunching his back, (3) keeping his caudal fin held at right angle to the axis of view to increase his apparent size, and (4) shaking his body with spasmodic oscillations. The shark appears frightened, and hence may perform the display to discourage any aggression directed at him by the cage with humans emitting a panoply of frightening stimuli. Alternative explanations of the motivation behind this behaviour are also discussed. We hope that it will lead other scientists to look for this behaviour when observing the behaviour of white sharks from a cage, so they can provide further evidence shedding light upon the shark's motivation for performing this conspicuous behaviour.

Keywords

aggressive display, white shark, spasmodic body oscillations.

1. Introduction

In this short note, we describe a single incidence of the convulsive body shuddering of a white shark as it approached two large metallic shark cages at Guadalupe Island, each with multiple divers standing within them. When animals feel threatened, they experience conflicting instincts — one is to escape and another is to fight. In this situation, they do not always fight but often perform a threat or agonistic display. Agonistic displays are conspicuous and exaggerated postures and movements, which convey the threatened animal's ill ease due to the presence of another animal or object and advertise their capacity to inflict harm should the object come any closer (Burghart, 1970). The hunching posture, erection of hair, baring of teeth, and hissing of a cat when confronted by a barking dog is a display that conveys to the dog the cat's readiness to inflict bodily harm should the dog move any closer. This display enables both the cat and dog to avoid the injuries that they would sustain in a fight.

The purpose of a threat display is to warn an unfamiliar animal or object not to approach any closer without resort to the actual physical contact that occurs during combat. Individuals could be stressed, and respond by performing an agonistic display. Although we strive to capture the intensity of the display with still-photographs within this note, we recommend that the reader view the video of it at [10.6084/m9.figshare.21856617](https://doi.org/10.6084/m9.figshare.21856617) due to the difficulty of capturing the spasmodic shivering of the body that accompanies the posturing of the tail and pectoral fins to make the shark appear larger and opening of the jaws to reveal its biological weaponry.

2. Materials and methods

Guadalupe Island (29°00' N, 118°26' W), which is comprised of 250 km² of area, is located 240 km offshore of the eastern coast of the Baja California Peninsula (Hoyos-Padilla et al., 2016). The volcanic island stretches 35 km north to south and 10 km east to west (Domeier et al., 2012). A narrow shelf surrounds the island with depths <200 m with the exception of the southern end, where the shelf extends away to Inner and Outer Islets,

0.5 and 2.5 km south of the main island (Hoyos-Padilla et al., 2016). The offshore waters reach depths of 3600 m. The island lies within the California Current System and has an average sea surface temperature of 18°C, ranging from 16°C in the spring to 20°C in the summer. Three species of pinnipeds occupy the shores of the island, the northern elephant seal (*Mirounga angustirostris*), Guadalupe fur seal (*Arctocephalus townsendi*), and California sea lion (*Zalophus californianus*). Northern elephant seals are present on the beaches along the coast throughout the year with the highest concentration of ca. 13 000 during the breeding season in late January (Gallo-Reynoso et al., 2005). High numbers of elephant seals exist on the northeastern and northwestern tips of the island and on either side halfway down the island and on the southeastern tip of the island.

The white shark ecotourism zone off Guadalupe Island is defined in the government management program of the Guadalupe Island Biosphere Reserve. A 100-m wide buffer zone was created that runs parallel to the coastline. This buffer zone serves to limit the approach of tourist boats to shore to minimize disturbance to the resting pinnipeds that are found along the shore (Santana-Morales et al., 2021). Only frozen fish (*Thunnus albacares*) bought in the departure port is allowed as bait for the activities conducted in this marine protected area. Nevertheless, operators often use fresh bait to attract sharks in the belief that the olfactory cue from a fresh fish could attract sharks more efficiently (Becerril-García et al., 2019). Tourist boats departing from San Diego and Ensenada visit the island from July to December each year, mooring close to the island off the northeastern end, where they are protected from the currents and wind from the northwest. From 2014 to 2019, the number of cage diving vessels in Guadalupe Island grew from six to ten, with an estimated 2800 tourists participating in white shark cage diving during the 2019 season (Santana-Morales, 2021). These boats have two to five shark cages suspended from their sterns close to each other off the beach with elephant seals not far from shore with a permitted separation distance of 450 m.

A video record (10.6084/m9.figshare.21856617) was obtained from an anonymous diver, depicting the convulsive body shuddering of a male white shark as it approached two large metallic shark cages, each with multiple divers standing within them. No history is available of this shark's prior record of behaviour upon approaching a shark cage. For this reason, the description of this behaviour has been limited to a brief scientific note. We

hope that it will lead other scientists to look for this behaviour when observing the behaviour of white sharks from a cage, so they can provide further evidence on the shark's motivation for performing this behaviour.

3. Results

A large male white shark approached two shark cages suspended from the stern of an ecotourism boat. A photograph shows what this particular shark would see as it approached a pair of cages with divers — it is captured from that person's film after the shark has passed the cage he was within and moving toward another two cages suspended from an adjacent ecotourism boat (Figure 1). The fact that the cages were within the photographer field of view, indicates the cages were probably no more than 30–40 m from each other in the clear waters off Guadalupe Island. Up to 10 boats are moored just offshore of the beaches with elephant seals on the northeastern coast of Guadalupe Island with a permitted separation distance of 450. In this case, the boats obviously violated this regulation. The boats and shark-protection cages may be an imposing sight to an animal following an olfactory stimulus, macerated fish, to its source. Having arrived at the source of the olfactory corridor, this shark was confronted not only by a dead fish or whale but highly visible cages made with aluminium or stainless-steel bars, which are usually 3 m high, 2 m wide and 2.5 m long. The divers use hookah air hoses to breathe, and are therefore releasing bubbles, which reflect light and generate sounds as they oscillate toward the surface. The photographers may also be taking pictures of the shark with their flash-bulb equipped cameras, which produce a sudden flash of irradiance, which likely also increases the magnitude of the stimuli emerging from the shark cages. These stimuli might be expected to elicit an aggressive display by a white shark as it moved toward the cages and the divers within the cages.

The shark's behaviour illustrated with a series of ten video frames, each separated by 0.4 s, over a period of 4 s as it approaches the cage, in which divers were standing. The shark initially swam toward the cage with its mouth closed (Figure 2a). The shark then opens its mouth by 0.8 s (Figure 2a, b). He keeps the mouth open for a prolonged period of 2.8 s as he passes close to the cage (Figure 2c–i) until he starts to close his jaws (Figure 2j). Note that the pectoral fins are depressed as he opens his jaws. This is particularly evident in frames d and e, but they fins are kept depressed until frame g. The



Figure 1. White shark approaching a pair of shark cages suspended from the stern of a ecotourism vessel at the main cage diving site at Guadalupe Island.

caudal fin is bent very little over this entire period, maximizing the size of the shark. The male also appears to hunch its back in Figure 2f and g. This appears to resemble a classical agonistic display with the (1) jaws held open to show its biological weaponry, (2) pectorals held down to make it appear large, (3) caudal fin held at right angle to the axis of view to increase its apparent size, and (4) his dorsum hunched also to appear larger.

What cannot be easily shown with still frames is the spasmodic oscillations that the shark passes along the entire length of his body. These can be seen on the video at [10.6084/m9.figshare.21856617](https://www.figshare.com/figure/21856617). However, presented here are ten successive frames, each 0.033 s apart (or 1 of 30 video scans/s), starting at the 1.2 s video frame (Figure 3e), when the shark began oscillating

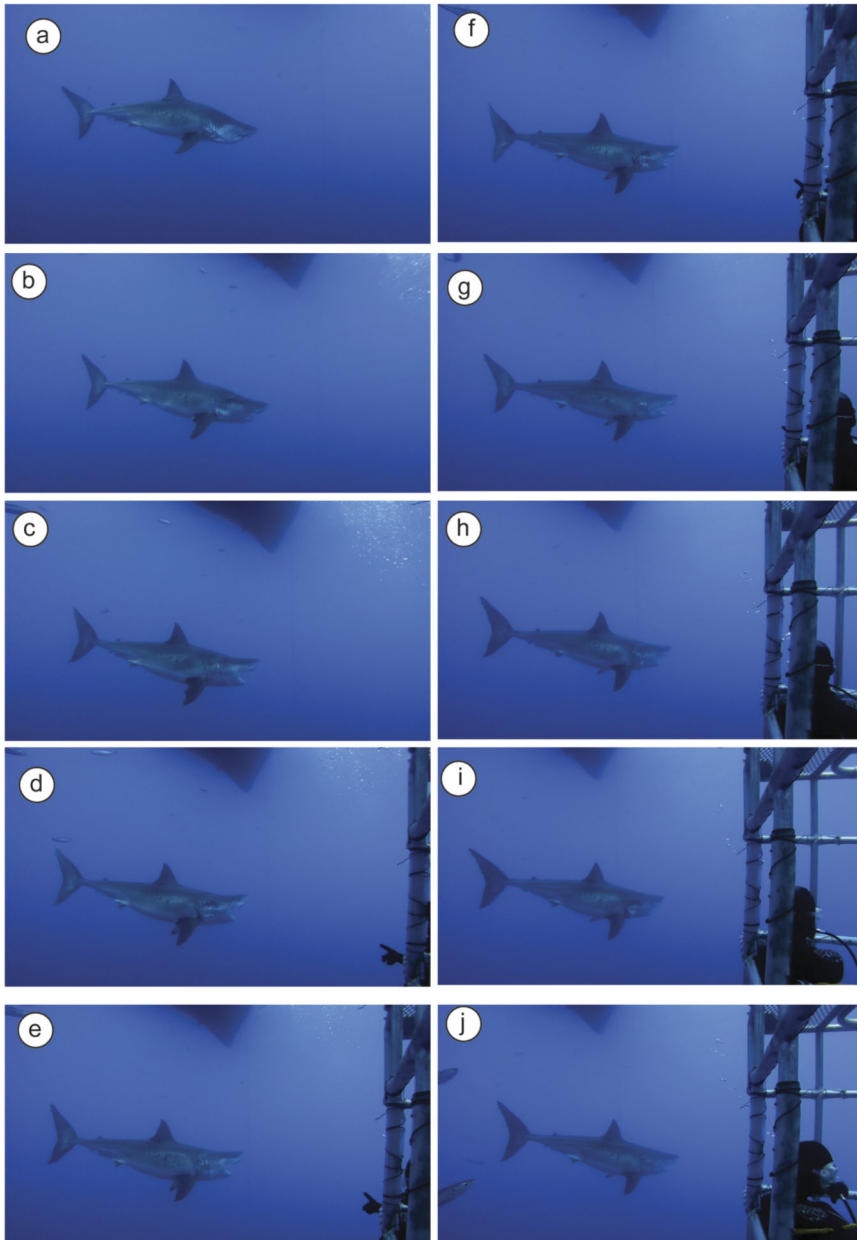


Figure 2. The white shark's jaw gaping agonistic display depicted with a series of 10 video frames (a–j), each separated by 0.4 s, over a period of 4 s as he approaches the cage, in which the photographer was standing.

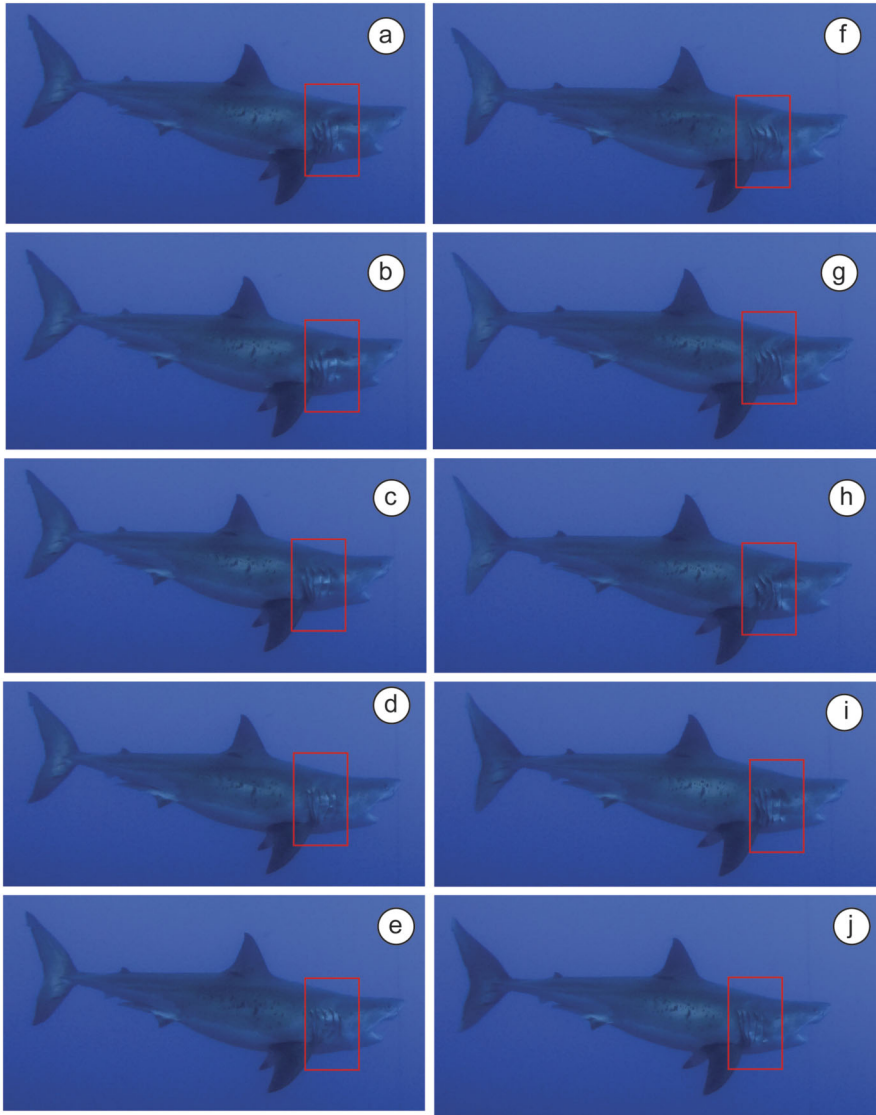


Figure 3. Ten successive video frames, each separated by 0.033 s (1 frame in the 30 frames per s) are shown, starting at the 1.2 s video frame in panel e, when the shark began oscillating in a spasmodic manner. The gill flaps are shown within red-bordered rectangles.

in a spasmodic manner. The wave of contraction can be seen in this series of images. The gill flaps are shown within red-bordered rectangles (Figure 3). The first two gill flaps are closed during the first four frames (Figure 3a–d); they are opened during the next four frames (Figure 3e–h); and they are closed during the next two frames (Figure 3i, j). The shark moved its gill flaps quickly over a period of only 0.33 s. Furthermore, see the dark shadow at the top of the first gill flap as the muscle is contracted in the first two frames (Figure 3a, b), its absence as the muscle is relaxed in the next five frames (Figure 3c–g), and its appearance again as the flap muscles are contracted again in the next two frames (Figure 3h, i), before being relaxed in the final frame (Figure 3j). The oscillations pass down the shark's body as evident by the reflection of light off the side of the body centred at the anterior base of the dorsal fin in the first four frames (Figure 3a–d), its absence in the next two frames (Figure 3e, f), and its reappearance in the next four frames (Figure 3g–j). All this time, the caudal fin is moved very little to maximize the size of the shark to the cage and the viewers within the cage.

4. Discussion

This display, performed by a stiff 'thunniform' swimming species, the white shark, has elements similar to the display, exhibited by a flexible 'carangiform' swimming species, the grey reef shark *Carcharhinus amblyrhynchos*. There are five postural components to the aggressive display of the grey reef shark (see Figure 4 in Johnston & Nelson, 1973). The first postural component is the upward pointing of the snout, the second is a bend between the chondocranium and vertebral column caused by the elevation of the snout, the third is a depressing of the pectoral fins to bring them close to each other, the fourth is the arching of the shark's back, and the fifth is lateral bending of the body with the tail pushed to either side in an exaggerated arc (Figure 4). In a sense, the shark is attempting to increase the size of its profile when viewed from the side.

The lemon shark (*Negaprion brevirostris*), another carangiform swimming shark, also performs an agonistic display, albeit slightly different than that of the grey reef shark. A lemon shark, approached by the senior author wearing a wetsuit with the white markings of a killer whale and a wooden cut-out dorsal fin, performed an analogous display. The shark arched his back, pulled its pectoral fin downward together to appear larger, opened

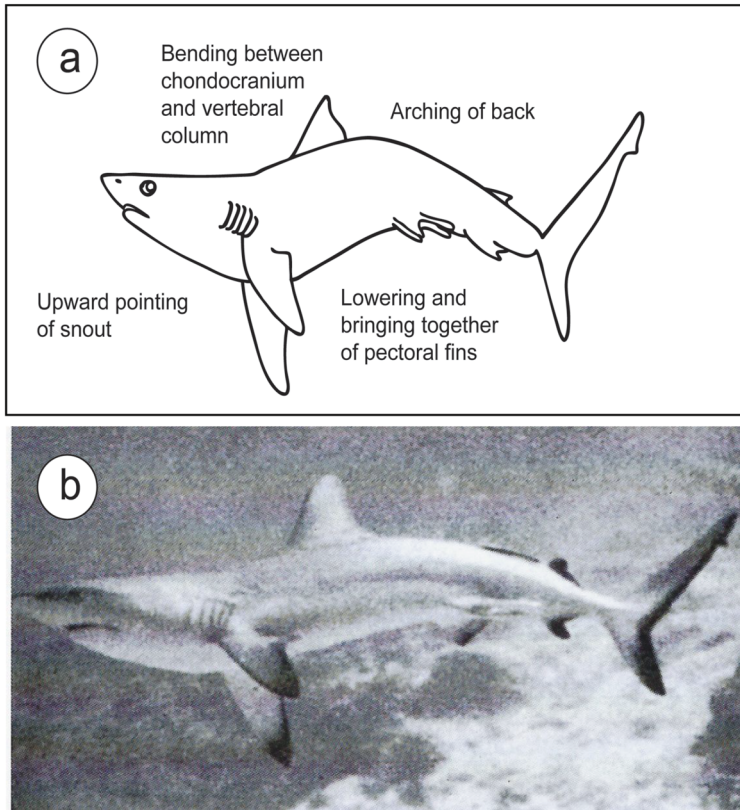


Figure 4. (a) Diagram of agonistic display of grey reef shark, showing the postural elements of the display. (b) Photograph of a shark performing the display.

and closed its mouth to reveal its teeth, which could inflict an injury to the diver, and swam back and forth in looping trajectories at a right angle to the approaching author (Klimley, 2019).

The thunniform swimming sharks are somewhat less flexible in body than the carangiform swimming sharks in that in the former sharks each of the lateral muscles are attached to different vertebrae while in the latter sharks all of the lateral muscles are attached to the base of the tail (Shadwick, 2005). The majority of the carangiform swimming sharks propel themselves forward with undulations from side to side along posterior half of the torso of the (see Figure 3.12 in Klimley, 2013). The grey reef and lemon shark swim in this manner. The white shark is a thunniform swimmer. It bends only the posterior quarter of their body. The caudal fin moves back and forth

while the rest of its body is held rigid. This makes the body appear stiffer when swimming than during the carangiform mode of locomotion. This may explain why the white shark does not arch its back in such a pronounced manner and does not swim in exaggerated looping trajectories as the former sharks when performing the behaviour within the video (see 10.6084/m9.figshare.21856617).

The tail slap display, exhibited during competition for prey at the surface of the water, has similar elements to this display (Klimley et al., 1996). The pectorals are brought together, providing maximum resistance within the water, to permit the shark to swing its tail out of the water and propel water toward the competitor. This posture is apparent in an image taken of a white shark directing a tail slap at a small boat positioned between the shark and seal carcass – the former being confused with a competitor, which might feed upon the rest of the prey (Figure 5). Tail slapping, a patently aggressive behaviour, directed at conspecifics has been observed at Seal Island, South



Figure 5. Photograph taken by underwater diver of white shark directing a Tail Slap at a small boat positioned between the shark and seal carcass — the boat is likely confused with a competitor, which might feed upon the rest of the prey. The pectorals are brought together, providing maximum resistance within the water, to permit the shark to swing its tail out of the water and propel water toward the competitor.

Africa (Martin et al., 2005; Martin, 2007) and at Guadalupe Island, Mexico (Becerril-García et al., 2019) as well as directed at boats and shark cages at Guadalupe Island, Mexico (Becerril-García et al., 2019) and at Dyer Island, South Africa (Sperone et al., 2012).

Are there alternative explanations for this behaviour? One alternative explanation may be that the shark suffers a fit of epilepsy. We were unable to find any published records of sharks exhibiting this behaviour. Why should this behaviour be shown only as the shark approached the cage with divers closely? Might it be caused by stress? However, the oscillating body movements were accompanied by the shark while it assumed many other elements of the agonistic display described by Johnson & Nelson (1973). Could the shark be clearing its gills? But why would it take 2.8 s to do this, and why just in front of the cage. White sharks have been filmed swimming in a sinuous manner while expelling faeces by Erick Higuera, a cinematographer, at Guadalupe Island (<https://www.earthtouchnews.com/oceans/sharks/great-white-sharks-flail-while-they-poop-yes-we-have-video/>). However, this shark did not exhibit body convulsions and did not exhibit the postural elements of an agonistic display. Furthermore, faeces evacuation was performed not in front of a cage with divers but a distance from a shark cage. Blacktip shark, *Carcharhinus melanopterus*, exhibited a tail flick, muscle spasm, head shake, and a fast direction change when the electrodes were energized when 10 cm from their snouts in a field experiment (Thiel et al., 2020). The white shark was too far from the shark cage, which does produce a small near field electrical potential but not near the high voltage applied in the experiment, to respond with such a manner. For the reasons above, we do not believe that the behaviour of the white shark in the video at 10.6084/m9.figshare.21856617 was explained other than as a response to the cage and the divers within it.

In this commentary, we describe an aggressive display, exhibited by a white shark upon approaching two large metallic shark cages. The white shark displays an agonistic display, apparently indicating ill ease due to the presence of the shark cages and divers within them. This brings up the possibility that white sharks are not without fear when they experience conflicting instincts – one is to escape and another is to fight. In this situation, the male white shark performed what we believe to be an agonistic display as they perform a Tail Slap display toward other white sharks attempting to feed upon the carcass of prey that they have killed.

References

- Becerril-García, E.E., Hoyos-Padilla, E.M., Micrelli, P., Galván-Magaña, F. & Sperone, E. (2019). The surface behaviour of white sharks during ecotourism: a baseline for monitoring this threatened species around Guadalupe Island, Mexico. — *Aquat. Conserv. Mar. Freshw. Ecosyst.* 29: 773-782.
- Burghart, G.M. (1970). Defining “communication”. — In: *Communication by chemical signals* (Johnston Jr., W.H., Moulton, D.G. & Turk, A., eds). New Appleton-Century-Crofts, New York, NY, p. 5-18.
- Domeier, M.L., Nasby-Lucas, N. & Lam, C.H. (2012). Fine-scale habitat use by white sharks at Guadalupe Island, Mexico. — In: *Global perspectives on the biology and life history of the white shark* (Domeier, M.L., ed.). CRC Press, Boca Raton, FL, p. 121-132.
- Gallo-Reynoso, J.P., Le Boeuf, B.J., Figueroa-Carranza, A.L. & Maravilla-Chávez, M.O. (2005). Los pinnípedos de la Isla Guadalupe. — In: *Isla Guadalupe: restauración y conservación* (Santos del Prado, K. & Peters, E., eds). Instituto Nacional de Ecología, Secretaría de Medio Ambiente y Recursos Naturales, Mexico City, p. 171-202.
- Hoyos-Padilla, E.M., Galván-Magaña, F. & Klimley, A.P. (2016). Movement patterns of juvenile and adult white sharks (*Carcharodon carcharias*) at Guadalupe Island, Mexico. — *Anim. Biotel.* 4: 1-14.
- Johnson, R.H. & Nelson, D.R. (1973). Agonistic display in the gray reef shark, *Carcharhinus menisorrhah*, and its relationship to attacks on man. — *Copeia*: 76-84.
- Klimley, A.P. (2013). *The biology of sharks and rays*. — University of Chicago Press, Chicago, IL.
- Klimley, A.P. (2019). *Dr. hammerhead swims with sharks*. — Fins Attached, Marine Research and Conservation, Colorado Springs, CO.
- Klimley, A.P., Pyle, P. & Anderson, S.D. (1996). Is the Tail Slap an agonistic display among white sharks?. — In: *Great white sharks: the biology of Carcharodon carcharias* (Klimley, A.P. & Ainley, D.G., eds). Academic Press, San Diego, CA, p. 241-255.
- Martin, R.A. (2007). A review of shark agonistic displays: comparison of display features and implications for shark–human interactions. — *Mar. Freshw. Behav. Physiol.* 40: 3-34.
- Martin, R.A., Hammerschlag, N., Collier, R.S. & Fallows, C. (2005). Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. — *J. Mar. Biol. Ass. UK* 85: 1121-1135.
- Santana-Morales, O., Hoyos-Padilla, E.M., Medellín-Ortíz, A., Sepulveda, C., Beas-Luna, R., Aquino-Baleytó, M., Becerril-García, E.E., Arellano-Millán, D., Malpica-Cruz, L., Lorda, J. & Castillo-Géniz, J.L. (2021). How much is too much? A carrying capacity study of white shark cage diving in Guadalupe Island, Mexico. — *Mar. Policy* 131: 104588. DOI:10.1016/j.marpol.2021.104588.
- Shadwick, R.E. (2005). How tunas and lamnid sharks swim: an evolutionary convergence. — *Am. Sci.* 93: 524-531.
- Sperone, E., Micarelli, P., Andreotti, S., Brandmayr, P., Bernabò, I., Brunelli, E. & Tripepi, S. (2012). Surface behaviour of bait-attracted white sharks at Dyer Island (South Africa). — *Mar. Biol. Res.* 8: 982-991.

Thiel, M., Mourier, J., Papastamatiou, Y., Ballestra, L., Chateauminos, E. & Huveneers, C. (2020). Response of blacktip reef sharks *Carcharhinus melanopterus* to shark bite mitigation products. — *Sci. Rep.* 10: 2563. DOI:10.1038/s41598-020-60062-x.