



REVIEW

Key issues in assessing threats to sea turtles: knowledge gaps and future directions

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ABSTRACT: Sea turtles are an iconic group of marine megafauna that have been exposed to multiple anthropogenic threats across their different life stages, especially in the past decades. This has resulted in population declines, and consequently many sea turtle populations are now classified as threatened or endangered globally. Although some populations of sea turtles worldwide are showing early signs of recovery, many still face fundamental threats. This is problematic since sea turtles have important ecological roles. To encourage informed conservation planning and direct future research, we surveyed experts to identify the key contemporary threats (climate change, direct take, fisheries, pollution, disease, predation, and coastal and marine development) faced by sea turtles. Using the survey results and current literature, we also outline knowledge gaps in our understanding of the impact of these threats and how targeted future research, often involving emerging technologies, could close those gaps.

KEY WORDS: Climate change · Illegal take · Fisheries · Pollution · Disease · Marine development · Marine turtles · Coastal development

1. INTRODUCTION

Sea turtles lead complex lives during which they are exposed to multiple anthropogenic threats, including those from climate change, coastal development, fisheries, direct take, and pollution (Fig. 1) (Donlan et al. 2010, Bolten et al. 2011, Fuentes et al. 2015, 2020a). These threats ultimately affect sea turtle

vital rates (Bolten et al. 2011) and can result in dramatic reductions in population size (Wallace et al. 2011). This is problematic since sea turtles have important ecological roles, contributing to the health and maintenance of coral reefs, seagrass beds, and sandy beaches, and act as biological transporters, introducing marine nutrients and energy to coastal ecosystems (Bjorndal & Jackson 2002, Bjorndal & Bolten

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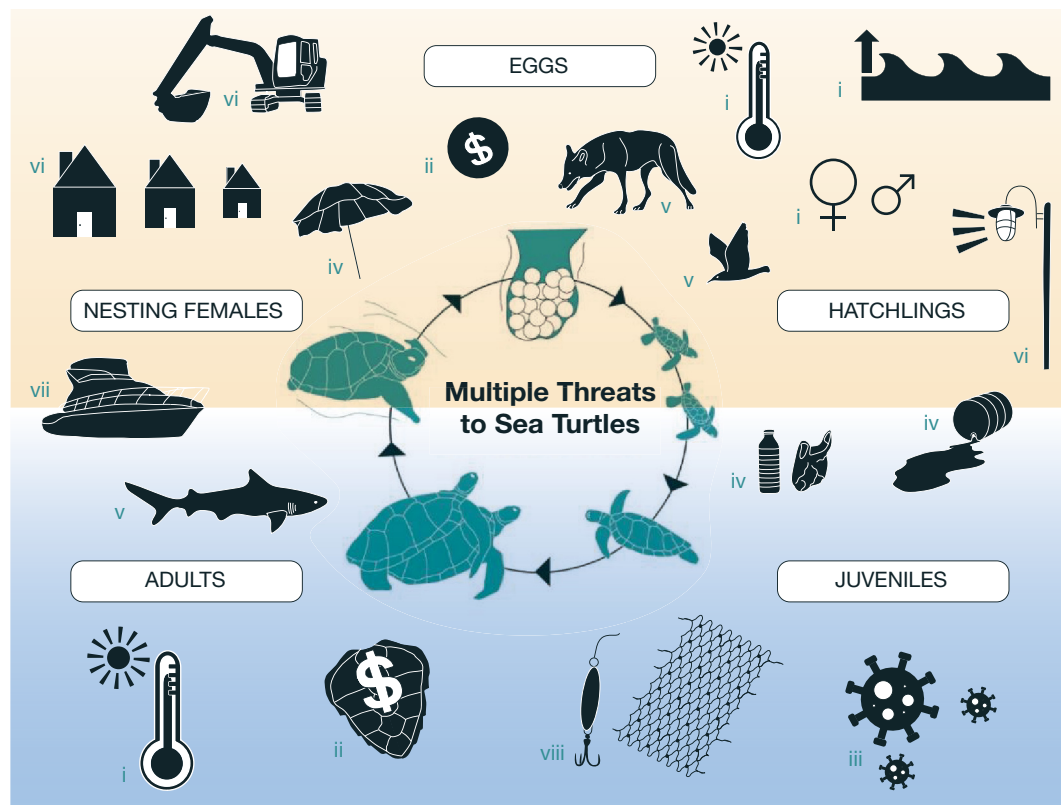


Fig. 1. Cumulative and synergistic threats that sea turtles face across their different life stages and habitats. The life history of turtles means they face threats both on land and in the ocean, and these cumulative threats may create conservation challenges. Depicted threats: (i) climate change; (ii) direct take; (iii) disease; (iv) pollution; (v) predation; (vi) coastal development; (vii) marine development; (viii) fisheries

2003). Decades-long conservation efforts aimed at mitigating some of these threats appear to have contributed to increases in abundance in certain populations (Mazaris et al. 2017). Nevertheless, some key threats remain, while others have recently emerged (Moore 2008, Hart et al. 2018, Fuentes et al. 2020a, López-Mendilaharsu et al. 2020). Taking thorough account of these threats is necessary to best inform contemporary conservation efforts. There is a broad understanding of individual threats that sea turtles are exposed to, and previous assessments based on literature reviews and expert knowledge highlight long-standing and remaining knowledge gaps (Hammann et al. 2010, Rees et al. 2016), with threat assessments usually focusing on spatiotemporally isolated issues (e.g. climate change; Patrício et al. 2021) or specific life stages (e.g. juveniles; Wildermann et al. 2018b). Relatively few studies explore the cumulative, synergistic, and secondary effects of different processes across broad spatial scales, which is required to determine the population consequences of disturbances and potential behavioral and physiological changes and their effects on vital rates (King et al.

2015, Pirota et al. 2018). Given the continued uncertainty about the impact of threats on sea turtles, we (1) identify current knowledge gaps, uncertainties, and challenges that hinder the assessments of the most pressing threats to sea turtles based on expert elicitation and a more recent literature search (up to July 2023); (2) discuss key conservation approaches used to address specific threats and identify associated data needs to improve the implementation and effectiveness of such approaches; and (3) outline how recent advancements in research and techniques may improve threat assessments and mitigation. In this way, we endeavor to provide clear guidance on how the field may move forward so that key threats can be better evaluated, understood, and mitigated.

2. METHODS

We considered the list of threats to sea turtles that were identified by the IUCN Marine Turtle Specialist Group during the second Burning Issues Assessment Workshop (Mast et al. 2005, Wallace et al. 2011). These

included climate change, coastal development, fisheries, direct take for use, and pollution. In this study, we added predation, disease, and marine development (e.g. port activities and expansion, wind energy, oil and gas extraction, aquaculture; Table A1 in Appendix 2) as threats because they have also been commonly reported to impact sea turtles (Heithaus et al. 2008, Bolten et al. 2011, Goodale & Milman 2016, Whittock et al. 2017, Butler et al. 2020, Mashkour et al. 2020). We used a Delphi technique (Mukherjee et al. 2015) to identify key knowledge gaps and potential conservation approaches associated with each threat. This approach consisted of an initial survey that gathered information on participants' background, area of expertise, and perception of knowledge gaps associated with a specific threat (Section A in the Supplement at www.int-res.com/articles/suppl/n052p303_supp.pdf). The initial survey was circulated to 65 volunteer participants that attended a virtual workshop entitled 'Understanding and quantifying cumulative and synergetic stressors to sea turtles' at the 40th International Sea Turtle Symposium in 2022. Ten additional participants with expertise in assessing specific threats to sea turtles also completed the initial survey. Based on responses from the initial survey (n = 37), respondents that indicated that they had some expertise (5–10 yr) and/or a lot of experience (>10 yr) with a particular threat were asked to complete a follow-up survey (Section B in the Supplement, example survey for climate change) for a maximum of 3 threats, based on their stated expertise. The follow-up survey asked specific questions related to each threat (up to 3) to

identify conservation approaches to mitigate those threats and a list of knowledge gaps that hinder our evaluation of each threat. Respondents were also asked to indicate how certain they were of the impacts of specific threats on sea turtles. Degrees of certainty were based on their knowledge of the threat and/or the existence of empirical work/literature (Section B in the Supplement). The results from the survey are mainly presented in Tables 1 & 2 and incorporated with our literature review on the background, conservation approaches, and knowledge gaps for each threat.

Along with the Delphi survey results, we summarized information within the literature to present the current knowledge of key threats to sea turtles, conservation approaches implemented to address specific threats, and outstanding gaps that hinder our understanding of impacts. We also included information on emerging research techniques, identified by respondents, to fill knowledge gaps in assessing threats to sea turtles.

3. RESULTS

The initial survey was completed by 37 respondents, of which 62% were academics, 19% were government employees, and 19% were associated with either for-profit or non-profit organizations. Most respondents (30%) indicated that they had 10 to 15 yr of experience working with sea turtles, followed by those with 5 to 10 yr of experience (27%), and those

Table 1. Certainty of survey respondents (in %) towards the impacts of specific threats on sea turtles

	Climate change (n = 12)	Direct take (n = 3)	Disease (n = 4)	Pollution (n = 5)	Predation (n = 6)	Coastal development (n = 10)	Marine development (n = 11)	Fisheries (n = 9)
Low certainty: very little or no empirical work/literature exists, or you have limited personal experience	0	0	0	0	0	0	9.09	0
Moderate certainty: some empirical work/literature exists, or you have some personal experience	16.67	33.33	75	20	33.33	30	63.64	33.33
High certainty: body of empirical work exists, or you have direct personal experience	50	33.33	0	80	66.67	40	27.27	33.33
Very certain: extensive empirical work exists, or you have extensive personal experience	33.33	33.33	25	0	0	30	0	33.33

Table 2. Key knowledge gaps associated with the impact and conservation strategy for each considered threat

Threat	Key questions related to impact	Key questions related to conservation
Climate change	<p>What is the effect of feminization on population dynamics and what is the number/proportion of males necessary to maintain a population at various levels?</p> <p>What is the impact of climate change on nesting and foraging habitats, and how might sea turtles adapt?</p> <p>How do cascading effects of climate change affect sea turtles (e.g. effect of climate change on fishing)?</p> <p>What are the physiological thresholds or tolerances at all life stages? Which populations are nearing or passing those thresholds?</p>	<p>What is the best approach for predicting which nesting areas to protect under future climate conditions?</p> <p>How do interventions at nesting beaches (e.g. clutch relocation and/or cooling) impact the ability of sea turtles to adapt to climate change (through behavior or evolutionary processes)?</p> <p>How will manipulating sand temperatures affect the operational sex ratio (OSR) and population dynamics? And what should the OSR of a healthy sea turtle population be?</p> <p>What are the risks of manipulating the nesting environment? What are the trade-offs?</p>
Direct take	<p>Where does direct take occur, how many turtles are taken, and what life stages are impacted?</p> <p>Why is direct take occurring and who is involved in these activities (e.g. supply chain and consumers), i.e. who are the drivers?</p> <p>What are the thresholds of take at each life stage that exceed sustainability?</p>	<p>Is there capacity to create a monitoring and/or enforcement body for direct take from specific populations?</p> <p>Are local communities supportive of cessation of direct take?</p> <p>How can we distinguish between retained bycatch vs. direct take?</p>
Disease	<p>What is the etiology of diseases?</p> <p>What is the prevalence and severity of disease on oceanic and neritic turtle populations?</p> <p>What are the environmental and/or human stressors causing immuno-suppression in sea turtles?</p> <p>What are the common factors associated with sites with high disease prevalence and severity?</p> <p>What are the contextual and/or site-specific factors affecting disease?</p>	<p>What conditions and/or treatments improve chances of recovery?</p> <p>What are the baseline and/or reference ranges of healthy turtle physiology?</p> <p>What are the appropriate diagnostic and treatment options for disease?</p>
Pollution	<p>What are the population-level impacts of plastic ingestion and entanglement?</p> <p>What are the effects of chemical contaminants on the long-term survival of animals treated for oil fouling?</p> <p>What are the sublethal health effects of pollutant exposure on sea turtles?</p>	<p>How can pollutants be traced back to their source to hold landholders and companies responsible?</p> <p>How willing is society to change their behavior to mitigate impacts from pollution?</p>
Predation	<p>What level of predation is sustainable?</p> <p>What abiotic and biotic factors affect predator and prey behaviors?</p> <p>How do predators affect sea turtle populations and behavior in the face of multiple anthropogenic and natural stressors?</p>	<p>Which available management actions are most effective at reducing predation? What are their associated demographic, ecological, logistical, and financial trade offs?</p> <p>How might management of synergistic threats interact with predation?</p>

Table 2. (continued)

Threat	Key questions related to impact	Key questions related to conservation
Coastal development	<p>What is the collective impact (additive, negative, synergistic) of different types of coastal development on nesting sea turtle behavior and reproduction?</p> <p>What level of adaptability do turtles have when it comes to coastal development? Does it differ among species and among populations of the same species?</p> <p>What factors influence turtle foraging site selection at regional or local scales? And how does coastal development affect it?</p>	<p>How effective are current regulations at protecting nesting beaches from coastal development threats?</p> <p>How do we best balance coastal development and ecological priorities?</p> <p>What are the disturbance thresholds for sea turtles, per life stage, for individual threats? How do these thresholds change for cumulative stressors?</p>
Marine Development	<p>What are the direct and indirect impacts of marine development on sea turtles?</p> <p>What marine development activities directly (vs indirectly) impact sea turtles the most, given a defined threshold for impact (e.g. habitat alteration, water column pollution, sound propagation, presence of vessels and/or other anthropogenic activities, or sedimentation)?</p> <p>What are the behavioral and demographic responses to different forms of marine development?</p>	<p>How can we better evaluate sea turtles' responses to direct and indirect anthropogenic impacts, and their interactions in pelagic waters?</p> <p>Is there sufficient knowledge on sea turtle spatio-temporal distribution and habitat use to determine the best conservation strategy?</p> <p>Are current key conservation strategies effective/efficient?</p> <p>Are current restriction boundaries accurately encompassing habitat-use?</p> <p>What metric defines success? Is this metric (or metrics) sufficiently tied to state/federal/international management goals?</p>
Fisheries	<p>What are the individual and population level effects of non-lethal impacts from fisheries (industrial, small scale, and recreational)?</p> <p>How do we develop the best estimate of bycatch when data are incomplete, especially when observer coverage is low?</p> <p>What is the rate of post-interaction mortality across species and fishery types? How can we assess post-release mortality?</p>	<p>How can we identify and effectively engage relevant stakeholders in development, implementation, and adoption of sustainable bycatch reduction solutions in various fishing sectors, communities, and cultures?</p> <p>What fishing gear characteristics most influence the magnitude and severity of bycatch impacts, and how can we prioritize bycatch reduction efforts for the fishing gears with the highest impacts on sea turtles?</p> <p>What is the scale of mitigation being undertaken, how effective is it, and how can this be augmented?</p> <p>What are some current mitigation measures that need more research and development on efficacy?</p>

with more than 20 yr of experience (22%). Most respondents indicated some experience (>5 yr) with working on impacts of climate change (60%), coastal development (46%), and/or marine development (48%) on sea turtles. In contrast, fewer respondents indicated experience (>5 yr) with fisheries (35%), pollution (35%), predation (30%), disease (27%), and direct take (27%). Based on the follow-up surveys, respondents indicated that they were most certain of impacts related to climate change, pollution, and coastal de-

velopment and least certain of impacts related to disease and marine development (Table 1).

3.1. Climate change

3.1.1. Background

Sea turtles are affected by multiple climate-related threats across their different life stages (Patrício et al.

2021). Considerable research effort has focused on the threat of population feminization due to the effect of rising incubation temperatures in light of temperature-dependent sex determination (TSD; e.g. Jensen et al. 2018, Patrício et al. 2021). Rising incubation temperatures can also decrease hatching success and hatchling fitness (Santidrián Tomillo et al. 2012, Hays et al. 2017, Montero et al. 2018). Additionally, sea level rise may cause the loss of nesting areas and higher clutch mortality due to seawater inundation (Fuentes et al. 2010, Varela et al. 2019, Lyons et al. 2020). Further, extreme weather events are predicted to occur more frequently with climate change, which may destroy nests and alter hatchling dispersal patterns (Fuentes & Abbs 2010, DuBois et al. 2020). For in-water life stages, future changes in climate conditions may push sea turtles into novel regions and habitats where they experience new anthropogenic, trophic, and ecological interactions (Pikesley et al. 2015, Fuentes et al. 2020a). Reduced fitness due to resource depletion or emerging diseases may further stress populations in a changing climate (Patrício et al. 2021). Climate change has therefore been described as a threat multiplier that interacts in additive and synergistic ways with almost all other stressors that sea turtles face (Staudt et al. 2013).

3.1.2. Conservation approaches

Several conservation mechanisms have been proposed to mitigate the effects of climate change on sea turtles (reviewed in Fuentes et al. 2012). Some mechanisms are focused on reducing egg incubation temperatures by shading or irrigating nests (Jourdan & Fuentes 2015, Esteban et al. 2018, Gatto et al. 2023). Others emphasize relocating clutches to cooler environments, to areas less prone to flooding and erosion on the nesting beach, or to hatcheries (Martins et al. 2021). Additional mechanisms include protecting nesting areas through sediment nourishing, revegetation, and regulated coastal development (Dellert et al. 2014). Monitoring incubation temperatures has been widely adopted, allowing direct assessments of temperature-related clutch mortality (Laloë et al. 2017, Bladow & Milton 2019) and baselines for sex ratio assessments. Discussions on the effectiveness and feasibility of different conservation approaches to mitigate the impacts of climate change on sea turtles can be found in Fuentes et al. (2012) and Patrício et al. (2021). To date, less effort has been directed towards understanding and mitigating the detrimental effects of climate change on turtles at sea (e.g. changes in condi-

tions at migratory corridors; Almpandou et al. 2019) when compared to efforts at nesting beaches. One of the strategies suggested to provide protection at sea and increase the resilience of sea turtles to climate change is the establishment of dynamic protected areas (Maxwell et al. 2015).

3.1.3. Knowledge gaps

Many assessments on the impact of climate change on sea turtles focus on individual stressors and/or specific sea turtle populations, with most to date focusing on the impacts of changes in temperature on sea turtle reproductive output (Patrício et al. 2021). As such, several knowledge gaps related to the impacts of changes in temperature on sea turtles have been identified in previous reviews (see Patrício et al. 2021) and addressed in recent research efforts (Rees et al. 2016). However, despite this work, the demographic consequences of projected skewed sex ratios are still poorly understood (Table 2; Heppell et al. 2022), and the minimum number of adult males needed to sustain a population remains unknown (Fig. 2b) (Santidrián Tomillo et al. 2021, Santidrián Tomillo 2022). Nesting beaches with heavily skewed female hatchling production may also exhibit a lower incidence of multiple paternity in clutches, which may be a precursor to further demographic consequences of a scarcity of adult males (Hays et al. 2022). Crucially, the point at which a scarcity of males starts to negatively impact clutch fertility is still unknown (Hays et al. 2022). Male hatchling production may increase with heavy rainfall (Staines et al. 2020, Laloë et al. 2021). While there are reasonable regional predictions for the likely extent of climate warming, there remains a high degree of uncertainty regarding how patterns of heavy rainfall may change in the future (Santidrián Tomillo et al. 2021) and how interactions with changes in temperature will affect the reproductive output of sea turtles.

The ability of sea turtles to adapt to projected changes in climate remains largely unknown. To counteract the impacts from increases in temperature, sea turtles may shift their nesting phenology to cooler times of the year (e.g. Weishampel et al. 2004, Mazaris et al. 2008). However, studies have now suggested that phenological shifts are unlikely to fully mitigate impacts of climate change (Saba et al. 2012, Monsinjon et al. 2019, Fuentes et al. 2023b, Laloë & Hays 2023) and may also be influenced by non-environmental phenomena (Robinson et al. 2016). It has been suggested that sea turtles may also gradually

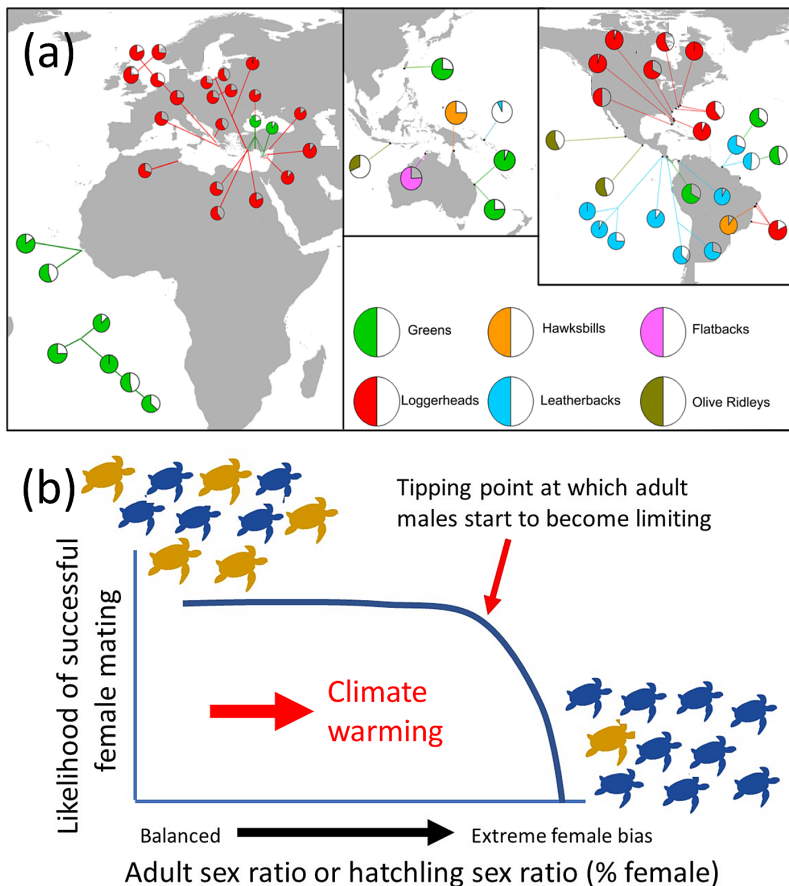


Fig. 2. Climate change and skewed sex ratios. (a) Hatchling sex ratio reported around the world. The estimated proportion of females is presented as the filled slices of the pie charts, with different species being presented by different colors (redrawn from Hays et al. 2014). (b) Theoretical considerations for how the likelihood of successful female mating might be expected to change at increasingly female-skewed sex ratios. As adult male turtles (yellow) become more scarce compared to females (blue), a tipping point may occur where not all breeding females encounter breeding males (figure modified from Hays et al. 2023)

shift their nesting ranges to areas that are climatically more suitable in the future (Abella Perez et al. 2016, Mainwaring et al. 2017, Fuentes et al. 2020a). Since nest site fidelity is not as high as previously thought, and because nesting beaches that are too warm will experience high embryonic mortality and hence will produce few to no hatchlings, recruitment will be reduced in specific areas (Raposo et al. 2023).

Less is known about the impacts of climate change on sea turtle foraging habitat and in-water behavior (Patrício et al. 2021). Storm systems can shape the movements of sea turtles in unusual ways (Monzón-Argüello et al. 2012, Ascani et al. 2016). Storms and climate warming can also profoundly impact foraging habitats, for example, causing seagrass die-offs and coral bleaching associated with marine heatwaves (Hays et al. 2020, Strydom et al. 2020), with likely cas-

cading effects on sea turtle foraging ecology. However, how foraging habitats are likely to change and the consequences for sea turtle growth, health, and reproductive output remain poorly understood (Stubbs et al. 2020).

Although progress has been made in projecting sea turtle habitat conditions under future environmental change scenarios (e.g. Almpantidou et al. 2016, Patel et al. 2021), advances are needed to better incorporate biological information and dynamic environmental conditions into models to inform possible conservation measures. A few studies have taken a more holistic approach, looking across multiple climate stressors or multiple sea turtle populations (e.g. Fuentes et al. 2011, Patrício et al. 2019, Lettrich et al. 2020). Expanding the scope and prevalence of multi-population and multi-stressor assessments will improve our ability to compare populations and prioritize conservation resources. Additionally, there is uncertainty surrounding how climate forecasts at global or regional scales apply at local scales.

Ultimately, without a robust understanding of the impacts of climate change on turtles and pre-existing baseline information on population structure and reproductive output, it becomes challenging to develop appropriate conservation interventions (see Table 1 in Patrício et al. 2021). For

example, relocation of clutches can change incubation conditions and hence hatchling sex ratios; however, relocations should not be conducted without adequate baseline data for primary sex ratios (Tolen et al. 2021, Ware et al. 2021). Further information is also needed on how microclimate conditions at hatcheries affect embryonic development (Robledo-Avila et al. 2022) or encourage fungal infections (Hoh et al. 2020), as well as on the overall risks of manipulating the nesting environment. Additionally, it can be challenging to predict which nesting areas will become inundated and may benefit from relocation (Ware & Fuentes 2018, Ware et al. 2019, 2021). Ultimately, the feasibility, costs, and ethics of implementing conservation approaches also need to be considered before implementation (Fuentes et al. 2015). Further, challenges exist with developing approaches to mitigate

climate change impacts on the ocean. This is mainly driven by the lack of knowledge about impacts themselves and also the effectiveness of proposed approaches (e.g. dynamic marine protected areas) in reducing those impacts.

3.2. Direct take

3.2.1. Background

For many centuries, sea turtles (eggs, meat, leather, oil, carapaces, and other body parts) have been an important resource for coastal inhabitants worldwide (Early-Capistrán et al. 2018, Miller et al. 2019). While such direct take is currently far below historical levels, the value of sea turtles in this regard persists in many regions (e.g. Nada & Casale 2011, Quiñones et al. 2017, Barrios-Garrido et al. 2018). Direct take impacts sea turtles at all life stages (Lutcavage et al. 1997). While some communities legally consume turtles domestically (Humber et al. 2014), others supply illegal market networks locally, regionally, and internationally, such as the illegal trade of tortoiseshell products sourced from hawksbill turtles (Vuto et al. 2019, Nahill et al. 2020, LaCasella et al. 2021). An estimated minimum of 1.1 million sea turtles were exploited illegally between 1990 and 2020, although direct take was found to be most frequent in large, stable populations (Senko et al. 2022b).

3.2.2. Conservation approaches

Understanding why certain human communities exploit sea turtles is a crucial step in developing and applying effective conservation mechanisms to address both legal and illegal take (Barrios-Garrido et al. 2018, Travers et al. 2019). Existing tools to assess direct take include direct and indirect observation, review of law enforcement records, and expert consultations; in most cases, these do not provide accurate information on the magnitude of take, targeted life stages, or locations where take is occurring (Gavin et al. 2010). Successful conservation measures must address the economic, traditional, and social needs of local communities to balance the interests of those involved and the conservation of target species (Campbell et al. 2002, Ferraro & Gjertsen 2009, Gjertsen & Niesten 2010). This may include identifying alternate livelihood opportunities to provide alternatives to commercialization of sea turtles and related products (Lutcavage et al. 1997). Work-

ing with communities towards co-management appears to be a successful strategy for sustainable harvest practices (Kamrowski et al. 2015) by involving local stakeholders in all aspects of conservation management decisions, including research, education, implementation, and enforcement of conservation programs (Pakiding et al. 2020, Yaakop et al. 2021). When working collaboratively with these communities, both sea turtle populations and local communities can benefit.

3.2.3. Knowledge gaps

Quantifying and locating direct take are challenging due to the frequently illegal nature of these activities (Hamann et al. 2010, von Essen et al. 2014). In areas where turtle consumption is socially normalized and even a symbol of wealth, traffickers know how to avoid detection, even when large numbers of turtles are trafficked (Mancini & Koch 2009, Quiñones et al. 2017, Lopes et al. 2022). Illegally harvested sea turtles and turtle-related products generally supply domestic markets (Nada & Casale 2011, Hancock et al. 2017, Quiñones et al. 2017), thus avoiding wildlife trafficking controls such as customs inspections. Even when traded internationally, wildlife products can pass undetected due to inadequate inspection systems (e.g. Bräutigam & Eckert 2006, Gomez & Krishnasamy 2019). Further challenges to quantify the effects of illegal take at sea are related to separating those impacts from fisheries bycatch mortality, as sea turtles are often regarded as a welcome bycatch and used for consumption (Mancini & Koch 2009). Moreover, a global synthesis of egg take is lacking. These information gaps, coupled with poor demographic information about the animals taken, can impede knowledge about the effect of direct take on population viability (Hamann et al. 2010).

Combating direct take has been further challenged by a shift from physical markets to online trade (Gomez & Krishnasamy 2019), which increases the difficulty of tracking transactions (Sung et al. 2021, Sardari et al. 2022). Ultimately, understanding the social, economic, and cultural drivers behind turtle consumption is fundamental to assessing the effects of direct take and its sustainability (Hamann et al. 2010) and to identifying appropriate conservation approaches. As such, there is a need to understand where sustainable levels of harvest exist within each population and the needs of the local communities relying on these fisheries.

3.3. Disease

3.3.1. Background

Determining the global extent and impacts of disease on sea turtles is often difficult due to the lack of knowledge on sublethal long-term chronic and cumulative impacts. Disease affects sea turtles across all ontogenetic life history stages (Mashkour et al. 2020) via bacterial and fungal pathogens (Smyth et al. 2019), parasites (Aznar et al. 1998, Gordon et al. 1998, Greiner 2013, Chapman et al. 2018), and viruses (e.g. fibropapillomatosis; Work et al. 2001). Susceptibility to these and other diseases is often tied to external factors such as anthropogenic activities, climatic variations, and pollutants from catastrophic events like the *Deepwater Horizon* oil spill and failure of the Fundão dam (Hamann et al. 2010, Rees et al. 2016, Deem & Harris 2017, Preece et al. 2017, Wallace et al. 2017, Miguel et al. 2022). More recently, research suggests that infectious and non-infectious diseases affect sea turtle health in a variety of ways that ultimately impact reproductive output and population viability on a global scale (Rees et al. 2016, Page-Karjian & Perrault 2021).

3.3.2. Conservation approaches

The diagnosis and management of disease is a complex process requiring various research tools and collaboration with multidisciplinary experts to advise conservation actions (Mashkour et al. 2020, Kophamel et al. 2022), as well as consideration of the connection between the health of humans, animals, and the environment, termed One Health (Mashkour et al. 2020). Mechanisms to assess and address impacts of disease on population health and population viability include disease risk analysis (DRA), rehabilitation of stranded animals, post-mortem examination, and reduction of disease stressors (Deem & Harris 2017, Flint et al. 2017, B. A. Stacy et al. 2017, Page-Karjian et al. 2020). DRA tools are especially helpful in providing an objective assessment of the risk of disease for a given (sub)population because a complete DRA assembles information on the etiology, management options, and impacts of specific diseases which can then be applied locally in the context of a specific habitat (Mashkour et al. 2020). Rehabilitation centers provide immediate treatment of diseased individuals (e.g. removal of tumors or ingested marine debris and assistance during mass stranding events; Lewbart et al. 2005, Innis et al. 2019). Moreover, vet-

erinary assessment and rehabilitation provide physiological insights on the impacts of anthropogenic and natural stressors (Innis & Dodge 2020). However, the role of rehabilitation for enhancing the survivorship of a population remains unclear and controversial (Flint et al. 2017). Postmortem examination of diseased individuals is crucial for determining the cause of mortality or illness, identifying disease agents and threats to population recovery and viability, and establishing treatment options for rehabilitating sea turtles (B. A. Stacy et al. 2017).

3.3.3. Knowledge gaps

Evaluating the impact of disease on sea turtles is mainly limited by (1) lack of knowledge on the link between environmental health, incidence of disease, and population viability; and (2) sample size and disease presentation variations that hinder the extrapolation of findings at the population level (Deem et al. 2001, Aguirre & Lutz 2004, Rees et al. 2016, Deem & Harris 2017, Stacy & Innis 2017, Kophamel et al. 2022, Young 2022). As a result, the cause, extent, and impact of disease on sea turtles are often unknown, making it hard to quantify and manage impacts (Flint et al. 2017). Moreover, impacts of emerging infectious diseases vary since modes of transmission, turtle immune responses, environmental factors, and genetics appear to play a role in the prevalence and manifestation of diseases (Mashkour et al. 2020, Martin et al. 2022). Determining the factors that influence disease emergence, severity, and recovery is a priority for assessing the impact of disease on population viability and reproductive fitness (Hamann et al. 2010, Deem & Harris 2017, Stacy & Innis 2017, Roost et al. 2022). Numerous studies link the increased human-induced environmental degradation of terrestrial and marine ecosystems and the emergence of wildlife disease (Dobson & Foufopoulos 2001, Brearley et al. 2013), and because most habitats are typically affected by a suite of anthropogenic stressors, identifying any 1 specific cause of deteriorating health or disease outbreak is often difficult (Smith et al. 2009, Giraudeau et al. 2018), leaving managers uninformed on what stressors to target in management plans. Once a better understanding of the links between the impacts of stressors on disease and health status is achieved, information from health assessment studies could be added as parameters to population viability analyses to enhance the accuracy of the predictions and provide an understanding of critical population trends (Fryxell et al. 2014).

3.4. Pollution

3.4.1. Background

Sea turtles are exposed to a variety of pollutants throughout their lives due to their reliance on a range of habitats (Lutcavage et al. 1997) and have been used as sentinels for environmental biomonitoring and toxicological studies (Andreani et al. 2008, Villa et al. 2017, Gaus et al. 2019, Leusch et al. 2021). Potentially dangerous pollutants to sea turtles include organic pollutants (e.g. persistent organic pollutants, organochlorine compounds, and biotoxins; Keller et al. 2006, van de Merwe et al. 2010, De Andrés et al. 2016, Perrault et al. 2017, Barraza et al. 2020) and inorganic pollutants (e.g. heavy metals; Cortés-Gómez et al. 2017, 2018a,b,c, Villa et al. 2017, Gaus et al. 2019, Finlayson et al. 2021) that enter coastal habitats as runoff from manufacturing, agricultural, and waste disposal activities (Keller et al. 2006, Camacho et al. 2014, Barraza et al. 2020). While impacts of offshore oil spills have received recent attention (Lauritsen et al. 2017, McDonald et al. 2017, Wallace et al. 2017, 2020), land-based runoff and discharge from industrial shipping remain the largest sources of oil in coastal and marine habitats (National Academies of Sciences, Engineering, and Medicine 2022). Anthropogenic debris, including plastic waste, is also a significant source of pollution affecting sea turtles (Tomás et al. 2002, Schuyler et al. 2016, Garrison & Fuentes 2019, Kuhn & van Franeker 2020).

The release of oil, chemicals, and anthropogenic debris can have direct and acute effects on the marine environment, and given that contaminants from these pollutants can persist in the marine environment, exposure can also result in chronic impacts to the health of sea turtles at various life stages (Milton & Lutz 2003, Perrault et al. 2011, Rees et al. 2016, du Preez et al. 2018, Senko et al. 2020, Wallace et al. 2020). Within the nest environment, pollutants can negatively impact sea turtle health by interfering with hatchling development, size, hatching success, and survivorship (Fritts & McGehee 1981, Phillott & Parmenter 2001, van de Merwe et al. 2010, De Andrés et al. 2016). In coastal and marine habitats, exposure to pollution can cause a variety of impacts including endocrine disruption and reproductive and immune system impairment (Keller et al. 2006, Barraza et al. 2020). These can, in turn, negatively impact immune function, growth, and physiological and metabolic pathways and can ultimately increase the incidence of infectious disease in affected popu-

lations (Sakai et al. 2000, Keller et al. 2006, Day et al. 2007, D'ilio et al. 2011, Candan 2018, Cortés-Gómez et al. 2018a,b,c, Gaus et al. 2019, Finlayson et al. 2021). Exposure to oil concentrated in oceanic convergence zones impacts multiple life history stages, both directly and indirectly (Witherington et al. 2012, Wallace et al. 2020) through physical fouling that can impede movement and cause physiological issues that leave turtles more vulnerable to predators, starvation (due to reduced foraging ability), and death by asphyxiation (Witherington et al. 2012, Wallace et al. 2020). Indirect impacts from chronic exposure to oil include negative impacts to the skin, blood, digestive and immune systems, and salt glands, all of which can impact individual fitness and survivorship (Milton & Lutz 2003, N. I. Stacy et al. 2017). Oil spills can also decrease nesting on beaches near the spill (Lauritsen et al. 2017).

Anthropogenic debris can present a physical barrier to hatchlings emerging from the nest environment (Sousa-Guedes et al. 2023) or entering the ocean (Nelms et al. 2015, Aguilera et al. 2018, Garrison & Fuentes 2019, Gündoğdu et al. 2019), leading to increased mortality from predation, desiccation, and dehydration, and possibly cause a reduction in population recruitment (Aguilera et al. 2018, Dimitriadis et al. 2018). In addition, microplastics (<5 mm in size) in beach sediments may alter nest properties, such as temperature and permeability, with potential negative implications for embryonic development, sex determination, and hatching success (Beckwith & Fuentes 2018, Lavers et al. 2021, Fuentes et al. 2023a). Debris is also a significant hazard to sea turtles in the marine environment and can cause entanglement, which can result in physical injuries such as abrasions, loss of limbs, reduced mobility, and reduced foraging efficiency. These injuries can culminate in starvation and drowning (Gregory 2009, Barreiros & Raykov 2014, Vegter et al. 2014, Senko et al. 2020). Additionally, ingesting plastic debris can cause internal physical injuries, gastrointestinal tract damage, malnutrition, further exposure to contaminants, and, ultimately, death (Barreiros & Raykov 2014, Nelms et al. 2015, Garrison & Fuentes 2019).

3.4.2. Conservation approaches

Most pollutants in coastal and marine habitats originate from land-based sources (UNEP 2007, Vikas & Dwarakish 2015), and as a result, land- and marine-based legislative and regulatory efforts are required. Although numerous agreements exist, they mainly

apply to subscribing nations, and enforcement is impractical, decreasing their effectiveness (Heimert 1997, Tan 2005, Xanthos & Walker 2017).

Countries may have legislation that governs the response to catastrophic chemical and oil spills. These can entail trained personnel, specialized equipment and facilities, and procedures to assess and minimize impacts (Wallace et al. 2020). Guidance protocols may include oil spill response training, action plans for damage assessment, and compensation for those damages (Wallace et al. 2020). Countries with oil production industries are required to have national oil spill contingency plans that are created with guidance from the International Petroleum Industry Environmental Conservation Association–International Association of Oil and Gas Producers (Owens & Sykes 2005, Glushik 2017).

Other methods to minimize pollution in coastal and marine habitats include targeting single-use plastic (SUP), recycling, replacing common pollutants with sustainable substitutes, and burning for fuel and green energy (Harding 2016, Jha & Kannan 2021). SUPs are one of the most common types of pollutants in the marine environment (for review see Schnurr et al. 2018). While reusable alternatives to SUPs often exist, replacement of SUPs is usually only successful when public engagement and education are sufficient to inform consumer knowledge and elicit behavioral change (Heidbreder et al. 2019). Management efforts should include facilitating an increase in plastic recycling through enhancing recycling infrastructure and increasing public awareness (Harding 2016). Recently, the United Nations Environment Programme has started negotiations to develop a legally binding instrument that would reflect diverse alternatives to address the full life cycle of all types and sizes of plastics, the design of reusable and recyclable products and materials, and the need for enhanced international collaboration to promote capacity building and collaboration (Hopewell et al. 2009, Senko et al. 2020, March et al. 2022). Regardless of the source or type of pollution, environmental persistence and widespread dispersal (Barnes et al. 2009) and increasing amounts of pollution in coastal and marine habitats (Laist et al. 1999, Derraik 2002, Moore 2008, Jambeck et al. 2015, Harding 2016, Löhr et al. 2017) make it difficult to manage and mitigate their effects.

3.4.3. Knowledge gaps

Determining the global extent and impacts of different sources of pollution on sea turtles is difficult

because several knowledge gaps exist in relation to sublethal impacts (e.g. chemical absorption; McCauley & Bjørndal 1999), and long-term chronic and cumulative impacts are understudied (Table 2). Moreover, coastal and marine pollution is increasing throughout most of the world (Laist et al. 1999, Derraik 2002, Moore 2008, Jambeck et al. 2015). The need to further evaluate the effects of pollution on turtle development, survivorship, health, reproduction, and habitat conditions has been previously highlighted, and recommendations for further studies on understanding non-point sources, pollutant dispersal patterns, and toxicology have been made (Hamann et al. 2010). Critical toxicity thresholds remain understudied and poorly understood, and quantitative data on direct mortality are lacking due to the opportunistic nature of observing the impacts of pollution on turtles in the marine habitat (Milton & Lutz 2003, Hamann et al. 2010, Wallace et al. 2020). In addition, impacts from pollution (e.g. oil) are rarely reported for specific life stages, namely those inhabiting open ocean habitats, and inhibit our understanding of vulnerability to specific pollutants (Wallace et al. 2020, but see N. I. Stacy et al. 2017). While direct physical impacts from oil contamination (e.g. fouling) may be easier to assess (Vargo et al. 1986, Westerholm & Rauch 2016), the toxicological effects of oil and oil dispersant chemicals on individual sea turtles and on populations in the short and long term remain poorly understood (Wallace et al. 2011, 2020). Similarly, population-level effects from other types and sources of pollution remain poorly investigated (NMFS et al. 2011, Wallace et al. 2011, but see Bembenek Bailey et al. 2017, 2019, Harms et al. 2019).

To better understand the global extent and impacts of plastic contamination on turtle nesting beaches, a standardized methodology for sampling marine debris and microplastics in beach sediment is needed to allow for more effective comparisons (Duncan et al. 2019). Additionally, experimental studies of nest environments under variable and experimentally controlled microplastic density are needed to better understand the threat to turtle nesting ecology from plastic pollution, such as desiccation, toxicology, and changes to hatchling sex ratios (Beckwith & Fuentes 2018, Duncan et al. 2019). Though some research efforts have focused on the prevalence of at-sea entanglement in plastic pollution and derelict fishing gear (or ghost gear) (Wilcox et al. 2013, Vegter et al. 2014, Duncan et al. 2018), the overall extent of mortality and implications for population-level and life stage-specific impacts are not well understood (Vegter et al. 2014, Nelms et al. 2015). In addition, our cur-

rent understanding of the sublethal impacts of microplastic ingestion due to the uptake of associated chemical contaminants (e.g. phthalates and other plasticizers) remains marginal (Duncan et al. 2019, 2021, but see Savoca et al. 2018, 2021). Furthermore, there is a paucity of data on the lasting impacts of debris on ecosystem degradation and interference with essential ecosystem functions in the various habitats that sea turtles rely on throughout their life cycle (Katsanevakis et al. 2007, Smith 2012, Vegter et al. 2014).

Ultimately, information regarding the extent and impact of pollution on turtles is needed to facilitate the design of appropriate mitigation strategies. Monitoring and better reporting (e.g. inclusion of negative results and observations from small sample sizes) will provide a more accurate representation of occurrence rates and extent of effects on individuals, on populations, and across species (Kühn & van Franeker 2020, Puskic et al. 2020, Ware & Fuentes 2020). This will also help to identify hotspots of risk for turtles, where distributions overlap with high concentrations of pollution, to identify areas where clean-up operations and policy changes are most needed.

3.5. Predation

3.5.1. Background

On nesting beaches, eggs, hatchlings, and adults face predation threats by native and introduced species (e.g. insects, crabs, feral hogs, diverse canids, and rats; Marco et al. 2015, Gronwald et al. 2019, Lovemore et al. 2020). Synchronous emergence of hatchlings increases the dilution effect, but when crawling across the beach, hatchlings can continue to face high predation rates (Erb & Wyneken 2019, Martins et al. 2021). The level of predation of hatchlings is affected by the amount of debris they encounter on the beach (Santidrián Tomillo et al. 2010, Aguilera et al. 2018), the numbers of hatchlings emerging, and the nest-to-surf distance (Erb & Wyneken 2019). When hatchlings initially enter the ocean, they are primarily at risk of predation by teleosts (Wilson et al. 2019), sharks (Bashir et al. 2020), and birds (Carneiro et al. 2017), and predation pressure is affected by tides, time spent in shallow water, and the predictability of time of release from nests (Gyuris 1994, Chung et al. 2009, Reising et al. 2015). Less is known about the threats turtles face during the pelagic stage, but with little refuge available in the open ocean, they are likely to continue to face predation by

teleosts, sharks, and birds. In nearshore habitats, juveniles, subadults, and adults primarily face predation risk by the largest ocean predators (e.g. sharks and killer whales; Pitman & Dutton 2004, Heithaus et al. 2008, Salmon et al. 2018, Stacy et al. 2021, Aoki et al. 2023). This risk of predation impacts sea turtle habitat use and foraging behavior in the neritic zone (Heithaus et al. 2007, Whitman 2018).

3.5.2. Conservation approaches

Selecting which management strategy to implement to mitigate predation depends on the current level of predation, identified predators, financial cost, and social support (Engeman et al. 2002, 2012, Silver-Gorges et al. 2021). Efforts to reduce losses may be predator or life-stage dependent, and previous efforts have included nest-level (e.g. screening, caging, relocation, hatcheries), predator-level (e.g. hunting, trapping, relocation), and ecosystem-level (e.g. habitat restoration, artificial light mitigation, waste management) activities (Table 2). Among the most common interventions are *in situ* screening of nests, relocation of the clutch to supervised hatcheries, and predator removal (Ratnaswamy et al. 1997, Engeman et al. 2005, 2010). However, predator management programs (including the removal of invasive predators such as feral pigs or rats) can have significant repercussions for ecosystem health and ethical concerns (e.g. single species-focused conservation effort; Barton & Roth 2008, Caut et al. 2008).

An important consideration in sea turtle predation management is the critical role that such losses play in broader ecosystem dynamics (Barton & Roth 2008). The predation of all sea turtle life stages is natural, though not socially popular, and is an integral part of marine ecosystem functioning (Bouchard & Bjorndal 2000, Ferretti et al. 2010). While the predation of sea turtles may be natural, the threat of predation may need to be managed and reduced in some circumstances, such as (1) predation by non-natural predators such as rats or feral pigs, (2) high levels of predation occurring in populations that also face other threats, and (3) increased levels of predation occurring due to other anthropogenic factors, such as light pollution aggregating hatchlings (Santidrián Tomillo et al. 2010, Silva et al. 2017). Decisions for managing sea turtle predation may be challenged by coastal development or habitat conservation and restoration activities, which may impact predator foraging patterns and prey selection (Arroyo-Arce et al. 2014, Butler et al. 2020). Further, climate change-induced shifts in

the spatiotemporal distribution of both sea turtles and their predators may create novel interactions with unknown management considerations in the future.

3.5.3. Knowledge gaps

Some of the biggest challenges in assessing predation levels and risk to sea turtles are due to a lack of (1) documentation of predation, including predator, frequency, and impact; (2) standardized definitions and protocols to quantify risk within and across habitat and predation types; (3) risk estimates at the population and landscape scales; and (4) understanding of complex trophic linkages and cascades of what predator removal does and how the predator that is removed reacts (Barton & Roth 2008, Ritchie & Johnson 2009). A broad understanding of whether human presence and coastal development affect predation is also needed. For example, urbanization of coastal areas in Florida increased the abundance of mesopredators (i.e. raccoons), consequentially increasing the levels of nest depredation on beaches closest to human development (Engeman et al. 2005). Similarly, decreased numbers of sharks may reduce predation on sea turtles (Heithaus et al. 2014). Broadly, researchers and conservationists need to take an ecosystem-level approach to manage predation and not limit it to a sea turtle-centric perspective. To assess when intervention may be needed to reduce predation risk, we must identify predation levels. However, natural predation rates across various sea turtle age, size, or life stage designations are generally poorly known (Crouse et al. 1987, Chaloupka & Limpus 2005). Determining the level of predation rates and turtle losses that require human intervention and how to execute the most cost-effective and least ecologically disruptive action(s) will be crucial to future sea turtle population management.

3.6. Coastal development

3.6.1. Background

Coastal areas and sandy beaches provide nesting habitat for sea turtles (Miller 1997). However, nesting areas are often impacted by coastal development, which includes associated pressures (e.g. artificial lighting, human disturbance/presence, noise, beach compaction) and modifications (e.g. beach armoring, beach sand placement, sand fencing; Brock et al. 2009, Rizkalla & Savage 2011, Kamrowski et al. 2012,

Drobes et al. 2019). Several studies have described the potential impacts of coastal development on sea turtles, including impacts from beach armoring (Rizkalla & Savage 2011, Hirsch et al. 2019, 2022), beach nourishment (Grain et al. 1995, Brock et al. 2009, Cisneros et al. 2017, Staudt et al. 2021, Reine 2022), and light pollution (Kamrowski et al. 2012, Hirama et al. 2021). Other threats, including beach driving (van de Merwe et al. 2012, Aguilera et al. 2019), mechanical beach cleaning (Nelson Sella & Fuentes 2019), recreational use of the beach (Ware & Fuentes 2020), and removal of vegetation (Schmid et al. 2008, Barrett & Sella 2022), have received less attention, as they may be less harmful. Coastal development can also aggravate potential impacts from sea level rise by preventing the natural movement of beaches and landward recession of shorelines (Fish et al. 2008, Fuentes et al. 2010). Impacts associated with coastal development threaten the quality of nesting areas, alter the behavior of both adults and hatchlings, and influence the reproductive output and success of marine turtles (Witherington 1992, Lorne & Salmon 2007, Harewood & Horrocks 2008, Berry et al. 2013).

3.6.2. Conservation approaches

Strategies to mitigate the impacts of coastal development on sea turtles primarily target specific pressures (e.g. light pollution, human disturbance) during the nesting and hatching season. Several coastal communities have ordinances requiring residents and businesses to turn off beachfront lights during turtle nesting season (Long et al. 2022), and some programs exist to help residents exchange external lights for turtle-friendly lighting systems (Nelson Sella et al. 2019). Similarly, several educational and media-based campaigns have been conducted globally to reduce light pollution at sea turtle nesting grounds (Swindall et al. 2019, Santos & Crowder 2021). Lighting studies are relatively easy and cost effective; therefore, several options and best practices have been explored (Jägerbrand & Bouroussis 2021), including lighting wavelength (Robertson et al. 2016) and dune vegetation shielding (Karnad et al. 2009, Hirama et al. 2021). Similar to light ordinances, Leave No Trace ordinances exist in parts of the USA, where municipalities mandate that residents and visitors remove all beach equipment and disposable items by a specified time or forfeit their equipment and potentially face civil penalties such as fines; however, the true effectiveness of such ordinances is unknown (see Ware & Fuentes 2020). Other

less studied pressures associated with coastal development, such as beach driving (Aguilera et al. 2019), mechanical beach cleaning, eco-tourism, recreational beach use (Ware & Fuentes 2020), and vegetation removal (Schmid et al. 2008, Barrett & Sella 2022), have limited conservation mechanisms established, apart from potential restrictions during nesting and hatching season (Drobes et al. 2019). Similarly, there is a lack of consistent global guidelines for coastal modifications (e.g. beach nourishment, seawalls) associated with protecting coastal development from storms, rises in sea level, and erosion at sea turtle nesting grounds (Staudt et al. 2021).

3.6.3. Knowledge gaps

Despite a general understanding of how coastal development and associated pressures impact sea turtles and their reproductive output, their actual impact is not typically quantified (Nelson Sella et al. 2019), and an understanding of the cumulative and synergistic impacts between the array of stressors associated with coastal development does not exist. Further, an understanding of how sea turtles might respond and adapt to coastal development and associated stressors has not been fully explored (Nelson Sella et al. 2019). These factors make it challenging to determine the overall impacts of coastal development on sea turtles and impacts on population stability. Assessments are also hindered by the lack of standardized monitoring protocols and systematic long-term data collection, particularly regarding coastal development activities at nesting grounds. Studies are often limited temporally, and therefore long-term sublethal impacts on the population are not captured (Knapp 2012). Addressing the identified knowledge gaps (Table 2) will help define and prioritize conservation strategies. However, there are still knowledge gaps regarding the efficacy of different regulations to protect sea turtles from impacts associated with coastal development, their overall effects on coastal ecosystems, and subsequent implications for coastal communities.

3.7. Marine development

3.7.1. Background

Globally, development in the marine environment continues to expand (Firth et al. 2016, Bugnot et al. 2021), along with greater amounts of altered habitat

and the potential increase of threats to sea turtles and other marine life. Anthropogenic activities that may impact sea turtles include artificial reefs (Barnette 2017), aquaculture (Moore & Wieting 1999, Lindell & Bailey 2015, Young 2015, Callier et al. 2018), oil and gas mining (Putman et al. 2015, Wallace et al. 2020), renewable energy technologies (Field & Gilbert 2019, Maxwell et al. 2022), seabed mining (Dickerson et al. 2004, Goldberg et al. 2015, Whittock et al. 2017, Williams et al. 2022), tourism (Hayes et al. 2017, Schofield et al. 2021, Zerr et al. 2022), and marine vessel traffic (Barco et al. 2016, Tyson et al. 2017, Santos et al. 2018, Thums et al. 2018, Field & Gilbert 2019). Impacts from these marine operations can include changes in sea turtle behavior, reductions in fitness, and mortality (Foley et al. 2019, Wallace et al. 2020, Schofield et al. 2021). Marine development activities also influence sea turtles by causing significant changes in their critical habitats (López-Mendilaharsu et al. 2020), predator and prey distributions (Erftemeijer & Robin Lewis 2006, Bastos et al. 2022, but see McLean et al. 2022), electromagnetic fields (Field & Gilbert 2019, Klimley et al. 2021), environmental noise and vibration (O'Hara & Wilcox 1990, Gena 2013, Tyson et al. 2017), light levels (Craig et al. 2001), amounts of toxins and contamination (Beyer et al. 2016, Wilson & Verlis 2017), and the flow of sediment, water, or other elements (Gena 2013).

3.7.2. Conservation approaches

The increasing amount of human activity in marine environments emphasizes the need for robust conservation mechanisms to mitigate impacts on sea turtles. Although sea turtles are currently afforded protection under various international legislative directives, conventions, and agreements that contribute to a legal framework for developing multinational and national conservation strategies (see Seminoff 2004, Ceriani & Meylan 2017), some actions have been more successful than others (Campbell et al. 2002, Hykle 2002). Marine management tools to minimize negative interactions with sea turtles include enacting monitoring plans that rely on protected species observers to inform necessary policy changes (Dickerson et al. 1991, Whittock et al. 2017), establishing exclusion zones (Wilson et al. 2006), setting interaction limits (e.g. takes), requiring gear modifications (Dickerson et al. 1991, 2004), altering construction techniques (e.g. use of bubble curtains; Lee et al. 2012), specifying temporal restrictions for active construction (Dickerson et al. 2007), physically relocating turtles out of project

zones (Dickerson et al. 1995), and setting vessel speed limits (Fuentes et al. 2021). In addition, area-based management tools (e.g. designating critical habitats, marine protected areas, marine reserves) have also been used to conserve key habitats or areas frequently used by sea turtles by restricting or requiring measures to minimize the impact of anthropogenic activities (Hilborn et al. 2022).

3.7.3. Knowledge gaps

Baseline data, frequent updates, and trends in marine construction and extractive processes on regional or global scales are essential for proper management, but this information is often difficult to obtain (Bugnot et al. 2021, Komyakova et al. 2022). Key anthropogenic stressors on marine ecosystems have been identified on a global scale (Halpern et al. 2008, 2015, 2019, Tulloch et al. 2020), and recent studies have put together baseline datasets for wind energy operations (Zhang et al. 2021) and other marine construction developments (Bugnot et al. 2021). However, more data on marine development activities at higher spatial and temporal resolutions are needed to enable more fine-scaled analysis to improve assessments and understanding of how these activities overlap with or affect sea turtles and their habitats. At the same time, comprehensive baseline data are lacking on sea turtle density and distribution, as well as the direct and indirect impacts of anthropogenic activities on sea turtles in the open ocean (Gitschlag et al. 1997, Viada et al. 2008, Elliott et al. 2019). This is likely a reflection of a lack of comprehensive line transect survey data, since density estimates are often available when these data exist (Benson et al. 2020, DiMatteo, et al. 2022). More empirical data are needed on the environmental issues and animal responses resulting from offshore aquaculture (Holmer 2010, Froehlich et al. 2017), dredging (Michel et al. 2013, Goldberg et al. 2015, Ramirez et al. 2017), oil and gas structures (McLean et al. 2022), wind energy development (Bailey et al. 2014, Goodale & Milman 2016), tourism (Landry & Taggart 2010, Hayes et al. 2017), and vessel traffic (Schoeman et al. 2020, Fuentes et al. 2021).

To date, potential marine development threats to sea turtles in offshore environments have primarily been assessed indirectly through the analysis of the spatial overlap patterns of sea turtle habitat use and anthropogenic activities (e.g. Maxwell et al. 2013, Hart et al. 2014, 2018). Current mismatches exist in the scale and placement of measures to regulate and

conserve areas in relation to sea turtle habitat use (Agardy 2005, Agardy et al. 2011, Santos et al. 2021, Connors et al. 2022), which may affect management effectiveness (Halpern 2003). Ultimately, more research is needed to comprehensively identify the suite of threats related to marine development that impact sea turtles, the environmental footprint of operations and stressors (spatially and temporally), the thresholds that correspond with sublethal and lethal responses in turtles, and how responses can vary among individuals, populations, and species (Komyakova et al. 2022). Until this research comes to fruition, mitigation measures may need to be implemented using a precautionary approach.

3.8. Fisheries

3.8.1. Background

Fisheries activities can impact sea turtles through ingestion of fishing hooks, entanglement in nets and lines, targeted and accidental captures, and interactions with vessels (Fig. 3) (Lewison et al. 2004, Fuentes et al. 2021, Dodge et al. 2022, Lamont et al. 2022). Bycatch, the incidental capture of sea turtles in fishing gear, is likely the greatest threat to sea turtles globally, with large numbers of turtles caught annually across multiple gear types (Lewison et al. 2004, 2014, Wallace et al. 2013). Further impacts from fisheries can occur from vessel traffic (e.g. collisions, noise), which may affect the fitness of individuals and energy spent avoiding vessels, cause displacement, and result in mortality (Hazel et al. 2007, Powell & Wells 2011). While the threat from industrial fisheries, such as pelagic longline fleets, overlaps with the global extent of sea turtles (Lewison et al. 2004, 2014), small-scale artisanal fisheries also catch disproportionately large numbers of sea turtles (Peckham et al. 2007, Alfaro-Shigueto et al. 2018). In addition, recreational and land-based fisheries (e.g. piers) may also impact sea turtles (Wildermann et al. 2018a, Lamont et al. 2022) but likely proportionally less than industrial and small-scale fisheries.

3.8.2. Conservation approaches

Managing fisheries is challenging due to the limitations of observation and enforcement at sea (Bartholomew et al. 2018). Furthermore, sea turtles frequently cross international boundaries, and protection measures often vary substantially across jurisdictions

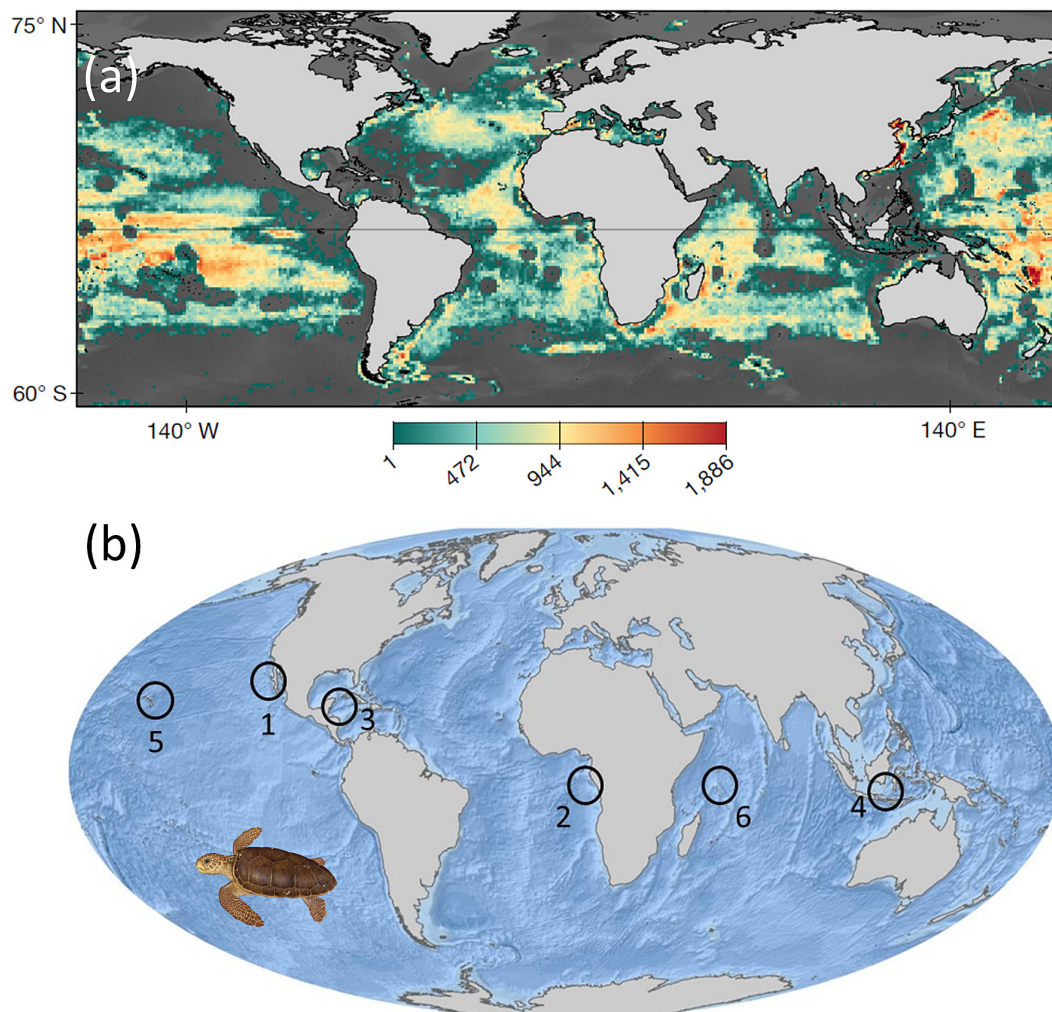


Fig. 3. Global threat of fisheries bycatch. (a) Mean annual distribution of fishing effort (mean days per grid cell) of automatic identification system-tracked longline fishing vessels from 2012 to 2016 (figure adapted from Queiroz et al. 2019). (b) Examples of regions where tracking marine turtles led to the introduction of evidence-based management to reduce turtle bycatch — (1) Mexico: loggerhead-focused reserve (8848 km²), now with limited fishing access; (2) Gabon: tracking data from leatherback *Dermochelys coriacea* and olive ridley *Lepidochelys olivacea* turtles were integral to the extension of a marine protected area (MPA) network to encompass 27 % of the nation's exclusive economic zone; (3) Mexico: satellite tracking data from hawksbill *Eretmochelys imbricata*, green *Chelonia mydas*, and loggerhead *Caretta caretta* turtles were used to show the importance of specific areas leading to federal authorities endorsing sea turtle sanctuaries; (4) Indonesia: leatherback turtle tracking data were used to enact legislation to extend protection and include waters adjacent to the nesting beaches; (5) Hawaii, USA: loggerhead turtle tracking data led to dynamic ocean management with targeted closure of fisheries when threat of bycatch is high; (6) Seychelles: tracking data of hawksbill turtles were used to justify the extension of the boundary of a no-take MPA (adapted from Hays et al. 2019)

(Fossette et al. 2014). Conceptually, the impacts of fisheries can be reduced in 2 ways: (1) avoid or reduce interactions in the first place, or (2) reduce the severity of unavoidable interactions (Fuentes et al. 2021). Several measures exist to reduce negative interactions among turtles, fishing gear, and vessels. Examples include spatial and/or temporal management of fishing activities (e.g. US Pacific coast swordfish gillnet fishery; US National Marine Fisheries Service 50 CFR 660.713), modifications to fishing op-

erations and/or gear (e.g. turtle exclusion devices [Mitchell et al. 1995], net illumination [Senko et al. 2022a], circle hooks [Swimmer et al. 2014, Gilman & Huang 2017]), changes in bait type (Watson et al. 2005), and use of alternative fishing gears that have limited or no probability of interacting with sea turtles (Dodge et al. 2022). Bycatch interactions can also be reduced through measures that decrease overall fishing effort, such as market-based incentives and alternative revenue streams (e.g. tourism, farming, handi-

crafts; Olale & Henson 2012). For interactions that cannot be avoided, mitigation measures can reduce the severity of impacts. Examples include changes in gear configuration and/or operation (Parga et al. 2015, Báez et al. 2019), authorization, training, and implementation of best practices for safe handling and release of bycaught sea turtles (Zollett & Swimmer 2019), and reducing vessel speed through go-slow zones (e.g. Hazel et al. 2007, Shimada et al. 2017). Ultimately, effective solutions reflect tradeoffs between conservation aspirations and logistical and socio-economic realities (Gilman & Huang 2017). Generally, measures that rely on top-down design and enforcement, or on complicated data-driven schemes, face significant social, economic, and technical obstacles to implementation (Howell et al. 2015). At the same time, solutions must involve appropriate authorities depending on the scales of operations and governance structure. Thus, holistic approaches that incorporate existing knowledge and are tailored to specific fisheries issues (e.g. entanglement, bycatch, interaction with vessels) are most likely to succeed (Arlidge et al. 2020).

3.8.3. Knowledge gaps

A relatively good understanding of the overlap between different commercial and artisanal fisheries and sea turtle distribution exists (Kroodasma et al. 2018, Sequeira et al. 2019). However, knowledge gaps still exist in relation to how the intensity of fishing and exposures translates to (1) the number of turtles being caught as bycatch; (2) the fate of those turtles, i.e. whether they die in the interaction or survive upon release; and (3) any subsequent short- or long-term sublethal impact (e.g. prolonged stress responses, gas emboli formation; Álvarez de Quevedo et al. 2013, Swimmer et al. 2014, Parga et al. 2020). Directly quantifying sea turtle mortality in fisheries bycatch can be difficult due to inconsistent regional management, observer coverage, and reporting of bycatch (Wallace et al. 2010, 2013). Calculating bycatch per unit effort is dependent on data collected by at-sea observers or monitors, and spatiotemporal coverage needs to be very high to ensure rare events are appropriately documented (Finkbeiner et al. 2011, Curtis & Carretta 2020). Although such fisheries observer programs are developing in some countries (e.g. Gabon; Casale & Heppell 2016), achieving sufficient coverage can be difficult, and alternative strategies, such as using on-board cameras, logbook reviews, or port-based surveys, can

provide similar information (Alfaro-Shigueto et al. 2018, Bartholomew et al. 2018, Baldi et al. 2022). Thus, the true magnitude of bycatch globally and how it varies by locations, species, populations, and life stages remain unknown (but see Lucchetti & Sala 2010, Wallace et al. 2013, Lewison et al. 2014). Even less is known about the sublethal impacts of fisheries on sea turtles, which can occur unnoticed following the interaction with vessels or after escape and/or release from fishing gear (Chaloupka et al. 2004, Wilson et al. 2014, Fahlman et al. 2017). Potential sublethal impacts from fisheries may include behavioral responses, physiological and energetic costs, and associated reductions in feeding, growth, or reproduction (Wilson et al. 2014). Thus, our understanding of the cumulative impacts of fisheries tends to be based on proxy information (Murray 2015) or extrapolations of limited bycatch data (Lewison et al. 2004, 2014), which can either over- or underestimate the impacts of fisheries (Casale & Heppell 2016). This highlights the need to further incorporate post-release survival estimates (e.g. Polovina et al. 2004, Roast et al. 2023) and long-term life history consequences of non-lethal interactions (Casale & Heppell 2016) into assessments of impacts from fisheries on sea turtles.

Not all fisheries impacts can be addressed and eliminated everywhere, making informed prioritization of limited conservation resources a necessity. To this end, assessments of both the relative population-level impacts of different fishing gears and gear characteristics as well as the relative efficacy and implementation feasibility of potential conservation measures are fundamental steps to guide the development and implementation of fisheries conservation priorities. These types of cumulative impact assessments should include all fisheries with known or presumed interactions—including industrial and small-scale fisheries as well as illegal, unreported, and unregulated fisheries—and where available information is limited, there should be a priority to fill the identified data gaps (Wallace et al. 2013, Lewison et al. 2014). Further, while development and improved understanding of bycatch mitigation techniques (e.g. gear modifications) and other conservation measures are vital (e.g. Swimmer et al. 2014, Senko et al. 2022a), we must look beyond the experimental academic research phase when prioritizing fisheries conservation approaches. Successful implementation of bycatch reduction measures must balance experimentally demonstrated efficacy in reducing turtle bycatch and the economic and operational costs to fishers. It must also minimize the logistical and resource needs

to implement and enforce changes at the appropriate scale. Along these lines, an important gap in fisheries conservation is how to identify and effectively engage relevant stakeholders—especially fishermen themselves—in the development, implementation, and adoption of sustainable bycatch reduction solutions in various fishing sectors, communities, and cultures (e.g. Arlidge et al. 2020).

4. EMERGING RESEARCH TECHNIQUES

In recent decades, a range of advancements have been made in research and techniques that may improve our understanding of various threats to sea turtles and can help guide their conservation. Here, we outline examples of key approaches that can provide baseline information (e.g. presence, abundance, trends) and thus be used to improve threat assessment and to inform sea turtle conservation. Although the emphasis here is on the natural sciences and technological tools, considering the importance of social science approaches (e.g. stakeholder engagement, expert elicitation, socio-economic surveys) and the need for integration with the natural sciences is critical (Campbell 2003, Lewison et al. 2018).

4.1. Chemical tracers

Chemical tracers are elements or chemicals in body tissues that, when analyzed, can help decipher turtle biology as well as exposure and/or ecological responses to anthropogenic threats. These tracers include stable isotopes, trace elements, fatty acids, and hormones (Cortés-Gómez et al. 2017, Haywood et al. 2019, Koutsos et al. 2021), and inferences are usually strengthened by comparing measurements from turtle body tissues with those from marine habitats, often across broad geographic ranges (e.g. Kurle & McWhorter 2017, Bell et al. 2019). Since different tissues have different turnover rates (e.g. hours [blood] to months [epidermis] to fixation in inert tissues [keratin]; Vander Zanden et al. 2015), characterization of temporal variability within and between individuals is possible (Silver-Gorges et al. 2023). In this context, chemical tracers can assist threat assessment both directly, by revealing environmental contaminants in turtle body tissues (Bezerra et al. 2013, Ylitalo et al. 2017, Finlayson et al. 2021), or indirectly, by revealing changes in sea turtle diet, distribution, habitat use, and residency duration in response to stressors (Turner Tomaszewicz et al. 2015, Ramirez et al. 2019,

Clyde-Brockway et al. 2022). These inferences can inform assessments of impacts from stressors such as fisheries bycatch (Williard et al. 2015), climate change (Jensen et al. 2018), and wildlife trafficking. Chemical tracers can also reveal sea turtle demographic patterns (e.g. somatic growth, primary sex ratios) and their changes related to disease, climate variability, and environmental disasters (Ramirez et al. 2020, Wallace et al. 2020). Several chemical tracers have been used in sea turtle research for decades (e.g. stable isotopes; Reich et al. 2007), yet they have generally been applied to understand basic biology and are thus underutilized for assessing responses to threats. In addition, there are promising tracers recently applied to sea turtles (e.g. lipidomics; Zhao et al. 2015, Ahmadireskety et al. 2020, Clyde-Brockway et al. 2021) that should be explored. Establishment of best practices and standardization of tissue collection, preservation, and analytical protocols is also needed (Barrow et al. 2008, Lemons et al. 2012), and more data are needed on spatiotemporal patterns of chemical tracers in sea turtles (Ceriani et al. 2017) and the marine environment. As tracer applications are refined, they will have even greater value when applied in combination (e.g. stable isotopes + trace elements + hormones + skeletochronology; Fleming et al. 2018, Turner Tomaszewicz et al. 2022) and/or with other techniques such as biologging and remote sensing (Ceriani et al. 2012).

4.2. Genomics

The advent of genomic technologies has greatly broadened the genetic toolbox (Komoroske et al. 2017), providing critical insights into our understanding of sea turtles and the impacts of major anthropogenic threats to guide conservation actions. Analyzing tens of thousands of nDNA markers (e.g. single nucleotide polymorphisms) and whole mitochondrial genomes at a relatively low cost is becoming common practice (Duchêne et al. 2011, Komoroske et al. 2019). Moreover, developing high-quality, publicly accessible genomic resources facilitates the generation of comparable data across laboratories (Bentley et al. 2023). These advances allow researchers worldwide to rapidly scale up global reference databases of both mtDNA and nDNA and will increase the resolution of genetic stock structure and the accuracy of genetic stock assignments in foraging areas (Jensen et al. 2020), fisheries bycatch (Stewart et al. 2019), and the illegal wildlife trade (LaCasella et al. 2021). High-throughput genotyping can also be

used in genetic mark–recapture and close-kin mark–recapture approaches to estimate key population parameters that are challenging to obtain for sea turtles, such as abundance, survival, and age to maturity (Bravington et al. 2016). Additionally, environmental DNA can detect the presence of sea turtles in an area from sand or water samples without the need to observe or directly sample animals (Ruppert et al. 2019, Harper et al. 2020), which may improve animal welfare by limiting necessary interactions to collect samples. These techniques are continuously improving and may soon be used to track relative abundance over time and resolve population-level identities (Farrell et al. 2022). Such approaches will be valuable in assessing how sea turtles overlap with fisheries and other ocean threats across large regions.

Early results on epigenetic markers to sex and age of reptiles (Bock et al. 2022, Mayne et al. 2022) bring a promising new way to accurately assess sex ratios of hatchlings and immature turtles. When coupled with high-throughput genomic markers, they will provide powerful techniques to quantify sex ratios and stock assignments in foraging grounds (Jensen et al. 2018) and detailed studies of kinship for breeding sex ratios (Stewart & Dutton 2011). Such studies may help the understanding of how populations react to extreme female biases seen in some populations (Booth et al. 2020) as a result of projected increases in temperature at nesting grounds. Combining organismal trait measurements with molecular assays to assess thermal stress and TSD processes can further our current limited understanding of how temperature affects reproduction and hatchling development, as well as the roles of local adaptation and plasticity in observed variability in these traits within and among populations (Bentley et al. 2017, Lockley & Eizaguirre 2021).

Functional genomic tools can also shed light on the impacts of pollution and pathogen exposure, which are often difficult to assess because they occur in tandem with other stressors and can have sublethal yet significant cumulative effects on long-term fitness. Transcriptomics can be used in combination with traditional approaches (e.g. body condition assessments and blood plasma biochemistry panels) to understand physiological responses and identify informative biomarkers (Connon et al. 2018, Gust et al. 2018), and there have been recent advances in minimally invasive sampling to facilitate monitoring in wild populations or during recovery in rehabilitation (Banerjee et al. 2021, Marancik et al. 2021). Additionally, examining linkages between immunogenomic diversity and disease susceptibility and recovery pro-

vides critical information on the roles of functional genomic diversity in population resilience to these threats (Martin et al. 2022). Finally, genomics can help determine when and how the loss of genetic diversity may hamper recovery efforts or future adaptability to changing environments (i.e. extinction vortex; Frankham 2005). Analyses using whole genome data such as genetic load, runs of homozygosity, and diversity metrics across neutral and functional genomic regions are likely to be particularly informative, as they can provide critical insight into affected genomic regions and demographic processes that may alter recommended recovery strategies (Khan et al. 2021, Robinson et al. 2022, Bentley et al. 2023).

4.3. Biologging

The term biologging refers to the large and rapidly growing field of research in which miniaturized electronic devices are attached to animals to collect data on animal movements, behavior, physiology, and the environment (Rutz & Hays 2009, Chung et al. 2021). Biologging can integrate animal movement and behavior with concurrent environmental conditions and interactions with sympatric species (Naito 2004, Hardin & Fuentes 2021). The data derived from biologging have been essential in investigating human impacts to sea turtles and their environment (Hays et al. 2019), such as determining post-release mortality after fisheries interactions (Álvarez de Quevedo et al. 2013, Swimmer et al. 2014, Parga et al. 2020) and determining the exposure of sea turtles to specific threats (Fuentes et al. 2020b, Santos et al. 2021). In particular, tracking approaches such as satellite and acoustic tracking have allowed informed decisions to be made to help sea turtle conservation, including the creation and strengthening of marine reserves and dynamic ocean management, such as restricting area closures to reduce bycatch or ship strike risk while maximizing sustainable use of the ocean (Hays et al. 2019, Hardin & Fuentes 2021). The widespread, and growing, use of tracking technologies (e.g. Hays & Hawkes 2018) means that there is still huge potential to use these datasets to drive conservation actions around the world.

Recent advancements in biologging have led to the development of devices that optimize battery life, data collection, data transmissions specifically for geographic location, and the use of multisensors (e.g. time–depth recorders, accelerometer, gyroscope, cameras; Chung et al. 2021). In particular, the use of

devices with multisensors can revolutionize our assessments of the behavioral responses of sea turtles to a variety of threats (e.g. interactions with vessels; Tyson et al. 2017) and increase our understanding of the sublethal impacts of anthropogenic activities on sea turtles (Jeantet et al. 2020, Hounslow et al. 2021). Despite the increasing range and availability of animal-borne sensors (e.g. camera, hydrophone, fluorometer, oxygen sensor, accelerometer), remote data acquisition is still a challenge, with most devices carrying multisensors needing to be recovered to retrieve the data. Advances in biologging technology have also made data analysis more complicated, time consuming, and computationally intensive; machine-learning algorithms can expedite this process (Jeantet et al. 2020), but in the near term, manual annotation is still necessary (Dujon & Schofield 2019). Future innovations in biologging should include remote data transmission capability for high-resolution archival tags, as well as continued miniaturization of tags for smaller taxa and rechargeable power sources for extending tag deployment durations. These features will help us further assess the impacts of anthropogenic activities on sea turtles.

4.4. Remote sensing

Remote sensing is the process of obtaining data on subjects or geographic areas from a distance, typically from high-flying aircraft or satellites (Sabins & Ellis 2020). At such altitudes, the sensors on these platforms can collect data on spatial scales that often encompass the globe within a time frame of days to weeks (Devi et al. 2015). Such extensive spatial coverage, accompanied by relatively short sampling frequencies, allows these remote sensing tools to provide insights into sea turtles and their threats at a population or species level (e.g. Bailey et al. 2012, Eguchi et al. 2017).

Arguably, the most prevalent use of remote sensing tools for assessing and addressing the threats faced by sea turtles is to combine remotely sensed oceanographic data (e.g. sea surface temperature, chl *a*, eddies/fronts) with information on the movements of sea turtles as determined via satellite telemetry and aerial surveys (Polovina et al. 2000, Robinson et al. 2016, Prosdocimi et al. 2021, Roberts et al. 2022). When analyzed simultaneously, these approaches can reveal which environmental factors best predict observed distributions of sea turtles (Patel et al. 2021). In turn, this can guide the imple-

mentation of protective measures that may be either spatially explicit, such as marine protected areas (Roberts et al. 2021), or spatially dynamic and adjusted based on real-time remotely sensed oceanographic data (Hazen et al. 2018). A well-known example of the latter is the TurtleWatch program in Hawaii (Howell et al. 2015). As remote sensing technologies continue to improve in both the resolution and frequency of oceanographic data collection, this will facilitate the creation of ever more accurate models to predict the distribution of sea turtles worldwide in relation to threats and inform management initiatives.

Another versatile application of remote sensing technology is to sample vast habitats through imagery. When such photos are collected at night, it can provide a practical measure of light pollution on turtle nesting beaches (Mazor et al. 2013, Hu et al. 2018). In addition, as the resolution of remote sensing imagery continues to improve, this may open new opportunities. High-resolution imagery could, in the future, be applied to photograph turtles at sea, as is already achievable with large mammals (Guirado et al. 2019), and at nesting grounds (Casale & Ceriani 2019), which could be used to conduct wide-scale assessments of population status and/or distribution. Assessments of sea turtle populations can also be facilitated with the recent advancements in the capability and use of uncrewed aerial vehicles (UAVs; Schofield et al. 2017, Rees et al. 2018), by allowing data to be collected at previously unprecedented spatial and temporal scales in diverse geographic locations (Rees et al. 2018). As such, UAVs have been used to monitor sea turtle nesting activity (Sellés-Ríos et al. 2022), quantify turtle abundance (Sykora-Bodie et al. 2017), explore sea turtle breeding dynamics (Schofield et al. 2017, Yaney-Keller et al. 2021), assess impacts from sea level rise (Varela et al. 2019, Rivas et al. 2023), and determine the effectiveness of conservation initiatives (Dickson et al. 2022). Further, UAVs equipped with stereo-video cameras can provide valuable information on individuals' body size, which is essential for population structure assessments and for eventually determining the size class of individuals exposed to different threats (Piacenza et al. 2022). Cameras may also be deployed as part of vessel monitoring systems to monitor fishing activities, bycatch, and the effectiveness and use of bycatch mitigation strategies (Jaiteh et al. 2014, Bicknell et al. 2016, Bartholomew et al. 2018), which have the potential to improve our understanding of the impacts of fisheries on sea turtles. All these approaches are complementary to short-, medium-, and long-term

monitoring and respond to various conservation issues facing sea turtles in their terrestrial and marine habitats. The association and these technologies, which are constantly innovating, will make it possible to considerably improve our understanding of the ecology of sea turtles and to better protect them.

4.5. Machine learning

As we enter the era of big data derived from biologging devices, remote sensors, electronic monitoring, and many other emerging data sources, machine learning tools will streamline the analysis of datasets that may otherwise be too large or complex for effective analysis by individuals (Peters et al. 2014, Lucas 2020). Machine learning is a field within artificial intelligence, which involves the study and development of computational models of the learning process (Carbonell et al. 1983), as such machine learning tools can be trained to identify patterns from pre-labelled datasets and apply this knowledge to identify similar patterns in novel datasets (Olden et al. 2008, Domingos 2012, Peters et al. 2014). Machine learning algorithms are increasingly used in ecology (e.g. neural networks [Hornik et al. 1989], support vector machines [Cortes & Vapnik 1995], random forests [Breiman 2001], deep learning [Goodfellow et al. 2016]), though their use has been relatively limited in studies of sea turtles and their threats. Machine learning techniques have also been identified as a potential analytical path to understanding additive and interactive effects of multiple stressors in complex systems (Dunne 2010, Hewitt et al. 2016, Betts et al. 2019), a key issue in ecology (Crain et al. 2008, Piggott et al. 2015, Orr et al. 2020).

There are several practical ways that machine learning tools can enhance our understanding of sea turtle stressors by leveraging existing research methods such as biologging, spatial analysis, and image recognition. Biologgers and satellite transmitters are expensive, and therefore sample sizes are often limited, but machine learning-based species distribution models that correlate satellite tracks with relatively inexpensive and widely available remote sensing data can generate new insights at minimal expense (Jeantet et al. 2020, 2021, Williams et al. 2020). Similar methods can improve estimation of fisheries bycatch (e.g. Pons et al. 2009, Stock et al. 2018, 2019) and are essential to implementation of dynamic ocean management (e.g. Hazen et al. 2018). Sea turtles are generally difficult to identify by the untrained eye, and field capture and tagging are logis-

tically demanding, making monitoring in-water populations and threat identification a challenge. However, image recognition algorithms (Wäldchen & Mäder 2018) used in concert with community science (e.g. social media; CoastSnap, a citizen science app [Harley & Kinsela 2022]; sea turtle observations by citizen scientists [Papafitsoros et al. 2022]), UAV (Rees et al. 2018, Varela et al. 2019), animal-borne camera (Nazir & Kaleem 2021), or electronic monitoring (Bartholomew et al. 2018, van Helmond et al. 2020) data streams can reduce logistical burdens, aid in threat assessment, and evaluate behavioral responses in sea turtles. For example, image recognition algorithms are a critical component of making electronic monitoring of fisheries more logistically and economically feasible as an alternative to human on-board observers.

It should be noted that machine learning algorithms are dependent on training data that are both high quality and abundant, as by definition algorithms can only learn patterns that they have been trained on (Christin et al. 2019). Machine learning algorithms can and will produce errors when extrapolating beyond training data, and it may not be obvious when this occurs, given the black box nature of many methods (Wearn et al. 2019). As with all analytical techniques, critical appraisal of results and careful consideration of the costs and benefits of choices made during analysis are necessary. With these caveats, the benefits of incorporating new or improved data analysis techniques are clear, especially for sea turtle science that faces many logistical difficulties and limited sample sizes.

5. CONCLUSIONS

We have highlighted that the threats to sea turtles identified in previous reviews (Hamann et al. 2010, Rees et al. 2016) continue to cause concern for sea turtle conservation. To determine the impact of a particular threat to a specific population, information on the exposure of a particular population to the threat is necessary, as well as knowledge of the lethal and sublethal impacts to different life stages (e.g. nesting females, eggs, hatchlings, swim-frenzy transitional stage, neritic and oceanic juveniles, neritic and oceanic adults) and consequences to population trajectories and dynamics based on the reproductive value of each life stage affected (Heppell & Crowder 1998, Wearn et al. 2019). However, such information rarely exists, with particular knowledge gaps on mortality and the impacts of oceanic immature life stages

(Wildermann et al. 2018b) as well as on the sublethal effects of threats on behavior, vital rates, and health of individuals. As a result, expert elicitation has been commonly used to identify and prioritize key threats to different populations (Nelson Sella et al. 2019, Williams et al. 2019, López-Mendilaharsu et al. 2020), with some studies focusing on the relative impact of different stressors within a threat (e.g. relative impact of coastal construction activities [Nelson Sella et al. 2019], climatic processes [Fuentes & Cinner 2010]). However, only a few studies to date have determined the relative impact of different threats to specific sea turtle populations (see Williams et al. 2019). Importantly, with any expert elicitation approach, there are limitations; in our study, for example, the low number of experts with experience with impacts of disease and coastal development might have biased the certainty scores for these threats.

Ultimately, the combined effect of synergies between stressors should be considered, to provide a robust understanding of impacts of stressors (Orr et al. 2020). For this, an understanding of the mechanisms that regulate the action of single stressors and their combined effects is needed, and for such, we need to identify the full range of anticipated combinations of stressor types and their magnitudes (Simmons et al. 2021, Pirota et al. 2022). However, currently we have a limited understanding of how stressors that impact sea turtles are interacting and the nature of such interactions (synergistic, antagonistic, or additive). Thus, empirical, and conceptual approaches should be developed to address this knowledge gap and advance our understanding of how sea turtles are impacted by multiple stressors, which will be crucial to inform future management and conservation. Ultimately, a first step to such an approach is to acquire a better understanding of the mechanisms of different threats and associated stressors, which may be accomplished by addressing some of the pressing questions identified here for each threat considered (Table 2). With this, effective conservation decisions may then consider the combined effects of threats to the stability of populations relative to the costs of recovery strategies, their effectiveness in mitigating threats, the existing resources and socio-political realities for implementation, and the impacts to various stakeholders and local communities (Bottrill et al. 2008, Carwardine et al. 2012). Importantly, most of the threats considered here are a transboundary issue not limited by political borders. Therefore, local, national, and international efforts are needed to manage them (da Costa et al. 2020, Conti et al. 2021). However, several knowledge

gaps still exist on the effectiveness, risks, and acceptability of various strategies to mitigate threats to sea turtles (Table 2). Addressing these will further ensure that decisions are more informed and conservation actions are likely to be successful. Optimistically, several emerging research techniques are available to improve our knowledge base for more targeted decisions to manage sea turtles. Because inequities exist globally with respect to access to and application of these advanced technological tools, effort should be made to make them more accessible and to facilitate their use within regions where they are not accessible.

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Appendix 2.

Table A1. Threats and associated stressors considered in our review

Threats	Associated stressors
Climate change	Sea level rise Hurricanes/storms Ocean circulation Changes in sea surface temperature Changes in precipitation Changes in temperature
Coastal development	Beach driving/beach traffic Beach renourishment Light pollution Beach armoring Tourism (nesting ground) Removal of vegetation Mechanical beach cleaning
Marine development	Dredging Oil and gas mining Wind energy aquaculture Tourism (in water) Marine traffic/vessel strike Ports
Fisheries	Bycatch Entanglement/ghost nets Vessel strike
Pollution	Plastics/marine debris Persistent organic pollutants Agricultural and industrial runoff
Predation	Invasive species Native/feral animals
Direct take	Legal harvest Illegal harvest
Disease	Infectious disease Disease fungus Non-infectious disease

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