Global patterns of illegal marine turtle exploitation

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Abstract

Human exploitation of wildlife for food, medicine, curios, aphrodisiacs, and spiritual artifacts represents a mounting 21st century conservation challenge. Here, we provide the first global assessment of illegal marine turtle exploitation across multiple spatial scales (i.e., Regional Management Units (RMUs) and countries) by collating data from peerreviewed studies, grey literature, archived media reports, and online questionnaires of incountry experts spanning the past three decades. Based on available information, we estimate that over 1.1 million marine turtles were exploited between 1990 and 2020 against existing laws prohibiting their use in 65 countries or territories and in 44 of the world's 58 marine turtle RMUs, with over 44,000 turtles exploited annually over the past decade. Exploitation across the 30-year period primarily consisted of green (56%) and hawksbill (39%) turtles when identified by species, with hawksbills (67%) and greens (81%) comprising the majority of turtles exploited in the 1990s and 2000s, respectively, and both species accounting for similar levels of exploitation in the 2010s. Although there were no clear overarching trends in the magnitude or spatial patterns of exploitation across the three decades, there was a 28% decrease in reported exploitation from the 2000s to the 2010s. The top ten RMUs with the highest exploitation in the 2010s included seven green and three hawksbill turtle RMUs, with most reported exploitation occurring in RMUs that typically exhibit a low risk of population decline or loss of genetic diversity. Over the past decade, the number of RMUs with "moderate" or "high" exploitation impact scores decreased. Our assessment suggests that illegal exploitation appears to have declined over the past decade and, with some exceptions, is primarily occurring in large, stable, and genetically diverse marine turtle populations.

Introduction

Human exploitation (or take) of wildlife is a global threat to biodiversity (Milner-Gulland et al., 2003) and has received increased attention as a major driver in the emergence and viral transmission of zoonotic diseases, especially in light of the COVID-19 pandemic (Volpato et al., 2020). Illegal exploitation of wildlife for food, medicine, curios, aphrodisiacs, spiritual artifacts, and other products is considered one of the most valuable illicit markets in the world (Haken, 2011; Challender & MacMillan, 2014), and has contributed to declines in terrestrial and marine species worldwide (Groombridge & Luxmoore, 1989; Bennett et al., 2002; Jerozolimski & Peres, 2003). Despite increased awareness of the problem and several measures to curb it, illegal trade of wildlife is increasing and worth an estimated 20 billion USD worldwide (Milliken & Shaw, 2012; Underwood et al., 2013; Challender & MacMillan, 2014). High profile examples include terrestrial species such as pangolins (Wu et al., 2004), elephants (Underwood et al., 2013), tigers (Sharma et al., 2014), and rhinoceroses (Ferreira et al., 2012), as well as marine species such as sharks (Clarke et al., 2006), totoaba fish (Valenzuela-Quinonez et al., 2015), cetaceans (Baker et al., 2010), humphead wrasse (Donaldson & Sadovy, 2001), and marine turtles (Miller et al., 2019; Lopes et al., 2022).

Marine turtles have been exploited for their meat, eggs, shell, skin, and internal organs since at least 13,000 years before present (Des Lauriers, 2006), and have historically been an important resource for coastal inhabitants worldwide (Barrios-Garrido et al., 2018; Frazier, 2003; Early-Capistrán et al., 2018; Early-Capistrán et al., 2020). By the 18th century, marine turtles were exploited on commercial and international-scales for food and other products (McClenachan et al., 2006; Cornelius et al., 2007; Bell et al., 2007; Limpus et al., 2008; Lam et al., 2012; Early-Capistrán et al., 2018). During the mid-19th century, industrial-scale trade in tortoiseshell products (i.e., carapace scutes from hawksbill turtles, *Eretmochelys imbricata*) was well underway, primarily serving the Japanese market (Mortimer & Donnelly, 2008). By the 20th century, rapidly increasing global demand, globalization, and advances in transportation technology (e.g. roads connecting remote areas to urban centers) that increased connectivity, paired with modern tools that facilitated capture (e.g. spear guns, nylon nets/rope, aluminum and fiberglass boats, outboard motors, and navigational systems), led to industrial-scale exploitation that peaked with over 17,000 tons of marine turtle meat and products (e.g. leather, tortoiseshell) taken in commercial fisheries during the 1960s (FAO, 2011), including over 380,000 marine turtles in a single year (1968) from Mexico alone (Cantu & Sanchez, 1999). Recent estimates suggest that 9 million hawksbill turtles (or 60,000 turtles annually) were traded globally over an approximate 150-year period (1844 to 1992) for their shells (Miller et al., 2019). Worldwide, largescale commercial exploitation has contributed to declines in several marine turtle populations over the past half-century (Stoddart, 1980; Jackson, 1997; Mortimer & Donnelly, 2008; Seminoff et al., 2015).

Today, while catch and utilization of marine turtles are still permitted in some parts of the world (see Humber et al., 2014), most countries have regulations that range from full protection (typically with permitted incidental take in commercial fisheries) to regulated take regimes (Brautigam & Eckert, 2006; Maison et al., 2010; Humber et al., 2014; CITES Secretariat, 2019; Lopes et al., 2022). Exploitation of marine turtles continues for food, but in some cases is driven by socio-cultural reasons that vary by -----Author Manuscrip region and culture (Mancini & Koch, 2009; Lam et al., 2012; von Essen et al., 2014; Barrios-Garrido et al., 2018). For example, marine turtle meat is considered a delicacy in some regions of Latin America, such as northwest Mexico (Senko et al., 2010; Senko et al., 2014; Mancini et al., 2011; Quiñones et al., 2017). In China and Vietnam, whole stuffed turtles are seen as a symbol of status and wealth (Hamann et al., 2006), while tortoiseshell products are a traditional component of Japanese dress and remain highly valued (Canin, 1991; Lam et al., 2012; Yifan, 2018). Turtle blood, fat, and testicles are considered aphrodisiacs in East Africa, and live turtles are offered to spirits in sacred religious ceremonies in the Pacific Islands region (Rudrud, 2010; Westerlaken, 2016; Alvarez-Varas et al., 2020).

Domestic and international conservation efforts, legislation, and intergovernmental conservation structures (e.g., the U.S. Endangered Species Act, Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Convention on the Conservation of Migratory Species of Wild Animals (CMS)) enacted over the past half-century appear to have had some success in reducing impacts of exploitation and other threats, with global-scale patterns that suggest more marine turtle populations appear to be increasing versus decreasing (Mazaris et al., 2017). Illegal exploitation (sourced via direct capture or accidental and retained bycatch) is still, however, likely prevalent in many regions worldwide. Moreover, an evaluation of the conservation status of all marine turtle Regional Management Units (RMUs) globally revealed that exploitation was scored as the threat category with the second-highest impact to marine turtle RMUs, behind only fisheries bycatch (Wallace et al., 2011). Assessing the magnitude, impacts, and trends of illegal exploitation would therefore improve our understanding of the drivers of population changes at both regional and global scales (Lopes et al., 2022), while helping researchers and resource managers identify conservation priorities across geographies, species, and populations. Nevertheless, such an assessment has yet to be conducted on a global scale.

Here, we assessed the global scope of illegal exploitation of marine turtles — defined broadly as the take or trade of turtles against established law in the locality where the exploitation occurred – for meat or products such as medicine, jewelry, leather, or taxidermies, excluding eggs. We focused explicitly on illegal exploitation (hereafter referred to as 'exploitation'), as legal fisheries generally have specific management measures in place that limit species, number of individuals, size classes, and/or seasons in which animals can be taken (Brautigam & Eckert, 2006; Maison et al., 2010; Humber et al., 2014; CITES Secretariat, 2019). Specifically, we analyzed data from peer-reviewed studies, grey literature, archived media reports, and online questionnaires to achieve the following research objectives:

- Evaluate the magnitude and potential trends of marine turtle exploitation globally, among countries, RMUs, and marine turtle species between 1990 and 2020;
- Characterize geographic and temporal patterns in reported trafficking of marine turtles and their products;
- Assess potential population-level impacts of exploitation on marine turtle RMUs.

We recognize the need to develop widely accepted, culturally appropriate terminology when describing the legality of marine turtle exploitation, as terms or activities can be difficult to interpret depending on cultural norms generally and on relevant rules of law in a specific country or territory (e.g., see Delisle et al. 2018). We also recognize that there may be variations in governance and application of the rule of law in a given country, how laws exist in relation to cultural norms, and whether or not they are ethical. Throughout this paper, we strived to handle these topics with sensitivity and respect while fulfilling our overarching goals, and recommend that standard, appropriate terminology and assessment approaches be developed.

Methods

Analytic goals

Our overarching goal was to assess the number of marine turtles illegally exploited worldwide, along with trends in exploitation over time, using data from peer-reviewed journal articles, grey literature, archived media reports, and online questionnaires of incountry experts spanning the past three decades, 1990 to 2020 (peer-reviewed, grey, and media sources are herein referred to as "documented" sources/data). Although not as robust as peer-reviewed articles, grey literature, media reports, and online questionnaires are utilized in addition to peer-reviewed articles to provide a more comprehensive picture of illegal exploitation by filling knowledge gaps in areas lacking peer-reviewed scientific research. For example, the news media plays an important role in shaping public understanding of societal problems, and analyses of media coverage have been conducted on sharks (Shiffman et al., 2020), panthers (Jacobson et al., 2012), grizzly bears (Hughes et al., 2020), and marine turtles (Santos and Crowder, 2021). Similarly, grey literature such as NGO reports and practitioner newsletters may constitute a significant proportion of available data used to inform management decisions and can contain vital information for conservation practitioners (Haddaway and Bayliss, 2015). Finally, online questionaries are an increasingly widespread tool, especially in light of the COVID-19 pandemic, which can provide ready access to large and diverse samples of people (Wardropper et al., 2021).

In our analysis, we included tallies of whole turtles or products that could be definitively linked to individual turtles (e.g., heads, tails, or shells), but did not include products that could not be (e.g., eggs or pieces of jewelry such as bracelets or earrings). To determine the legality of marine turtle exploitation, we first reviewed and updated the Humber et al. (2014) global review of legal marine turtle fisheries. We then reviewed available information and/or responses from in-country experts describing the legislation in each country with documented exploitation. Marine turtles that were exploited under cultural or indigenous take provisions (e.g., Australia), irrespective of broader legislation in the country, were not included in the analysis. All illegal exploitation of individual turtles, including non-permitted take within legal take regimes, was included in our analysis. In cases where legislation was unclear, or if we were unable to verify legislation, the study and country were not included. Data from farming or ranching operations were not included, while animals taken as fisheries bycatch were only included if they were illegally retained.

We specifically sought data on the global magnitude and distribution (i.e. country or territory and RMU, the latter of which describes spatially explicit marine turtle populations above the level of individual nesting rookeries and below the global species level, using "georeferenced available data on marine turtle biogeography – including individual nesting sites, genetic stocks, and geographic distributions based on monitoring research – to spatially integrate sufficient information to account for complexities in marine turtle population structures"; Wallace et al. 2010b)) of exploitation, along with data on which species were exploited. We classified turtles as "trafficked" in the context of exploitation if they were known to have moved across international bodies, if they were seized by authorities during international transit, or if the data source otherwise stated that the animal was internationally traded.

Data compilation and considerations

We assessed the number of marine turtles exploited worldwide from January 1, 1990 to December 31, 2019 (our last searches were conducted on July 29, 2020) through a comprehensive collation and synthesis of: 1) publications in peer-reviewed journals; 2) technical and agency documents, non-governmental organizations including the IUCN Species Survival Commission's Marine Turtle Specialist Group regional reports, TRAFFIC technical reports, and symposia proceedings (collectively termed 'grey literature'); 3) archived media reports; and 4) an online questionnaire sent to in-country marine turtle experts.

Our review of peer-reviewed and grey literature was conducted by searching the following databases: ISI Web of Knowledge (i.e., Zoological Record, ISI Web of Science, and BIOSIS), Google Scholar, Index of Online Theses and Dissertations, Directory of Open Access Journals, and IUCN Library Databases (i.e., IUCN, CITES, TRAFFIC, WIDECAST). We examined the first 150 document hits from each Internet source for inclusion criteria. We used the following search terms in our literature review (*indicates a wildcard), with terms searched both independently and combined using AND/OR features: 1) sea turtle utilize* OR utilis*; 2) marine turtle utilize* OR utilis*; 3) sea turtle illegal; 4) marine turtle illegal; 5) sea turtle harvest*; 6) marine turtle harvest*; 7) sea turtle hunt*; 8) marine turtle hunt*; 9) sea turtle poach*; 10) marine turtle poach*; 11) sea turtle trade*; 12) marine turtle trade*.

Our review of media articles was conducted by searching Arizona State University's international newspaper database "Access World News", which houses more than 12,000 newspapers from all continents except Antarctica, for news articles (photographs without associated articles were not included) using the aforementioned search terms (results dated from Jan 1, 1990 to December 31, 2019, with the last search completed on July 29, 2020). All documented sources assessed were in English. The use of an international news database allowed us to integrate news articles from a broad array of sources, as opposed to using a handful of traditional outlets (Santos and Crowder, 2021).

To ensure that we did not count duplicate incidents of marine turtle exploitation, we compared the number of turtles exploited as well as the year and location of exploitation for each new peer-reviewed, grey, or media source against our existing database. If the location and year of exploitation matched or were similar to any entry in our existing database, we examined the details of the information (e.g., number of turtles, people involved) to determine whether the new source was a duplicate. If details of exploitation matched an existing entry, the new source was not included.

While we treated each type of documented source equally when counting illegally exploited turtles in our analysis, we calculated a data quality score for each country to provide additional information to interpret the robustness of results (*sensu* Wallace et al. 2011) (Dataset S1). To calculate the data quality scores, we assigned each literature source a weight based on data quality as follows: media articles were assigned a weight of 0.25; grey reports were assigned a weight of 0.5 when a single method was used to assess illegal exploitation (e.g. only dumpsite surveys) and < 50% of a country was covered, and a weight of 0.75 when multiple methods were used to assess illegal exploitations were assigned a weight of 0.75 when a single method was used to assess illegal exploitation and < 50% of a country was covered and a weight of 1 when multiple methods were used to assess illegal exploitation and < 50% of a country, a weighted average was calculated to produce a data quality score by summing each weight multiplied by the number of sources assigned that weight, then dividing that by 1.5, the sum of the weights.

We used an online questionnaire of in-country marine turtle experts to fill in data gaps (i.e., countries in which we were unable to locate peer-reviewed, grey, or media sources), as illegal exploitation is likely underreported due to its clandestine nature (Humber et al., 2011; Martin et al., 2012). Our voluntary confidential online questionnaire (Google Forms) was distributed in English to known in-country experts in marine turtle research and conservation living in or known to work in target nations, and included experts identified in a database developed by Humber et al. (2014). Experts were first identified if they had previously authored research on illegal exploitation within a target nation. In cases where there were no previous studies, we could not get in contact with the author(s) of previous work, or there were no experts included in the Humber et al. (2014) database, we used our collective experience in the field of marine turtle research to identify in-country experts. We contacted 104 experts from 80 countries via email and did not offer compensation to participate. Experts were asked to provide estimates on the levels of illegal exploitation over the past two decades (i.e., 2000s and 2010s) for the applicable country or territory they were requested to provide information on. Exploitation ranges provided in the questionnaire included: 0; 1-100; >100-1,000; >1,000-10,000; >10,000-25,000; >25,000-50,000; >50,000-75,000, >75,000-100,000; and >100,000 turtles per year, irrespective of life stage or species. Respondents could also write a specific exploitation value other than the ranges provided. In cases where experts provided different exploitation ranges for the same country or territory, we used the lowest exploitation range to provide a conservative estimate. Supplementary Table S1 contains the final exploitation estimates for each country we received questionnaire responses for.

Data analysis

Each documented data source was evaluated and filtered to only include cases where exploitation was clearly illegal (i.e., performed against existing laws prohibiting the use of marine turtles) during the time it was documented. For countries whose legislation changed during the study period (e.g., Vietnam), cases of exploitation were only included

when they occurred during active legislation prohibiting marine turtle exploitation. From each documented source, we extracted data for all relevant variables, which included the number of turtles of all life stages, decade of exploitation, location (i.e., country or territory and RMU), species, and whether trafficking had occurred. We only summarized data directly reported in data sources, and did not calculate our own estimates or extrapolations, although we did include annual estimates of exploitation reported in our collated sources. When estimates were given as a total value for a range of years that spanned multiple decades, we divided the number of turtles exploited by the number of years provided to obtain a mean estimate of annual exploitation so that the total number of turtles exploited could be correctly apportioned by decade. Additionally, when single annual estimates were given for a multiple-year study, we multiplied the annual estimate by the length of the study in years to find the total number of individuals. When no documented data for a country or territory existed for a specific decade, we incorporated the exploitation estimates provided by the online questionnaire sent to in-country experts for that decade by multiplying the median of the annual exploitation range by 10 to account for the entire decade (see Dataset S1). We rounded all estimates of exploitation that included questionnaire data to the nearest thousand when possible to account for the imprecise nature of the ranges gathered from the questionnaire data. We identified exploitation by species and trafficked turtles only in cases where they were explicitly mentioned in the documented source. RMUs and trafficking status could not be specified where the species and/or location of exploitation were not provided, which included all questionnaire data. When RMUs overlapped, we split the number of turtles evenly between the overlapping RMUs.

We created an exploitation impact score for each RMU to contextualize the magnitude and risk of exploitation relative to nesting female population size, a standard population abundance metric for marine turtles (NRC, 2010). This approach is akin to 'bycatch impact scores' developed by Wallace et al. (2013) to estimate population-level impacts of fisheries bycatch on marine turtle RMUs. Exploitation impact scores were created for the entire study period along with each respective decade. To calculate the exploitation impact scores for the entire study period, we divided the average number of turtles (of all life stages, males as well as females) exploited per decade by estimates of abundance of nesting females obtained by calculating the midpoints of population ranges provided in Wallace et al. (2011). For each individual decade, we divided the total number of turtles exploited in that decade by the same estimates of nesting female populations. An exploitation impact score, then, can be interpreted as the approximate number of turtles exploited per nesting female per decade. Therefore, when an exploitation impact score is greater than 1, more turtles of all life stages and both sexes are being exploited within a 10-year period than there are adult females nesting annually in the population. Additionally, we plotted the exploitation impact scores for each RMU against the RMU risk scores (i.e., indices of population viability that include criteria such as annual nesting female abundance, trends, and genetic diversity) reported in Wallace et al. (2011) to evaluate the impacts of exploitation relative to other threats, as well as current population size and trajectory.

To provide appropriate context for strategic conservation priority setting, we developed conservation priorities for each RMU that were based on our exploitation impact scores and risk scores from Wallace et al. (2011). To create these conservation

priorities, we classified risk scores as either "low" or "high" according to the method used in Wallace et al. (2011), and classified exploitation impact scores as "low", "medium", or "high," where "low" scores were less than 0.5, "medium" scores were between 0.5 and 1, and "high" scores were greater than 1. For the final conservation priority, we reported both the level of risk and exploitation (i.e., low/medium/high risk–low/medium/high exploitation).

Where data was available for multiple decades, we analyzed decadal trends for the total number of turtles exploited, the species exploited, RMUs (not including RMU exploitation impact score since the trends follow those for the number of turtles exploited in RMUs exactly), countries, and trafficking. In each trend analysis, the trend was classified as "increasing", "decreasing", "no change", or "unclear". An "unclear" classification was used for any case where exploitation changed over time but did not consistently increase or decrease across all decades for which data was available. We used ArcDesktop 10 geographic information systems software to depict the magnitude of exploitation for countries and territories using a choropleth map for data from the literature review and graduated symbols for data from the expert questionnaires. We also created choropleth maps depicting exploitation for each species in their respective RMUs. We used R 3.5.3 to plot and analyze all data (R Core Team, 2019).

Results

Overview of global exploitation

Summarizing 39 peer-reviewed publications, 42 grey reports, 82 media reports, and 46 expert questionnaire responses, an estimated total of 1,128,000 marine turtles were reported to have been exploited between 1990 and 2020 across 65 countries or territories and in 44 of the world's 58 marine turtle RMUs, representing approximately 38,000 turtles annually across the three decades (Supplementary Table S2; Dataset S1). Documented data (1990-2020) and questionnaire data (2000-2020) revealed changes in the magnitude of exploitation over time, with 7,875 turtles per year exploited in the 1990s, 61,000 turtles per year exploited in the 2000s, and 44,000 turtles per year exploited in the 2010s (Figure 1; Dataset S1), indicating a 28% decrease in reported exploitation from the 2000s to the 2010s.

Global trends in exploitation by species

Peer-reviewed, grey, and media sources documenting illegal marine turtle exploitation between 1990 and 2020 reported 66% (131,519 turtles) of exploitation to the level of species (not including questionnaire data, which did not report on species). Across all decades, green turtles (*Chelonia mydas*, 56%) were the most exploited species, followed by hawksbills (39%), loggerheads (*Caretta caretta*, 3%), olive ridleys (*Lepidochelys olivacea*, 2%), leatherbacks (*Dermochelys coriacea*, <1%), and Kemp's ridleys (*Lepidochelys kempii*, <1%) (Dataset S1). Exploitation of flatback turtles (*Natator depressus*) was not reported in the documented sources we reviewed.

On a finer decadal scale, 56% of exploited marine turtles were reported by species in the 1990s, 95% in the 2000s, and 51% in the 2010s. Decadal analysis revealed changes

over time in the proportion of turtles of each species that were exploited. In the 1990s, hawksbills were exploited most frequently (67%), followed by green turtles (30%), loggerheads (2%), leatherbacks (0.5%), olive ridleys (0.05%), and Kemp's ridleys (< 0.001%) (Figure 2a; Dataset S1). In the 2000s, the decade with the highest proportion of exploited turtles with data reported to the level of species, green turtles were exploited the most (81%), followed by hawksbills (9%), loggerheads (6%), olive ridleys (4%), leatherbacks (0.1%), and Kemp's ridley turtles (0.002%) (Figure 2b; Dataset S1). For the most recent decade (2010 to 2020), hawksbills (54%) were the most abundant species, followed by greens (45%), olive ridleys (0.4%), loggerheads (0.2%), and leatherbacks (0.04%) (Figure 2c; Dataset S1). No Kemp's ridley turtles were reported exploited in the 2010s. Of all species of marine turtles reported to be exploited between 1990 and 2020, leatherbacks were the only species to show a decline in numbers exploited across all three decades.

Global distribution and trends in exploitation by marine turtle RMUs

Sources that provided species-specific exploitation data revealed illegal marine turtle exploitation in 44 of the world's 58 marine turtle RMUs (Figure 3; Dataset S2). The RMUs with the highest exploitation for each species between 1990 and 2010 included the Southwest Pacific green turtle RMU, the West Pacific/Southeast Asia hawksbill RMU, the Northeast Atlantic loggerhead RMU, the East Pacific olive ridley RMU, the Southeast Atlantic leatherback RMU, and the Northwest Atlantic Kemp's ridley RMU, the only RMU for Kemp's ridley turtles (Figure 3; Dataset S2).

In the 1990s, 22 RMUs had documented exploitation, with the West Pacific/Southeast Asia hawksbill RMU having the highest number of turtles (n = 750 per year) (Figure 3; Dataset S2). In the 2000s, 34 RMUs had documented exploitation, with the Southeast Indian green turtle RMU having the most exploited turtles (n = 1,001 per year) (Figure 3; Dataset S2). Finally, the 2010s had documented exploitation in 28 RMUs, with the most turtles exploited from the West Pacific/Southeast Asia hawksbill RMU (n = 922 per year) (Figure 3, Dataset S2).

Of the 44 RMUs with documented exploitation, 30 had documented exploitation in multiple decades, allowing for the analysis of trends over time. Ten RMUs had documented exploitation in all three decades, but none showed consistent trends in exploitation across the entire period (Figure 3; Dataset S2). Twenty RMUs had documented exploitation in only two decades, seven of which had exploitation increase over time, ten of which had exploitation decrease, and three of which exhibited no change in exploitation (Figure 3; Dataset S2). Among the RMUs with an overall increase in exploitation, four were "high risk" populations (West Pacific/Southeast Asia hawksbill RMU, East Atlantic hawksbill RMU, Southwest Atlantic hawksbill RMU, South Caribbean green RMU) (Dataset S2).

RMU exploitation impact scores

Across the entire study period, we were able to calculate exploitation impact scores for 29 RMUs, including two with high exploitation (East Atlantic green and East Atlantic hawksbill RMUs) and two with moderate exploitation (East Pacific green and South

Caribbean green RMUs) (Dataset S2). Over the 30-year study period, the East Atlantic hawksbill RMU was the only RMU classified as a "high risk" – "high exploitation" RMU, with an exploitation impact score of 1.16, meaning, on average, the number of turtles exploited within a given decade was greater than the number of nesting females in the population, with 1.16 turtles exploited per nesting female per decade.

In the 1990s, we were able to calculate exploitation impact scores for 17 RMUs. Only the East Atlantic green turtle RMU had high exploitation (3.5 turtles exploited per nesting female per decade) and only the Southwest Pacific hawksbill RMU had moderate exploitation (0.6 turtles exploited per nesting female per decade) (Figure 4a; Dataset S2). However, both of these RMUs are considered to be low-risk populations (Wallace et al. 2011). In the 2000s, exploitation impact scores were calculated for 23 RMUs, of which four had high exploitation and two had moderate exploitation (Figure 4b; Dataset S2). Two of the RMUs with high exploitation in the 2000s – the East Atlantic hawksbill RMU (3.1 turtles exploited per nesting female per decade) and the North Pacific loggerhead RMU (1.4 turtles exploited per nesting female per decade) – were classified as "high risk" – "high exploitation". We were able to calculate exploitation impact scores for 19 RMUs in the 2010s, none of which had high exploitation and only one of which had moderate exploitation (0.87 turtles exploited per nesting female per decade).

Global distribution and trends in exploitation by countries

We obtained peer-reviewed publications from 25 countries or territories, grey reports from 27 countries or territories, and archived media reports from 21 countries or territories published between 1990 and 2020, covering 51 countries when combined (herein referred to as documented sources). The mean data quality score for these 51 countries ranged from 0.17 to 6.83, with an average of 1.15. The majority of countries (n = 33, 65%) had a data quality score less than 1, indicating low data availability and/or quality. Likewise, we received questionnaire responses corresponding to 34 countries, including 13 countries for which we found no documented exploitation (Supplementary Table S1). In total, we acquired estimates of illegal marine turtle exploitation from at least one data source for 65 countries and territories. When all data sources are taken into account, nearly 75% of exploitation (i.e., number of turtles exploited) between 1990 and 2020 occurred in five countries: Haiti (31%), Tanzania (20%), Honduras (10%), Indonesia (7%), and Mexico (6%) (Dataset S1). Of these five countries, Haiti, Honduras, and Tanzania were only represented in the questionnaire data.

Of the 65 countries with available data, 43 had exploitation estimates across multiple decades, allowing for the analysis of trends over time. Fourteen countries had estimated increases in exploitation over time, with Mexico having the largest rise in exploitation (~ 60,000 turtle increase) (Figure 1; Supplementary Table S3). Fifteen countries had estimated decreases in exploitation over time, with Tanzania having the largest decrease in exploitation (120,000 turtle decrease) (Figure 1; Supplementary Table S3). Colombia, the Turks and Caicos Islands, and the United States did not have clear trends in exploitation (Figure 1; Supplementary Table S3). The remaining eleven countries had no change in exploitation estimates (Figure 1; Supplementary Table S3). Discrepancies between documented and questionnaire data are presented in Supplementary Table S4.

Global distribution and trends in international trafficking by countries

Of the 198,297 total marine turtles reported in documented data between 1990 and 2020, 42,771 (22%) were reported to have been traded internationally (questionnaire data is not applicable here, as trafficking was not reported in the questionnaire). Across all three decades, the top five places of origin included Vietnam (34%), the Philippines (8%), Venezuela (4%), Malaysia (3%), and the Coral Triangle (2%), the latter of which could include Indonesia, Malaysia, the Philippines, Papua New Guinea, Timor-Leste, and the Solomon Islands. The top five destinations for traded marine turtles included China (46%), Japan (43%), Colombia (4%), Vietnam (2%), and Malaysia (2%). The five most common routes for international trade between 1990 and 2020 were Vietnam to China (34%), the Philippines to China (5%), Venezuela to Colombia (4%), the Coral Triangle to China (2%), and Malaysia to China (2%).

There was no clear decadal trend regarding the number of turtles trafficked, with 18,022 turtles traded in the 1990s, 4,776 traded in the 2000s, and 19,973 traded in the 2010s. Four countries were documented as origins of marine turtle trafficking in multiple decades, with the number of trafficked turtles originating from Indonesia and Malaysia decreasing over time and trafficked turtles coming from the Philippines and Vietnam increasing. Six destination countries had documented trafficking in multiple decades, with Australia, Indonesia, and Japan showing a decrease in imported turtles and China, Vietnam, and Russia showing an increase in imported turtles. Five trafficking routes showed trends in the number of turtles trafficked over time. Indonesia to China and Malaysia to China showed reduced trafficking of marine turtles, while the Philippines to China, the Philippines to Vietnam, and Vietnam to China all showed increased trafficking over time.

Discussion

Overview and caveats of illegal marine turtle exploitation

Our assessment revealed that over 1.1 million marine turtles were reported to be illegally exploited in 65 countries and territories and in 44 of the world's 58 marine turtle RMUs between 1990 and 2020, with over 44,000 turtles exploited per year in the most recent decade. While there was no consistent trend in the number of turtles exploited across all three decades, there was a 28% decrease in reported exploitation from the 2000s to the 2010s. Green turtles (56%) and hawksbills (39%) comprised most of the reported exploitation across all three decades. With a few exceptions highlighted herein, most of the reported exploitation over the past decade occurred in 'low-risk' marine turtle RMUs that are typically genetically diverse and characterized by large, relatively stable, or increasing abundances, suggesting that current levels of illegal exploitation – at least relative to other contemporary threats – may not exert major population-level impacts on most marine turtle RMUs (Figure 4).

While we may have missed obscure literature or media reports and were unable to reach all of the experts we sought, we are confident that our assessment reflects the current state of available information regarding illegal exploitation of marine turtles

worldwide. Nonetheless, our estimates of marine turtle exploitation are almost certainly biased negatively for several reasons, including: 1) assessing prohibited exploitation is difficult due to its typically clandestine nature (von Essen et al., 2014; Senko et al., 2014); 2) there are significant data gaps due to a lack of reporting in many areas, limited spatial scope of assessment, or difficulty accessing obscure data (e.g., programmatic grant or contract reports) that was not searchable or available for our assessment; 3) data represented herein are likely more indicative of hotspots where researchers have published data, as well as extemporaneous reports of trade seizures, than actual illegal exploitation; 4) international trade of marine turtles may be on the rise due to increasing demand from Southeast Asia, and especially China (Yifan, 2018); 5) turtles may be butchered at-sea in nearshore waters for meat or products, and stranding probabilities of marine turtle carcasses tend to be low (usually 5-30% of total mortality; Epperly et al., 1996; Hart et al., 2006; Koch et al., 2013), limiting detection of exploitation; 6) a general lack of law enforcement leads to limited successful documentation of illegal exploitation (Mancini et al., 2011); 7) our online questionnaire and use of media sources were conducted and assessed in English, representing a potential language bias that likely resulted in missed coverage from non-English speaking countries; and 8) our assessment included only whole turtles or products that could be linked to individual turtles (e.g., heads, shells, or tails), and did not account for eggs or products that could not be linked to individual turtles (e.g., bracelets or earrings made from tortoiseshell).

Trends in illegal marine turtle exploitation over the past three decades

Although there was no consistent trend in the number of turtles exploited across all three decades, there was a 28% decrease in reported exploitation from the 2000s to the 2010s. Considering that more information was available for the most recent decade compared to the 2000s (we found more sources documenting illegal marine turtle exploitation and trade for the 2010s than the 1990s and 2000s combined; Supplementary Table S2), we expected an overall increase in reported exploitation. However, we observed the opposite, suggesting that the reported decrease in exploitation over the past decade may indicate an actual decrease. This could be due to a combination of increased protective legislation, awareness of the problem, global grassroots conservation efforts, changing local norms and traditions, reduced research attention or shifting conservation priorities (especially for emerging threats such as plastic pollution), fewer documented exploitation interventions or quantifications, or declining marine turtle populations (i.e., fewer turtles available for exploitation) at local scales. Decreased exploitation may also be attributed to greater avoidance of the activity due to increased protective legislation or risks to assessing the activity, especially if it becomes more organized or connected with crime syndicates.

There were inconsistent trends concerning the species exploited, RMUs, countries, and marine turtle trafficking. While exploitation across the entire study period consistently comprised mostly hawksbill and green turtles, exploitation in the 1990s was primarily hawksbills, while the 2000s experienced a large spike in green turtle exploitation (Figure 2). This may be due to lingering effects of shifting legislation in bekko trade, increases in green turtle populations (Broderick et al. 2006), and

discrepancies in data collection (e.g., the 2000s having a much higher proportion of exploitation reported by species compared to the other two decades).

Trends in the number of marine turtles exploited in each country were also inconsistent, with Mexico having the largest increase in exploitation and Tanzania having the largest decrease in exploitation. Country trends were the only trends, besides overall exploitation, that could be informed by both documented and questionnaire data. While this provides a more complete picture of exploitation, using all data sources to assess trends in a country's exploitation has some important caveats. For example, questionnaire data reported consistently higher exploitation than documented data (Supplementary Table S4), which may lead to incorrect trends for countries that utilize both documented and questionnaire data for trend analysis. However, this issue is only pertinent to Guinea-Bissau, Jamaica, and Mexico, all of which showed increased exploitation in the analysis with both documented and questionnaire data, but decreased exploitation from questionnaire data alone (Supplementary Table S4).

While there was no clear decadal trend in the number of turtles trafficked internationally from 1990 to 2020, trend analysis revealed that patterns of trafficking shifted in Indonesia and Vietnam. Over the course of three decades, the number of turtles exported from Indonesia to other countries decreased, but the number of turtles imported to Indonesia increased during the same period. Vietnam has shifted in the opposite direction, with more turtles being exported and fewer imported in recent times compared to the 1990s. However, trafficking trends should be interpreted with caution for several reasons. For example, it was not always known whether marine turtles were traded domestically or internationally, nor whether seizures were a result of international trade or local use, an issue that could be resolved using genetic testing to determine a marine turtle's origin. Further, many instances of international trade are not documented, particularly in cases involving transport of marine turtle products on the high seas or open oceans, where avoiding detection (akin to illegal, unregulated, and unreported [IUU] fisheries) is easier than in cases where turtles are exploited in coastal areas.

Conservation priorities based on RMU exploitation impact scores

Assessment of exploitation by RMUs based on documented data and exploitation impact scores allows for the identification of "high risk" and "high exploitation" global hotspots, which can inform conservation and management priorities (Wallace et al., 2010b; Wallace et al., 2011; Wallace et al., 2013; Barrios-Garrido et al., 2020). At the RMU scale, most of the RMUs with increasing exploitation are "low risk" populations, while some "high-risk" RMUs (i.e., hawksbills in the West Pacific/Southeast Asia, East Atlantic, and Southwest Atlantic RMUs, green turtles in the South Caribbean RMU) also experienced increases in documented exploitation. The only RMU that emerged with a "high risk" and "high exploitation" conservation priority across the three-decade period of this study was the East Atlantic hawksbill RMU. Thus, our analysis showed that most of the world's exploitation over the past decade has been documented in "low-risk" marine turtle RMUs that tend to be genetically diverse and exhibit large, stable, or increasing population abundances. Our analysis, therefore, suggests that illegal exploitation may not represent a major, population-level threat to most of the world's marine turtle RMUs, with some exceptions. These exceptions include the four "high risk"

RMUs that exhibited increasing trends in exploitation over time (i.e., West Pacific/Southeast Asia hawksbill RMU, East Atlantic hawksbill RMU, Southwest Atlantic hawksbill RMU, and South Caribbean green RMU). However, we note that our assessment is based on limited data availability and estimates are likely negatively biased and geographically incomplete.

Despite the utility of RMUs and exploitation impact scores for assessing conservation priorities for marine turtle populations, these results should be interpreted cautiously for the following reasons. First, RMUs could only be assigned to turtles that were reported by species, which excluded online questionnaire data and 34% of documented data. Second, the location of capture is also necessary to assign an RMU. Thus, for trafficked turtles seized en route to or at their destination, an RMU could not be assigned unless the location of capture was specifically stated. Furthermore, some countries such as Malaysia, Indonesia, and the Philippines are included within the boundaries of multiple RMUs, making it difficult to assign the correct RMU unless the exact location of capture or the genetic stock to which turtles belong to are known. Third, the exploitation of marine turtles at higher risk RMUs may be more difficult to detect due to low population numbers and potentially stricter enforcement or penalties. Additionally, the RMU classifications and population estimates used for the analysis were published a decade ago (i.e., Wallace et al., 2011), though drastic changes in nesting abundance within one decade that would substantially alter the conclusions of our study were unlikely because marine turtles are long-lived and their population sizes vary across large temporal and spatial scales. Another limitation of sourcing data from Wallace et al. (2011) is that exploitation impact scores could not be calculated for some RMUs because an estimate of female nesting abundance was unavailable. With these limitations in mind, RMU-scale evaluations of potential population-level impacts of exploitation enabled identification of conservation priorities as well as knowledge gaps that require attention.

Marine turtle trafficking and hawksbill exploitation as a global conservation priority

When our analysis is combined with the most recent global assessment of legal exploitation that reported an annual take of greater than 42,000 marine turtles since 2010 (Humber et al., 2014), at least approximately 80,000 turtles are exploited – legally or illegally – per year, most of which are green and hawksbill turtles. Humber et al. (2014) found that > 95% of legal marine turtle exploitation was comprised of green (89%) and hawksbill turtles (8%). However, in the present analysis, hawksbills made up over half of the illegal exploitation where species was reported over the past decade—more than six times higher than the proportion of hawksbills reported in Humber et al. (2014). Regardless, our estimate underestimates the true exploitation of hawksbills given that we were unable to ascribe tortoiseshell products (e.g., pieces of jewelry) to individual turtles. A recent global assessment of the tortoiseshell trade reported that more than 46,000 individual tortoiseshell products have been offered for sale since 2017 (> 17,000 inperson and >29,000 online) in at least 10 countries with substantial illegal markets (Nahill et al., 2020).

Madagascar and countries in Southeast Asia (i.e., China, Vietnam, Indonesia, Malaysia, and the Philippines) emerged as contemporary hawksbill exploitation hotspots in our study. Based on known cases that resulted in hundreds of animals confiscated from vessels over the past decade, it is believed that vessels leave ports with the express purpose of targeting hawksbills from Malaysia, the Philippines, and Indonesia to supply international black market circuits, including high-end consumer markets of East Asia, with theoretical flight and vessel routes flowing from these countries directly to China or through Vietnam into China (CITES Secretariat, 2019; Gomez & Krishnasamy, 2019). Anecdotal evidence suggests that hawksbill turtles in Southeast Asia are targeted by vessels originating from the Hainan Province in China as well as Vietnam and Thailand (Lam et al., 2012; CITES Secretariat, 2019), while Africa may be supplying marine turtles seized in China via transshipment through Indonesia (anonymous survey respondent; this study).

Traded turtles may also be obtained directly from fishers who capture turtles as bycatch and then warehouse them to supply black market circuits (Yifan 2018). Tortoiseshell is nonperishable and thus easily stockpiled, which distances consumers from suppliers, reduces traceability, and decouples the feedback of reduced demand with increased cost over value (McClenachan et al., 2016; Miller et al., 2019; Nahill et al., 2020). For example, in 2014, Vietnamese authorities seized 7,000 turtle carcasses in a warehouse, the single largest seizure of marine turtles ever recorded; hawksbill turtles comprised the majority of carcasses, almost all of which were either fully or partially taxidermied and assumed to be bound for sale in China (Nuwer, 2016).

For these reasons, special attention should be paid to hawksbill RMUs, particularly the West Pacific hawksbill (Pacific Ocean/Southeast Asia) RMU. Despite the lack of an exploitation impact score (due to lack of population abundance data), this population should be considered another high-priority RMU due to the large number of turtles exploited, the region's high concentration of countries that serve as sources and sinks for international trade, the large number of individual tortoiseshell products documented in a recent global assessment (Nahill et al., 2020), and the global conservation status of hawksbills (Spotila, 2004; Mortimer & Donnelly, 2008; Barrios-Garrido et al., 2020).

Contextualizing illegal marine turtle exploitation with other threats

Contextualizing exploitation with other marine turtle threats is vital for strategic conservation priority-setting. Wallace et al. (2010a) reported that published information documented a minimum of 85,000 turtles reported as bycatch globally from 1990 to 2008, a value that the authors suggested was underestimated by at least two orders of magnitude due to low (< 1%) observed international fishing effort and underrepresented bycatch in small-scale fisheries. In the Mediterranean alone, Casale (2011) estimated that 44,000 turtles are killed annually as bycatch. In contrast, illegal exploitation may not be comparable to bycatch impacts on a global scale, although better data for both bycatch and exploitation is needed. Regardless, most populations impacted by exploitation appear to be from RMUs characterized by relatively high population sizes and stable or increasing population trends, with the likely exceptions of hawksbill turtles in the West Pacific/Southeast Asia and Caribbean. Nonetheless, because exploitation often affects older life stages (i.e., large juveniles and adults) that have the largest influence on marine turtle population dynamics (Crouse et al., 1987), it can be a serious threat to marine turtle populations.

To successfully address illegal marine turtle exploitation, a combination of outreach, enforcement, and research is necessary, particularly to protect "high-risk" marine turtle populations from further declines. However, before such strategies can be developed, how "illegal" hunting is defined, described, and quantified must be considered carefully. Specifically, enhanced culturally appropriate outreach is crucial to balancing goals of sustaining turtle populations and preserving important cultural and socioeconomic traditions. For example, indigenous Australians have a legally recognized right to use marine turtles for food and other customary activities within their ancestral territories (Weiss et al., 2013); similar characterizations likely exist elsewhere. Further, turtle exploitation can help sustain food insecure or otherwise marginalized communities, and prohibiting exploitation or fully enforcing laws that prohibit exploitation will likely be detrimental to human welfare (Liles et al., 2014; Barrios-Garrido et al., 2019).

Moving forward, increased support for governments lacking the resources to properly enforce illegal exploitation of marine turtles is needed, as well as support for communities to sustain human well-being in the face of restrictions or bans on marine turtle exploitation. Communities living near marine turtle supply centers could be provided with incentives—i.e., investments in healthcare, education, and infrastructure, as well as increased economic opportunities—to protect wildlife while sustaining important cultural practices (Challender & MacMillan, 2014; Gjertsen & Niesten, 2010; Pakiding et al., 2020). Co-design of legislation between stakeholders and governments could offer a pathway for developing conservation strategies that benefit both people and turtles.

Further data collection and reporting by governments and enforcement agencies will be essential for researchers and managers to accurately prioritize conservation efforts to address illegal exploitation in the context of other threats to marine turtle populations, particularly in countries that are lacking robust data regarding exploitation, which comprised the majority of countries in our assessment (Dataset S1). Improving assessments of exploitation (and other threats) are needed to better understand population-level impacts to marine turtles. Future research should strive to develop population models that estimate the number of turtles of harvestable size in each RMU, while enforcement officers could collect genetic data on seized marine turtles to allow for correct RMU attribution or record size classes to better understand population-level effects of exploitation. Further research looking at how marine turtle exploitation relates to factors such as population size, food insecurity, and the Human Development Index will help researchers elucidate the drivers behind supply and demand for marine turtle products (Barrios-Garrido et al., 2020). Additionally, given the importance of public perceptions, greater conservation and regulatory buy-in by local government and influential community leaders could be beneficial (Liles et al., 2016; von Essen et al., 2014). Traditional practices (i.e., taboo systems or cultural rules) which once encouraged the protection of and responsibility to care for sensitive or depleted resources are currently experiencing a renaissance in numerous Pacific Island locations (Summers et al., 2018), and may be replicated elsewhere as well as complement current management efforts.

With effective conservation and management, marine turtle populations have shown remarkable potential for recovery from long-term abundance declines caused by persistent threats (Chaloupka et al., 2008; Mazaris et al., 2017). While the results herein almost certainly represent only a fraction of actual illegal exploitation, this study provides a foundation for further research and conservation efforts focused on addressing the illegal exploitation of marine turtles throughout the world's oceans.

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Figure 1. Global maps depicting the magnitude of illegal exploitation by country during the 1990s, 2000s, and 2010s. Data from peer-reviewed, grey literature, and media reports are shown by colored countries, while data from the in-country expert online questionnaire (2000s and 2010s) are shown with the diamond symbols (no questionnaire data were collected for the 1990s). Country-specific data represented herein are presented in Dataset S1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 2. Total number of marine turtles illegally exploited annually by species in the A) 1990s, B) 2000s, and C) 2010s based on an assessment of documented sources (online questionnaire data were not included due to the absence of species-specific data). Species on the x-axis are abbreviated as green turtle (Cm), hawksbill turtle (Ei), loggerhead turtle (Cc), olive ridley turtle (Lo), and leatherback turtle (Dc), while turtles not reported by species are denoted as NR. Species-specific data represented herein are presented in Dataset S1.

Figure 3. Global maps for green, hawksbill, olive ridley, loggerhead, and leatherback turtle Regional Management Units (RMUs) showing the total number of recorded turtles illegally exploited for each species' respective RMUs across the three decades based on an assessment of peer-reviewed literature, grey literature, and media reports (online questionnaire data were not included due to the absence of species-specific data). RMUs are defined as "georeferenced available data on marine turtle biogeography – including individual nesting sites, genetic stocks, and geographic distributions based on monitoring research – to develop multi-scale RMUs that spatially integrate sufficient information to account for complexities in marine turtle population structures" (Wallace et al., 2010, see for a full list of the 58 global marine turtle RMUs). RMU data represented herein are presented in Dataset S2. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 4. Risk and exploitation impact scores for each Regional Management Unit (RMU) with documented exploitation in the A) 1990s, B) 2000s, and C) 2010s. RMUs are defined as "georeferenced available data on marine turtle biogeography – including individual nesting sites, genetic stocks, and geographic distributions based on monitoring research – to develop multi-scale RMUs that spatially integrate sufficient information to account for complexities in marine turtle population structures" (Wallace et al., 2010, see for a full list of the 58 global marine turtle RMUs). The RMU in each decade with the highest exploitation impact score is highlighted. To calculate the exploitation impact scores, estimates for the total number of turtles exploited from each RMU in each decade were divided by estimates of nesting females from the respective RMU. Risk scores and estimates of nesting females were sourced from Wallace et al. (2011). RMU conservation priorities increase moving towards the upper-right corner of the plot. RMU exploitation impact scores represented herein are presented in Dataset S2.

Supp. Table S1. Estimated annual illegal exploitation of marine turtles provided by incountry experts. Values for countries depict ranges provided to expert respondents. Countries or territories for which data were not found in the documented exploitation are bolded.

Supp. Table S2. Number of documented sources per decade split by data source type and the number of turtles exploited or traded for each decade, showing increasing data availability and decreasing exploitation of marine turtles over time. This table does not include online questionnaire data.

Supp. Table S3. Decadal trends in exploitation over time for the 43 countries with exploitation reported in documented and/or questionnaire data across multiple decades. All country-specific data are presented in Dataset S1.

Supp. Table S4. Discrepancies between illegal exploitation reported by the online questionnaire and documented data sources. On average, the discrepancies were larger in the 2000s than the 2010s. Questionnaire exploitation data presented here is the median of the annual exploitation ranges provided in the questionnaire responses multiplied by 10 to account for the entire decade.

Dataset S1 [Excel file]. Estimated annual illegal exploitation of marine turtles partitioned by species and data source type for the entire study period as well as for each decade, including a complete list of references (i.e., documented sources) used in the assessment. References for each data source used in the assessment are included here, along with data quality scores for each country.

Dataset S2 [Excel file]. Exploitation impact scores, conservation priorities, and other relevant information for each RMU for the entire study period, along with each decade, split by data source.



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