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Observations of skin color aberrations in four shark species off the coast of southern California, USA

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Abstract Skin color aberrations are naturally occurring abnormal pigment patterns that are generally rare among chondrichthyans. In this study, we highlight different skin color aberrations from observations of four shark species native to southern California, USA. We report the first recorded instance of apparent leucism (regional pigmentation loss), in a California horn shark *Heterodontus francisci* (Girard 1855) and tope shark *Galeorhinus galeus* (Linnaeus 1758). We also report the apparent second documented occurrence of albinism in the swell shark *Cephaloscyllium ventriosum* (Garman 1880) from a newly hatched captive individual with parents of normal pigmentation. Lastly, we redescribe a rare secondary color morph in the leopard shark *Triakis semifasciata* Girard 1855 using previous literature and new sightings/images from sharks in the wild. Color aberrations may lead to different advantages (e.g., certain color morphs may offer additional camouflage) or disadvantages (e.g., reduced pigmentation may limit camouflage and protection from ultraviolet light). Documenting these rare color aberrations augments our understanding of how color patterns can vary between individuals and taxa, and ultimately how these conditions potentially impact shark biology.

Keywords Elasmobranch · Pigment · Hypomelanosis · Leucism · Albinism · Color morph

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Skin color aberrations are abnormal skin patterns including conditions leading to excessive pigmentation (i.e., hypermelanosis) or pigment deficiencies (i.e., hypomelanosis) as well as general polymorphism (different color morphs). Skin color aberrations have been attributed to both inheritable homozygous and heterozygous mutations, as well as epigenetic responses to environmental factors including diet, disease, injury, inbreeding, and temperature (Sage 1962; Sandoval-Castillo et al. 2006; Espinal et al. 2016; Gervais et al. 2016). In fishes, there are six identified chromatophores that contribute to skin pigmentation and each produce pigments of varying colors and functions (Bechtel 1995; Bagnara and Matsumoto 2006). Observations of pigment deficiency in chondrichthyans (i.e., sharks, rays, and chimaeras) are overwhelmingly attributed to loss of melanin (Supplemental Table 1), which is responsible for black or brown coloration and is produced within melanophores (Bechtel 1995; Bagnara and Matsumoto 2006). Hypomelanosis, a collective term for all conditions leading to the full (i.e., albinism) or partial (e.g., leucism, piebaldism) loss of melanin pigmentation (Shipley et al. 2023), is quite rare in chondrichthyans and has only been described in $<5\%$ of chondrichthyan species (69 of the 1483 identified species) (Fricke et al. 2023; Supplemental Table 1). Albinism is a genetic condition in which the individual completely lacks the ability to produce melanin, typically resulting in completely white skin and often red irises of the eyes (Clark 2002; Sandoval-Castillo et al. 2006; Bigman et al. 2016). Leucism, or partial albinism, is the term for a broad suite of conditions in which the individual can still produce pigmentation but lacks melanin across certain regions of the body where melanin is typically present (Berdeen and Otis 2011; Bigman et al. 2016; Wargat et al. 2023). Leucistic sharks often retain normal-colored eyes (Clark 2002; Bigman et al. 2016; Arronte et al 2022). In addition to conditions that affect pigment production, skin color aberrations can include uncommon color morphs, in which individuals of a single species exhibit distinct color patterns. In fish species that exhibit color polymorphism, color morphs can vary with sex, time (ontogenetic or seasonal changes), and habitat (Gray et al. 2008; Korzan et al. 2008; Maan and Sefc 2013; Dahl et al. 2019).

Here, we document macroscopic observations of irregular skin patterns in four shark species native to the coast of southern California, USA. We report an apparent case of leucism in the California horn shark *Heterodontus francisci* (Girard 1855) made from four separate observations of the same individual in the wild between 2019 and 2023. In addition, we report an apparent case of leucism within the tope shark *Galeorhines galeus* (Linnaeus 1758) from a chance encounter in the wild in 2023. We also report an apparent case of albinism in the swell shark *Cephaloscyllium ventriosum* (Garman 1880) from a captive individual in 2019. Lastly, we report additional observations of an anomalous color pattern in the leopard shark *Triakis semifasciata* Girard 1855 made from various observations. While this secondary color morph has previously been documented by Schott (1964) and Castro (2011), we provide unique images of these individuals in the wild and discuss this trait in context of historical sightings.

Leucism in the California horn shark

Here we report four independent sightings of a male California horn shark with apparent leucism from the coastal waters of La Jolla, CA, across a 4-year time span (Fig. 1). This individual had a blotchy complexion, with the apparent lack of skin pigmentation in various regions, while maintaining normal eye pigmentation. This same individual, identified by its distinct pigmentation patterns, was observed on four confirmed occasions: (1) resting in the rocky reef habitat of La Jolla Cove along with normally pigmented horn shark individuals (Fig. 1A–C, daylight hours, May 9, 2019, approximately 32.851 N, 117.266 W); (2) approximately 2 km northwards over a sandy bottom near Scripps Institution of Oceanography pier (Fig. 1D, night time hours, June 24, 2019, 32.867 N, 117.257 W); (3) in La Jolla Cove (Fig. 1E, daylight hours, June 18, 2020, exact coordinates not provided); and (4) among normal pigmented conspecifics in the rocky reefs of La Jolla Cove less than 0.5 km from the first sighting (Fig. 1F, Supplemental Videos 1 and 2, daylight hours, April 6, 2023, 32.851 N, 117.270 W). The shark was briefly retained on the June 2019 encounter during the collection of other horn sharks for non-related work (Prinzing et al. 2021, 2023) and estimated to be between 55 and 60 cm total length. This is the first record of a California horn shark with apparent leucism and the second *Heterodontus* species (out of nine) with a documented case of hypomelanosis. A unique case of leucism has

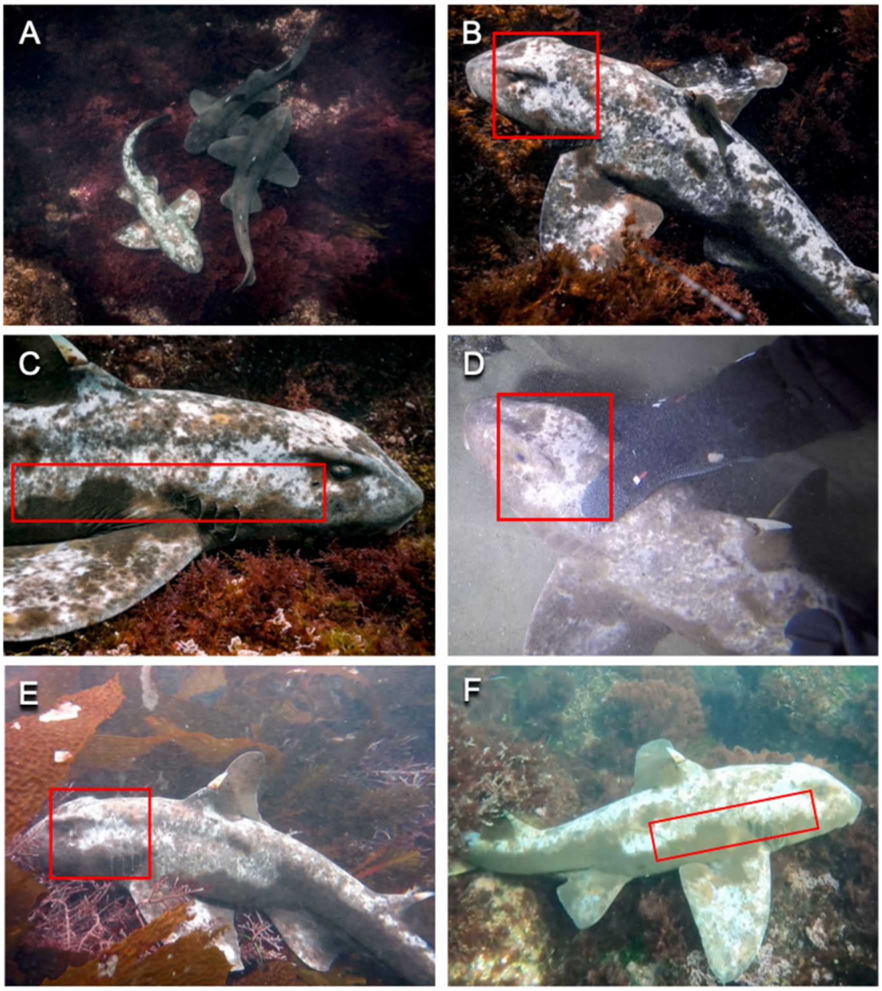

Fig. 1 Underwater images of a mature male California horn shark (*Heterodontus francisci*) with apparent leucism encountered in La Jolla, CA, USA, over a 4-year period: **A**–**C** May 5, 2019 (La Jolla Cove, photos by Zoey Vagner), **D** June 24, 2019 (Scripps Institution of Oceanography Pier, screenshots from video by Tanya Prinzing), **E** July 18, 2020 (La Jolla Cove, screenshots from video by "Diver Jackie"), **F** April 6, 2023 (La Jolla Cove, screenshots from videos by Kevin Smith). Note the partial lack of skin pigmentation in comparison to conspecifics with normal pigmentation (**A**) and normal-colored eyes (**C**) which is indicative of leucism. Red rectangles indicate similar pigmentation between **B**, **D**, and **E**, as well as **C** and **F** showing this is the same individual across sightings. In the most recent encounter (**F**), the white (pigment-lacking) areas of the shark appeared to be brighter than previous encounters, but these differences appear to be associated with reduced image quality rather than real pigmentation change that are occasionally observed with ontogeny, UV exposure, or other environmental stimuli in elasmobranchs (Ari 2014; Domeier and Nasby-Lucas 2007; Dudgeon et al. 2008; Lowe and Goodman-Lowe 1996; Robbins and Fox 2012), including in horn sharks (Ebert 2003)

previously been reported in the closely related Port Jackson shark *H. portjacksoni* (Meyer 1793) from Australia, although this individual still appeared to produce yellow pigmentation (Jha 2004; The Sydney Morning Herald 2004; Veena et al. 2011).

Hypomelanosis often leads to certain biological disadvantages including lack of protection from ultraviolet rays and increased risk of predation due to the conspicuous nature of a white body against the contrasting environmental background. This may ultimately reduce animal survival and further contribute to the rare observation of hypomelanosis in the wild (Uieda 2000; Sandoval-Castillo et al. 2006; Acevedo et al. 2009). However, our multiple observations of the mature horn shark over several years suggests that leucism may not adversely affect its health and survival. Horn sharks generally seek shelter in rocky crevices during the day, when a hypomelanistic individual would be most conspicuous to predators, and then feed at night when a lack of skin pigmentation would be of less concern (Nelson and Johnson 1970; Strong 1989; Meese and Lowe 2020a; Meese and Lowe 2020b). Horn sharks also exhibit high site fidelity and often return to the same feeding grounds and resting places (Strong 1989; Meese and Lowe 2020a, 2020b), which in this case has allowed for multiple observations and unique insight into the continued health and survival of this leucistic individual.

Fig. 2 A tope shark (*Galeoorhinus galeus*) with apparent leucism swimming over a shallow rocky reef in La Jolla, CA, USA (screenshot from a video taken by Peter Demman on August 6, 2023)

Leucism in the tope shark

On August 6, 2023, an adult tope shark with apparent leucism was observed swimming within La Jolla Cove, CA (32.850 N, 117.266 W), above a shallow rocky reef (Fig. 2), among an aggregation of conspecifics characterized as mostly pregnant females (Nosal et al. 2021). The individual exhibited typical gray pigmentation with a noticeable blotch of non-pigmented skin between the first and second dorsal fin on the right lateral body and had normal-colored eyes. Hypomelanosis in the form of albinism has been reported twice before from two tope individuals caught in the north Atlantic Ocean (Deynat 2003; Quigley et al. 2018), but this represents the first report of apparent leucism within the species, and the first reported individual with hypomelanosis within the Pacific Ocean. While topes are found circumglobally in coastal temperate waters, there is little to no gene flow between populations or oceans (Chabot and Allen 2009; Chabot 2015).

Albinism in the swell shark

In December 2019 at Scripps Institution of Oceanography, a swell shark lacking any skin pigmentation (Fig. 3) hatched from an egg laid by a captive female with normal pigmentation. This is the second known observation of apparent albinism in this species. The other known instance of albinism in swell sharks is from a mature female caught near Cabo San Lucas, Baja California Sur, Mexico, in 2016 (Becerril-García et al. 2017). While in many species, including chondrichthyans, albino individuals are often characterized by red eyes (Reum et al. 2008; Lipej

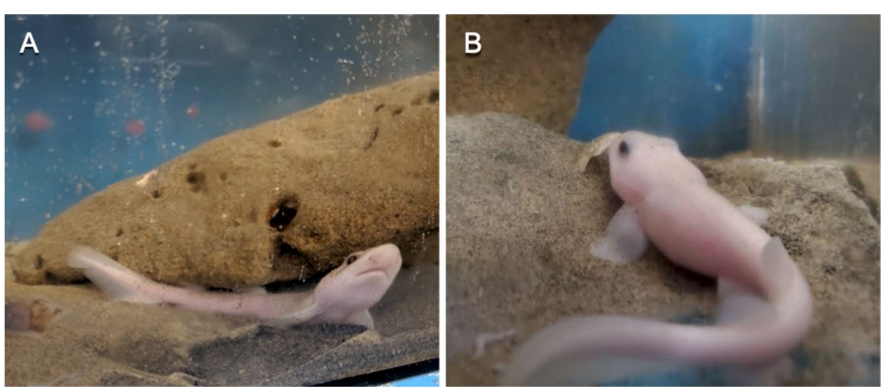

Fig. 3 A newly hatched albino swell shark (*Cephaloscyllium ventriosum*) from parents of normal pigmentation on **A** November 7, 2019 (photo by Alma Trinidad Javier) and **B** December 13, 2019 (photo by Zachary Skelton)

et al. 2011), both known albinistic swell shark individuals appeared to have normal-colored eyes, likely attributed to the presence of chrysopsin and rhodopsin pigments, both of which would not be affected by changes to melanin production as they are produced by different enzymes in different chromatophores (Denton and Warren 1956; Crescitelli et al. 1985; Crescitelli 1991; Wang et al. 2007; Becerril-García et al. 2017).

Secondary color morph in the leopard shark

Lastly, we document additional cases of an anomalous color pattern in leopard sharks (Fig. 4; Table 1). This species' primary color morph (initially called "primary chromatic pattern" by Schott (1964) and included in the original species descriptions as referenced in Pietsch et al. (2012)) is characterized by small spot marks and larger dark saddle bars that straddle the dorsal and lateral surface of the shark (Fig. 4A). In contrast, a separate, anomalous pattern (first introduced as a "secondary chromatic pattern" by Schott (1964)), is characterized by more irregular saddle bars with strong longitudinal marks, concave indents, or branches, and often accompanied by smaller and numerous irregular marks and spots extending laterally along the sides of the shark (Fig. 4B–D; Schott 1964; Castro 2011). These irregular patterns and longitudinal streaks have resulted in nicknames for this color morph such as "scribbled," "tire treads," or "zig zags" (personal observations) and are easy to identify when compared with individuals with the primary color morph (Fig. 4E–F). To be consistent and avoid confusion moving forward, we suggest that this anomalous pattern in leopard sharks be referred to as the "secondary" color morph. While most sharks appear to group within one of these two

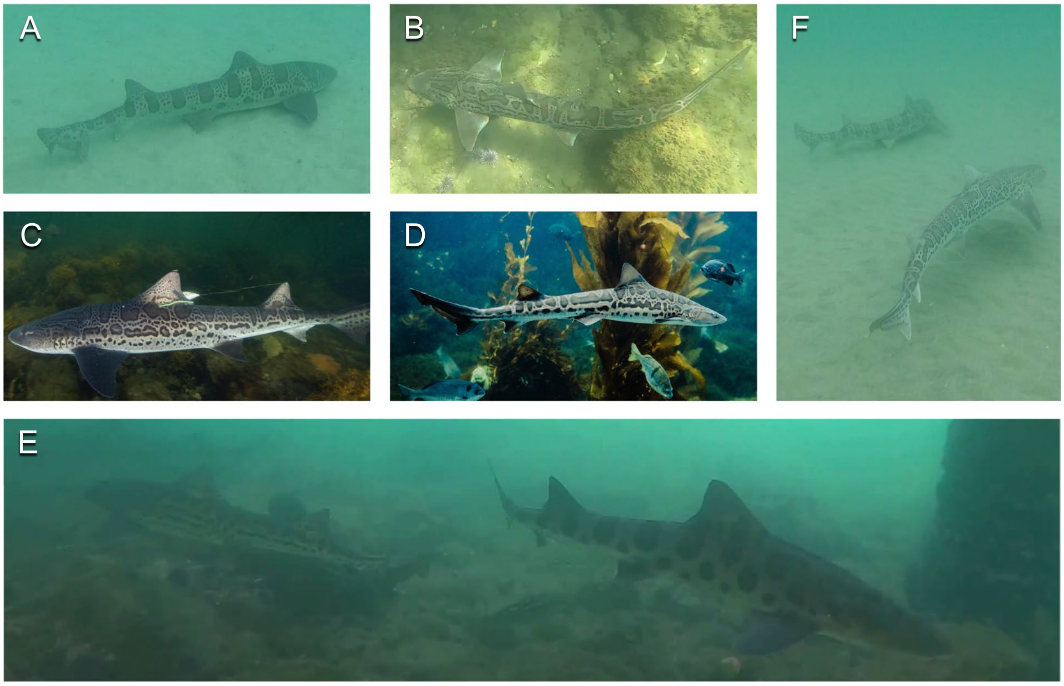

Fig. 4 Comparison of the primary color morph with traditional saddle pattern (**A**, **E** [right] and **F** [top]), and the unusual secondary color morph (**B**–**D**, **E** [left], **F** [bottom]) in the leopard shark (*Triakis semifasciata*). These sharks were spotted in La Jolla, CA on August 10, 2015 (**C** by Ralph Pace Photography) and on September 8, 2020 (**A**, **F** by Zachary Skelton), under the Santa Cruz Island pier on August 16, 2020 (**E**, by Zachary Skelton), and from a captive individual at the Birch Aquarium (**D**, by Jordann Tomasek). The individuals with the secondary color morph reported here from La Jolla and Santa Cruz Island were encountered among aggregations of dozens of individuals with the primary color morph. The leopard shark pictured in **C** was equipped with a satellite tag; unfortunately, shark movement data was not recovered from the tag due to tag malfunction

Table 1 Review of reports of the secondary color morph in the leopard shark (*Triakis semifasciata*)

Year	Size (cm)	Sex	Life stage	Encounter	Location	Description	Source
1946	68.4	F	Juvenile	Caught	San Quintin Bay, Baja California	Photo, Morphometrics	Schott (1964)
1953	28.2	F	Juvenile	Caught	Goleta, California	Photo, Morphometrics	Schott (1964)
NR	27.8	M	Juvenile	Caught	California	Illustration	Castro (2011)
2009	170	F	Adult	Captivity	Birch Aquarium	In captivity (died 2011)*	Castro (2011), Birch Aquarium
2010	44	M	Juvenile	Caught	Del Mar, California	Tagged	A. Nosal
2015	152	F	Adult	In wild	La Jolla, California	Photo*, tagged	Ralph Pace Photography
2020	> 100	F	Adult	In wild	La Jolla, California	Photo*	Z. Skelton
2020	> 100	–	Adult	In wild	Santa Cruz Island, California	Photo*	Z. Skelton
2021	~ 120†	F	Adult	Caught	Santa Catalina Island, California	Video	Landshark Outdoors YouTube Channel[1]
2023	~ 190	M	Adult	Captivity	Living Coast Discovery Center	In captivity since 2002*	Living Coast Discovery Center
2023	–	M	Adult	Captivity	Birch Aquarium	In captivity since 2008*	Birch Aquarium
2023	–	–	Adult	In wild	La Jolla, California	Video*	J. Gailey
2023	–	–	Adult	In wild	La Jolla, California	Video*	P. Demman
–	–	–	Adult	Caught	–	Photo	B. Hervery-Murray[2]
–	–	–	Adult	In wild	La Jolla, California	Photo	A. Murch[3]

In addition to the recorded sightings listed here, Schott (1964) mentions a sighting from a personal communication. Similarly, we have heard of other anecdotal observations of the secondary color morph (R. Herrmann, and A. Carlisle, personal communications); however, observations without accompanying photographs are not recorded in this table

†Size estimated in ImageJ (Schindelin et al. 2012) using the known length of a knife that was on the same plane as the shark in the video

*Photo or video available in the attached repository: https://figshare.com/s/88dba2835756b69def9a

[1] https://www.youtube.com/watch?v=nJN1XM5O0vE

[2] https://wonews.com/summer-shark-fishing-tackle-baits-and-tactics-for-targeting-big-leopards/

[3] https://www.sharksandrays.com/leopard-houndshark/

descriptions, it is important to note that there is large variation in both the primary and secondary color morphs. Specifically, the number, size, and placement of both saddles and spots can vary in both morphs and the shape of the secondary marks can vary greatly in the secondary color morph. Thus, it is possible these morphs could be further divided into more distinct sub-groupings or viewed as a graded spectrum between the two morphs, although more in-depth demographic research would be needed to discern these scenarios.

Here, we report 11 additional observations of the secondary color morph to the original reports by Schott (1964) and Castro (2011). These observations were collected from various sources including our own in situ observations (Fig. 4A–C, E–F), and information we collated from online posts (i.e., videos and blog articles by fishermen and outdoor enthusiasts), and from captive individuals located at the Birch Aquarium (Fig. 4D) and the Living Coast Discovery Center (Table 1). Included in our observations were five individuals observed at a local female aggregation site in La Jolla, California. Combining our new dataset with rare historical records (Table 1), this secondary color morph has now been documented across a 76-year time span encompassing regions from Goleta, California, USA, to San Quintin Bay, Baja California, Mexico (over 350 miles apart), including the offshore Channel Islands. Considering leopard sharks live upwards of 25–30 years (Smith 1984; Kusher et al. 1992; Smith et al. 2003), this represents at least three generations of individuals with this color morph, indicating its persistence as a rare, but regularly encountered trait.

The driving mechanism behind these divergent color morphs and their relative proportion is not known. Of the 150 individuals that Schott (1964) sampled ($n = 49$), observed ($n = 100$), or mentioned via personal communication ($n = 1$), three individuals (2%) were of the secondary color morph. While it is possible that this is simply a rare genetic mutation with little biological significance, Dahl et al. (2019) hypothesized the "sandy" color morph for the Zebra Shark *Stegostoma tigrinum* (Forster 1781), a species known for its variegated patterns similar to the leopard shark, may provide camouflage advantages for individuals inhabiting sandy habitats. Leopard sharks are known to occupy a wide variety of habitats including sandy flats, eelgrass beds, and rocky reefs (Ebert 2003; Castro 2011), in which different color morphs could potentially provide some benefit. Although we observed both color morphs over both rocky reefs and sandy flats, a larger sample size and a more exhaustive survey of leopard shark color morph demography and habitat use would be needed to understand any potential correlations between a specific morph and habitat type. Interestingly, we were unable to find documented reports of the secondary color morph from leopard sharks north of Point Conception, CA, which is a known barrier to gene flow between leopard shark populations to the north and south (Barker et al. 2015), although this could simply reflect underreporting in northern areas where there are fewer interactions with leopard sharks.

Implications

Similar to other documented instances of hypomelanosis and rare color morphs, this paper is based on chance observations rather than a directed study of the topic. Thus, our results and those of other papers on skin aberrations generally suffer from a few challenges. First, due to the rarity of encounters, chance observations do not allow for a clear understanding of the prevalence and variation of color aberrations within and between species. Second, because observations of skin conditions are mostly described from external color alone, the underlying physiological (e.g., lack of pigment production, lack of melanocytes) and genetic causes are generally not assessed. For example, of the 84 studies listed in Table S1 documenting chondrichthyan hypomelanosis, only one study (Wargat et al. 2023) included histological examination to show that the described leucism in this animal was caused by a loss of melanin in the skin. Histological and genetic testing can thus be used to discern specific causes in rare cases in which skin aberrations occur in captivity or in wild animals that are captured and retained. While most skin aberrations are thought to fall under the umbrella of hypomelanosis, there are other chromatophores and pigments that contribute to coloration, and it is often unclear to what extent those chromatophores and pigments play a role. Finally, it is also possible that such encounters may go unreported in the literature due to the topical nature of the subject or because it may not be broadly known how atypical these occurrences are. As an example, we falsely assumed that hypomelanosis had been previously recorded in California horn sharks, and it took us four years before we realized this was a unique observation. Examining individuals with skin aberrations in captivity also provides a rare opportunity to further study the genetics and inheritance of such traits. For instance, mating between a male and female of known phenotypes can allow for studies of inheritance in pups born in captivity. Thus, due to their rarity, it is important to document both wild and captive observations of skin aberrations in order to help understand color patterns and their biological significance across time, space, and taxa, and to help inform future observations.

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Author contribution Contributed to conception and design: Z.R.S.

Contributed to acquisition of data: Z.R.S., T.S.P., Z.V., P.D., A.P.N., P.J.Z.

Contributed to analysis and interpretation of data: Z.R.S., A.P.N., N.C.W.

Edited and approved the submitted version for publication: All authors.

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Data availability All data is provided within the manuscript and supplementary material.

Data accessibility Raw picture and videos files are available at https://figshare.com/s/88dba2835756b69def9a.

Declarations

Ethical approval The results of this study are from field observations and thus no ethical approval was required. However, the brief handling of the leucistic horn shark during collection of horn sharks for other studies (Prinzing et al. 2021, 2023) was approved by the Institutional Animal Care and Use Committees of the University of California, San Diego (protocol no. S00080) and National Oceanic and Atmospheric Administration Southwest Fisheries Science Center (protocol no. SW1801) and in accordance with California Fish and Wildlife Scientific Collecting Permit SC-13908.

Competing interests The authors declare no competing interests.

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