Short Note

Cookiecutter Shark Bite Wounds on Cetaceans of the Gulf of Mexico

Mark A. Grace,¹ Laura Aichinger Dias,^{2,3} Katherine Maze-Foley,^{2,3} Carrie Sinclair,¹ Keith D. Mullin,¹ Lance Garrison,³ and Lauren Noble⁴

¹NOAA/SEFSC/NMFS/Mississippi Laboratories, Pascagoula, MS, USA E-mail: Mark.A.Grace@noaa.gov ²Cooperative Institute for Marine and Atmospheric Studies, University of Miami, Miami, FL, USA ³NOAA/SEFSC/NMFS/Miami Laboratory, Miami, FL, USA ⁴NOAA/SEFSC/NMFS/Mississippi Laboratories Affiliate, Pascagoula, MS, USA

Cetaceans can be observed in the field with external wounds produced by cookiecutter sharks (Chondrichthyes: Squaliformes: Dalatiidae: *Isistius* spp.). Cookiecutter sharks are ectoparasitic predators, and the distinct feeding wounds they inflict on their prey are typically oval to round-shaped, ranging from superficial tooth puncture marks for incomplete bites to deeply incised scoops of flesh for fully completed bites (Jones, 1971; Shirai & Nakaya, 1992; Figure 1). Cookiecutter shark bite wounds that are unique in their shape and location have been used as a distinguishing feature for tracking specific cetaceans (e.g., Dwyer & Visser, 2011; Best & Photopoulou, 2016), and their occurrence can be important for verifying cetacean stock designations (Goto et al., 2009), establishing cookiecutter shark distribution ranges (Muñoz-Chápuli et al., 1988), and for describing cookiecutter shark foraging ecology (Papastamatiou et al., 2010).

Host fatalities from cookiecutter shark bite wounds have not been conclusively documented, although for smaller-sized host fauna, such as squids or cetacean calves (e.g., Baird, 2016), the



Figure 1. Cookiecutter shark (*Isistius* spp.) bite wound (pale oval forward of the dorsal hump) on a sperm whale (*Physeter macrocephalus*) in the Gulf of Mexico (GOM) (2009 SWAPS survey), 20 June 2009, Lat. 25 34.40 N/Long. -084 44.26 W. *Photo credit:* Carrie Sinclair, NOAA/SEFSC/NMFS/Mississippi Laboratories

bites could be fatal due to the bite size in proportion to host size. Cookiecutter sharks are relatively small (up to 54 cm; Compagno, 1984); however, their upper trophic-level prey can include killer whales (Orcinus orca; Dwyer & Visser, 2011), white sharks (Carcharodon carcharias; Gallo-Reynoso et al., 2005; Hoyos-Padilla et al., 2013), and, infrequently, humans (Honebrink et al., 2011; Ribéreau-Gayon et al., 2017, 2018). Given the external appearance of cookiecutter shark bites, evidence of wounds can be seen on the body of cetaceans observed during visual line-transect surveys as well as on live or dead stranded cetaceans. Bite wounds can be fresh, which appear as conspicuous pink to red-colored circles on their bodies, or scars, which display a white to gray color pattern. Herein, we examine the presence of cookiecutter shark bites on several cetacean species of the Gulf of Mexico (GOM) and discuss how this predator-prey association may have a species distribution and prey-trophic-level basis.

The GOM cetacean visual surveys were a useful documentation source for examining whether cetacean species are differentially preyed upon by cookiecutter sharks. These surveys were conducted by NOAA/SEFSC/NMFS aboard NOAA ships Gordon Gunter (https://www.omao.noaa.gov/ learn/marine-operations/ships/gordon-gunter) and Pisces (https://www.omao.noaa.gov/learn/ marine-operations/ships/pisces) (2007 to 2015; 9 surveys). Those surveys utilized line-transect survey methods (e.g., Mullin & Fulling, 2004) primarily during daylight hours (0700 to 1900 h) and were manned by rotating teams of marine mammal observers from the flying bridges of vessels. Visual observations were made with the unaided eye, with 7× hand-held binoculars, and with high-powered mounted binoculars (25 × 150). Among other data, cetacean sighting reports included location, date, time, species identifications, group size, and behavior. A cetacean sighting consisted of one or more individuals of the same or different species. Usually when a cetacean was sighted, the ship deviated course toward the sighting location to better identify species and count group size. Deviating the ship's course allowed a close approximation to the group and, depending on the species, animals would often come toward the ship to bowride. Bowriding animals, predominantly delphinids, provided the best opportunity to observe and occasionally photograph cookiecutter shark bites. In some instances, a rigid-hulled inflatable boat would be deployed to document larger cetaceans such as sperm whales (*Physeter macrocephalus*). Cookiecutter shark bites were reported as present (Yes), absent (No), or could not be determined (CBD). For positive records (Yes), at least one cookiecutter shark bite (fresh or scar) had to be present on at least one animal of the sighting. Negative records (No) indicated observers did not see bite wounds, and CBD records indicated that it was not possible to determine cookiecutter shark bite wound occurrence given the distance to the group or any other factor rendering determination. It is worth noting that negative records may have been attributed to sightings for which not all of the animals were evaluated for bites. For example, a portion of the group came to bowride and was therefore evaluated (in this case as no bites observed), while other animals were not close to the ship for accurate observations and therefore not evaluated for bites (but the whole sighting was assigned a "No" value). Further, cookiecutter shark bite wounds for each sighting were not enumerated nor measured and, in general, were not described in reports (e.g., fresh or partial bite, healed or not healed, and/or body location). When available, survey photographs from specific sightings were reviewed to confirm cookiecutter shark bite wound occurrences.

The cumulative distance for line transects during the cetacean visual surveys was 48,807 km (23,114 nmi) with a total of 1,844 cetacean visual sightings (single or group) of 19 different species (non-identified taxa not included; Table 1). Of the total sightings, 600 could be evaluated for evidence of cookiecutter shark bite wounds (Yes + No). More than half of the evaluated sightings were of bottlenose dolphins (Tursiops truncatus) (n = 321 or 53%), followed by Atlantic spotted dolphins (Stenella frontalis) (n = 142 or 24%)and pantropical spotted dolphins (Stenella atten*uata*) (n = 92 or 15%). The evaluated sightings had 148 positive records of cookiecutter shark bites (25% of the total evaluated sightings) for 12 different species (Figure 2). The pantropical spotted dolphin had the most positive cookiecutter bite records (n = 77 or 52% of the total positive records; 84% of its total evaluated sightings), followed by the bottlenose dolphin (n = 36 or)25% of the total positive records; 11% of its total evaluated sightings), which was also the most frequently sighted cetacean, and the spinner dolphin (Stenella longirostris) (n = 11 or 7% of the total positive records; 79% of its total evaluated sightings).

There are several biases that potentially affect the detection of cookiecutter shark bites on cetaceans. One of the most important biases is the approachability of cetaceans by large research ships or small boats. During cetacean visual surveys, most of the positive records of bites were detected in delphinids, especially smaller species with the tendency to bowride. Generally, only dolphins, porpoises (absent in the GOM), and smaller

evaluated, and bowfider – known to bow				OAA/NMI-5/SEI-SC cetacea	all visual surveys.
Taxon (total sightings)	Yes	No	CBD	Yes/ Yes+No	Bowrider
Bryde's whale (35) Balaenoptera edeni	0	1	34	0.00	No
Cuvier's beaked whale (9) Ziphius cavirostris	0	0	9	0.00	No
Blainville's beaked whale (1) Mesoplodon densirostris	0	0	1	0.00	No
Beaked whales (50) (Genus/species not determined)	1	0	49	1.00	No
Sperm whale (145) <i>Physeter macrocephalus</i>	4	0	141	1.00	No
Dwarf sperm whale (3) <i>Kogia sima</i>	0	0	3	0.00	No
Kogia spp. (29) (Species not determined)	0	0	29	0.00	No
Pygmy killer whale (1) Feresa attenuata	0	0	1	0.00	No
Short-finned pilot whale (15) Globicephala macrorhynchus	0	0	15	0.00	No
Risso's dolphin (52) Grampus griseus	1	0	51	1.00	No
Fraser's dolphin (2) Lagenodelphis hosei	1	0	1	1.00	Yes
Killer whale (2) Orcinus orca	1	0	1	1.00	No
Melon-headed whale (7) Peponocephala electra	1	2	4	0.33	Yes
False killer whale (2) Pseudorca crassidens	0	0	2	0.00	No
Pantropical spotted dolphin (189) Stenella attenuata	77	15	97	0.84	Yes
Clymene dolphin (2) Stenella clymene	1	0	1	1.00	Yes
Striped dolphin (8) Stenella coeruleoalba	2	1	5	0.67	Yes
Atlantic spotted dolphin (207) Stenella frontalis	6	136	65	0.04	Yes
Spinner dolphin (37) Stenella longirostris	11	3	23	0.79	Yes
Stenella spp. (41) (Species not determined)	0	0	41	0.00	N/A
Rough-toothed dolphin (26) Steno bredanensis	6	9	11	0.40	Yes
Bottlenose dolphin (611) Tursiops truncatus	36	285	290	0.11	Yes
Unidentified dolphin (294) (Genus/species not determined)	0	0	294	0.00	N/A
Unidentified cetacean (76) (Genus/species not determined)	0	0	76	0.00	N/A
Totals (1,844)	148	452	1,244	0.25	

Table 1. Cetacean sightings (as a single or a group) with cookiecutter shark bites; yes = bite wound or bite scar present, no = bite wound or bite scar absent, CBD = could not be determined, yes/yes+no = bite wound or scar present/total sightings evaluated, and bowrider = known to bowride or observed bowriding during NOAA/NMFS/SEFSC cetacean visual surveys.



Figure 2. GOM distribution of cetacean visual survey and coastal cetacean stranding observations with occurrence of cookiecutter shark bite wounds. The dalatiid shark captures are the two cookiecutter sharks and the closely related pocket shark. Coordinates are °W longitude and °N latitude.

toothed whales bowride (Würsig, 2008). Larger cetaceans (e.g., sperm whales) do not bowride (Table 1) and often spend a considerable amount of time under water (Okamura, 2003; Watwood et al., 2006; Soldevilla et al., 2017); therefore, observations can be more problematic for larger cetaceans compared to smaller cetaceans with shorter dive intervals (Davis et al., 1996; Klatsky et al., 2007; Wells et al., 2009). In addition, small delphinids often occur in large groups and may increase opportunities for bite wound or bite scar observations, and, incidentally, most delphinids tend to be very active and conversely under certain circumstances, which may make observations difficult.

Another observation factor for smaller cetaceans is interspecific differences that are appearance related. For instance, the Atlantic spotted dolphin and the Risso's dolphin (*Grampus griseus*) can be extensively spotted and scarred, thus potentially masking healed cookiecutter shark bite wound scars as evidenced by the relatively large number of negative bite records for Atlantic spotted dolphins in the surveys. Additionally, cookiecutter shark bite wounds or healed scars can be found along the cetacean lower body or ventrum (Baird, 2016) and are not always visible by surface observations, especially for species that do not bowride, an observation bias that would be particularly prevalent for larger cetaceans. When considering the variety of field and observation limitations, the positive bite records are the most reliable sighting data element and represent a minimum level of cookiecutter shark bite occurrence. The potential visual observation biases for reporting the occurrence of cookiecutter shark bites was typified by 67% of all observations being CBD (Table 1).

The Marine Mammal Health and Stranding Response Program (MMHSRP) database (https:// mmhsrp.nmfs.noaa.gov/mmhsrp) is another information source useful for assessing GOM cetaceancookiecutter shark predator-prey associations. Stranding-network scientists respond to live or dead stranded cetaceans in the GOM states of the U.S. and, although not a requirement, the reporting of cookiecutter bite wounds can be noted on the Level A data form (https://www.fisheries.noaa.gov/ national/marine-mammal-protection/level-datacollection-marine-mammal-stranding-events). The MMHSRP database was queried by using "cookie cutter" for all stranding records in GOM states between 2007 and 2015. For the nearly 4,500 stranding records, 54 included comments on the

Species	#	n	%	Location
Fin whale	1	1	1.00	TX
Short-finned pilot whale	57	2	0.04	FL
Risso's dolphin	22	2	0.09	FL
Dwarf sperm whale	25	4	0.16	FL, TX
Pygmy sperm whale	37	7	0.19	FL, TX
Unidentified dwarf/pygmy sperm whale	15	1	0.07	FL
Melon-headed whale	30	4	0.13	AL, TX
Sperm whale	19	1	0.05	LA
Spinner dolphin	20	2	0.10	FL
Striped dolphin	4	1	0.25	FL
Atlantic spotted dolphin	33	1	0.03	FL
Bottlenose dolphin	4,225	30	0.01	FL, TX, MS

Table 2. GOM marine mammal stranding reports with occurrences of cetaceans with cookiecutter bite wounds (2005 to 2017). # = number of strandings, n = number of strandings with cookiecutter shark bite wounds, % = percentage with cookiecutter shark bite wounds, and Location = GOM state stranding location.

presence of cookiecutter shark bites on cetaceans (Table 2). It is worth emphasizing that comments on the presence of cookiecutter shark bites is not a requirement for filling Level A data and that the absence of comments does not always imply that bites were not seen. However, similar to the bite occurrences recorded during the cetacean visual line-transect surveys, the positive records do indicate predation of cookiecutter sharks upon various species of cetaceans. Eleven species of stranded cetaceans were documented with bites, with at least one of these cetacean species with bites from each of the GOM states (Figure 2; the area of the Florida Keys/Monroe County, Florida, was excluded due to uncertainties related to carcass drift from the Atlantic Ocean). Bottlenose dolphins were the most common species to strand and accounted for more than half of the positive bite wound records (56%). The pygmy and dwarf sperm whales (*Kogia* spp.) and the melon-headed whale (Peponocephala electra) also showed relatively high numbers among the positive records but, except for the pygmy killer whale that was not reported with bites (MMHSRP), strand at lower rates. The fin whale (Balaenoptera physalus) was the only stranded cetacean with cookiecutter shark bites (Table 2) that was not reported with bites during cetacean visual surveys. Cetaceans with cookiecutter shark bites reported from cetacean visual surveys but not reported with bites from their stranding reports were the Fraser's dolphin (Lagenodelphis hosei; n = 5) and the rough-toothed dolphin (*Steno bredanensis*; n = 13).

Assessing predator-prey associations between cetaceans and cookiecutter sharks was not a primary research objective of the cetacean visual surveys; however, there was applicable stable isotope sampling during the 2010 survey (Sperm Whale Autonomous Prey Study [SWAPS]; L. Garrison et al., unpub. data). A useful comparison for identifying trophic and food web relationships across a broad range of taxa and ecosystems is by stable isotope fractionation (Newsome et al., 2010; Ben-David & Flaherty, 2012); and during SWAPS, a survey objective was to collect tissue samples from sperm whales and probable sperm whale prey for stable isotope ratio analysis. Midwater trawling was conducted in depths ranging from 160 to 1,700 m primarily in sperm whale habitat. Thirty-two squid taxa and 39 fish taxa were collected and sampled for stable isotope ratio analysis, including two species of cookiecutter sharks (largetooth cookiecutter shark [Isistius plutodus] and cookiecutter shark [Isistius brasiliensis]; Figure 3). The stable isotope ratios for *I. plutodus* and *I. brasiliensis* ranged from $\delta^{15}N$ 11.0 to 11.6 and δ^{13} C 16.9 to 16.6, respectively (Table 3), which place them in a similar trophic level to sperm whales (δ¹⁵N 11.2 to 13.5; δ¹³C 16.9 to 14.0; Ruiz-Cooley et al., 2012) and also indicates they did not feed exclusively on sperm whales because otherwise their $\delta^{15}N$ values would be expected to be higher than sperm whales (Newsome et al., 2010). In addition, both the cookiecutter sharks and sperm whales were placed higher in trophic level than most of their potential prey sampled during the survey ($\delta^{15}N$ 6.9 to 12.4 and δ^{13} C 20.0 to 16.7; Table 3). It is not certain whether the entire group of the 74 trawl-captured taxa were probable sperm whale prey because the conclusive methods for determining prey taxa would have been to sample sperm whale stomachs or to observe sperm whales actively feeding on prey (that can be conclusively identified) which were not survey objectives.



Figure 3. Isistius brasiliensis (left) and Isistius plutodus (right) ventral view of mouth and teeth (2010 SWAPS survey). Photo credit: Mark Grace, NOAA/SEFSC/NMFS/Mississippi Laboratories

Table 3. Stable isotope ratios for sperm whales, cookiecutter sharks, and probable sperm whale prey. Sperm whale mean values are from Ruiz-Cooley et al. (2012); cookiecutter shark, squid, and fish taxa prey values (mean by taxa) are from SWAPS. Muscle tissue sample preparation and stable isotopic composition analysis followed standard extraction and analysis methods per Rossman et al. (2013) (P. Ostrom, Michigan State University, pers. comm., 11 November 2017). Fish taxa do not include the cookiecutter sharks nor a gulper shark (*Centrophorus granulosus*).

Source (<i>n</i>)	Stable isotope ratios
Sperm whales (71)	δ ¹⁵ N 11.2-13.5; δ ¹³ C 16.9-14.0
Cookiecutter sharks (2) Isistius brasiliensis Isistius plutodus	$\delta^{15}N 11.0; \delta^{13}C \ 16.9 \\ \delta^{15}N 11.6; \delta^{13}C \ 16.6$
Sperm whale prey (32 squid taxa)	δ ¹⁵ N 6.9-12.3; δ ¹³ C 20.0-16.7
Sperm whale prey (39 fish taxa)	δ ¹⁵ N 8.6-12.4; δ ¹³ C ⁻ 19.0-17.3

Stable isotope ratios are important for assessing trophic levels, but there are numerous factors that affect broad-based comparisons between similar and dissimilar species, time series years, and geographic regions (e.g., Walker et al., 1999; Ruiz-Cooley et al., 2004, 2012; Barros et al., 2009; Hussey et al., 2011; Ben-David & Flaherty, 2012). With regards to other possible predatorprey commonalities between cetaceans and members of Dalatiidae, it is relevant to note that also captured during the SWAPS survey was a closely related pocket shark (*Mollisquama* sp.; Grace et al., 2015; not sampled for stable isotopes) which has jaw and dental morphological similarities to cookiecutter sharks that also make it well-suited for ectoparasitic feeding.

Despite a small sample size, the cookiecutter shark bite occurrence observations shed some light into the little known and documented feeding ecology. Even though there was a relatively low number of survey sightings for several cetaceans, and cookiecutter shark captures are relatively rare considering published literature only accounts for five GOM cookiecutter sharks (*Isistius* spp.) and the closely related GOM pocket shark (all were captured in midwater above bottom depths 823 to 3,038 m; Garrick & Springer, 1964; Grace et al., 2015; SWAPS survey), the minimum distribution overlap between cetaceans and cookiecutter sharks is evidenced by the reported bite occurrences. The graphic plot of the positive records of bite wounds from the cetacean visual surveys with the locations where the cookiecutter sharks were captured during the trawls (Figure 2) also demonstrates the minimum distribution overlap between predator and prey. Additionally, the minimum distribution overlap is to some extent supported by GOM habitat-based mean year-round cetacean density plots (Roberts et al., 2016; for supplemental information for species-specific or guild mean yearround predicted density plots, see http://seamap. env.duke.edu/models/Duke-EC-GOM-2015). As an example, some of the higher-level mean year-round density areas for the pantropical spotted dolphin (a species with a high percentage of sightings with bite wounds) overlap to a greater extent with the deepwater cookiecutter shark capture locations from the SWAPS survey than some of the other more coastal cetaceans reported with cookiecutter shark bites. Conversely, bottlenose dolphins that have higher-level density coastal distributions were also detected with bites (albeit at a relatively low percentage when compared to the other more frequently sighted cetaceans), and that may indicate that cookiecutter sharks can have a broader, shallower water depth distribution than indicated by their GOM capture locations. Also, several cetaceans that were not evaluated for cookiecutter shark bite wounds during GOM surveys have been documented with cookiecutter shark bite wounds from other areas (e.g., Bryde's whale and beaked whales; Jefferson et al., 2015).

Even though visual observations of ectoparasitic predator-prey associations between cetaceans and cookiecutter sharks are often problematic, the GOM cetacean visual surveys and cetacean stranding reports were useful for documenting important attributes of a complex predator-prey dynamic. Of the 21 cetacean species known to regularly inhabit the U.S. waters of the GOM (https://www.nefsc.noaa.gov/publications/tm/tm223), this study documented 13 with evidence of cookiecutter shark bites. In spite of the paucity of documentation and limitations for observations, the bite records accounted for 62% of the various cetacean species in the GOM with cookiecutter shark bites. Given this high diversity in prey species, ranging from the coastal bottlenose dolphin to the deep diver sperm whale, it can be inferred how generalist the diet and widespread the habitat of cookiecutter sharks might be. Cookiecutter shark bite wounds on cetaceans are reported from many of the world's oceans (Dwyer & Visser, 2011), and cookiecutter sharks have GOM distributions that frequently overlap with cetaceans as evidenced by the cookiecutter shark

bite wounds reported by the cetacean visual surveys and stranding records. There are prey-based commonalities between sperm whales and cookiecutter sharks as indicated by the stable isotope fractionation results, and the occurrences of other GOM cetacean species reported with cookiecutter shark bites suggests cookiecutter sharks may also forage on some of the prey of other cetaceans. While cookiecutter shark feeding behavior and their feeding mechanisms are considered to be specialized (Munroe et al., 2014), with regards to them targeting a variety of prey that includes cetaceans, their resource use strategy may be an example of a generalist foraging niche with individuallevel variations and specializations (Bolnick et al., 2002; Matich et al., 2011). Additional research is needed to fully understand the trophodynamics of the enigmatic cetacean-cookiecutter shark predator-prey association.

Acknowledgments

The cetacean research surveys were conducted under National Marine Fisheries Service Permit Numbers 779-1633 and 14450. Thanks are extended to Anthony Martinez and Jesse Wicker (NOAA/ SEFSC/NMFS) who were the chief scientists for surveys and to the many marine mammal observation scientists who collected survey data as well as the command and crews of NOAA ships Gordon Gunter and Pisces. Karen Mitchell, Kevin Barry, Christian Jones and William Driggers III (NMFS Mississippi Laboratories), Illiana Ruiz-Cooley (NOAA SWFSC; sperm whale stable isotope ratio analysis), and Peggy Ostrom (Michigan State University, SWAPS fishes and squid stable isotope ratio analysis) are thanked for their assistance. Elizabeth Stratton of the Gulf of Mexico Marine Mammal Disaster Response is thanked for assistance with the National Marine Mammal Stranding Database. Likewise, the Southeast U.S. Marine Mammal Stranding Network is thanked for its tireless efforts during stranding responses. The anonymous reviewers are thanked for their time and comments that significantly improved the manuscript. The U.S. Department of the Interior (Bureau of Ocean Energy Management, Environmental Studies Program, Washington, DC), through Interagency Agreement M09PG0014 with NOAA/NMFS, is recognized for their SWAPS funding contribution.

Literature Cited

- Baird, R. W. (2016). The lives of Hawaii's dolphins and whales: Natural history and conservation. Azalea: Journal of Korean Literature and Culture, 10.
- Barros, N. B., Ostrom, P. H., Stricker, C. A., & Wells, R. S. (2009). Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Marine Mammal Science*, 26, 324-336. https://doi.org/10.1111/j.1748-7692.2009.00315.x
- Ben-David, M., & Flaherty, E. A. (2012). Stable isotopes in mammalian research: A beginner's guide. *Journal of Mammalogy*, 93(2), 312-328. https://doi. org/10.1644/11-MAMM-S-166.1
- Best, P. B., & Photopoulou, T. (2016). Identifying the "demon whale-biter": Patterns of scarring on large whales attributed to a cookie-cutter shark *Isistius* sp. *PLOS ONE*, 11(4), e0152643. https://doi.org/10.1371/ journal.pone.0152643
- Bolnick, D. I., Svanbäck, R., Fordyce, J., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1-28. https://doi.org/10.1086/343878
- Compagno, L. J. V. (1984). FAO species catalogue (Vol. 4). Sharks of the world: An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. Rome: Food and Agriculture Organization of the United Nations.
- Davis, R. W., Worthy, G. A., Würsig, B., Lynn, S. K., & Townsend, F. I. (1996). Diving behavior and at-sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. *Marine Mammal Science*, 12(4), 569-581. https://doi.org/10.1111/j.1748-7692.1996.tb00069.x
- Dwyer, S. L., & Visser, I. N. (2011). Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (Orca) (*Orcinus orca*). Aquatic Mammals, 37(2), 111-138. https://doi.org/10.1578/AM.37.2.2011.111
- Gallo-Reynoso, J. P., Le Boeuf, B. J., Figueroa, A. L., & Maravilla, M. O. (2005). Los pinnípedos de Isla Guadalupe [The pinnipeds of Guadalupe Island]. In K. Santos-del-Prado & E. Peters (Eds.), *Isla Guadalupe: Hacia su restauración y conservación* [Guadalupe Island: Towards its restoration and conservation]. Delegación Coyoacán, México, DF: Instituto Nacional de Ecología.
- Garrick, J. A. F., & Springer, S. (1964). *Isistius plutodus*, a new squaloid shark from the Gulf of Mexico. *Copeia*, 678-682. https://doi.org/10.2307/1441443
- Goto, M., Kanda, N., Pastene, L. A., Bando, T., & Hatanaka, H. (2009). Differences in cookie cutter shark-induced body scar marks between J and O stocks of common minke whales in the western North Pacific (SC/J09/JR18).
- Grace, M. A., Doosey, M., Bart, H. L., & Naylor, G. J. (2015). First record of *Mollisquama* sp. (Chondrichthyes: Squaliformes: Dalatiidae) from the Gulf of Mexico, with a morphological comparison to the holotype description of *Mollisquama parini* Dolganov. *Zootaxa*, 3948(3), 587-600. https://doi.org/10.11646/zootaxa.3948.3.10

- Honebrink, R., Buch, R., Galpin, P., & Burgess, G. H. (2011). First documented attack on a live human by a cookiecutter shark (Squaliformes, Dalatiidae: *Isistius* sp.). *Pacific Science*, 65(3), 365-374. https://doi.org/10.2984/65.3.365
- Hoyos-Padilla, M., Papastamatiou, Y. P., O'Sullivan, J., & Lowe, C. G. (2013). Observation of an attack by a cookiecutter shark (*Isistius brasiliensis*) on a white shark (*Carcharodon carcharias*). *Pacific Science*, 67(1), 129-134. https://doi.org/10.2984/67.1.10
- Hussey, N. E., Dudley, S. F. J., McCarthy, I. D., Cliff, G., & Fisk, A. T. (2011). Stable isotope profiles of large marine predators: Viable indicators of trophic position, diet, and movement in sharks? *Canadian Journal* of Fisheries and Aquatic Sciences, 68(12), 2029-2045. https://doi.org/10.1139/f2011-115
- Jefferson, T. A., Webber, M. A., & Pitman, R. L. (2015). Marine mammals of the world: A comprehensive guide to their identification (2nd ed.). New York: Elsevier/ Academic Press. 616 pp. ISBN 978-0124095427.
- Jones, E. C. (1971). Isistius brasiliensis, a squaloid shark, probable cause of crater wounds on fishes and cetaceans. Fishery Bulletin, 69(4), 791-798.
- Klatsky, L. J., Wells, R. S., & Sweeney, J. C. (2007). Offshore bottlenose dolphins (*Tursiops truncatus*): Movement and dive behavior near the Bermuda pedestal. *Journal of Mammalogy*, 88(1), 59-66. https://doi.org/ 10.1644/05-MAMM-A-365R1.1
- Matich, P., Heithaus, M. R., & Layman, C. A. (2011). Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal* of Animal Ecology, 80, 294-305. https://doi.org/10.1111/ j.1365-2656.2010.01753.x
- Mullin, K. D., & Fulling, G. L. (2004). Abundance of cetaceans in the oceanic northern Gulf of Mexico. *Marine Mammal Science*, 20(4), 787-807. https://doi. org/10.1111/j.1748-7692.2004.tb01193.x
- Muñoz-Chápuli, R., Rel Salgado, J. C., & De La Serna, J. M. (1988). Biogeography of *Isistius brasiliensis* in the north-eastern Atlantic, inferred from crater wounds on swordfish (*Xiphias gladius*). Journal of the Marine Biological Association of the United Kingdom, 68, 315-321. https://doi.org/10.1017/S0025315400052218
- Munroe, S. E. M., Simpfendorfer, C. A., & Heupel, M. R. (2014). Defining shark ecological specialization: Concepts, context, and examples. *Reviews in Fish Biology and Fisheries*, 24, 317-331.
- Newsome, S. D., Clementz, M. T., & Koch, P. L. (2010). Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, 26(3), 509-572. https://doi.org/10.1111/j.1748-7692.2009.00354.x.
- Okamura, H. (2003). A line transect method to estimate abundance of long-diving animals. *Fisheries Science*, 69, 1176-1181. https://doi.org/10.1111/j.0919-9268.2003.00743.x
- Papastamatiou, Y. P., Wetherbee, B. M., O'Sullivan, J., Goodmanlove, G. D., & Lowe, C. G. (2010). Foraging ecology of cookiecutter sharks (*Isistius brasiliensis*) on pelagic fishes in Hawaii, inferred from prey bite

wounds. Environmental Biology of Fishes, 8, 361-368. https://doi.org/10.1007/s10641-010-9649-2

- Ribéreau-Gayon, A., Carter, D. O., & Regan, S. (2018). New evidence of predation on humans by cookiecutter sharks in Kauai, Hawaii. *International Journal of Legal Medicine*. https://doi.org/10.1007/s00414-018-1786-8
- Ribéreau-Gayon, A., Rando, C., Schuliar, Y., Chapenoire, S., Crema, E. R., Claes, J., . . . Morgan, R. M. (2017). Extensive unusual lesions on a large number of immersed human victims found to be from cookiecutter sharks (*Isistius* spp.): An examination of the Yemenia plane crash. *International Journal of Legal Medicine*, 131(2), 423-432. https://doi.org/10.1007/s00414-016-1449-6
- Roberts, J. J., Best, B. D., Mannocci, L., Fujioka, E., Halpin, P. N., Palka, D. L., . . . Lockhart, G. G. (2016). Habitatbased cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports*, 6, 22615. https://doi. org/10.1038/srep22615
- Rossman, S., Barros, N. B., Ostrom, P. H., Strickler, C. A., Hohn, A. A., Gandi, H., & Wells, R. S. (2013). Retrospective analysis of anthropogenic ecosystem disturbance. *Marine Mammal Science*, 29(4), 705-718. https://doi.org/10.1111/j.1748-7692.2012.00618.x
- Ruiz-Cooley, R. I., Engelhaupt, D. T., & Ortega-Ortiz, J. G. (2012). Contrasting C and N isotope ratios from sperm whale skin and squid between the Gulf of Mexico and Gulf of California: Effect of habitat. *Marine Biology*, 159, 151-164. https://doi.org/10.1007/s00227-011-1795-3
- Ruiz-Cooley, R. I., Gendron, D., Aguíñiga, S., Mesnick, S., & Carriquiry, J. D. (2004). Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Marine Ecology Progress Series*, 277, 275-283. https://doi.org/10.3354/meps277275

- Shirai, S., & Nakaya, K. (1992). Functional morphology of feeding apparatus of the cookie cutter shark, *Isistius brasiliensis* (Elasmobranchii, Dalatiinae). *Zoological Science*, 9(4), 811-821.
- Soldevilla, M. S., Hildebrand, J. A., Frasier, K. E., Aichinger Dias, L., Martinez, A., Mullin, K. D., . . . Garrison, L. P. (2017). Spatial distribution and dive behavior of Gulf of Mexico Bryde's whales: Potential risk of vessel strikes and fisheries interactions. *Endangered Species Research*, 32, 533-550. https://doi.org/10.3354/esr00834
- Walker, J. L., Potter, C. W., & Macko, S. A. (1999). The diets of modern and historic bottlenose dolphin populations reflected through stable isotopes. *Marine Mammal Science*, 15, 335-350. https://doi. org/10.1111/j.1748-7692.1999.tb00805.x
- Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T., & Tyack, P. L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology, 75, 814-825. https://doi.org/10.1111/ j.1365-2656.2006.01101.x
- Wells, R. S., Manire, C. A., Byrd, L., Smith, D. R., Gannon, J. G., Fauquier, D., & Mullin, K. D. (2009). Movements and dive patterns of rehabilitated Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico and Atlantic Ocean. *Marine Mammal Science*, 25(2), 420-429. https://doi.org/10.1111/j.1748-7692.2008.00251.x
- Würsig, B. (2008). Bow riding. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (p. 133). New York: Academic Press.