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RESEARCH ARTICLE

Predation on sea turtles at sea: A multi-source synthesis and research perspectives

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Abstract

1. Predation is a key ecological process shaping sea turtle populations, yet - unlike predation of eggs, hatchlings and adults on nesting beaches - its role at sea remains poorly quantified due to observational challenges.
2. This study synthesizes multiple, rarely integrated data sources—including unpublished data—to examine global patterns of sea turtle predation at sea. Sources include field observations (turtles found stranded, nesting, admitted to rescue centers, or captured in-water for research), literature records, predator diet data, and non-conventional online sources (NCS; images and videos).
3. A literature review compiled 206 report/predator/turtle species/turtle life stage/area combinations involving all seven extant sea turtle species and 51 predator species. Although predators span several taxa (including teleost fishes, crocodilians, and mammals), most reports involve a few shark species. To estimate predation rates, we analysed 156,726 turtle records (dead or alive), of which 5,107 individuals (3.3%) showed evidence of shark-bite injuries. These rates varied significantly among species, size classes, regions, and over time. Stomach content analysis of 3,927 sharks from 12 species identified turtle remains only in tiger and white sharks, with tiger sharks emerging as the dominant predator. NCS yielded 34 shark-turtle interactions, 73% of which were videos that offered rare insights into sea turtle defensive behaviours such as dorsal shielding, rapid manoeuvring, fleeing, and even counterattacks.
4. Together, these multiple approaches provide complementary insights and highlight the dominant role of large sharks, particularly tiger sharks, in sea turtle predation. However, current knowledge is largely confined to predation in neritic waters because of the inherent difficulties of studying this topic in oceanic

environments. Predation on small juveniles and in oceanic waters remains the most significant knowledge gap due to the likelihood of whole-body ingestion and occurrence in oceanic habitats. Tracking such early life stages may become feasible with advances in tag miniaturization. Meanwhile, visible shark-bite injuries on large turtles—if adequately standardized—represent a promising tool for monitoring spatial and temporal trends in predation pressure on large turtles in coastal waters. With improved data collection, analytical methods, and citizen science contributions through NCS, we can begin to address critical knowledge gaps in the at-sea predation ecology of sea turtles.

KEYWORDS

gut contents, in-water capture, nesting females, non-conventional sources, shark bite, strandings

1 | INTRODUCTION

A thorough comprehension of predator–prey interactions is crucial for understanding the ecology of prey species and for designing effective conservation strategies. Moreover, the ecological impact of predation extends beyond the individual prey species, with predators exerting a regulatory role through several trophic levels (Estes et al., 2011; Ripple & Beschta, 2012). Ultimately, predation influences community structure, functioning and biodiversity (Stier et al., 2017).

Sea turtles are recognized as keystone species due to their pivotal roles in marine ecosystems. For instance, green turtles (*Chelonia mydas*) control seagrass bed density, which is essential for the productivity and nutrient cycling of these habitats (Bjorndal, 1980). Additionally, the nesting activities of sea turtles affect the beach ecosystem through nest construction (Madden et al., 2008) and introduction of nutrients (unhatched eggs) (Vander Zanden et al., 2012). Predators of sea turtles may also modulate the extent to which sea turtles influence their environment through direct predation and/or by causing behavioural modifications that reduce predation risk. They are also important to limit overgrazing on seagrass meadows (Heithaus et al., 2008). Therefore, mortality factors such as predation affect both turtle populations and their ecosystems. Unfortunately, while interactions of sea turtles with anthropogenic activities have received great attention from the scientific community, predator-turtle interactions and the function of turtles as prey are still poorly understood (Heithaus, 2013; Rees et al., 2016).

Turtle eggs and nesting females and hatchlings on the beach are known to be taken by a variety of predators (e.g. jaguars, feral dogs and cats, foxes, coyotes, raccoons, ghost crabs, armadillos) (Heithaus, 2013). Several programs routinely monitor predation events, particularly on egg clutches and several studies have estimated predation rates (e.g. Butler et al., 2020; Erb & Wyneken, 2019; Espinoza-Rodríguez et al., 2023; Stokes et al., 2023). In contrast, information on predation at sea is scarce. Predation rates on hatchlings are relatively high in the waters off their natal beaches (e.g. Stewart & Wyneken, 2004; Witherington & Salmon, 1992), due to the high diversity and abundance of animal species in shallow coastal waters. As a strategy for reducing predation risk, hatchlings engage in rapid vigorous swimming immediately after entering the sea. This behaviour enables them to quickly distance themselves from the predator-rich coastal waters and reach offshore waters where the predator density is usually lower, thereby enhancing their survival chances (Salmon et al., 2009; Scott et al., 2014; Wyneken & Salmon, 1992). Subsequently, small juveniles of some species (*Caretta caretta* and *Lepidochelys kempii*) develop dorsal spines thought to deter predators (Salmon et al., 2015). Nevertheless, as sea turtles grow, increasing size gradually reduces their number of potential predators, as larger turtles are less likely to be preyed upon due to the physical limitations imposed by the mouth gape of predators (Salmon et al., 2018; Salmon & Scholl, 2014; Vose & Shank, 2003). Eventually, few potential predators remain for older turtles and these are primarily large sharks (Heithaus, 2013).

Our limited knowledge of at-sea predation of turtles hinders our understanding of the overall impact of predation on sea turtle populations as well as the strategies sea turtles use to evade predators in the open ocean. For instance, the impact of predation likely varies across regions and populations and if predator distributions change (Hammerschlag et al., 2022), geographic patterns of these impacts can also shift over time. Predator abundance may also have sub-lethal effects on turtle behaviour and habitat use, with possible population-level consequences for turtles (Heithaus et al., 2007). However, the actual predation rate at the population level remains unknown and elusive to investigation.

Studying the level of predation on sea turtles in their marine environment poses significant challenges, particularly in oceanic waters. The distribution range of these animals, encompassing entire oceans and their low density in open waters make observing predation events extremely difficult. With the exception of a few specific studies on predation of sea turtle hatchlings after they enter the sea (e.g. Gyuris, 1994; Wilson et al., 2019; Witherington & Salmon, 1992), information on turtle predation at sea comes primarily from turtles found successfully predated or just injured by a predator. Moreover, scavenging and actual predation are difficult to distinguish from turtles found dead (Aoki et al., 2023; Bornatowski et al., 2012; Stacy et al., 2021). Most of the current information is obtained from turtles observed during studies on other topics or from incidental observations (usually posted on the internet by recreational sea-goers). The latter category of 'non-conventional data sources' has increased with the spread of social media, smartphones and the general use of the internet and represents a citizen science opportunity for studies on animal conservation (Chowdhury et al., 2024; Morais et al., 2021; Sullivan et al., 2019; Toivonen et al., 2019). However, such information does not provide a quantification of the predation level (e.g. proportion of turtles predated) which is necessary to estimate the mortality of the juvenile stage at the population level (e.g. Mazaris et al., 2006).

The information about predation on turtles at sea has largely been collected opportunistically, without ties to greater objectives; it is fragmentary and lacks a comprehensive synthesis. This study therefore aims to synthesize available information on sea turtle predation at sea (vs. on nesting beaches) and to evaluate the potential of different approaches to advance the study of sea turtle predation ecology. To this end, we integrated multiple, complementary data sources—including a literature review, field observations of sea turtles with evidence of predation by sharks, observations of sharks with evidence of sea turtles in their diet and non-conventional online sources—to characterize predator diversity, identify patterns of predation across turtle species, life stages and regions. We hypothesized that, given adequate data, predation rates would differ across areas, species, life stages and time.

2 | MATERIALS AND METHODS

We collated data from four sources: (1) literature reviews; (2) field observations (stranding reports, nesting monitoring, rescue centre intakes or in-water captures) of sea turtles with evidence of predation (or attempted predation) by a shark; (3) field observations of sharks with evidence of sea turtles in their diet; and (4) non-conventional sources.

2.1 | Literature reviews

Because predation of turtles at sea is rarely the focus of a published article and is much more likely to be reported or mentioned among other observations or as additional information, a comprehensive literature review is difficult. However, a sample of literature sources can provide insights about general patterns, like the relative occurrence of different types of predation cases reported. With this approach, literature (published as of 2021) reporting cases of predation on sea turtles at sea was searched through two research engines: Scopus (SC) and Google Scholar (GS). SC searches for keywords only in the title, abstract and keywords of the source and combinations of sea turtle and predator taxa were used as keywords for the search: '[sea turtle genus and species]' AND '[predator keyword]'. For the latter, the common name of a predator group was used when it covered multiple potential predator species (i.e. when the group name was also embedded in the common names of individual species, such as 'shark' or 'seal'). Differently, the specific predator genus or species was used for groups with just a few species of interest, where the common name of the group (e.g. birds, fish) would mostly return non-relevant articles. Taxa most likely to be considered as possible turtle predators based on their size and/or trophic ecology were considered. Predation by other turtles was not considered. A total of 60 predator keywords (two higher-level groups and 58 genus or species; Table S1) representing six taxonomic groups (cartilaginous fish, bony fish, reptiles, birds, mammals) were used in combination with turtle species. A more extensive search was attempted through GS, which searches for keywords also in the body of the article. Since GS returns an overwhelming number of results, a third keyword ('predation') was added. Even so, GS typically returns thousands of results and potentially useful articles were selected based on the title and the text excerpt provided by GS in the search results window rather than reading every single article (which implies also obtaining the whole article) as that would not have been feasible. Since this approach is expected to produce false negatives (i.e. discarding articles with information of interest), to estimate the frequency of false negatives, 100 of the discarded articles were randomly selected and examined. Naturally, the choice of search tools may have influenced the results, as the publishing habits of sea turtle and shark biologists can affect the coverage these tools provide. Additional articles were found serendipitously (e.g. mentioned in other articles or communicated by people). All the resulting articles were examined and cases of predation upon sea turtles at sea were extracted and coded in terms of turtle and predator species, type of interaction (predation of live turtles or scavenging of carcasses), turtle life stage (as indicated by the original source: hatchling, adult and juveniles, that is all immature stages beyond hatchling but not yet adult), zone (neritic, oceanic) and geographic area (North and South Atlantic, Mediterranean, North and South Pacific and Indian Ocean, with 'north' and 'south' defined relative to the equator).

2.2 | Turtles with evidence of predation by shark

Evidence of predation by sharks (i.e. a shark-bite injury) represents the relatively most obvious and common evidence about marine predators of turtles. Data were assembled from published sources and from unpublished data (including turtle size) provided directly by the organizations that collected them, as represented by the authors (see Table 1 for all data sources). In the latter case, data were originally collected within local projects, each authorized by the relevant national authority for turtle handling. These studies were focused on turtles found under one of the following scenarios: those found dead or debilitated floating in the water or washed up on shore ('strandings'), those collected by 'rescue centres' (admitted for rehabilitation to rescue centres, usually after being found as strandings or captured in fishing gear; in some cases, these datasets include also stranding data), those observed while nesting ('nesting'), and those intentionally captured at sea

TABLE 1 Percentage of live and dead individual turtles documented with a shark-bite injury (*n* total individuals).

	Caretta caretta		*Chelonia mydas*		*Dermochelys coriacea*		*Eretmochelys imbricata*		*Lepidochelys kempii*		*Lepidochelys olivacea*		*Natator depressus*
Area/type	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**
Mediterranean Sea													
Nesting females													
Greece[a]	6.3 (2061)												
Turkey[b]	0.2 (1092)												
Spain[c]	20.0 (5)												
Stranding													
Spain[d]	0.3 (1410)	0.6 (169)											
Rescue center													
Israel[e]	9.3 (1191)		9.5 (305)		0.0 (4)								
Italy-Lampedusa[f]	1.6 (3282)												
Italy-Molfetta[g]	1.2 (414)												
Turkey[b]	0.0 (330)		0.7 (139)										
Spain[c]	0.0 (588)	3.0 (132)											
N Atlantic Ocean													
In-water captures													
Cayman Islands[h]							0.4 (232)						
Florida total[i]	7.8 (6725)		2.7 (4260)		0.0 (23)		0.9 (115)		3.6 (250)		100 (1)		
A—Gulf of Mexico N	0.0 (24)		0.7 (290)				0.0 (1)		0.6 (179)				
B—Gulf of Mexico S	2.6 (425)		1.3 (391)				0.0 (67)		0.0 (2)				
C—Atlantic coast S*	8.1 (6276)		3 (3579)		0.0 (23)		2.1 (47)		11.6 (69)		100 (1)		
Canada[j]	12.9 (62)												
Nesting females													
Florida[k]	2.0 (450)												
Florida[l]					71.2 (118)								
US Virgin Islands[m]					88.9 (9)								
Strandings													
Florida total[n]	3.2 (3341)	6.2 (22067)	3.0 (6742)	6.7 (14020)	1.4 (74)	4.4 (613)	0.4 (264)	2.8 (496)	1.7 (587)	8.3 (3929)	0.0 (4)	0.0 (1)	
A—Gulf of Mexico N	5.0 (239)	7.2 (1621)	3.9 (334)	8.9 (707)	0.0 (10)	0.0 (73)	0.0 (5)	0.0 (11)	3.2 (158)	11.8 (1100)			

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TABLE 1 (Continued)

Area/type	*Caretta caretta* Alive	*Caretta caretta* Dead	*Chelonia mydas* Alive	*Chelonia mydas* Dead	*Dermochelys coriacea* Alive	*Dermochelys coriacea* Dead	*Eretmochelys imbricata* Alive	*Eretmochelys imbricata* Dead	*Lepidochelys kempii* Alive	*Lepidochelys kempii* Dead	*Lepidochelys olivacea* Alive	*Lepidochelys olivacea* Dead	*Natator depressus* Alive
B—Gulf of Mexico S	3.7 (1086)	9.9 (6586)	2.6 (1949)	8.2 (4578)	0.0 (32)	0.0 (40)	1.0 (96)	6.4 (218)	1.5 (273)	7.9 (2094)	0.0 (1)		
C—Atlantic coast S*	3.2 (1082)	5.3 (5501)	5.0 (2155)	6.4 (6580)	4.0 (25)	0.0 (151)	0.0 (145)	0.0 (247)	0.0 (71)	0.0 (119)	0.0 (3)	0.0 (1)	
D—Atlantic coast N*	2.2 (934)	3.6 (8359)	1.2 (2304)	3.6 (2155)	14.3 (7)	7.7 (349)	0.0 (18)	0.0 (20)	1.2 (85)	5.0 (616)			
SW Atlantic Ocean													
Strandings													
Brazil total	0.0 (142)	0.2 (6430)	3.9 (5109)	1.8 (48952)	0.0 (3)	0.0 (338)	0.0 (26)	1.0 (300)			2.9 (67)	0.3 (3613)	
A—North coast[o]	0.0 (4)	0.0 (10)	0.0 (24)	0.2 (534)			0.0 (1)	0.0 (1)			0.0 (6)	0.0 (21)	
B—Northwest coast[p]			2.4 (41)	10.9 (566)			0.0 (10)	4.3 (23)			33.3 (3)	14.2 (7)	
C—Central coast[o]	0.0 (4)	1.1 (95)	0.0 (26)	0.2 (545)			0.0 (3)	0.0 (11)			0.0 (24)	0.2 (1719)	
D—South coast[o]	0.0 (134)	0.2 (6325)	3.9 (5018)	1.0 (47307)	0.0 (3)	0.0 (338)	0.0 (12)	0.8 (265)			2.9 (34)	0.3 (1866)	
Cape verde[q]	0.5 (11090)												
Pacific Ocean													
In-water captures													
Australia[r]	2.0 (118)		0.5 (273)										
Australia[s]	0.3 (320)												
Nesting females													
Papua New Guinea[t]					70.6 (34)								
Strandings													
Australia[u,*]	2.3 (217)		0.6 (2324)				0.0 (334)				6.3 (16)		2.7 (37)
Hawai'i[v]							12.5 (72)						
Indian Ocean													
In-water captures													
Australia total*	30.7 (352)		6.1 (428)										
Australia[w]	22.0 (132)		4.1 (170)										

(Continues)

TABLE 1 (Continued)

	Caretta caretta		*Chelonia mydas*		*Dermochelys coriacea*		*Eretmochelys imbricata*		*Lepidochelys kempii*		*Lepidochelys olivacea*		*Natator depressus*
Area/type	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**	**Dead**	**Alive**
Australia[x]	35.9 (220)		7.4 (258)										
Rescue centre													
Israel[e]							20.0 (10)						
Reunion (France)[y,*]	0.7 (288)	0.0 (19)	1.7 (60)	7.7 (52)			9.7 (31)	12.0 (25)					

Note: The sea turtles were either encountered while nesting (nesting females; $n=3769$), documented as a stranding that was found floating or washed ashore (stranding; 132,787), documented after rescue (rescue centre; $n=6870$) or captured during targeted studies (in-water captures; 13,159).

[a]a = ARCHELON [years: 2012–21].

[b]Pamukkale University [2008–21].

[c]Fundación Oceanogràfic [2010–22].

[d]Orós et al. (2016) [1998–2014].

[e]Israel Sea Turtle Rescue Center [1999–2022].

[f]Associazione Caretta caretta [2001–21].

[g]Associazione Panda Molfetta [2021].

[h]Blumenthal et al. (2009) [2000–07].

[i]In-water Research Group [2001–22].

[j]Hall and James (2021) [2011–18].

[k]Ataman et al. (2021) [2019–20].

[l]Klingshirn (2021) [2019–2021].

[m]Asada et al. (2021) [2015–18].

[n]Fish and Wildlife Research Institute [1980–2022].

[o]Instituto de Pesquisas Ambientais Littoralis [2015–22].

[p]Bornatowski et al. (2012) [2002–11].

[q]Sanchez-Sierra Campillo (2017) [2005–15].

[r]Limpus et al. (1992) [1968–89].

[s]Limpus et al. (1994) [1990–92].

[t]Hirth et al. (1993) [1989].

[u]Flint et al. (2017) [1996–2013].

[v]Brunson et al. (2022) [1982–2018].

[w]Heithaus et al. (2002) [1999–2000].

[x]Heithaus et al. (2005) [2000–03].

[y]Kelonia Turtle Care Center [2002–20].

*Areas where proportions of turtles with a shark-bite injury varied significantly among species (Fisher exact test).

for research ('captures'). Crescent-shaped bite marks on flippers, carapace or plastron were specifically sought in photos and information related to turtle records, and only these records were considered. Live and dead turtles were treated separately as predators can scavenge on turtles that died from other causes (Stacy et al., 2021). Records for which the sea turtle species was not identified were not included. Records were grouped by geographic area, turtle record type (strandings, rescue centre, nesting), turtle species and turtle condition (dead or alive). Geographic areas were defined arbitrarily as entire countries when the coastline was relatively short or bordered only one marine area, and as sub-country sectors when coastal heterogeneity warranted further subdivision (Table 1; Figure S1).

To assess shark scavenging on dead carcasses, proportions of turtles with bite marks among live and dead turtles were compared through a Fisher exact test, within the same country-species-type combination. A larger proportion of turtles with bite marks was expected in dead turtles due to scavenging in addition to predation. The following analyses were conducted on live turtles only.

To assess possible temporal trends of predation rates, a binomial Generalized Linear Model (GLM; *glm* function in R v 4.3.0, R Development Core Team, 2024) with year as a predictor was performed on those organization-area-type-species combinations with >1000 records of live turtles. To assess different predation rates among turtle species, for each area-type combination, a Fisher test with a Monte Carlo simulation was performed using the *fisher.test* function of the *stats* package. To investigate if the predation rate varied among marine regions, the proportions of turtles with a shark-bite injury in different areas were compared, with a Fisher test, for each turtle species-type combination occurring in at least two areas. To investigate if predation rate varied among size classes, the proportions of turtles with a shark-bite injury by 10-cm size class of stranded turtles were compared with a Fisher test, for species and area where such data were available at an adequate sample size. Then a *post hoc* pairwise comparison with Benjamini–Hochberg correction was conducted using the *pairwise.prop.test* function of the *stats* package.

2.3 | Sharks with evidence of turtles in their diet

Evidence of predation upon turtles was sought in the form of stomach contents of sharks examined in the context of studies on shark diet. Data were assembled from published sources and unpublished data of the authors. Data consisted of the presence/absence of turtle parts in the stomach of individual sharks with non-empty stomachs. When sample size was adequate, differences in the frequency of ingested turtles among shark species or among different sexes and life stages of the same shark species were investigated through a Fisher Exact test followed by a *post hoc* pairwise comparison with Benjamini–Hochberg correction, using the functions *fisher.test* of the stats package and *fisher.multcomp* of the RVAideMemoire package, respectively.

2.4 | Non-conventional sources

Non-conventional sources of information (hereafter NCS) were explored to identify turtle and predator interactions and the geographic areas with a higher frequency of these interactions. Searches for turtle predators were limited to sharks only because other predators were assumed to be less likely to be reported by NCS, for different reasons such as predator size, visibility from the sea surface, abundance and overlapping distribution with turtles and tourists. NCS vary from general to specific search engines for multimedia content, including digital newspaper libraries. We excluded social media, which largely reshare the same content and proved redundant in a pilot search (Twitter, Facebook and Instagram). For the aims of the present study, six NCS were selected because they have a wide coverage in regions where turtle predation events are assumed to occur and provide open access information in the form of news, images and videos. These were Google News, Google Images and You Tube, Baidu News, Baidu Images and Youku.com (the latter three for areas not covered or less covered by the first three). All these NCS can be searched by setting a specific period and language.

All searches were constrained to the period 2000–2022, reflecting the advent of widespread internet and smartphone use during that period. To minimize geographical biases, searches were repeated in six languages assumed to be used in most of the regions frequented by turtles: Arabic, Chinese (simplified), English, French, Portuguese and Spanish. Hindi was not considered because it was assumed that English is spoken throughout India and sources and contents are frequently translated into English or have an English version. Search keywords were translated to these other languages from English either by native speakers or simultaneously by two online translators (DeepL Translator, https://www.deepl.com/en/translator; Google Translator, https://translate.google.com/). Search keywords were 'turtle' and 'shark' combined with other terms related to a predation event: 'attack', 'bit' (included in bite, bites, bitten) and 'eat' (included in eats, eaten). When the number of results provided by a search was very high (e.g. with Google Images), only the first 100 results were considered. Records without information on place and date or where the spontaneity of the event was in doubt (e.g. use of bait or attractants) were not considered. All the retained records were examined and coded in terms of turtle and shark species, type of interaction (predation or scavenging) and geographic area (North and South Atlantic, North and South Pacific, Indian).

3 | RESULTS

3.1 | Literature review: Predator diversity by area and habitat

Searches in GS and SC provided a total of 47,326 results (46,990 GS, 336 SC), which were reduced to 6977 after removing duplicates (6728 GS, 249 SC). The selection process for GS results was estimated to provide 2% of false negatives. A total of 297 potentially useful articles were identified, of which 45 were found to contain relevant information. Serendipitous sources (citations in other articles or author communications) contributed an additional 93, for a total of 138 useful articles (see the Supporting Information for a complete list). These reported on at least 51 different predators (41 identified at species level and seven belonging to a genus or a family different from those of the other species), seven turtle species and 206 different predator/turtle species/turtle stage/area combinations (Table 2, Figures 1 and 2). Most reports with known habitat were from the neritic zone (Figure 1). Sharks were the most reported predators and predated on all turtle life history stages. Tiger sharks (*Galeocerdo cuvier*) were by far the most important species, with white shark (*Carcharodon carcharias*) and bull shark (*Carcharhinus leucas*) also of note. Bony fish predators were only reported for predation on the smaller size classes of turtles (hatchlings and juveniles), with dolphinfish (*Coryphaena hippurus*) and Atlantic tarpon (*Megalops atlanticus*) being the relatively more represented species. Other taxa of note were crocodilians and killer whale (*Orcinus orca*). *Caretta caretta* and *Chelonia mydas* were the most reported turtle prey. Hatchlings were the least reported turtle stage, but also the only category for which predation rates were purposely quantified, ranging from 1.5 to 93.6% (Table 3).

3.2 | Turtles with evidence of shark predation

A total of 156,726 turtle records from 1980 to 2021 were assembled, including all the seven species (82,680 *Chelonia mydas*, 62,415 *Caretta caretta*, 4768 *Lepidochelys kempii*, 3725 *L. olivacea*, 1883 *Eretmochelys imbricata*, 1218 *Dermochelys coriacea*, 37 *Natator depressus*), across 15 countries (Table 1) and six ocean sub-basins (Figure 3). Of these, 5107 turtles were found to have evidence of a shark-bite injury (Table 1).

The proportions of live and dead turtles with evidence of shark-bite injury were significantly different in several cases, with a higher proportion observed among dead turtles (suggesting scavenging), except in one case where the opposite was observed (Table S2). To exclude cases of scavenging, all subsequent results were only for turtles that were found alive.

Positive temporal trends of proportions of turtles with a shark-bite injury were detected by GLM in eight out of the nine tested groups (combinations of organization-area-type-species) (Table 4; Figures S2–S4). The proportion of turtles with a shark-bite injury varied significantly among species (Fisher exact test; $p<0.05$) in six areas (see Table 1 for which areas and for proportions). The proportion of turtles with a shark-bite injury varied significantly among areas (Fisher exact test; $p<0.01$) in *C. caretta* (all types), *C. mydas* (captures, strandings and rescue centre), *E. imbricata* (strandings) and *L. kempii* (captures) (Table S3). Significant differences in the proportions of stranded turtles with a shark-bite injury by size class were detected in Florida *Chelonia mydas* (Fisher exact test; $p<0.001$; $n=5882$) and Brazil (Fisher exact test; $p<0.001$; $n=2698$)—with a higher proportion observed in large size classes in Florida and the opposite in Brazil (Table S4)—while in *Caretta caretta* in Florida the difference was just close to the significant threshold (Fisher exact test; $p=0.052$; $n=1657$).

3.3 | Sharks with evidence of turtles in their diet

Cases of parts of turtles found in the gut of a total of 3927 sharks examined of 12 different species are reported in Table 5. Among these cases, ingested parts of turtles were reported only from tiger sharks (*Galeocerdo cuvier*) and white sharks (*Carcharodon carcharias*), although the sample sizes for other shark species were small. In one area (Reunion), the sample size was adequate to compare between two shark species, showing that the proportion of individuals that ingested parts of turtles was significantly higher in adult tiger sharks (*Galeocerdo cuvier*) than in adult bull sharks (*Carcharhinus leucas*), where no turtle remains were observed (Fisher Exact test; $p<0.001$; $n=190$). Proportions of tiger sharks that ingested turtles were higher in adults than in immatures (Fisher Exact test; $p<0.01$; $n=527$). No significant difference was detected between the sexes (Fisher Exact test; $n=527$).

3.4 | Non-conventional sources

A total of 34 events of turtles predated or scavenged by sharks were collected from NCS (Figure 4; Table S5). These events were found in Google Images ($n=18$, 53%, which redirected to other websites) or YouTube ($n=16$, 47%). Sources were either Images (27%) or Videos (73%). Most of the events were reported in English ($n=27$, 79%), followed by Spanish ($n=3$, 9%), French ($n=2$, 6%), Portuguese ($n=1$, 3%) and Arabic ($n=1$, 3%). The events were reported within the following oceans: Indian ($n=17$, 50%), North Atlantic ($n=10$, 29%), North Pacific ($n=4$, 12%), South Atlantic ($n=1$, 3%), South Pacific ($n=2$, 6%). Most event types were attempted predation ($n=14$, 41%), successful predation ($n=10$, 29%), with few incidents of scavenging ($n=1$, 3%), while 9 (26%) of the interactions could not be confidently assigned (uncertain). The turtle species involved in the reported events were the following: *Caretta caretta* ($n=12$, 35%), *Chelonia mydas* ($n=10$, 29%), *Eretmochelys imbricata* ($n=5$, 15%), *Lepidochelys kempii* ($n=1$, 3%), *Lepidochelys olivacea* ($n=1$, 3%), *Natator depressus* ($n=1$, 3%) and unknown ($n=4$, 12%). The shark species involved were tiger shark ($n=22$, 65%), bull shark ($n=1$, 3%), white shark ($n=1$, 3%) and unknown ($n=10$, 29%). Fifteen videos showed the interaction between sharks and turtles, with turtles displaying specific defence behaviours like orienting the dorsal part of the carapace to the shark, turning faster than the shark to elude bites, fleeing and biting the shark.

4 | DISCUSSION

Despite the limited and often anecdotal nature of existing data, assembling a large number of dispersed records enabled this study to outline several general aspects of sea-turtle predation at sea, including predation diversity, spatio-temporal patterns, differences among turtle species and size classes and the most challenging knowledge

TABLE 2 Occurrence (%) in 138 scientific articles (see Section 3) of interaction between each species of predator and the species or life stage of sea turtles (206 combinations in total), listed in decreasing order of total value.

	Turtle species								Turtle stage					
Predators	**CC**	**CM**	**DC**	**EI**	**LK**	**LO**	**ND**	**UN**	**A**	**JA**	**J**	**H**	**NA**	**Tot**
Chondrichthyes	21.5	14.1	2.4	4.9	2.0	2.9	1.0	16.6	8.3	24.9	5.4	5.4	21.5	65.4
Galeocerdo cuvier	7.3	8.3	1.0	3.9	0.5	1.0	1.0	11.2	4.4	12.2	2.0	–	15.6	34.1
Unidentified shark	7.8	2.4	0.5	0.5	1.0	0.5	–	0.5	2.9	8.3	1.0	–	1.0	13.2
Carcharodon carcharias	2.9	0.5	0.5	–	–	–	–	1.0	1.0	2.4	1.0	–	0.5	4.9
Carcharhinus leucas	0.5	0.5	0.5	–	–	1.0	–	1.0	–	1.5	–	–	2.0	3.4
Carcharhinus sorrah	1.0	1.0	–	0.5	–	–	–	–	–	–	–	2.4	–	2.4
Carcharhinus falciformis	0.5	0.5	–	–	–	–	–	1.0	–	0.5	0.5	0.5	0.5	2.0
Carcharhinus melanopterus	–	1.0	–	–	–	–	–	–	–	–	–	1.0	–	1.0
Rhizoprionodon terraenovae	1.0	–	–	–	–	–	–	–	–	–	–	1.0	–	1.0
Sphyrna mokarran	–	–	–	–	0.5	–	–	0.5	–	–	0.5	–	0.5	1.0
Carcharhinus brevipinna	0.5	–	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Carcharhinus obscurus	–	–	–	–	–	–	–	0.5	–	–	–	–	0.5	0.5
Carcharhinus plumbeus	–	–	–	–	–	–	–	0.5	–	–	–	–	0.5	0.5
Isurus oxyrinchus	–	–	–	–	–	0.5	–	–	–	–	0.5	–	–	0.5
Mustelus antarcticus	–	–	–	–	–	–	–	0.5	–	–	–	–	0.5	0.5
Osteichthyes	4.9	7.8	2.0	1.0	0.5	0.5	0.5	2.9	–	–	2.9	17.1	–	2–
Coryphaena hippurus	1.0	1.0	–	–	0.5	0.5	–	–	–	–	–	2.9	–	2.9
Megalops atlanticus	1.0	–	1.0	–	–	–	–	0.5	–	–	–	2.4	–	2.4
Choerodon cyanodus	–	1.0	–	–	–	–	–	–	–	–	0.5	0.5	–	1.0
Lutjanus griseus	0.5	–	0.5	–	–	–	–	–	–	–	–	1.0	–	1.0
Sphyraena barracuda	–	0.5	–	–	–	–	–	0.5	–	–	–	1.0	–	1.0
Promicrops lanceolatus	–	0.5	–	0.5	–	–	–	–	–	–	1.0	–	–	1.0
Arius felis	–	–	–	–	–	–	–	0.5	–	–	–	0.5	–	0.5
Caranx crysos	–	–	–	–	–	–	–	0.5	–	–	–	0.5	–	0.5
Caranx latus	–	–	0.5	–	–	–	–	–	–	–	–	0.5	–	0.5
Centropristes striatus	0.5	–	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Cromileptes altivelis	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Dicentrarchus labrax	0.5	–	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Epinephelus itajara	–	–	–	0.5	–	–	–	–	–	–	0.5	–	–	0.5
Epinephelus morio	–	–	–	–	–	–	–	0.5	–	–	–	0.5	–	0.5
Epinephelus sp.	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Epinephelus tauvina	–	0.5	–	–	–	–	–	–	–	–	0.5	–	–	0.5
Lethrinus mahsena	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Lophius sp.	0.5	–	–	–	–	–	–	–	–	–	0.5	–	–	0.5
Lutjanus argentimaculatus	–	–	–	–	–	–	0.5	–	–	–	–	0.5	–	0.5
Lutjanus bohar	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Lutjanus carponotatus	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5
Lutjanus griseus	–	–	–	–	–	–	–	0.5	–	–	–	0.5	–	0.5
Muraenidae	–	0.5	–	–	–	–	–	–	–	–	–	0.5	–	0.5

(Continues)

TABLE 2 (Continued)

Predators	Turtle species								Turtle stage					Tot
	CC	CM	DC	EI	LK	LO	ND	UN	A	JA	J	H	NA	
Pomatomus saltatrix	0.5	—	—	—	—	—	—	—	—	—	—	0.5	—	0.5
Scaridae	—	0.5	—	—	—	—	—	—	—	—	—	0.5	—	0.5
Serranidae	—	0.5	—	—	—	—	—	—	—	—	—	0.5	—	0.5
Tylosurus	—	0.5	—	—	—	—	—	—	—	—	—	0.5	—	0.5
Unidentified fish	0.5	—	—	—	—	—	—	—	—	—	—	0.5	—	0.5
Reptilia	1.0	1.5	0.5	—	—	0.5	1.0	—	2.9	1.0	0.5	—	—	4.4
Alligator mississippiensis	1.0	1.0	—	—	—	—	—	—	0.5	1.0	0.5	—	—	2.0
Crocodylus porosus	—	0.5	—	—	—	—	1.0	—	1.5	—	—	—	—	1.5
Crocodylus acutus	—	—	—	—	—	0.5	—	—	0.5	—	—	—	—	0.5
Crocodylus sp.	—	—	0.5	—	—	—	—	—	0.5	—	—	—	—	0.5
Aves	—	—	0.5	—	—	—	0.5	—	—	—	0.5	0.5	—	1.0
Haliaeetus leucogaster	—	—	0.5	—	—	—	—	—	—	—	—	0.5	—	0.5
Mammalia	1.0	0.5	2.4	—	—	0.5	—	0.5	2.4	2.0	0.5	—	—	4.9
Orcinus orca	—	—	2.4	—	—	0.5	—	0.5	1.5	2.0	—	—	—	3.4
Monachus monachus	1.0	0.5	—	—	—	—	—	—	1.0	—	0.5	—	—	1.5
Cephalopoda	—	—	—	—	—	—	—	0.5	—	—	—	0.5	—	0.5
Sepiateuthis sepiodea	—	—	—	—	—	—	—	0.5	—	—	—	0.5	—	0.5
Unidentified predators	2.4	1.0	0.5	—	—	—	—	—	0.5	—	0.5	2.9	—	3.9
Total	30.7	24.9	8.3	5.9	2.4	4.4	2.9	20.5	14.1	27.8	10.2	26.3	21.5	100.0

Note: Relative occurrence may be skewed by research biases and therefore may not represent actual biological occurrence. CC = *C. caretta*, CM = *C. mydas*, DC = *D. coriacea*, EI = *E. imbricata*, LK = *L. kempii*, LO = *L. olivacea*, ND = *N. depressus*, UN = Undefined; H = Hatchling, J = Juvenile, A = Adult, JA = unknown if Juvenile or Adult (not hatchlings), NA = not available.

gaps. In particular, current knowledge is almost entirely restricted to predation in neritic waters, due to the inherent challenges of studying this topic in oceanic environments. This study shows that, while conducting a comprehensive review of the subject is challenging and all approaches have inherent limitations, each can nonetheless offer valuable insights into specific aspects and contribute to the overall picture.

4.1 | Predator diversity and turtle life-stage predation gradient

Sea-turtle predation risk varies strongly across life stages, with many predators targeting small turtles and far fewer capable of preying on larger juveniles and adults. The literature review identified 44 marine predators, primarily bony and cartilaginous fish, with the latter dominating reported occurrences. The data presented here indicate that predation risk declines sharply from hatchlings to large juveniles and adults, thereby providing empirical support for the common assumption that mortality rates decrease with age. Beach-run studies (Table 3) report predation rates on hatchlings only during the very short period immediately after they enter the sea. It is therefore likely that the overall predation rate for turtles of that size—over a period much longer than the observed window—is substantially higher. Although comparable predation rates are not available for large turtles—because such estimates would require monitoring free-ranging individuals as is done for hatchlings—dead stranded turtles can still provide some insight. Stranded turtles represent animals that died from a variety of causes, including predation. However, the proportion of dead turtles showing evidence of predation is much lower than the true predation rate because it must be scaled by the (unknown) overall mortality rate in the population. For example, if 5% of dead turtles show predation marks and the overall mortality rate is 10%, then predation would account for only 0.5% mortality. Thus, although we cannot estimate predation-related mortality in stranded turtles without knowing overall mortality, the true predation rate must be far lower than the observed proportion of turtles with bite marks—also because some of these marks are due to scavenging rather than predation. Given that the bite-mark frequencies observed in dead stranded turtles (a strong overestimate of predation rate) are of the same order of magnitude as the predation rates reported for hatchlings (a strong underestimate), it follows that predation on larger turtles is much lower than predation on hatchlings.

Both these size classes (hatchlings and large turtles) are studied in coastal neritic waters where predator density is presumed to be higher. In contrast, post-hatchlings and small juveniles frequenting oceanic waters remain understudied because they disperse beyond

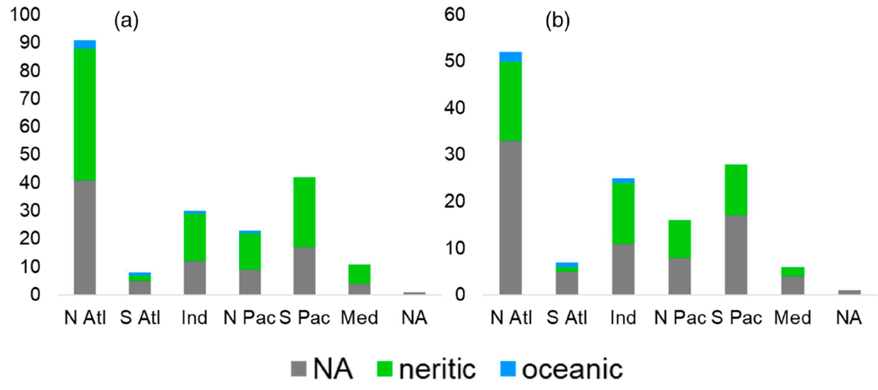

FIGURE 1 Number of predator-turtle interaction (a; $n = 206$) and number of shark-turtle interaction (b; $n = 135$) in different habitats from 138 scientific articles (see Section 3) (NA = not available) and Oceanic sub-basin (N Atl = North Atlantic, S Atl = South Atlantic, Ind = Indian Ocean, N Pac = North Pacific, S PAc = South Pacific, Med = Mediterranean).

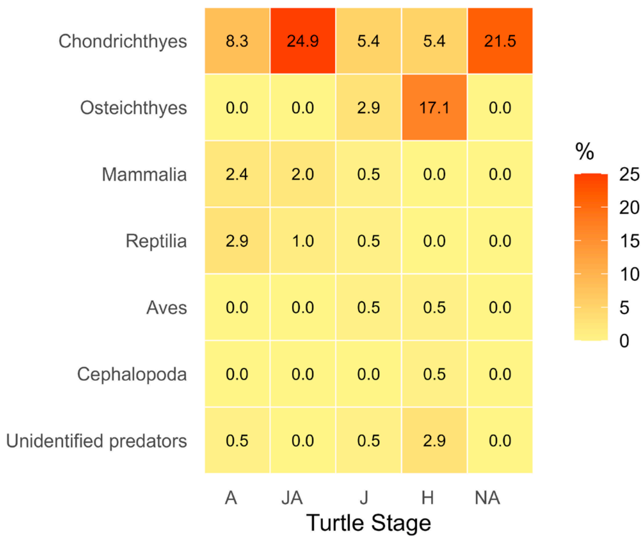

FIGURE 2 Occurrence (%) in 138 scientific articles (see Results) of interaction between predator group and life stage of sea turtles (see Table 2; $n = 206$). H = Hatchling, J = Juvenile, A = Adult, JA = Juvenile to Adult, NA = not available.

direct observation. While their small size makes them vulnerable to predators capable of ingesting them whole, this vulnerability may be partly mitigated by the typically lower predator density of oceanic zones. This ontogenetic pattern aligns with known turtle antipredator adaptations: cryptic colouring and frantic swimming in hatchlings, rapid growth to escape gape-limited predation, and finally a large body with a thickened carapace which limits the predator assemblage from many taxa—mostly bony fishes—preying on hatchlings and small juveniles, to a few large predators such as seals, crocodiles and large sharks preying on large juveniles and adults (Heithaus, 2013; Salmon et al., 2015, 2018; Salmon & Scholl, 2014; Vose & Shank, 2003).

However, the number and proportion of predator species reported in the scientific literature cannot, alone, truly inform about the relative importance of different predators for the turtle populations, because of inherent biases. Most records reported here involved *Caretta caretta* and *Chelonia mydas*, reflecting the general bias in published turtle research efforts (Rees et al., 2016). Similar biases may also affect the representation of turtle size (and life stage) and predator species. The observed bias toward larger turtles is likewise consistent with the overall research bias on large turtles (Wildermann et al., 2018), even though sea turtle populations consist predominantly of small (young) individuals (e.g. Casale & Heppell, 2016), a trait likely evolved in response to high predation pressure at small sizes. As a consequence of the greater focus on large turtles, predators of small turtles are likely underrepresented in the scientific literature.

4.2 | Predation by sharks

Sharks emerge as the dominant predators of sea turtles across all evidence sources, shaping turtle behaviour, influencing mortality patterns and driving substantial variation in predation risk across species, sizes and regions. However, this dominance can also be due to the general research bias toward large turtles in neritic waters. A strong predation pressure by sharks would explain the behavioural toolkit of sea turtles against sharks, of which the NCS videos here reported show some examples: keeping the dorsal carapace facing the attacker, biting the shark and rapid directional changes that exploit the shark's poorer manoeuvrability. These innate defensive behaviours are triggered by visual cues, as evidenced by turtles' reactions to shark-shaped decoys (Bostwick et al., 2014). The effectiveness of these tactics might differ among species, as suggested by the faster speed and turns of *Chelonia mydas* than *Caretta caretta* when chased by humans (Heithaus et al., 2002). With an adequate sample size, videos showing interactions could allow us to describe the fine components of defence behaviour evolved by sea turtles and possible differences among species.

Results indicate a great difference in predation on turtles among shark species, with tiger sharks being by far the main shark predator of turtles. This was suggested by several authors (Bornatowski et al., 2012; Fitzpatrick et al., 2012; Witzell, 1987) and is here supported by three different lines of evidence: (i) higher predation rates by tiger than bull sharks in the same area, (ii) the predominance of tiger shark reports in published accounts and (iii) their dominance among NCS. Tiger sharks seem to be specialized feeders of sea turtles (Witzell, 1987), and the results presented here provide further evidence that the importance of turtles in their diet increases as sharks grow (Lowe et al., 1996; Simpfendorfer et al., 2001). This can

TABLE 3 Predation rates on sea turtle hatchlings after entering the sea.

Region/country	Turtle species	Predation rate % (*n*)	Monitoring period (min)	Source
Atlantic				
Bermuda	*Chelonia mydas*	5.6 (18)	60–240	Frick (1976)
	Caretta caretta	13.3 (45)	5–15	Frick (1976)
Cape Verde	*Caretta caretta*	9.1 (11)	20–480	Scott et al. (2014)
Costa Rica	*Dermochelys coriacea*	2.3 (43)	83 (average)	Hoover et al. (2020)
Florida	*Caretta caretta*	7.2 (235)	15–30	Glenn (1996)
	Caretta caretta	5.1 (217)	15	Stewart and Wyneken (2004)
	Caretta caretta	4.6 (240)	15	Whelan and Wyneken (2007)
	Caretta caretta	6.8 (74)	50–120	Wyneken and Salmon (1992)
	n/a	26.3 (152)	15	Wyneken (2000)
Mediterranean				
Turkey	*Caretta caretta*	4.8 (62)	30	Türkecan and Yerli (2007)
Indo-Pacific				
Australia	*Chelonia mydas*	93.6 (47)	10–20	Gyuris (1994)
	Natator depressus	72.0 (61)	80	Wilson et al. (2019)
Malaysia	*Chelonia mydas*	61.9 (21)	1–240	Pilcher et al. (2000)
Papua New Guinea	*Dermochelys coriacea*	1.5 (68)	30–300	Tapilatu et al. (2019)

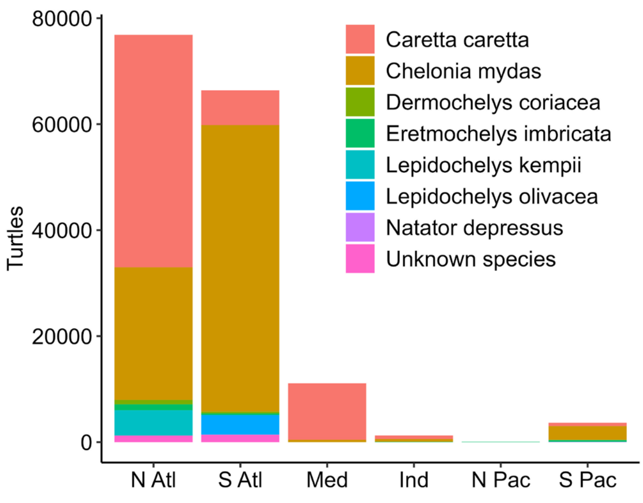

FIGURE 3 Number of turtle records by Oceanic sub-basin (N Atl = North Atlantic, S Atl = South Atlantic, Ind = Indian Ocean, N Pac = North Pacific, S PAc = South Pacific, Med = Mediterranean; see Table 1 for details).

be intuitively related to the increase in mouth size, bite power and teeth size and shape.

Although the proportion of live turtles documented with a shark-bite injury represents just an index of the actual predation rate, such an index allows valuable comparisons. For instance, results show that different turtle species may have varying vulnerabilities to shark predation. This difference cannot be explained by species size only, since a higher proportion of shark-bite injuries of *Caretta caretta* than of both smaller and larger species was observed in turtles stranded in the same region. Fine-scale distribution (preferred habitat) and behaviour are more likely explanatory factors. For instance, different escape abilities were the factor suggested for the lower predation rate observed among *Chelonia mydas* than *Caretta caretta* in Australia (Heithaus et al., 2002). In this respect, the higher proportion of *Dermochelys coriacea* with evidence of shark-bite injuries than *Caretta caretta* among turtles nesting in Florida may be more likely due to different areas and habitats frequented by the adults of these species, although *Dermochelys coriacea* is known to frequent the oceanic zone (Bolten, 2003) where predators are supposed to occur at lower density than in neritic waters. A high proportion of *Dermochelys coriacea* with shark-bite injuries was also reported from the US Virgin Islands, where females tend to move offshore during the internesting period to reduce the likelihood of shark encounters (Asada et al., 2021).

Within a single species, predation rate by sharks varied among size classes. However, the fact that different size effects in different areas were observed in the same species (*Chelonia mydas*) and that no size effects were detected in another species (*Caretta caretta*) suggests that other factors associated with size (e.g. different spatial distribution among size classes) primarily affect the observed predation rate, confounding the general decrease in predation rate with turtle size discussed above. Accordingly, in the same turtle species and area, shark predation rates can vary among subareas, probably due to different turtle-to-shark ratios or different fine-scale overlapping due to ecological differences, although potential artefacts from partially opportunistic data collection cannot be ruled out.

TABLE 4 Results of a binomial GLM with year as predictor of the proportion of turtles with shark-bite injury.

Ocean	Area	Type	Turtle species	Years	*N*	Slope	p_value
NWA	Florida-B	Stranding	*Caretta caretta*	1980–2022	1086	0.145	–
NWA	Florida-B	Stranding	*Chelonia mydas*	1980–2022	1949	0.054	0.011
NWA	Florida-C	Stranding	*Caretta caretta*	1980–2022	1082	0.044	0.027
NWA	Florida-C	Stranding	*Chelonia mydas*	1980–2022	2155	0.054	0.000
NWA	Florida-C	Capture	*Caretta caretta*	2001–2022	6234	0.045	–
NWA	Florida-C	Capture	*Chelonia mydas*	2001–2022	3051	0.067	0.000
MED	Israel	Rescue	*Caretta caretta*	1999–2022	1191	0.041	0.023
MED	Italy-Lampedusa Island	Rescue	*Caretta caretta*	2001–2021	3282	−0.037	0.136
SWA	Brazil-D	Stranding	*Chelonia mydas*	2015–2022	5018	0.240	–

Note: For area sectors of Brazil and Florida see Figure S1.

Abbreviations: MED, Mediterranean Sea; NWA, northwest Atlantic Ocean; SWA, south-west Atlantic Ocean.

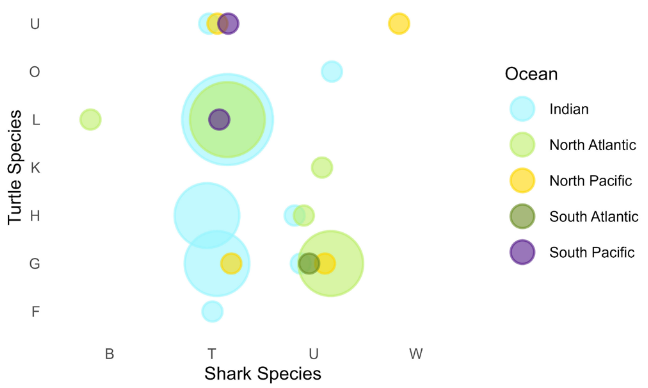

FIGURE 4 Shark versus turtle interactions by species recorded in non-conventional sources (NCS, $n=36$, see text) by Ocean. Turtle species: F = Flatback, G = Green, H = Hawksbill, K = Kemp's Ridley, L = Loggerhead, O = Olive Ridley, U = Unidentified. Shark species: B = Bull shark, T = Tiger shark, U = Unidentified, W = White shark. The smallest and largest circles represent 1 and 6 interactions, respectively. Circles are jittered on the *x* axis for better visualization.

Predation rate by sharks seems to vary among regions too, as expected because of different turtle (abundance) and shark (species and abundance) occurrence, although methodological differences among different projects cannot be ruled out. However, such differences may not be static and the loss (or recovery) of apex predators is likely to shift local predation regimes on turtles in divergent directions.

In this respect, the observed increase in predation rates across different areas and species is intriguing. It may indicate an increasing shark-to-turtle ratio resulting from local changes in shark or turtle abundance, although the opposite would be expected with the general decline of shark populations (Pacoureau et al., 2021) in contrast to sea turtles (Mazaris et al., 2017). It may also be an artefact due to heightened attention to turtle injuries. These results encourage continued monitoring of predation rates in relation to the population size of both turtles and sharks.

Inferring the importance of mortality induced by shark predation on large turtles is difficult. While live turtles are not the appropriate category to estimate mortality rates by different causes, in dead turtles predation and scavenging are confounded, and the proportion of carcasses with evidence of attack can be considered as the maximum mortality. Even so, shark predation seems to be a minor mortality factor compared to anthropogenic threats (e.g. bycatch, vessel strike) but probably also compared to other natural factors either identified or hidden, at least in part, under the 'unknown' category (Brunson et al., 2022; Casale et al., 2010; Flint et al., 2017; Foley et al., 2019). It is possible, however, that the current level of shark predation is lower than the natural one if shark populations have been reduced (Pacoureau et al., 2021; Simpfendorfer et al., 2023) more than sea turtle populations.

4.3 | Most promising approaches for investigating sea turtle predation at sea

Among the approaches currently available for studying sea-turtle predation at sea, evidence of predation on turtles encountered in the field—whether captured, nesting, incidentally caught or stranded—emerges as the most informative, although each method has important limitations that shape what can and cannot be learned. In particular, this approach can provide limited or no information on the smaller size classes of the turtle population (the size that is more likely to be ingested as a whole) and on large predators that can attack large turtles (notably sharks). First, such data can provide information on turtle species more vulnerable to predation and on the predator species (only for a few species of sharks that can be recognized by the signs left). Second, since present results show that spatial and temporal differences can be statistically detected, this approach can be used for comparing predation levels among places or, even more interesting, to monitor trends, assuming that other factors remain constant over time. For spatial comparisons, potentially affected by differences among local research projects,

TABLE 5 Percentage of sharks with part of sea turtles found in the gut.

Ocean	Country	Shark species	% sharks with turtles (*n*)	% non-empty sharks with turtles (*n*)	Source
WIO	Reunion	*Carcharhinus albimarginatus*	0.0 (1)		1
		Carcharhinus amblyrhynchos	0.0 (1)	0.0 (1)	1
		Carcharhinus leucas	0.0 (301)	0.0 (138)	1
		Carcharhinus obscurus	0.0 (1)		1
		Carcharhinus plumbeus	0.0 (4)	0.0 (2)	1
		Carcharodon carcharias	0.0 (1)		1
		Galeocerdo cuvier Juveniles	4.3 (327)	11.0 (127)	1
		Galeocerdo cuvier Adults	18 (200)	32.1 (112)	1
		Isurus oxyrhincus	0.0 (2)		1
		Loxodon macrorhinus	0.0 (13)	0.0 (4)	1
		Sphyrna lewini	0.0 (20)		1
		Sphyrna zygaena	0.0 (3)	0.0 (1)	1
	South Africa	*Galeocerdo cuvier*	12.8 (39)	12.8 (39)	2
		Galeocerdo cuvier	4.4 (778)	5.5 (628)	3
EIO	Australia	*Galeocerdo cuvier*	18.2 (225)	45.0 (84)	4
		Galeocerdo cuvier	1.6 (252)	27.0 (15)	5
PAC	Australia	*Galeocerdo cuvier*	1.7 (59)	4.5 (32)	6
		Galeocerdo cuvier	20.9 (86)		7
		Galeocerdo cuvier	6.9 (835)	10.4 (558)	8
	Hawaii	*Galeocerdo cuvier* (<200 cm)	0 (28)		9
		Galeocerdo cuvier (200–300 cm)	5.9 (118)	7.5 (93)	9
		Galeocerdo cuvier (>300 cm)	11.9 (135)	15.1 (106)	9
		Galeocerdo cuvier	15.4 (201)	17.6 (176)	10
	Philippines	*Galeocerdo cuvier*	30.2 (43)	59.1 (22)	11
	Malaysia	*Galeocerdo cuvier*	40.0 (5)	66.6 (3)	12
MED	Central Mediterranean	*Carcharodon carcharias*	17.0 (24)	17.0 (24)	13
ATL	USA	*Galeocerdo cuvier*	20.6 (34)	20.6 (34)	14
		Galeocerdo cuvier	71.4 (7)	71.4 (7)	15
		Galeocerdo cuvier	26.7 (15)	28.6 (14)	16
		Galeocerdo cuvier (<101 cm)	0.0 (53)		17
		Galeocerdo cuvier (101–250 cm)	15.3 (111)	16.4 (104)	17
		Galeocerdo cuvier (>250 cm)	40 (5)	40 (5)	17

Note: If available, the percentage is also given for the subsample of sharks with non-empty gut, that is excluding those sharks where no gut contents were found. Sources, 1: Present study (M. Barret, S. Jaquemet), 2: Bass et al. (1975)*, 3: Dicken et al. (2017), 4: Simpfendorfer et al. (2001), 5: Heithaus (2001), 6: Stevens (1984)*, 7: Present study (B. Holmes), 8: Simpfendorfer (1992), 9: Lowe et al. (1996), 10: Balazs (1980), 11: Kauffman (1950)*, 12: (Hendrickson, 1958)*, 13: Fergusson et al. (2000), 14: Bell and Nichols (1921)*, 15: Gudger (1949)*, 16: Dodrill (1977)*, 17: Aines et al. (2018). *in Witzell (1987).

Abbreviations: ATL, Atlantic Ocean; EIO, east Indian Ocean; MED, Mediterranean Sea; PAC, Pacific Ocean; WIO, west Indian Ocean.

a careful standardization of what type of sign is considered a predator bite is needed. For instance, missing limbs are often attributed to shark attacks, even though they can also be the result of entanglement in fishing gears, so they represent a maximum level of attack rate. Although shark wounds may vary by region and life stage, a semi-circular pattern of multiple sharp wounds (created by the shark's teeth) provides stronger evidence of a shark attack and would represent a simple standardization easy to implement. Standardization would also help in monitoring trends at the same site by the same research team, although in this case possible biases due to different methods over time are less likely. In addition to turtles alive at time of capture (i.e. directly captured for research, encountered while nesting or incidentally captured in fishing gear), stranded turtles represent an easily accessible sample in several countries. However, they can be found either dead or alive and—as also shown by present results—the two categories should be analysed separately because true predation and scavenging are confounded among dead turtles (Stacy et al., 2021). Although a careful examination of the injuries may allow distinction between pre- and post-mortem attacks, as well as identification of the shark species (Aoki et al., 2023; Bornatowski et al., 2012; Stacy et al., 2021), this approach requires specific skills and relatively fresh carcasses. Therefore, a standardization that considers only live turtles for monitoring shark predation may be more feasible, easier to implement and ultimately more effective for increasing the amount of data suitable for calculating predation rates worldwide.

Predation of small size classes of turtles is clearly a major knowledge gap and challenge. Since small turtles can be swallowed whole and typically disperse across wide oceanic areas, predation on this stage is extremely difficult to investigate, except when they aggregate off their natal beaches. A few studies (Table 3) estimated predation rates on hatchlings immediately after they left the beach by directly monitoring them. A similar approach is needed for investigating predation rates during subsequent phases, that is hours or days after entering the sea and until turtles reach a size that can be investigated through the approach based on visible evidence of predation attempts. However, these turtles cannot be followed directly in open sea and remote tracking systems are necessary. Sea turtles can be monitored through satellite tracking and advances in tag miniaturization are promising. For instance, hardshell turtles as small as 9 cm of straight carapace length have been recently tracked by fixing very small satellite tags to the carapace (Candela et al., 2024). However, such attachments make it difficult to distinguish predation events from other possible factors causing transmission loss. For this reason, pop-up archival tags (PATs) are the preferred method to infer survival rates but can be used only on larger turtles. These tags have been used to estimate predation rates (0.13; $n=62$) in medium-sized loggerhead turtles (minimum 57.3 cm CCL) (Hall & James, 2021). Miniaturized pop-up tags will be required to estimate predation rates in very small turtles.

Finally, NCS represents a useful approach to obtain valuable information (in the form of videos) about the behaviour of turtles and predators during their interactions, which would otherwise be very difficult to obtain through dedicated field work, even with recent technological improvements (Ryan et al., 2022). Based on present results, the search for such videos should focus directly on video platforms (rather than on social media due to redundancy) and specifically on YouTube and content in English (among the different sources and languages explored here). These guidelines could streamline future studies on this topic. Promoting citizen science by local projects would help increase the availability of such videos initially, enhancing our ability to unravel at-sea turtle–predator dynamics. The growing use of drones for video recording is likely to increase the potential contribution of citizen science in the future.

5 | CONCLUSIONS

Combining multiple data sources that have rarely been assembled together, this study provides the most comprehensive synthesis to date of the available evidence on turtle predation at sea, although this information is mostly limited to the neritic zone. By incorporating field observations, literature records, predator diet data and non-conventional sources, it reveals patterns of predator diversity, life-stage-specific vulnerability and the dominant role of large sharks, particularly tiger sharks. Despite methodological challenges, the approaches reviewed here demonstrate a growing potential for addressing key unanswered questions on sea turtle predation ecology.

Based on all the above results and considerations, four valuable research lines emerge as achievable through the approaches explored in this study (Table 6), and the following recommendations can be derived. First, estimating population-level predation rates (i.e. the proportion of turtles predated) can greatly contribute to sea turtle population modelling, which is particularly valuable for species of conservation concern but are hampered by the lack of survival rate estimates (Heppell et al., 2003). It can be achieved through intensified monitoring of individual turtles (by acoustic and pop-up tags), also through technology improvement. Second, monitoring spatio-temporal changes in predator-to-turtle population ratio would be particularly interesting because both turtles and their predators are subjected to anthropogenic threats, causing a complex dynamic among the three groups (turtles, predators, humans). Such information can be obtained through predation rates as above or, alternatively, through an index of predation rate, much simpler to obtain from stranding networks

TABLE 6 Potential approaches for investigating specific aspects of predation on sea turtles.

Knowledge type (application)	Turtle size class	Approach
Predation rate (turtle population modelling)	Hatchlings	Acoustic tags
	Hatchlings to small juveniles	Not available
	Small juveniles and larger	Pop-up satellite tags
Index of shark predation rate (trends, interspecies differences)	Large	Injuries (from turtle projects)
List of predators, predator sex/stage (ecology/trophic web)	Any	Literature search
	Any	Stomach contents (from experts on predators)
Defence behaviour against sharks (evolutionary ethology)	Large	Videos posted on the internet
	Medium-large	Shark-borne/ sea turtle-borne cameras

or capture-mark-recapture programs in the form of injury rates. Assembling existing data and collecting new data should be promoted, together with the use of standardized criteria and the separate analysis of dead and live turtles. Third, a better understanding of the ecological implications of sea turtles as prey requires more information on the variety of predators of different sea turtle life stages. Such information may already exist and can be extracted by enhancing the literature search and by engaging predator experts in sharing existing data on stomach contents of predators, especially small ones in oceanic zones. Fourth, the behavioural repertoire that sea turtles have evolved to evade predators, and its interspecies variation, represents an interesting ethological topic that could be adequately studied only through a large number of videos. Social media represent a promising source of such videos, especially if enhanced by citizen science approaches.

AUTHOR CONTRIBUTIONS

Conceptualization, *writing—original draft*, *supervision*: Paolo Casale; *Methodology*: Paolo Casale, Alec B.M. Moore, Enrique González-Bernardo; *Formal analysis*: Alessandro Servolini, Giulia Baldi, Paolo Casale; *Investigation*: Alessandro Servolini, Enrique González-Bernardo, Alicia Tagliolatto, Allen Foley, Michael Bresette, Ryan Welsh, Daniela Freggi, Dimitris Margaritoulis, Yakup Kaska, Yaniv Levy, Shir Sassoon, Jose Luis Crespo-Picazo, Daniel García-Párraga, Mathieu Barret, Pasquale Salvemini, Bonnie Holmes, Alec B.M. Moore; *Data Curation*: Alessandro Servolini, Giulia Baldi, Enrique González-Bernardo; *Writing—Review and Editing*: All authors; *Visualization*: Giulia Baldi, Paolo Casale.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All sources of non-original data are fully provided in the paper. Original data are provided in the paper (including the Supporting Information) in a form that allows a third party to replicate all the analyses and recreate all results, with the exception of the dataset for the temporal analysis, available on Zenodo (https://doi.org/10.5281/zenodo.17878060).

STATEMENT ON INCLUSION

Our study brings together authors from a number of different countries, who also directly contributed with their own unpublished data they collected locally in the field. The study also includes a literature review and all sources of the data included in the study are properly cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Keywords used in the literature search for potential predators of sea turtles.

Table S2. Percentage of live/dead turtles (total *n*) with evidence of a shark-bite injury.

Table S3. Results of comparisons (Fisher exact test) among areas of the proportions of live sea turtles determined to have shark-bite injuries (see Table 1 for details).

Table S4. Percentage of live sea turtles with a shark-bite injury (total number with and without such injuries) in Brazil (BR; source: Instituto de Pesquisas Ambientais Littoralis) and Florida, USA (FL; source: Fish and Wildlife Research Institute), by size class.

Table S5. Shark-turtle interactions recorded in Non-Conventional Sources (NCS).

Figure S1. Maps of Sectors in Florida (A) and Brazil (B), where they are named in anti-clockwise and north-south order, respectively.

Figure S2. Raw data and binomial GLM results of annual trends of predation rate observed in live *Caretta caretta* turtles found stranded or captured (in-water captures, IWC) in Florida (see Table 4).

Figure S3. Raw data and binomial GLM results of annual trends of predation rate observed in live *Chelonia mydas* turtles found stranded or captured (in-water captures, IWC) in Florida (see Table 4).

Figure S4. Raw data and binomial GLM results of annual trends of predation rate observed in live turtles found stranded or admitted to rescue center (RC) in Brazil and Israel, respectively (see Table 4).

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