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Sharks as exfoliators: widespread chafing between marine organisms suggests an unexplored ecological role

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Ectosymbionts, such as bacteria and parasites, are found on the body surface of the host organisms throughout the ecosystems across the world. Hosts have evolved a variety of mechanisms across ecosystems to rid themselves of ectoparasites or other skin irritants, including chafing behavior, whereby an organism curves their body to rub the convex portion of their body along a rough surface (Eibl-Eibesfeldt 1955, Wicklund 1969, Myrberg and Gruber 1974, Wyman and Walters-Wyman 1985, Mooring et al. 2004, Papastamatiou et al. 2007, Grossman et al. 2009, Ritter 2011, Berthe et al. 2017). Chafing has been well documented in aquatic environments (Eibl-Eibesfeldt 1955, Wicklund 1969, Myrberg and Gruber 1974, Wyman and Walters-Wyman 1985, Papastamatiou et al. 2007, Grossman et al. 2009, Ritter 2011, Berthe et al. 2017). Most of the documented incidents occur between an organism and an inanimate object, such as sandy or rocky substrate (Myrberg and Gruber 1974, Wyman and Walters-Wyman 1985, Ritter 2011, Berthe et al. 2017). Few sources have documented the evidence of an organism chafing against another living organism, such as sharks or turtles (Eibl-Eibesfeldt 1955, Wicklund 1969, Papastamatiou et al. 2007, Grossman et al. 2009). Here, we compiled the observations on the natural history of 47 incidents of fish chafing against sharks in 13 locations across the world's oceans. This appears to be the only phenomenon, whereby a prey actively seeks out and rubs up against a predator. We hypothesize several ecological implications and suggest future research to better understand this phenomenon.

Of our 47 recorded chafing incidents, we recorded 25 events using a drone: six incidents were recorded subsurface by divers, five were documented photographically, and the rest were anecdotal observations (Appendix S1: Table S1). Twelve teleosts and one shark species were recorded chafing against eight different species of shark (Figs. 1, 2), though only one species was observed chafing against one shark species at a time (Appendix S1: Table S1). The chafing events varied in duration from eight seconds to over five minutes (Appendix S1: Table S1). For many instances, we could not determine the entire duration of the event because the video did not record the entirety of the event or no video was recorded due to the reduced under water visibility. The observed chafing events occurred in 13 locations, spanning three oceans, and ranging from temperate to tropical ecosystems. Many chafers and sharks exhibited life histories with partial or dominant pelagic stages (Skomal 2016; FishBase). In all incidents, the number of fish chafing against sharks ranged from one to over 100 individuals (Appendix S1: Table S1). Given the logistical difficulties in observing sharks in the wild, the prevalence of reports of chafing involving multiple species in multiple locations around the world raises several ecological questions.

What is the benefit of rubbing against a shark? In several instances, fish actively changed their behavior to pursue a nearby shark (Fig. 3, Video S1). For example, we recorded *Lichia amia* (leervis) turning abruptly to pursue a passing white shark 19 times in Plettenberg Bay, South Africa (Fig. 3, Video S1, Appendix S1: Table S1). This behavior appeared to increase the risk of predation. In six instances, the white shark directly pursued a leervis that had stopped chafing and started to swim away. There was no detectable change in the shark's speed during the pursuit, but the leervis increased its speed in response to the shark's attempt. The repeated chafing movements of fish suggest that shark's skin may offer a better mechanism for parasite removal compared to other rough surfaces used for chafing, like the available surrounding sandy and rocky benthos (Myrberg and Gruber 1974, Wyman and Walters-Wyman 1985, Ritter 2011, Berthe et al. 2017). Future studies are needed to determine the efficacy of dermal denticles in removing parasites compared to other mechanisms and the potential benefit of chafing against a shark given the associated costs of predation. In 46 of 47 incidents (98%), we noticed that fish chafed in localized regions along the shark's body, specifically around the caudal peduncle and below the dorsal fin (Fig. 1, Videos S1, S2; Appendix S1: Table S1). We hypothesize that fish chafe in specific regions on the shark's body because the dermal denticles in these areas are more effective in removing parasites due to variation in dermal denticle morphology across the shark's body (Ankhelyi et al. 2018, Popp et al. 2020). However, it could also be because those regions are associated with the lowest predation risk. No predation attempts of chafers were observed, likely due to sharks' lack of agility needed to catch them. In comparison, *Carcharhinus falciformis* (silky shark) are seen chafing around the head of *Rhincodon typus* (whale shark), a species that poses no risk to the chafers (Fig. 1c, Video S3). Future studies investigating the profilometry of sharks' dermal denticles and their efficacy in removing skin irritants with respect to the location on the body will provide further insights into the function of dermal denticle as a cleaning mechanism.

Second, how does chafing affect the shark? In 18 of 47 events (38%), where sharks' behavior could be adequately observed, sharks appeared to negatively respond to chafing. For example, 18 drone recordings showed white sharks abruptly diving, changing directions, or both, when pursued by chafing fish. Dives were characterized by a steep descent from the surface to the seabed. Directional changes were categorized as (1) a sharp 90° to 180° turn, (2) sinusoidal swimming, (3) a tight corkscrew dive resulting in the upper lobe of the caudal fin breaking the surface, or (4) some combination of all three (Fig. 3, Video S1). This aversive behavior could be because sharks incur some cost or negative consequence from the fish's contact. There is increasing evidence to show that transfer between cleaner and client is possible and that parasites take advantage of these interactions as an avenue to spread (Narvaez et al. 2021). However, this behavior occurred in only 38% of our observations; so, it could be the reason that sharks simply dislike the fish's contact. Still, little is known about the composition of dermal microbiomes of and sharks and the possibility of transfer of microbial and parasitic infections.

Lastly, how does chafing behavior influence fish and shark ecology? To our knowledge, only three other studies published evidences of fish chafing against sharks (Eibl-Eibesfeldt 1955, Wicklund 1969, Papastamatiou et al. 2007). Our evidence extrapolates upon their findings that sharks potentially act as mobile cleaning stations for fish with a variety of life histories, including reef, coastal, and pelagic species. Fish that live in the pelagic zone do not frequent to go to cleaning stations or have access to other cleaning mechanisms in coastal ecosystems. Sharks play a vital role in the removal of ectoparasites or other skin irritants, thereby improving health and fitness of pelagic fish. If parasite transfer is possible, another potential ecological impact could be the transmission of parasitic infections or other diseases. We noticed that the areas of a shark's body, where

Fig. 1. Evidence of chafing on multiple shark species in multiple locations. (a) *Trachurus symmetricus* chafing large *C. carcharias* off of Guadalupe Island, Mexico. Image taken from video recorded during underwater cage dive on 23 August 2011. (b) *Pomatomus saltatrix* chafing *Cetorhinus maximus* off of Gloucester, MA, USA. Image taken by pilot of spotter plane, Dan d'Hedouville. Exact date unknown. (c) Four *Carcharhinus falciformis* chafing *Rhyncodon typus* near Darwin Island, Galapagos, Ecuador. Image taken from a fin camera recording from 18 September 2016.

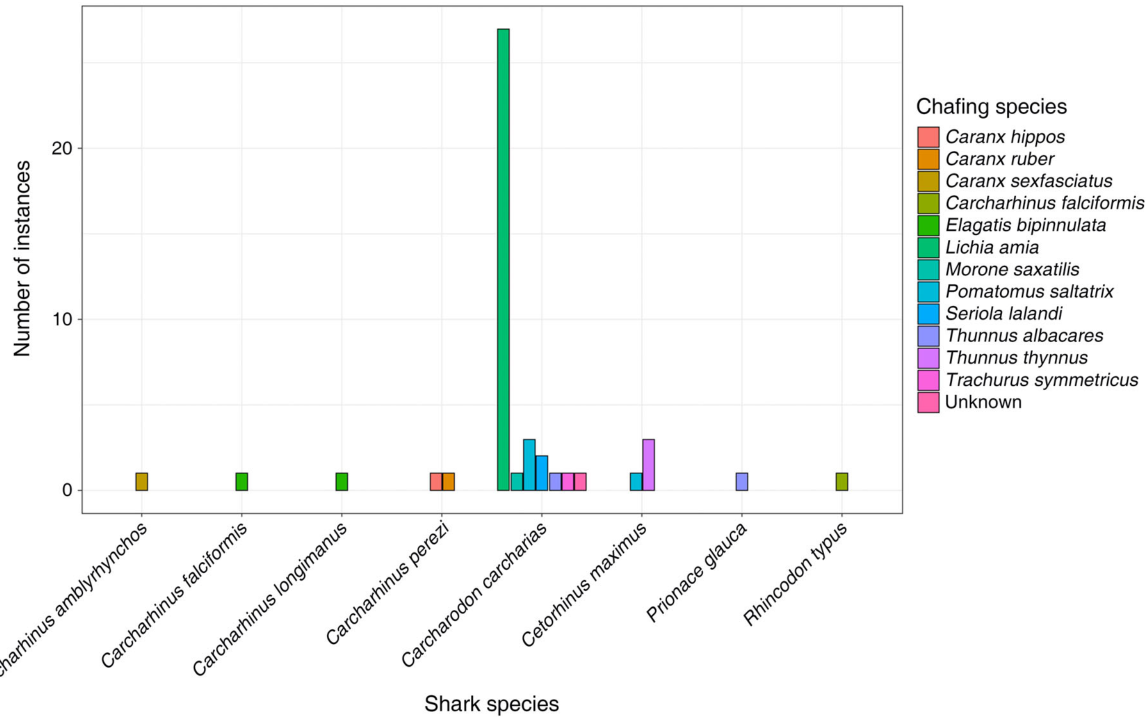

FIG. 2. Bar graph showing the number of chafing incidents by chafing species for each shark species.

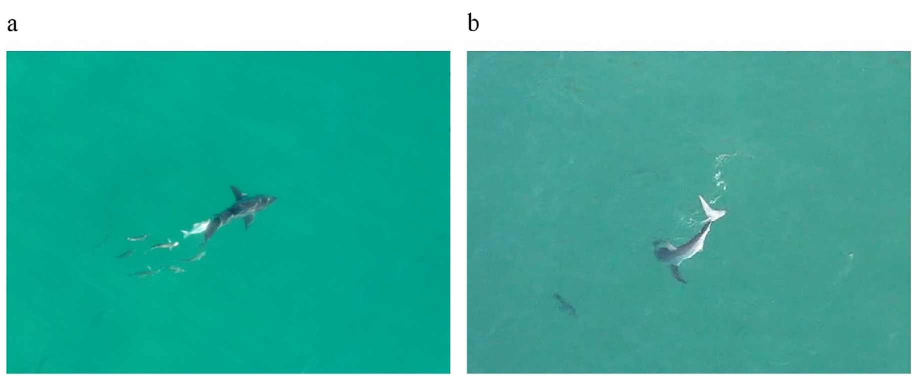

FIG. 3. (a) A school of ten *L. amia* following a small *C. carcharias* with one individual mid-chafe against the left, ventral caudal peduncle region. Image taken from video recorded on 14 June 2019. (b) *C. carcharis* negatively reacting to two chafing *L. amia* through an abrupt directional change and a steep dive. Image was taken from video recorded on 19 June 2019. Both videos were recorded in Plettenberg Bay, South Africa using a DJI Mavic 2 Pro.

cleaner fish spend most of the time (Oliver et al. 2011), are the same areas where we have seen the most chafing occur, namely the caudal fin and peduncle regions (Appendix S1: Table S1). If a transfer is taking place, sharks that are chafed against, particularly the pelagic species, could potentially be vectors for microbial or parasitic transfer when they migrate across ecosystems. However, the current literature is only the beginning to discuss the possibility of transfer of microbial and parasitic infections between organisms, no studies exist yet that explore potentially broader ecological consequences.

The frequency and global occurrence of interspecies chafing against shark's skin suggests that it holds a greater significance in marine ecology than previously known. To our knowledge, no terrestrial analog exists for cross-species chafing behavior, let alone prey seeking out and rubbing up against a predator. This leads to the broader ecological question as to why this phenomenon does not appear to occur in terrestrial ecosystems.

Moreover, many terrestrial animals have rough or scaly skin, but there is no terrestrial equivalent for dermal denticles, whose sandpaper-like texture and posterior orientation appear to evolve primarily for hydrodynamic efficiency in a dense, viscous medium (Popp et al. 2020). This unique functional morphology could be why chafing behavior is found exclusively in aquatic systems. If sharks act as vectors for ectoparasite removal or transfer between systems, they could play a role in pathogen or parasite transmission. Therefore, changes or spatial shifts in shark populations could interrupt vector pathways and have implications for species and systems. We acknowledge several hypotheses about the costs and benefits of chafing against sharks and why it has no terrestrial analog, but the true ecological significance remains unknown, representing an area for future research.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3570/suppinfo

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Data (Williams et al. 2021) are available in FigShare at https://doi.org/10.6084/m9.figshare.15078894