



SEA TURTLES IN THE ANTHROPOCENE

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ABSTRACT

Sea turtle species have life cycles that have common features such as oviparity, nesting on sandy beaches, growing as juveniles in surface waters and moving to foraging grounds before migrating—often over long distances—to natal beaches to breed. They are therefore exposed to aquatic and terrestrial influences, both abiotic (e.g. temperature, weather) and biotic (e.g. food availability, predation). Humans have exploited sea turtles for millennia and pressure on their populations has increased dramatically during the ongoing Anthropocene as human influences have increased both in power and global reach. Fishing bycatches generated by powerful unselective gears have largely replaced direct fishing as an existential threat, but meat and egg poaching persist, while burgeoning global wildlife crime threatens sea turtles, especially hawksbills. Habitat loss caused by coastal development and exponential increases in beach-based tourism have reduced nesting success. Sustained losses of coral reef and seagrass habitats have removed foraging grounds for adult turtles and both habitat types are currently projected to disappear before 2100. Environmental degradation has taken several forms. Chemical pollution through the accumulation of organics and heavy metals have affected reproduction and facilitated the transmission of fibropapillomatosis. An emerging threat due to eutrophication also needs to be considered. Marine plastic pollution is already highly damaging to sea turtles; plastic fishing gears ‘ghost-fish’ indefinitely, capturing and killing all life-history stages except eggs, while ingestion of macro and microplastics blocks/damages guts. Rising global temperature has been identified as a potential existential threat for all species because of temperature-dependent sex determination and substantial sea level rise. However, climate change is also projected to cause an order of magnitude increase in the frequency of heat waves and extreme sea level highs, both of which can kill turtle embryos. This Praeger Review concludes with a description of sea turtle occurrences around the British Isles and the anthropogenic influences upon them.

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INTRODUCTION

There are seven living species of sea turtles (Table 1). Six (*Chelonia mydas*, *Natator depressus*, *Caretta caretta*, *Lepidochelys olivacea*, *Lepidochelys kempi* and *Eretmochelys imbricata*) are members of the hard-shelled sea turtles (Family Cheloniidae); the remaining species is the leatherback turtle *Dermochelys coriacea* (Family Dermochelyidae). The fossil history of sea turtles is complex and polyphyletic (Cadena and Parham 2015). The leatherback turtle has existed in more-or-less its current form for around 50 million years and is only distantly related to the cheloniid turtles which are all of Neogene origin; common (probably freshwater) ancestors lived in the early Cretaceous around 140 million years ago (Parham and Pyenson 2010; Cadena and Parham 2015). According to the International Union for Conservation of Nature (IUCN), all species of sea turtle are ‘vulnerable’, but most are ‘critically endangered’, although information on the flatback hard shell turtle is limited.

Despite their varied phylogeny, living sea turtle species largely share basic life history characteristics.

All hatch from eggs laid in nests on sandy shores. The hatchlings climb out of their nests and crawl to the sea where most species rapidly swim to oceanic (>200m depth) waters in which they remain (often associated with floating seaweed, e.g. Mansfield *et al.* 2021) for periods of years before they return as juveniles to neritic waters (<200m deep) where they grow to sexual maturity and forage before making oceanic migration(s) back to their natal breeding grounds, known as ‘natal homing’ (Bowen and Karl 2007). The females of all seven species sometimes mate with several males; females store sperm and often lay mixed paternity clutches (Lee *et al.* 2018). The females make multiple beach climbs at intervals of days/weeks, usually at night, to dig nests and lay clutches of numerous eggs in damp (or dampened via urine and mucus) sand. Females usually breed at intervals of 2–3 years.

There are many divergences from this general pattern. The leatherback is oceanic throughout almost all its life cycle, only moving into neritic waters to mate and nest, though it is limited to tropical/subtropical waters as a hatchling, post

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Table 1—Living sea turtles, their distribution and feeding ecology.

<i>Species name</i>	<i>Common name</i>	<i>Distribution</i>	<i>Feeding ecology</i>
A. Family Dermochelyidae			
<i>Dermochelys coriacea</i>	Leatherback	Oceanic, global, tropical to cold temperate	Specialist gelativore. Eats medusae, salps, pyrosomas.
B. Family Cheloniidae			
<i>Caretta caretta</i>	Loggerhead	Oceanic and neritic, tropical to warm temperate	Carnivorous. Eats benthic and pelagic invertebrates (mostly molluscs and crustaceans).
<i>Chelonia mydas</i>	Green	Oceanic, global and neritic, tropical and subtropical	Adults and juveniles herbivorous (on seagrass and macroalgae); hatchlings omnivorous.
<i>Eretmochelys imbricata</i>	Hawksbill	Oceanic, global and tropical.	Omnivorous, particularly feeding on sponges and corals.
<i>Lepidochelys kempii</i>	Kemp's ridley	Neritic. Largely limited to Gulf of Mexico and E. Coast USA.	Carnivorous. Eats swimming crabs, shrimp, jellyfish, fish in water column, benthic molluscs.
<i>Lepidochelys olivacea</i>	Olive ridley	Oceanic and neritic, tropical to warm temperate	Omnivorous. Eats wide variety of invertebrates and seaweeds.
<i>Natator depressus</i>	Flatback	Neritic, Australia and Papua New Guinea only	Omnivorous. Eats wide variety of invertebrates and seaweeds.

hatchling or juvenile. Adult leatherbacks are endothermic (e.g. Frair *et al.* 1972; Davenport *et al.* 1990; Bostrom and Jones 2007; Davenport *et al.* 2009a, 2009b; Davenport *et al.* 2014a), can survive indefinitely in southern and northern cold temperate waters, migrate thousands of kilometres to forage and breed, with the capability of diving into near-freezing waters to forage (James *et al.* 2006). They can occasionally dive to great depths (<1280m; Doyle *et al.* 2008) although most dives are <300m (Houghton *et al.* 2008). Hard-shelled turtles such as the green, hawksbill and loggerhead turtles spend most of their lives in the top 50m, although Polovina *et al.* (2002) found that olive ridleys sometimes dived beyond 100m.

While green, loggerhead, hawksbill and olive ridley turtles have global distributions, the flatback appears to be limited throughout its aquatic life to neritic waters around Australia and Papua New Guinea and therefore has short breeding migrations (<https://www.qld.gov.au/environment/plants-animals/animals/discovering-wildlife/turtles/species/flatback-turtle>). Kemp's ridley, the smallest and rarest sea turtle, has a limited nesting area and 95% of females nest communally during daytime ('arribadas') at a single nesting beach near Rancho Nuevo, Mexico. Adults and juveniles usually forage in the

northern Gulf of Mexico (<https://www.fisheries.noaa.gov/species/kemps-ridley-turtle>).

Female sea turtles vary considerably in terms of the number and size of eggs they lay during a single nesting occasion, the number of clutches they lay during a single nesting season and in the interval between breeding seasons. Jorgewich-Cohen *et al.* (2022) recently published a comprehensive evaluation of optimal egg size theory for all chelonians. Broadly, sea turtle data are compatible with this theory, but some examples illustrate their variability. Bjorndal and Carr (1989) analysed a 30-year green turtle dataset from Costa Rica. They found that egg diameter varied between 39 and 44mm and that clutch size varied from 3 to 219 eggs (mean 112) and was greater in older turtles. Flatbacks lay much smaller numbers of eggs (around 50 per clutch; Pendoley *et al.* 2014), but the eggs are larger (50mm diameter) and yield the largest sea turtle hatchlings (60mm carapace length) that are believed to make them less susceptible to predation (Limpus 2007; Turner Tomaszewicz *et al.* 2022). Finally, the largest sea turtles—leatherbacks—have the biggest and deepest nests in which they lay about 80 large eggs (53mm diameter), plus about 20 shelled albumen globs (each 10–50mm diameter) (Wallace *et al.* 2006), whose function is unclear but may help

hatchling emergence (Patiño-Martinez *et al.* 2010). Leatherbacks lay up to 11 clutches per breeding season, but average about 7 clutches laid at intervals of about 10 days (Rivalan *et al.* 2006).

All sea turtle species are believed to be long-lived. Readable internal identity tags have not been in use for sufficient time to allow multi-decadal age/growth measurements. Early studies of captive animals and mark/recapture studies on summer feeding grounds suggested rapid growth, but more recent skeletochronological studies based principally on the forelimb humeri have indicated that growth to maturity is slow (see Avens *et al.* 2009). Green turtles have been most studied, particularly the Hawaiian population (Zug *et al.* 2002). These are now believed to take about five years to grow in the oceanic pelagic phase before recruiting to neritic foraging grounds. They take 30–50 years to reach sexual maturity and breed for several decades, perhaps reaching 75 years of age. Data for loggerheads are similar, though the pelagic phase of Atlantic specimens that circulate in the North Atlantic Gyre may last 7–12 years (Bjorndal *et al.* 2003; Bolten 2003). Smaller cheloniid sea turtles mature rather more quickly; Snover *et al.* (2013) estimate 17–22 years for hawksbills, while Avens *et al.* (2017) reported 11–13 years for Kemp's ridleys, comparable to the closely related olive ridleys. Most recently, Turner Tomaszewicz *et al.* (2022) have reported flatbacks to mature at 12–23 years. Leatherback turtles had been thought to mature early, but the most recent study, based on analysis of scleral ossicles (Avens *et al.* 2009), indicates that they may take around 25–30 years to reach sexual maturity, like greens and loggerheads. This gives them generation times that are comparable with those of large mammals, such as humans and elephants.

It should be noted that skeletochronological studies are bedevilled by remodelling of the structures analysed during growth, the invasiveness of the procedure (almost always performed on dead specimens) and the limited possibilities of validation. Recently Mayne *et al.* (2022) have introduced a new DNA methylation ageing method based on skin biopsies that they tested on green turtles of known ages (<43 years) reared at the Cayman Turtle Centre (Cayman Islands) and at a facility at Réunion, France. They validated this technique in the field by repeat testing (intervals of 2–3 years) on wild caught green turtles in Australia. They demonstrated the accuracy of this approach (median absolute error 2.1 years) and showed that the CpG DNA sites used were also present in leatherbacks, hawksbills, flatbacks, loggerheads and olive ridleys. They have effectively developed a robust 'universal marine turtle epigenetic clock' that should greatly improve the study of sea turtle population dynamics.

Finch (1998) introduced the concept of 'negligible senescence' that is shown by a small number

of vertebrates including naked mole rats and Greenland sharks that combine long life with sustained reproductive capacity and low mortality rate. They avoid the poor health and declining reproductive output of most ageing vertebrates. Chelonians in general, and sea turtles in particular, have been thought to be examples of this phenomenon (e.g. da Silva *et al.* 2022). Data for wild sea turtles are however unavailable. Glen *et al.* (2023) have recently interrogated the 27-year Cayman Turtle Centre captive green turtle fecundity database; their results were equivocal and they found that older turtles laid more eggs than first-timers but some older turtles retained high fecundity whereas others did not. Natal homing is an important feature of sea turtle biology. Its existence has been assumed for many decades, but direct evidence was lacking until relatively recently, primarily because of the difficulty of tagging hatchlings and detecting the tags many years later in nesting females. This is despite the extensive evidence of turtles' abilities to navigate geographically, both in hatchlings/juveniles (Lohman *et al.* 2008) and in adults migrating between foraging and breeding grounds (Sale and Luschi 2009). Limited direct evidence for natal homing has only been obtained in the case of 'living tagged' juvenile Kemp's ridleys that later nested as adults (Shaver and Caillouet 2015). However, more general evidence has been revealed by molecular genetic analysis (Bowen and Karl 2007), which showed that feeding aggregations, particularly of green turtles, dispersed to different breeding beaches and that there was little if any genetic mixing of the breeding groups. The geographical scale of homing, however, is less clear: while some groups of green turtles exclusively home to small sites (Raine Island off the Northern Australian Barrier Reef; Hamann *et al.* 2022), others home to extensive beaches many kilometres in length. Bermuda provides a cautionary tale: although sea grass beds around the archipelago have until recently supported large populations of juvenile and subadult green turtles that disperse to breed when they are sexually mature, no nesting has been recorded since the early 1800s when nesting females became extinct because of exploitation. This absence of nesting is unusual, particularly in light of a ten-year head-starting programme carried out between 1967 and 1977, during which over 25,000 hatchlings were translocated from Caribbean sources and released (Godley *et al.* 2004). Loggerheads generally show somewhat weaker nesting fidelity and there is convincing evidence for the establishment of new nesting sites since the peak of the last glacial maximum *c.* 18,000 years ago (Bowen and Karl 2007). Leatherback turtles, the most widely distributed reptiles on Earth (Hays *et al.* 2004) have a relatively low level of natal site fidelity and a propensity for establishing new nesting colonies (Dutton *et al.* 2007).

Sea turtles were an evolutionary and ecological success story until relatively recent geological time and have been exposed to considerable changes in temperature and sea level over millions of years. Green turtles have been keystone grazing species for seagrass meadows for millennia (Gangal *et al.* 2021; de Kock *et al.* 2023), while leatherback turtles have been top predators in gelatinous food webs for millions of years, each turtle consuming thousands of tons of medusae, salps and pyrosomes in its lifetime (Jones *et al.* 2012). Spongivorous hawksbills have helped structure coral reef ecosystems throughout the world (Meylan 1988). All sea turtles have impacted beach ecosystems by virtue of the addition of marine-derived nutrients in the form of eggs, hatchlings and waste products that support predators and detritivores (Bouchard and Bjorndal 2000).

Problems have arisen for turtles because of human activities that have become intense enough to affect global ecology, atmosphere, hydrosphere and geology to measurable extents during what is informally known as the Anthropocene. As Crutzen and Stoermer (2000) point out, the start date of the Anthropocene is controversial—they favoured a preindustrial date (when global human population was <1 billion), which will be loosely followed here.

Sea turtles are charismatic species, and their conservation has been supported more and more since the 1950s, although the earliest legal probation on killing green turtles, enacted in Bermuda (<https://www.thebermudian.com/>) dates from 1620 CE (Carr 1967). Most recent efforts have focused on managing breeding beaches, including protecting nests against predation, patrolling beaches to deter egg poachers, rescuing doomed nests as the result of high tide levels or beach erosion, closing fishing seasons and improved fishing gear, plus the rehabilitation of injured or sick turtles. These measures have been very successful in several cases (Mazaris *et al.* 2017). The rescue from extinction of Kemp's ridleys is perhaps best known, but recent meta-analyses (Weber *et al.* 2014; Mazaris *et al.* 2017; Gangal *et al.* 2021; Hays *et al.* 2022a) have also revealed substantial increases in breeding populations of green and loggerhead turtles where direct exploitation (of eggs or adult females) ceased several decades ago. The USA has been particularly successful in promoting the recovery of green turtle populations since the passing of the Endangered Species Act in 1978. In Hawaii green turtles had been reduced by unrelenting commercial exploitation to a single nesting site by 1950, but numbers today are high, though long-abandoned nesting beaches have not been recolonised (Van Houtan and Kittinger 2014). Similarly, nesting of green turtles in the state of Florida increased from around 4,000 nests in the 1980s to more than 230,000 in the 2010s. However, McClenachan *et al.* (2006), who looked at the considerable historic loss of breeding beaches in the

Caribbean, pointed out that such population increases can mask the loss of genetic diversity and an over-reliance on the fewer remaining breeding beaches.

The main aims of this review are to consider the global effects of a variety of anthropogenic impacts including climate change (The Royal Society 2020) on sea turtles, and to evaluate their likely consequences. However, as the review is one of a series in memory of the great Irish naturalist Robert Lloyd Praeger (1865–1953), a final section specifically devoted to the occurrence of, and threats to, sea turtles around the British Isles is also included.

DIRECT IMPACTS

EXPLOITATION

All sea turtle species have been exploited by humanity for millennia, though the impacts of direct fisheries were limited by technology and human population numbers until around 700 years ago, after which they became increasingly intense (e.g. McClenachan *et al.* 2006). Adults have been captured for shells, meat, fat and blood, while eggs have been collected from newly laid clutches. Historically, turtles were often collected by seafarers and stored on deck as long-lasting fresh meat; in the nineteenth and twentieth centuries, canning and freezing opened worldwide trade (Lee 2012; Ching 2016) and populations of some species plunged (Van Houtan and Kittinger 2014). Turtle meat/soup was commercially marketed into the 1980s and 1990s (Davenport 1988), and meat is still extensively traded illegally, especially in Asia and Africa (the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) 2019; Vieira *et al.* 2024). Egg collection persists world wide, not least because of a prevailing myth that turtle egg-eating is aphrodisiacal, but also because of cultural and historical influences. In many countries of Central America egg collection is technically illegal, but poaching remains a widespread activity of low-level crime networks (Pheasey *et al.* 2020).

Unremitting egg collection can play a dominant role in local extinction (e.g. leatherback turtles, Terengganu, Malaysia: Chan and Liew 1996) as egg poachers can collect >90% of eggs during nesting seasons. Kemp's ridleys, nesting on a single beach, were nearly exterminated by egg collection and fisheries' bycatch between the 1930s and 1980s. Currently Kemp's ridley adult numbers are believed to be around 10% of historical values (Bevan *et al.* 2016).

The hawksbill turtle has been exploited in large quantities for its shell scutes, which are the source of decorative tortoiseshell. Millions of hawksbills have been killed over the past two centuries (Mortimer

and Donnelly 2008). Although international trade in tortoiseshell by CITES signatory countries was banned in 1977, Japan did not cease importing tortoiseshell until 1992 and a recent report (Kitade *et al.* 2021) confirms that substantial illegal imports persist, with tortoiseshell arriving from other Asian countries and the Caribbean. Although hawksbills have been the most important source of curios and decorative items, green turtles have also contributed shells and stuffed specimens.

Senko *et al.* (2022) recently published a comprehensive world wide review of illegal trade in sea turtles over the past three decades. They estimated that at least 1.1 million turtles (green turtles 56%; hawksbills 39%) were illegally killed for trading between 1990 and 2020. Rising human populations, increased prosperity and a burgeoning international luxury trade, particularly in Asia, have fuelled demand and offset legislative and other conservation measures. This estimate, itself likely to be a substantial underestimate, does not include legal killing or accidental bycatch.

BOAT/SHIP INTERACTIONS

All sea turtles spend much time at or near the sea surface when breathing, basking or foraging. They are consequently vulnerable to being injured by boats or ships, either by blunt force trauma or by propeller damage (Davenport and Davenport 2006) (see Figure 1A, B).

Such vulnerability is greatest in coastal waters, given the enormous increase in recreational boating since World War II (there are now about 33 million registered recreational boats worldwide, plus about 2–3 million personal watercraft (PWCs); roughly half of which are used in the USA: <https://www.giornaledellavela.com/2022/09/29/analysis-how-many-boats-there-are-in-the-world-where-they-are-and-who-uses-them-most/?lang=en>). Three production developments have underpinned this increase: a) the construction of glass fibre and resin hulls from the 1940s onwards; b) the mass production of increasingly powerful outboard motors that have enabled higher boat speeds, and c) the introduction of 1–3 seat personal watercraft PWCs powered by water jets from the 1970s onwards (Davenport and Davenport 2006). Small and fast vessels are particularly likely to impact turtles as their drivers' forward view is limited. The hiring of PWCs is common in tourism hotspots, so the drivers are often inexperienced and less likely to spot turtles, particularly at high speeds.

The importance of boat impacts on sea turtles has been most studied in the USA, where recreational boating (by motor sailboats, speed boats, rigid inflatable boats, PWCs, etc) is regionally intense and Florida alone has around 1 million registered vessels (<https://www.statista.com/statistics/1155988/us-recreational-boating>). Foley *et al.*

(2019) analysed Floridan turtle strandings data from all Floridan coastal counties between 1986 and 2014. They found that about one-third of stranded turtles had been killed by propeller damage or blunt force trauma. Loggerheads were most vulnerable, but greens, hawksbills, olive/Kemp's ridleys and leatherbacks all showed some mortality caused by boats. During the study period about 11,000 turtles had been killed by boats: 70% by propeller damage and 30% by blunt force trauma. The authors estimated that the true mortality was 5–10 times greater (i.e. 55,000–110,000) because few dead turtles strand. There were significant increases in boating mortalities as boat numbers rose during the study period, with a peak in 2007. The USA has some of the most rigorous boating regulations in the world and uses speed limits and exclusion areas far more than elsewhere, yet boats continue to cause substantial mortality. By extrapolation from the work of Foley *et al.* (2019), it is likely that hundreds of thousands of turtles are killed globally each year by recreational boating, especially as recreational boating is expanding rapidly and is expected to grow at a compound annual growth rate of 5.3% from 2023 to 2030 (<https://www.grandviewresearch.com/industry-analysis/global-leisure-boat-market>).

FISHERY INTERACTIONS

Modern fishing, whether for finfish or invertebrates, is essentially mechanised hunter-gathering. Marine capture fisheries showed continual and considerable production growth from the 1950s to the 1980s, rising from less than 20 million tons y^{-1} in 1950 to around 90 million tons y^{-1} by the late 1980s. At this point production stalled and has plateaued throughout the 21st century (source: Food and Agriculture Organisation of the United Nations, FAO, 2022) despite continuing increases in fishing effort, both by large-scale fisheries and by the proliferation of small-scale fishers, including artisanal fishers as coastal human populations rise. Illegal fishing has also increased and is estimated to be responsible for about a quarter of present catches (Agnew *et al.* 2009).

Globally, fishing/overfishing has had profound ecological consequences in the last seven decades, with reductions in populations of large, predatory marine animals such as sharks, tuna, cod and grouper ('fishing down food webs'; Pauly *et al.* 1998) as well as population decreases in small industrial species (e.g. anchoveta, sardines, capelin), which are used, after processing, in a much expanded livestock agriculture and/or mariculture ('fishing down and farming up the food web'; e.g. Pauly *et al.* 2001).

Large-scale fishing can be broadly divided into trawling, drift netting, long-lining and purse-seining. All have been implicated in causing substantial bycatch mortality in air breathing vertebrates including seabirds, cetaceans and pinnipeds (Soykan *et al.*

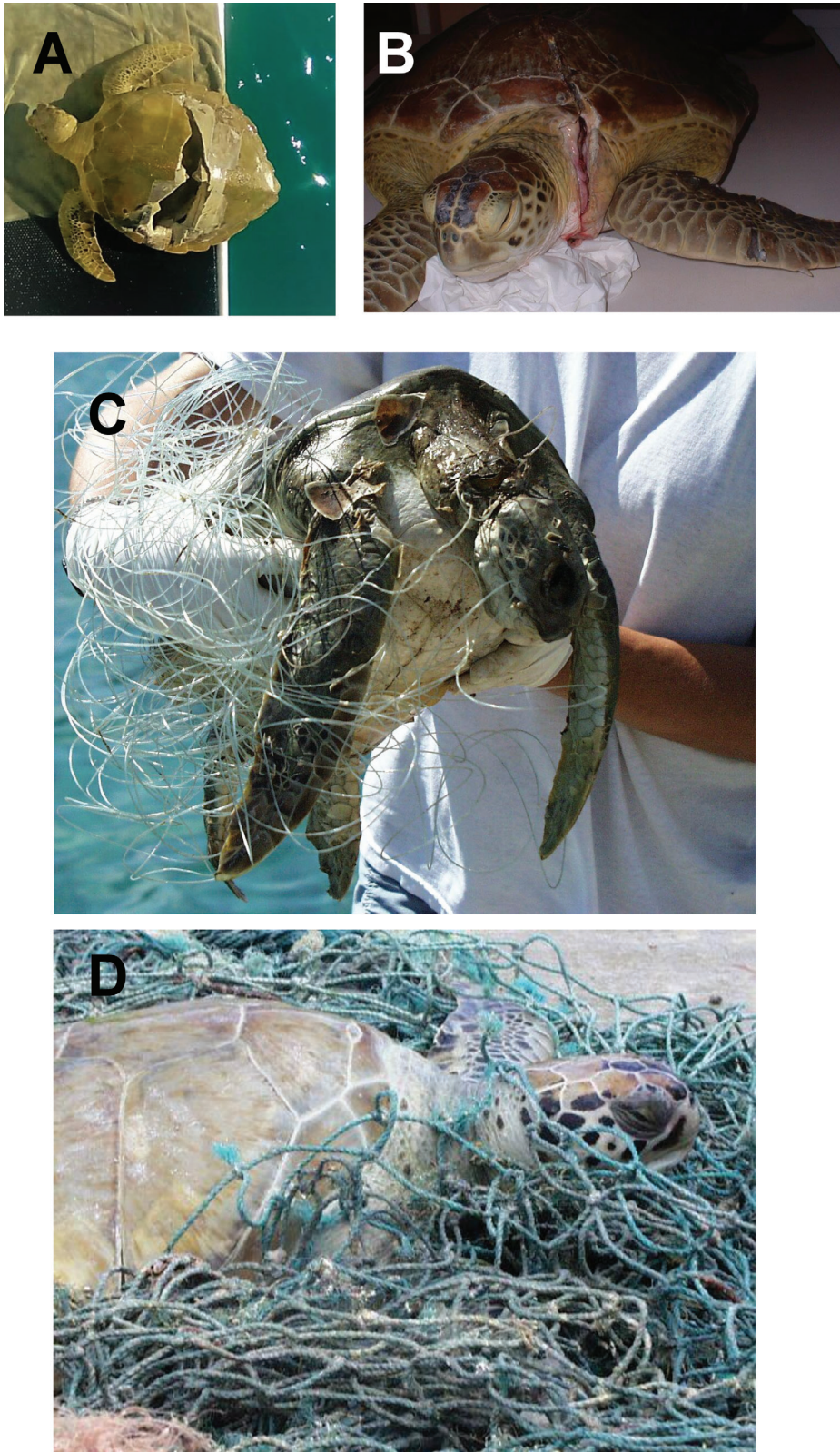


Figure 1—Boat and fishing gear impacts on sea turtles. A. Green turtle killed by blunt trauma impact of high-speed boat/jetski. B. Green turtle killed by boat propellor wound. C. Green turtle drowned by monofilament nylon. D. Green turtle killed by entanglement in drifting ghost fishing net. All images courtesy of Jennifer Gray/Bermuda Turtle Project.

2008; Petrossian *et al.* 2022). Purse-seining appears to have a low impact on sea turtles (Bourjea *et al.* 2014) but trawling, drift netting and long-lining have all caused considerable turtle mortality.

Trawling involves nets being pulled either along the seabed (bottom trawling), usually to catch demersal fish or crustacea, or in midwater, mainly catching shrimp/prawns, pelagic fish and squid. Bottom trawls damage the seabed and usually catch many non-target species; they are dangerous to sea turtles, particularly when the trawls are deployed or recovered and are close to the sea surface, but bottom-foraging turtles such as loggerheads can be entangled and drowned. Midwater trawls are used in the middle of the water column and are dangerous to cetaceans and turtles swimming at the same depth. Shrimp fishing, whether by bottom or mid-water trawls, requires fine mesh nets and was identified in the 1970s and 1980s as a major killer of coastal turtles—a minimum of 71,000 turtles per annum according to Finkbeiner *et al.* (2011). In the USA, the National Oceanic and Atmospheric Administration (NOAA) developed turtle excluder devices (TEDs) that were introduced in the 1970s and became mandatory for shrimping vessels in 1987 (Jenkins 2012). A TED is effectively an escape chute upstream of the end of the trawl that is guarded by a coarse grid that allows shrimp to pass through to the net end but excludes larger forms such as turtles. The USA required imported shrimp to be caught using TED-equipped nets from 1989 onwards (Jenkins 2012), which forced fishers around the world to use TEDs. India introduced TEDs in 1996 to try to reverse falls in olive ridley nesting numbers in Odisha (Behera 2000).

Although TEDs reduced turtle mortality, there have been multiple problems that have arisen in field use (<https://www.fisheries.noaa.gov/southeast/by-catch/history-turtle-excluder-devices>). They have not allowed large loggerheads or leatherbacks to escape, while fishers have sometimes deactivated them to improve shrimp catches. They are also easily blocked by debris. In the 2010s more efficient trash and turtle excluder devices (TTEDs) were designed to exclude unwanted 'trash' fish (e.g. sharks, rays) as well as turtles. Finkbeiner *et al.* (2011) calculated that mortality in the USA SE/Gulf of Mexico shrimp fisheries had dropped to around 4,600 turtles y^{-1} by 2007 thanks to TEDs and other mitigation methods. A recent review (Jenkins 2023) summarises the history and problems associated with bycatch reduction devices.

The extinction of the large Pacific leatherback population at Terengganu, Malaysia, although mainly due to legal and illegal egg collection over many years, was partly caused by offshore demersal trawling (Chan and Liew 1996), which captured and killed adult leatherbacks before they could breed. The current largest leatherback nesting site in the world is a major source for Atlantic leatherbacks and is located on the west African coast, especially Gabon. Around

16,000–41,000 adult females nest each year, making multiple nesting beach crawls (Witt *et al.* 2009). Casale *et al.* (2017) reported that Gabon was also a nesting site for other sea turtles, particularly olive ridleys (1,400–8,200 adult females) and the country has widespread conservation measures in place to protect most (80%) nesting sites. Casale *et al.* (op. cit.) made a preliminary study of the impact of various trawl fisheries on turtles. Gabon has offshore industrial shrimp and bottom trawlers (the former using TEDS), as well as inshore artisanal fisheries. In 2012–13 no turtles were caught by TED-equipped vessels. Most turtles caught (80%) were olive ridleys, despite their far lower nesting numbers, and very few leatherbacks were impacted, perhaps because they swam in surface to mid waters, while the olive ridleys foraged on the bottom. Casale *et al.* (2017) indicate that the olive ridley catch is high enough to threaten the local future of the species. Gabon is in the process of setting up Marine Protected Areas that will hopefully enhance turtle conservation, however it should be noted that vessels from the EU, Japan and South Korea are allowed to fish from 6 to 200 miles off the coast of Gabon where turtle catches are unknown, while the inshore artisanal fishery is understudied.

Overall, trawling is highly damaging to sea turtles globally; Maruyama *et al.* (2024) recently published estimates of loggerhead turtles killed by shrimp and pair trawls (i.e. single large, bottom trawls pulled by two vessels) off the coast of Brazil. Their findings indicated that thousands of turtles are killed each year, but they had to use indirect measures to make these estimates, which have extremely large confidence intervals. They point out that TED use in shrimp trawls has been mandatory for 30 years, yet effective use by fishers is poor. Fishers using pair trawls do not keep records of turtle captures unless observers are aboard, which is financially and logistically difficult.

Drift netting, whether large or small-scale, is a fishing technique that requires relatively low powered boats. A drift net is a curtain-like net that hangs from a line supported by floats (see He *et al.* 2021 for detail). A single fishing vessel can deploy several nets, which are then left to 'soak' for hours/days before the vessel returns to collect the nets and the catch. Historically, drift nets were made of natural fibres, but these were replaced by lightweight synthetic materials in the 1950s. By the 1960s these permitted enormous oceanic nets to be used, up to 50km long and 30m high. Such large nets have been banned since the late 1980s, but drift nets had already done enormous damage to turtle populations, including the eastern Pacific leatherback (Eckert and Sarti 1997).

Several legal fisheries still use drift nets that are around 2.5km long and 60m high with an approximately 150 thousand m^2 of capture area. Drift nets are extremely unselective and generate high levels of bycatch, including turtles and marine mammals as

well as ‘trash’ fish. Drift nets also catch seabirds, but less than long-lining (see below). Drift net impacts have been studied off the west coast of the USA where part of the West Pacific component of the whole Pacific leatherback population forages each year (Carretta 2020). Current catches are small (tens per annum) and declining because of reduced fishing effort and changes in the closed season, but West Pacific leatherback populations are now so reduced that these low capture numbers still represent significant losses.

Hays *et al.* (2004) used satellite tag records to demonstrate that leatherback turtles ranged widely in the Atlantic, moved independently of current directions and spent about 60% of their time below the sea surface with 99% of dives being <250m depth. It is well known that leatherbacks in the north Atlantic can cross the ocean when foraging (including around the British Isles: see below). Less well known is that leatherbacks from the west African rookeries cross the ocean to forage off the South American coast. Here they encounter fisheries including oceanic Brazilian drift nets, which are often of illegal length (Fiedler *et al.* 2012). Fiedler *et al.* (op. cit.) reported that these nets caught leatherbacks, loggerheads and greens, with leatherbacks making up 77% of the take. They estimated that the annual catch ranged from 1,212 to 6,160 leatherback turtles, around 29% being killed.

Longlining is also employed at various scales and is common world-wide. It relies on baited fish-hooks rather than the net mesh to catch target fish. The hooks are connected via side lines (snoods) to a main line that can be short in small-scale fisheries, but can exceed 50km in large-scale mechanised fisheries (see He *et al.* 2021). Hooks can be set fixed on the bottom, anchored dangled in mid water, or allowed to drift in deeper water, usually with the fishing vessel attached at one end. Longlining has resulted in substantial historical bycatch, particularly of seabirds, but also sea turtles. Loggerheads are especially vulnerable to bottom-set longlines, but they and other species, including leatherbacks and ridleys are also attracted to midwater baits. The Pacific and Atlantic longline fisheries of the USA were closed in 2001 because of concerns about their impacts on sea turtles. The introduction of circle hooks (instead of J-shaped hooks) and whole fish bait allowed the reopening of the fishery in 2006 (Solis *et al.* 2021) as turtle bycatch was much reduced. However, pelagic longlining takes place worldwide and is largely unmonitored. Parra *et al.* (2023) reported on the Portuguese longline pelagic fishery that intersects the North Atlantic Gyre, which carries foraging juvenile and subadult loggerheads that originate from the USA and Cabo Verde. These longliners are still using J-hooks to target swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*). Parra *et al.* (op. cit.) found that loggerheads and leatherbacks (mostly adults) were caught and in such cases, mortality in loggerheads

was significant, but leatherbacks—caught when the seawater temperatures were lower—mostly survived.

Alfaro-Shigueto *et al.* (2011) studied Peruvian small-scale fisheries that used longline, bottom-set nets and drift nets and their effects on loggerheads, greens, olive ridleys and leatherbacks. They showed that these numerous and diffuse fisheries (>100 ports, >9,500 vessels, >37,000 fishers) caught tens of thousands of turtles per year. Although most (91.8%) were released, the impacts on Pacific turtles were severe because of the large numbers of fishing gears in use. Additional problems included the difficulty of regulation or monitoring, plus illegal use of turtle products as ‘marine bushmeat’: around 30% of live turtles caught in gillnets were retained for consumption. Clearly, many thousands of turtles were killed.

Alfaro-Shigueto *et al.* (2018) later examined, using questionnaire-based estimates, the impact of small-scale gillnet (= drift net) fisheries in the south-eastern Pacific, extending the geographical investigation to 43 fishing ports in Ecuador, Peru and Chile. The ports surveyed constituted 16.4%, 41% and 22% of the national gillnet fleets, respectively. They found that that this subset of the total fishing fleet was responsible for the death of about 13,000 turtles annually, implying a real total several times higher. The authors of these two studies noted that the turtles caught by the diffuse fisheries had origins not only in the eastern Pacific (e.g. Galapagos, Mexico, Costa Rica and the small east Pacific component of the Pacific leatherback population), but also in the West Pacific (e.g. Australia, New Caledonia). They also found that effective regulation of small-scale fishing and bycatch was extremely difficult because the fishers were characterised by poverty, lack of knowledge of regulations and a need for protein. They and their vessels were so numerous and based at so many remote ports that monitoring by observers was logistically unfeasible.

The Mediterranean Sea is another area that features multiple diverse small and medium scale fisheries, with extra complications for turtles. The sea has populations of green turtles that nest (predominantly in Cyprus, Turkey and Syria) and forage neritically in the eastern Mediterranean. There are also larger numbers of loggerheads that nest in Greece, Turkey and Libya, but forage widely in the sea, including in the western Mediterranean, using both pelagic and neritic resources (Camiñas *et al.* 2020). In addition, large numbers of loggerheads originating from the North Atlantic enter the western Mediterranean to forage (Álvarez de Quevedo *et al.* 2013). In the Mediterranean, all types of fishing are practiced: bottom trawling, purse seining, drift netting, long-lining. There is also a complex network of national and international fishing regulations because so many nations fringe this sea. There are about 80,000 fishing vessels in total in the region, and it is estimated that 75% of overall Mediterranean fish stocks are

overfished, rising to 93% within EU waters. Total fish populations have fallen by over a third over the past half-century (source: https://www.wwfmmi.org/what_we_do/fisheries/).

Lucchetti *et al.* (2019) estimated that 10,000 loggerheads were killed annually by fishing activities in Italian waters alone. Lucchetti *et al.* (op. cit.) reported promising tests of upgraded TEDs in Italian trawl fisheries, which do not normally use them, but pointed out that the main aim of their studies was to retain profitability of the fishery whilst reducing turtle mortality.

Conversely, there are some hopeful signs. Báez *et al.* (2019) analysed data (2000–16) for the Spanish pelagic longline fishery focused on swordfish, bluefin tuna and albacore, all of which are high-value catches in the western Mediterranean. In 2000 the fleet had an annual turtle bycatch of about 10,000, which led to 6,000 mortalities (including post-release mortalities of 30.8–36.5%, following Álvarez de Quevedo *et al.* 2013). By 2016 captures had fallen to around 3,000 per annum, but mortalities were reduced to near zero. Partly this was due to a smaller fleet, but a greater setting depth and changes in the timing of fishing both played a role.

Abandoned, lost and discarded fishing nets/fishing gear continue to function indefinitely in the marine environment ('ghost fishing'), partly because rotting carrion continues to attract scavengers to the gears, which are in turn caught and killed. In tropical/subtropical areas nets may snag on coral reefs and trap fish or sea turtles, or they may float at the surface and aggregate to form mats that resemble seaweed mats, but entangle sea turtles so that they drown, starve or are mutilated (Stelfox 2020). Ghost fishing is increasing because fishers normally have no access to port recycling facilities and therefore have little incentive to dispose of this marine litter on land (UN Environment Programme at <https://www.unep.org/technical-highlight/fishing-nets-double-edged-plastic-swords-our-ocean>) and instead they dispose of worn out or damaged gear at sea.

Historically, fisheries bycatches have probably caused the death of millions of turtles per year. The World Wide Fund for Nature (WWF) estimated that at least 250,000 sea turtles are currently killed by entanglement in fishing gear each year (Course *et al.* 2020). However, this is probably a considerable underestimate as it does not include dead turtles that fall off gears so are never observed, nor does it include turtles of all life history stages that are lost to ghost fishing.

HABITAT LOSS

BREEDING BEACHES

Sea turtles nest, mostly nocturnally, on sandy beaches throughout the tropics and subtropics. Unaltered beaches are fringed on the landward side by vegetation.

Nests are dug above the high-water mark and eggs laid in them. Newly emerged hatchlings head towards the lightest part of the night-time horizon over the sea and away from the dark vegetation (Limpus 1971). Nesting females, eggs and hatchlings are preyed upon by guilds of native terrestrial/aerial predators, including crabs, birds, crocodiles and mammals (Heithaus 2023). Females and hatchlings that descend the beach to enter the sea run a gauntlet of marine predators, predominantly fish, including sharks, before escaping to open water. Beaches are ephemeral geological structures that change markedly as the processes of erosion and deposition vary in dominance (Gallop *et al.* 2020) and they may disappear entirely during violent storms or reappear as currents and weather systems alter. These natural changes have local consequences for sea turtles but are relatively unimportant over long timescales as new nesting sites replace those lost.

The availability of pristine beaches to turtles has been greatly reduced during the last two centuries. Coastal development in the form of roads, human habitation, businesses, ports, industry, tourist resorts and cities has increased exponentially, particularly since the 1950s (Davenport and Davenport 2006); for example, approximately 40% of the Mediterranean coastline is now covered by man-made structures (source: <https://www.unep.org/unepmap>). Of the remaining coastline, most sandy beaches have been developed for tourism and brightly lit hotels/restaurants, nightclubs and roads line their landward sides rather than vegetation. This light pollution disorients nesting females and emerging hatchlings (Carr 1967; Kamrowski *et al.* 2012).

Ariano-Sanchez *et al.* (2023) recently looked at the consequences of development and vegetation loss in Guatemala, where beaches are dark as the sand is derived partly from volcanism rather than sedimentation. They found that developed beaches were significantly hotter, with likely feminisation of egg clutches (see 'Temperature' section below). Informal tourist infrastructure (e.g. loungers, umbrellas, boat/board hire hubs) encroaches on potential nesting sites. Beaches are 'groomed' to remove 'unsightly' seaweed and smooth out blemishes cause by tourist activities. Grooming often involves nocturnal beach scraping by machinery while light-polluting headlights and security lighting attract any newly emerged hatchlings (Witherington *et al.* 2014). Use of vehicles often creates tyre tracks that are traps for emerging hatchlings. Similar developments occur world-wide, particularly in tourist hotspots. Although local conservation efforts have often been successful, globally they support small fractions of the original populations because of beach loss combined with natal homing and slow colonisation of new nesting sites.

CORAL REEFS

Shallow-water coral reefs are also important to the life history of at least three sea turtle species,

the hawksbill, green and loggerhead. Hawksbills are omnivores that specialise in eating sponges that are toxic and contain glass spicules, but they also consume coral polyps and macroalgae; they therefore have had a keystone ecological role for reefs. Loggerheads regularly hunt their benthic prey in the complex 3D geometry of reef habitats. All three species spend part of their time on coral reefs at 'cleaning stations' having macroalgae and vagile epifauna removed from their shells and soft parts by reef fish and shrimp (Sazima *et al.* 2010).

Coral reefs require a narrow range of environmental conditions to thrive. Guan *et al.* (2015) found that the global limits were 21.7°–29.6°C for temperature, 28.7–40.4 for salinity, 4.51 μmol L⁻¹ for nitrate, 0.63 μmol L⁻¹ for phosphate, and 2.82 for aragonite in its saturation state. The minimum light level needed in coral reefs was found to be 450 μmol photon m⁻² s⁻¹. This means that corals cannot live in cool waters but cannot be too warm either; they are vulnerable to eutrophication and ocean acidification is an almost inevitable consequence of raised atmospheric CO₂ levels (Takahashi *et al.* 2014), and heightened turbidity, which reduces light penetration and inhibits photosynthesis by coral zooanthellae.

Coral reefs have declined markedly in extent over the last two centuries, especially in the Caribbean and SE Asia (Carpenter *et al.* 2008). Coastal developments, intensive logging, clearance of coastal mangrove communities, plus inputs of untreated sewage from human populations have all caused high turbidity plumes that have killed coral. Direct mining of coral exoskeletons (for construction material, for jewellery and for medical purposes) has been widespread on African and Asian coasts for many decades (Brown and Dunne 1988). Removal of live coral for the aquarist trade is practiced worldwide. Hugely damaging fishery practices including dynamite fishing, cyanide fishing and trawling using modern powerful gears continue to be in routine use especially around the Coral Triangle of SE Asia (Tahiluddin and Sarri 2022) despite their illegality. Mining, dynamite fishing and trawling reduce reefs to rubble and so are essentially irreversible as coral reefs take centuries or millennia to grow. Countries that once had coral reefs had already lost them by the late 1980s, and rising human populations are driving continued coral reef loss (Wilkinson *et al.* 1996). Coastal dredging is still a threat to coral reefs, including the Great Barrier Reef, as it causes turbidity that greatly reduces light levels and results in the expulsion of coral zooanthellae as well as having a wide range of deleterious biochemical consequences (Jones *et al.* 2020).

To add to these direct anthropogenic effects, the consequences of global climate change for coral reef survival have been increasingly evident since the 1980s. The first major world-wide coral bleaching event took place in 1998 after many years of localised

events (Souter *et al.* 2021). Coral bleaching mainly follows sharp rises in shallow-water sea temperature that cause corals to expel their symbiotic zooxanthellae, which support coral metabolism. Since 1998 the frequency of bleaching events has increased and Souter *et al.* (2021) found that hard coral cover on reefs has declined significantly by about 20% since 2011, while algal cover has replaced it. Algal cover provides much less reef complexity and hence diversity for foragers and cleaner fish. Current projections (European Environment Agency Integrated Pollution Prevention and Control 2018) suggest that 70% of coral reefs will disappear if global warming reaches a sustained 1.5°C above pre-industrial levels (Lamboll *et al.* 2023). This risk increases to 99% if the temperature rises by 2°C. It is therefore probable that reefs will disappear as useful habitats for sea turtles, especially the hawksbill, by around 2050.

SEAGRASS MEADOWS

Seagrasses form shallow water meadows from the tropics to the Arctic circle, especially in relatively sheltered areas. Seagrass beds are highly productive, biodiverse and fix far more carbon than terrestrial forests (Serrano *et al.* 2021). About 30% of their area has disappeared since 1900 because of climate change, typhoons and hurricanes, coastal development, dredging, eutrophication, unregulated fishing and boating activities, and disease. A recent meta-analysis of SE Asian seagrass beds (Sudo *et al.* 2021) showed that 80% were shrinking, 20% were growing and that the net rate of loss was 4.7% year⁻¹. Tropical, subtropical and warm temperate seagrass beds are important resources for a wide range of animals, including sea turtles, particularly green turtles which forage very flexibly on a wide variety of seagrass species in different parts of the world as well as associated macroalgae, molluscs and jellyfish (Bjørndal 1997; Howell and Shaver 2021). The loss of seagrass beds can be a serious problem for turtle population survival where alternative food sources are absent, and use of the beds may have a history of millennia (de Kock *et al.* 2023). Again, Bermuda provides a cautionary tale. Sea grass bed areas have declined over several decades (for multiple reasons, including dredging, boating activities, eutrophication from runoff and septic tanks, high levels of pollution by organic pollutants and petroleum products) and this has been accompanied by declines in green turtle size, body mass and body condition (Meylan *et al.* 2022). Their long-term 50-year study also revealed that the resident juvenile and subadult greens showed a high degree of fidelity to feeding sites. As their food source disappeared, the remaining seagrass stands were overgrazed (Fourqurean *et al.* 2010), so their ability to grow declined. This has future implications for the breeding grounds that adults eventually disperse

to, particularly as sea grass beds have been lost at an enhanced rate in recent years. Christianen *et al.* (2014) revealed an additional problem based on a ten-year-old study of a marine protected area (MPA) that consisted of seagrass fields around Derawan Island, Indonesia. Such fields are highly biodiverse and important to the conservation of many species. They found that the MPA had attracted immigrant green turtles which had risen to unprecedented densities (*c.* 20 individuals ha⁻¹) and had overgrazed the seagrass, which became less biodiverse. In addition, predominantly juvenile turtles displayed a hitherto unknown foraging strategy: they dug up the sediment with their foreflippers to reveal seagrass roots and rhizomes, which they consumed. This resulted in the seagrass becoming patchy and more prone to erosion. Overall, they found that the seagrass fields would only recover if all the turtles were removed indicating that the conservation of seagrasses and their associated green turtle population is clearly complex.

ENVIRONMENTAL DEGRADATION

CHEMICAL POLLUTION

Sea turtles are vulnerable to environmental degradation caused by chemical pollution, especially by petrochemicals; persistent organic pollutants (POPs) including 'legacy' compounds such as polychlorinated biphenyls (PCBs) and dichloro-diphenyl-trichloroethane (DDT); 'forever chemicals' per- and polyfluorinated alkyl substances (PFAs), (Brunn *et al.* 2023) and heavy metals (Arienzo 2023). Exposure to such pollution is greatest in shallow neritic waters, especially when sediments are contaminated, and pollutants are transmitted up food chains to juvenile/subadult/adult turtles. Due to the particular life history characteristics of sea turtles, such as their great longevity and multiple long-distance migrations between different environments, the accumulation of long-lived materials is particularly likely (Arienzo 2023). The sources of pollutants are extremely diverse, and include runoff of herbicides, pesticides and heavy metals effluents from coastal shipbuilding/repair operations, degradation of plastic rubbish plus spills of petroleum products from personal watercraft such as jet skis, small boats, general shipping, oil tankers and petroleum storage/processing facilities. Many of the materials have accumulated in the marine environment over more than a century as chemical industries have developed and promoted compounds that had great initial utility, but eventually proved to be highly damaging and persistent such as PCBs, DDTs, PFAS and tetraethyl lead.

In 2010 the Gulf of Mexico was seriously polluted by the BP *Deepwater Horizon* environmental disaster when a mobile drilling rig exploded 64km

off the coast of Louisiana and oil spilled from the 1,600m deep wellhead for 87 days, releasing about 3.19×10^6 barrels of oil (Wallace *et al.* 2017), making it the worst oil spill in history. Unlike most other oil spills, it contaminated the entire water column, affected over >112,000km² of sea surface, and fouled 2,100km of coastline. Five sea turtle species were impacted: the loggerhead, Kemp's ridley, green, hawksbill and leatherback. It was estimated that about 400,000 turtles were affected and 4,900–7,600 large juvenile and adult sea turtles were killed. Worst affected were small pelagic phase juveniles that were associated with floating *Sargassum* weed, which concentrated the surface oil. Some 56,000–166,000 juveniles died, either because they were coated in oil or ingested tar (McDonald *et al.* 2017).

Heavy metals accumulate in the tissues of sea turtles (Savoca *et al.* 2022). They reported relatively low levels from loggerhead egg yolks, except in the case of barium. Barazza *et al.* (2023) have recently studied green turtle hatchlings from Heron Island, a small coral sand cay on the southern Great Barrier Reef (GBR) of Queensland, Australia. This is famous for >99% of hatchlings being female. Barazza *et al.* (2023) showed that this is partially caused by metals such as Ba, Cr and Cd, and metalloids including Sb, which have oestrogenic effects promoting feminisation of embryos, rather than being solely due to high temperatures. In 2015 a catastrophic dam failure in a Brazilian mining area led to widespread heavy metal contamination of turtle breeding beaches and foraging areas north and south of the mouth of the Doce River. Miguel *et al.* (2022a, 2022b) reported its effects on loggerhead and green turtles. Both species showed deleterious effects with green turtles showing elevated blood and tissue levels of heavy metals, evidence of kidney and liver damage as well as heightened parasite loads.

Since the 1930s, green turtles have been increasingly affected by an epidermal tumour disease, fibropapillomatosis (FP), that is infectious and caused by a herpes virus (ChHV-5). The tumours are benign but often disabling by inhibiting feeding and vision, and are occasionally fatal. Tumours can be removed by laser in rehabilitation facilities. First detected in Florida green turtles in 1938, the disease is now found throughout the world's oceans and has reached incidences of 70–90% in some green turtle populations. It has also been reported from loggerheads, both ridley species, and even the leatherback. Alfaro-Núñez *et al.* (2016) found high levels of virus in clinically healthy green turtles, indicating latency. Many studies have suggested that poor water quality is associated with high FP incidence, pollutants implicated including sewage, POPs and heavy metals (e.g. Miguel *et al.* 2022a, 2022b). Vanstreels *et al.* (2023), in a large study in coastal Brazil, found higher levels of FP in juvenile green turtles foraging near to a metallurgical processing site, but also found that the anatomical distribution of tumours could be

linked to clusters of environmental variables. Overall, it appears that FP is a good indicator of environmentally stressed turtles.

EUTROPHICATION

Over the last two centuries, exponentially rising human and livestock populations and their corresponding faecal and urinary outputs, plus agricultural intensification, the development of artificial fertilisers, deforestation and the burning of fossil fuels have delivered greatly increased quantities of nitrogen and phosphorus to aquatic habitats (Devlin and Brodie 2023). Nutrient enrichment by N and P causes enhanced plant growth both in the water column and on the substratum. Photosynthesis and an increased plant biomass causes hyperoxia during the day, but at night respiration results in hypoxia and a lower pH. Blooms of phytoplankton and macroalgae die and decay with bacterial metabolism further reducing oxygen concentrations, eventually to anoxic levels. Global warming worsens the problem as higher temperatures reduce oxygen solubility and enhance plant metabolic rates.

Once primarily a problem of freshwater and estuarine habitats where P is the limiting nutrient, eutrophication now affects coastal waters where N is limiting around the world, creating extensive benthic dead zones (Osterman *et al.* 2009), plus mass mortality of fish and invertebrates. One symptom of this eutrophication is the accumulation of very large quantities of seaweed on sandy beaches, creating a nuisance for tourism and other forms of coastal exploitation. Rotting seaweed mounds release sulphides, which have even caused mortality in wild boars and horses (van Alstyne *et al.* 2015) and hospitalised humans. ‘Green tides’, composed predominantly of *Ulva* sp. have been seen since the 1970s in temperate areas, notably in China and Brittany (Schreyers *et al.* 2021). However, in the last two decades, ‘golden tides’ have appeared repeatedly in tropical and subtropical areas of the Atlantic (Smetacek and Zingone 2013). These are composed of floating brown seaweed mats of the genus *Sargassum* that have been carried by currents or blown ashore. Lapointe *et al.* (2021) have shown that *Sargassum* tissues have increased in N content by 35% since the 1980s due to coastal and oceanic eutrophication, ‘turning a critical nursery habitat into harmful algal blooms with catastrophic impacts on coastal ecosystems, economies, and human health’.

Copious *Sargassum* mats have spread on several occasions to beaches of the Caribbean islands, Mexico, Brazil, Florida and West Africa from Sierra Leone in the North to Ghana in the South in beach-covering quantities of hundreds of thousands of tons (Ackah-Baidoo 2012). All these affected areas have turtle breeding beaches. Satellite images confirm that *Sargassum* sp., once limited largely to

the Sargasso Sea of the western Atlantic, are now forming the recurrent great Atlantic Sargassum belt (Wang *et al.* 2019), so such algal stranding is likely to continue for the foreseeable future. Reversing coastal eutrophication would take many decades and there are no current initiatives designed to achieve this.

Large quantities of seaweed arriving on breeding beaches in summer have multiple effects on sea turtles. First, gravid females are unable to climb the beach to nest and at a minimum they are likely to search out less affected areas (Maurer *et al.* 2021). Second, emerging hatchlings will be unable to climb over *Sargassum* accumulations to reach the sea and will die of dehydration (Gavio and Santos-Martínez 2018). Less obviously, beached *Sargassum* can alter the thermal environment of the embryos within nests (Maurer *et al.* 2022), cooling in summer and warming in winter. Since the sex ratio of hatchlings is determined by their thermal history, this may have implications for population dynamics.

Presently unknown are the effects of increasing quantities of floating *Sargassum* across the Atlantic Ocean. Young loggerheads are known inhabitants of *Sargassum* mats where they are well-camouflaged and where there is an abundance of small prey items associated with the weed. This might suggest that eutrophication will generate more habitat for them. Most other species have been observed rarely after they leave the natal beaches as hatchlings until they recruit years later to near-shore feeding grounds as sizeable juveniles. The whereabouts of leatherback hatchlings and small juveniles in the ocean are unknown. Young leatherbacks are known to lack manoeuvrability (Davenport 1987) and if they encounter extensive oceanic weed lines, entanglement may be an issue.

PLASTICS

Plastic compounds were discovered from the mid-nineteenth century onwards and commercially exploited throughout the twentieth century, especially from the 1950s. Plastics have now polluted all oceans and seas. In 2023 it is estimated that these waters already contain about 200 million tons of plastic, and that this is being added to at a rate of about 12 million tons per annum rising to about 30 million tons per annum by 2040 if no changes are made (Reddy and Lau 2020). Plastic materials are generally less dense than seawater so tend to accumulate at or near the sea surface and are only likely sink when sufficiently biofouled. Plastic items range downwards in size from large monofilament nylon or polypropylene nets, through polythene bags and polyethylene terephthalate (PET) bottles and expanded polystyrene, to microplastics (<5mm) either in the form of plastic feedstocks (e.g. styrene beads) or generated from fragmentation of larger items and

fibres from textiles (Thompson *et al.*; 2004; Barnes *et al.* 2009). Microplastics and even smaller plastic particles (nanoplastics <0.1mm: Ng *et al.* 2018) are now universal in a range of environments, including the atmosphere (Allen *et al.* 2022). Most plastics do not biodegrade rapidly, so the material already present will endure for centuries or even millennia with abrasion and the action of UV light generating rising proportions of smaller and smaller particles. Plastic material is not evenly distributed with roughly 90 million tons occurring in six oceanic concentrated garbage patches (Leal Filho *et al.* 2021) created by the current systems that form the ocean gyres in both hemispheres. The largest is the Great Pacific Garbage patch in the Northern Pacific Gyre, half of which is made up of plastic rubbish from fishing gear which reflects the extensive use of trawls, drift nets, purse seines and longlines in this basin. In addition to visible plastic pollution, Napper *et al.* (2022) showed that many microplastic particles were generated by rope abrasion, and that loss of microplastics from ropes increased as ropes age.

In contrast, the South Atlantic patch is mostly composed of plastic bottles of Asian origin. These patches are expected to grow exponentially by 2.5% per annum for the foreseeable future (Leal Filho *et al.* 2021). Plastic debris are also known to aggregate at frontal structures in the sea where turtles also accumulate (González Carman *et al.* 2014). Microplastics are known to accumulate toxic chemicals, including heavy metals and POPs, by adsorption from the environment; effectively acting as microsponges and

stripping toxins from the sea. After ingestion of the microplastics, the toxins can be desorbed and transferred to biota (Verla *et al.* 2019).

Sea turtles have long been known to be vulnerable to plastic pollution. Early worries concerned ingestion of plastic bags (Fritts 1982), while Mrosovsky *et al.* (2009) analysed necropsy records for 408 adult leatherback turtles from 1885–2007. No plastics were recorded in the guts until 1968. Thereafter, 37.2% of leatherback intestinal tracts contained plastics, sometimes blocking the gut.

Boxes 1 and 2 show case histories of two studies of individual turtles, the studies being more than 30 years old. They both showed that plastic pollutants were already far more diverse than simply polythene bags and included multiple materials of a wide range of sizes. They also show that plastics caused damage and death. The leatherback faecolith packaging of plastic garbage was mineralised by struvite known medically in humans from gallstones/kidney stones/gastrointestinal faecoliths, so was clearly a pathological response (Ramanathan *et al.* 2017), while the juvenile hawksbill starved to death because the intestinal tract was impacted by thousands of macroplastic and microplastic materials that filled the stomach and intestines. Nelms *et al.* (2016) provided a seminal world-wide review of plastic pollution and marine turtles, confirming the widespread damage caused by plastic materials of a range of sizes. In more recent years the effects of nanoplastic pollution have attracted attention. It has been shown recently in humans that nanoparticles of PET, polythene and

BOX 1—Leatherback turtle.

A fresh carcase of an adult *Dermochelys* (killed by sharks in 1991) was necropsied in Hawaii. It had a hard, stone-like ball 13cm in diameter in a pouch in the wall of the lower rectum. The object proved to be mineralised faecal material, the mineral being struvite (NH_4MgPO_4). When broken up, the ball was found to contain the following plastic items:

1. 300mm length of tangled, blue polypropylene twine, 5mm thick.
2. 4 strands (105–130mm length, 1mm wide) of old, unravelled polypropylene tarpaulin fabric.
3. 160mm length of monofilament nylon fishing line.
4. 4 pieces of hard, flat green plastic (9×13mm, 10×7mm, 6×5mm, 6×5mm).
5. 1 piece hard white plastic (9×5×2mm).
6. 1 piece yellow/hard plastic (5×5mm).
7. 3 small strands of unidentified plastic (20-, 20- and 25mm length).
8. 6 pieces (each about 4mm diameter) expanded polystyrene.
9. Large number (hundreds) of polystyrene beads (<1mm diameter).
10. 3 pieces of abraded polythene bag material (c. 20mm diameter).

This information demonstrates that leatherback turtles already ingested a wide range of micro- and macro-plastics more than three decades ago.

Source: Davenport *et al.* (1993).

N.B. Similar faecoliths have been found in other adult leatherbacks (e.g. Eckert and Luginbuhl 1988)

BOX 2—Post-pelagic juvenile hawksbill

Found moribund in 1991 off Bermuda, carapace length 158mm, weight 750g. The turtle was grossly distended (image above). Rehabilitation was attempted but failed as the gut was completely blocked. At necropsy the lower oesophagus, stomach and intestines were found impacted with fragments of plastic and monofilament nylon with very little organic matter present (a few squid beaks and macroalgal material). The gut contents weighed 14.4% of the turtle weight and contained 2,297 plastic particles including monofilament nylon and styrene beads.

Source: Jennifer Gray 1991. Bermuda Turtle Project (with permission).

polystyrene are detectable in blood samples (Leslie *et al.* 2022), indicating passage across organ membranes and in principle there is no reason to expect this not to happen in sea turtles.

Finally, Wilcox *et al.* (2018) quantified the risks to turtles associated with plastic pollution. Using extensive necropsy databases, they estimated that ingestion of a mere 14 pieces of plastic is likely to carry a 50% risk of increased mortality due to gut blockage or perforation. Those sea turtle species with prolonged oceanic life history stages that intersect the main ocean gyres and their associated garbage patches (Leal Filho *et al.* 2021) are clearly facing an increasing existential risk.

CLIMATE CHANGE

TEMPERATURE

It has long been known that sea turtles are profoundly affected by temperature. All cheloniid turtles, plus the young and juveniles of leatherbacks, are ectothermic and are essentially constrained by the 20°C surface oceanic water isotherm and at lower temperatures they stop feeding and hibernate or eventually become cold-stunned and uncoordinated (Davenport 1997). Feeding, metabolic activity and growth rates increase with temperature, reaching a maximum at the highest tropical oceanic seawater temperatures that slightly exceed 30°C. Near-shore water temperatures can be higher, but the exact

upper lethal temperature for turtles has not been established for ethical/logistical reasons.

Since the 1970s, much research effort has been concerned with the effects of nest temperature on sea turtle eggs and embryos. Bustard (1972) established that, at constant temperatures, green turtle eggs only developed between 25–27°C and 35–37°C, taking 6–13 weeks between laying and hatchling emergence; at lower or higher temperatures development failed. In the 1980s, the discovery that all sea turtle species then examined featured temperature-dependent sex determination (TSD), with pivotal constant temperatures (i.e. temperatures that yielded a 50–50 sex ratio) close to 29°C, soon generated interest in the possible consequences of global climate change (Mrosovsky 1982; Davenport 1989; Mrosovsky and Pieau 1991; Mrosovsky 1994). One species, the flatback, is apparently rather more resilient to a global temperature rise. Flatbacks have significantly higher pivotal temperatures (30.4°C) and tolerated longer term exposure to nest temperatures <35°C (Howard *et al.* 2015).

TSD means that turtle eggs exposed to low temperatures are predominantly masculinised by hormonal cascades whilst at high temperatures they are feminised. Mrosovsky and Provanha (1989) were the first to report high levels of female loggerhead hatchlings (>93%) from Florida beaches, while cooler beaches in Georgia and South Carolina yielded 56% females. These data suggested that a warming climate risked the eventual extermination of populations as too few males would eventually be available for mating.

This scenario was simplistic as egg/embryo temperatures vary with seasons, sand type/colour, nest depth and location of nest including shade vs solar exposure. Hypothetically, sea turtles could adjust to rising temperatures by changing their behaviour in relation to these variables. Over geological timescales they have certainly done so. For example, flatback turtle populations in hot areas of Australia breed in winter, while genetically distinct populations nesting in cooler areas do so in summer (Poloczanska *et al.* 2009), so that the eggs are incubated over similar temperatures and yield both male and female embryos. These differences in phenology of breeding probably evolved over thousands of years.

The nesting behaviour of female sea turtles and its periodicity, both in terms of numbers of clutches laid by individuals and the intervals between their breeding seasons, is well studied, notably with the contributions of volunteers/citizen scientists. All of this has been accomplished by the increasingly sophisticated tagging of adult females, plus remote monitoring of nest temperatures. However, adult male turtles are rarely seen and rarely tagged because adult males of most populations never emerge on land. Hays *et al.* (2010) suggested that, if adult males bred more frequently than adult females, the operational sex ratio would be more balanced; this was confirmed experimentally for Mediterranean loggerheads by Hays *et al.* (2014). Hays *et al.* (2022b) have shown that the known breeding habits of males including shorter inter-nesting intervals, multiple matings with females and breeding at several nesting sites reduce the risks of clutch feminisation.

Another possibility that might allow turtles to retain their thermal/geographical niche in the face of rising environmental temperatures would be a change in nesting phenology to take advantage of cooler/earlier parts of the nesting season. Laloč and Hays (2023) have recently modelled this possibility for 58 geographically separated nesting sites for all sea turtle species and concluded that even an unlikely forward shift in nesting date of 18 days would not completely counteract likely warming. Fuentes *et al.* (2024) published a comprehensive global consideration of the likely effectiveness of phenological adjustments in green, loggerhead and olive ridleys and found that even extreme forward or backward movement of nesting date would only prevent extinction of about half of the nesting populations.

Blechschmidt *et al.* (2022) concentrated on the large (200,000) northern GBR green turtle population (pivotal temperature of 29.3° C), which is heavily female biased (*c.* 80% of adult breeders, 99% of subadult turtles). They considered all possible methods of 'escaping extinction' such as deeper nest-digging to lower incubation temperature, an earlier breeding season, a greater frequency of male breeding, migration of males from the cooler southern GBR population where the sex ratio is currently

67% female and evolution of higher pivotal incubation temperatures. Their modelling indicated that all these responses, including rapid evolution, were needed under all scenarios in which extinction was avoided. Based on this information, it is highly likely that the northern population will die out, though the southern population is likely more resilient.

An additional thermal problem for sea turtles is that global air temperatures are not only rising, but their variability is increasing. A NOAA (2022) showed that heat wave frequency in USA cities had doubled between the 1960s and the 2020s. Heat wave intensity and duration were also significantly increased, the latter by about 30%. Heat waves were also likely for much longer periods of the year—the heatwave season was about 25 days long in the 1960s, and around 75 days in the 2020s. Similar data for turtle nesting beaches is currently unavailable, but prolonged heat waves certainly carry the risk of exceeding embryo viability temperature ranges. This has recently been modelled for green turtles nesting in Turkey up to 2100 (Turkozan *et al.* 2021). They found that the likelihood of heat wave nest temperatures exceeding lethal temperatures would rise to 19.3% by 2100, assuming moderate climate warming.

Mancino *et al.* (2023) have recently used scenario modelling of likely temperature increases for the Mediterranean and concluded that potential new green turtle nesting areas will become available in the cooler Western Mediterranean. However, this implies that green turtles will colonise such new areas. Nesting sites are currently confined to Cyprus, Turkey and Syria. Natural recolonisation of the Western Mediterranean is highly unlikely because of natal philopatry, implying that assisted colonisation would be needed. Only one successful green turtle example is available; Barbanti *et al.* (2022) evaluated the fifty-year history of assisted colonisation on nesting frequency on the Cayman Islands. Nesting frequencies have increased exponentially, but the conservation programme, which included headstarting (rearing in captivity to a size where predation risk is reduced) for one year, has required considerable expenditure. It is also noteworthy that this programme was aimed solely at replacing an exterminated population, not the recolonising of 'new' beach habitats. Identifying new thermal refuges and funding re-introduction programmes for several decades for several sea turtle species would require considerable political, financial and logistic commitment.

An alternative to assisted colonisation lies in cooling existing nesting sites. Jensen *et al.* (2018) reported extreme temperature-driven feminisation in one of the largest green turtle rookeries in the world on Raine Island, a small, treeless, windswept island of the GBR in Queensland, Australia (BBC 2023). This contrasted greatly with the resilience to climate-induced temperatures shown by turtles

nesting at the pristine Conflict Islands at a similar latitude near Papua New Guinea, whose sandy breeding beaches fringe rainforest interiors where rainfall remains high and hatchling sex ratios have remained balanced over the last two decades (Staines *et al.* 2023). Raine and Hillman Islands in the GBR are now the focus of experiments to compare various approaches such as shading and watering with sea water to the cooling of nests: the Turtle Cooling Project (see <https://wwf.org.au/blogs/behind-the-scenes-of-the-turtle-cooling-project/>).

SEA LEVEL RISE AND EXTREME SEA LEVEL EVENTS

Global mean sea-level (GMSL) has risen by 0.016–0.021m since the nineteenth century, half of that since 1993 (IPCC 2021; <https://www.climate.gov/news-features/understanding-climate/climate-change-global-sea-level>). This rise has almost entirely been because of global warming of sea water, which causes expansion of the oceans, rather than because of melting of the Greenland and Antarctic ice sheets. Horton *et al.* (2020) reported on likely sea level rise by 2100 relative to 1986–2005 assuming little moderation of carbon emissions. They accept that a rise of about 1m (or 50 times the increase that has already occurred) in GMSL is probable by 2100, but recent studies on melting of the Antarctic ice sheets imply that a rise of <2m is possible. Such rates of increase in GMSL are historically unprecedented. In theory beaches can move inland as sea level rises, but in practice this is likely improbable in many areas because of ‘coastal squeeze’, where armoured coastlines characteristic of developed areas provide a rigid inland limit and features such as groynes limit the lateral movement of sand (Lyons *et al.* 2020). Cheng *et al.* (2024) have recently presented a review of the progress of heating of the top 2000m of the world ocean between 1960 and 2023. Changes in ocean heat content (OHC) form one of the strongest and most unequivocal signals of climate change and reveal a steady rise over the study period and is far less variable than air temperatures or sea surface temperatures. These data also reveal that the world ocean is becoming more stratified so that less mixing with deeper, colder, oxygen-rich water is taking place. This means that the upper part of the ocean becomes less able to absorb CO₂, resulting in a fall in pH (Takahashi *et al.* 2014), but also means that incoming solar energy heats a smaller proportion of the ocean, promoting increased sea surface temperatures, which will in turn increase GMSL.

The Climate Emergency is not simply triggering changes in GMSL. Changes in global temperatures are increasing storminess and the consequent frequency of extreme sea levels (ESLs). These ESLs are caused by a combination of storm surges, tides and waves, which in turn cause highly damaging short-term increases in local sea level that damage

or destroy coastal man-made and natural habitats. Traditionally, ESLs are described as those that are expected once in a century, once in 500 years or once in a millennium. Tebaldi *et al.* (2021) summarised projections from multiple studies and projected the frequency of events that are currently expected once a century (100-yr ESL). Assuming a moderate increase in mean global temperature of 1.5°C by 2100, they expect a 50% chance of an ESL occurring every year or a 50-fold increase in frequency with the chances being even greater in the tropics. An ESL can have multiple effects on sea turtle reproduction. Most obviously, a large storm surge during the breeding season will flood nests with sea water, killing eggs by asphyxiation or salt poisoning. In addition, storms can redistribute sand around affected beaches; they can lower beach levels, or pile sand up, depending upon beach aspect.

Predicting the consequences of rising GMSL and increased frequency of ESLs is complex, Lyons *et al.* (2020) presented the likely effects on nesting loggerheads and greens on the barrier islands of the southeastern USA. They found that predictions varied greatly even between geographically close sites. Also, although predicted decreases in nesting areas because of a GMSL increase by 2100 were modest overall, around 2–6%, effects on some of the currently most densely used nesting areas were sufficient for females to start to dig up each other’s nests—a problem already evident on some degraded sites, such as Raine Island, Australia, with high nesting densities (BBC 2023). Interestingly, Lyons *et al.* (2020) found that projected changes in GMSL had little effect on the likelihood of nest inundation by hurricanes—this was already greater than 99%. At present, projections for hurricane frequency reveal no clear pattern, but it is accepted that hurricane intensity and rate of associated precipitation have significantly increased over the last half century.

Rivas *et al.* (2023) modelled the likely loss of nesting sites due to sea level rise for seven sea turtle rookeries in the Caribbean, Americas and Australia that are currently visited by five nesting species, leatherbacks, greens, hawksbills, loggerheads and olive ridleys. They found that, under a moderate GMSL rise, 100% of some sites would disappear by 2050, with leatherbacks and loggerheads nesting upon open, shallow-sloping beaches being particularly vulnerable.

SEA TURTLES AND IRELAND/U.K.

Five sea turtle species have been recorded from waters around Ireland and the UK: leatherback, loggerhead, hawksbill, green and Kemp’s ridley (Pierpoint 2000). From 1990 onwards, the UK Department for Environment Food and Rural Affairs and regional UK governments have funded a cumulative TURTLE database of marine turtle records for the

United Kingdom and Ireland that contains all earlier (as far back as 1756) and subsequent records supplied by citizen and professional scientists (Pierpoint and Penrose 2002). Scientists from Ireland and the UK, together with the National Parks and Wildlife Service of Ireland and the Department of Agriculture, Environment, and Rural Affairs of Northern Ireland, have contributed much to the creation and maintenance of this database. Notable inputs have been the efforts of Gabriel King in the 1980s to collate more than a thousand early records of sightings of leatherback turtles (e.g. King and Berrow 2009), plus the extensive studies of leatherback turtle ecology and oceanic migrations by Tom Doyle (e.g. Doyle 2007) and Jon Houghton (e.g. Houghton *et al.* 2006).

From the late nineteenth century onwards it has been realised that sea turtles observed around the UK and Ireland fall into two categories: 1) leatherback turtles, which are migratory and temporary summer residents of waters around the UK and Ireland that forage on pelagic

jellyfish (Hays *et al.* 2004; Houghton *et al.* 2006; Witt *et al.* 2007a) and 2) cheloniid turtles (mostly juvenile loggerheads and Kemp's ridleys), which predominantly arrive in autumn/winter and are assumed to be present thanks to accidental displacement from their normal range of the North Atlantic Gyre by adverse weather/currents in the North Atlantic Ocean (Witt *et al.* 2007b). Live specimens do not feed and are often moribund (termed debilitated turtle syndrome DTS, see Sloan 2011 and Fig. 2) so that NE Atlantic waters are a sink for cheloniid turtles.

Davenport *et al.* (2014b) noted that leatherback turtles entered cold summer waters on both sides of the Atlantic and had been observed feeding north of the Arctic circle. They interrogated the TURTLE database and hypothesised that leatherback turtles foraged in northern shelf waters but turned south at around the time of the autumn equinox (equal day and night length) in late September (days of year 267–69).



Figure 2—Juvenile loggerhead (*Caretta caretta*) stranded moribund in Cornwall, UK in November 2023. Note that the rear of the carapace and plastron is fouled by numerous specimens of the goose barnacle *Lepas anatifera*, which covered the hindflippers. Juvenile loggerheads mainly use the hindlimbs for routine propulsion (Davenport and Pearson 1994), so this turtle would have been reduced to floating with negligible swimming ability. The capitulum length of the barnacles was about 20 mm, suggesting that they were at least 40 days old (Evans 1958; Mesaglio *et al.* 2021). Image courtesy of Steve Byrne.

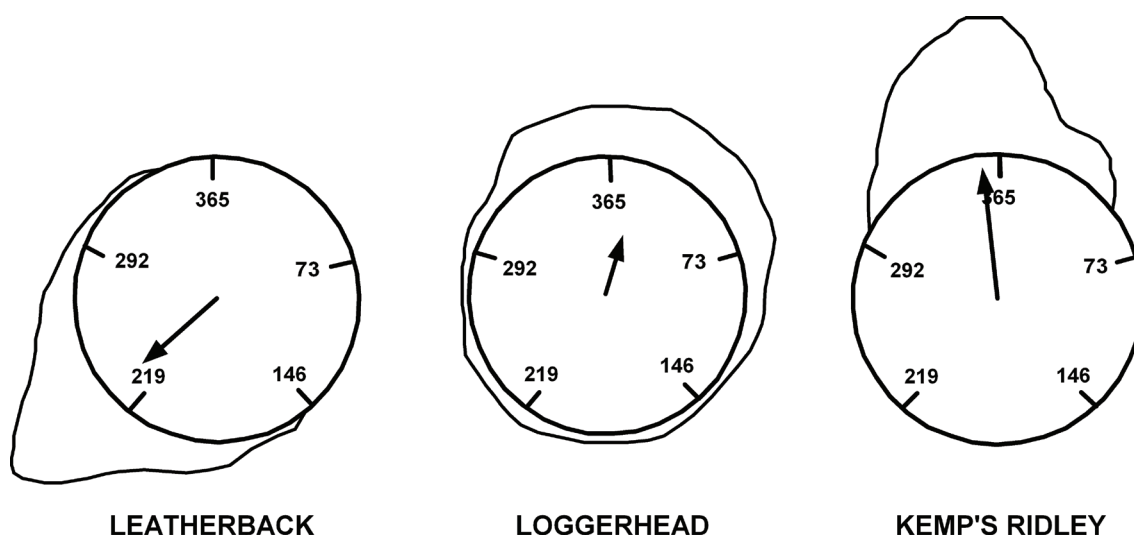


Figure 3—Circular data plots showing the sighting/stranding day-of-year (DOY) distributions for Leatherback, Loggerhead and Kemp’s ridley sea turtle species in the TURTLE database for waters around the UK and Ireland (redrawn from Feeseey 2018). Plots represent DOY distributions for all (alive and dead) 1950–2016 records. Numbers inside the circles refer to the DOY. Arrow directions indicate the sample mean dates, while the arrow length indicates the strength of seasonality.

Feeseey (2018) analysed 1950–2016 records from the TURTLE database (1,587 in total). She found that 86% of records were of leatherbacks, 11% of loggerheads and 2.8% of Kemp’s ridleys. Using circular statistics the mean day-of-year of recorded occurrence for the three species was determined (Figure 3, Table 2).

The means of the three were different from one another to a highly significant extent ($p < 0.0005$) and confirmed the summer occurrence of leatherbacks. Approximately 18% of leatherbacks were found dead, either stranded or at sea, while mortality, which occurred predominantly in winter, was much higher in loggerheads (44%) and Kemp’s ridleys (61%). Sea surface temperatures around the UK in winter are close to the 10°C ‘cold stunning’ temperature reported for cheloniid sea turtles that is associated with impaired swimming and coordination (Schwartz 1978).

Trend analysis using the TURTLE database data is difficult because of variation in survey effort over the years and the difficulty of finding/observing turtles at sea. However, an analysis of

1910–2018 records by Botterell *et al.* (2020) indicates a decline in incidence of all species of turtles in recent years. It is unclear whether this reflects changes in temperatures or current temperature patterns, or, in the case of leatherback turtles, whether more direct anthropogenic effects are involved. Certainly, leatherbacks have been trapped or killed by fishing gear, mainly through the use of trawls or crab/lobster pot lines, or have ingested plastic bags in northeast Atlantic waters (Doyle 2007). Boat/ship impacts have also caused mortality (Davenport *et al.* 2014b) and it is worrying that the waters around the British Isles may have turned into a sink for leatherback turtles.

CONCLUDING REMARKS

This review demonstrates that anthropogenic threats to sea turtle populations are multiple, interactive and potentially existential. Despite this, some species—particularly loggerheads, greens

Table 2—Phenology of occurrence of sea turtles (live or dead) around the British Isles (1950–2016). Calculated using circular statistics from the TURTLE database by Feeseey (2018).

Species	Mean day- of- year of recorded occurrence	Corresponding date of the year
Leatherback turtle <i>Dermochelys coriacea</i>	232	20 August
Loggerhead turtle <i>Caretta caretta</i>	15	15 January
Kemp’s ridley turtle <i>Lepidochelys kempii</i>	358	24 December

and Kemp's ridleys—have shown a degree of resilience, and some populations have increased, largely through the efforts of government agencies, charities and volunteers. Hopefully, continued conservation efforts, underpinned by targeted research, will sustain and extend these increases. However, the world human population nearly quadrupled between 1950 (2.5 billion) and its current (2024) level of about 8 billion. Although population increase, once exponential, has now slowed, it is still predicted to peak at about 10 billion late in the twenty-first century. Clearly the human population and its demand for resources will continue to be high for the next century at least, as will poverty and the resulting conflicts between conservation efforts and the needs of poor people sourcing protein (Vieira *et al.* 2024).

There is no prospect of a reduction in global fishing effort. Reduced turtle bycatch will therefore depend on enhanced measures to minimise/mitigate bycatch and their enforcement. The omens are not good. Large scale fisheries can mitigate their impacts by using more effective TEDS, changes in fishhook designs, alterations in gear usage, exclusion zones and closed fishing seasons. However, much fishing is in international waters and effective monitoring/enforcement is difficult. Also, Solís *et al.* (2020) demonstrated that mitigation can be expensive; avoidance of a single turtle catch was estimated to cost about US\$37,000. Small-scale fisheries are also responsible for much bycatch, but such fisheries are usually highly subsidised as they employ large and increasing numbers of poor people. Regulation is therefore difficult or impossible.

All sea turtle species are affected by bycatch and ghost fishing, but leatherbacks and olive ridleys are particularly sensitive because of their widespread pelagic foraging and migrations. The Laúd OPO Network (2020) reported on the much depleted, genetically distinct eastern Pacific leatherback population. They investigated populations nesting in Mexico and Costa Rica; both were reported to have declined dramatically because of fisheries bycatch many years ago (Eckert and Sarti 1997), but egg and meat poaching also persists, particularly in Costa Rica. The Laúd OPO Network (2020) found that the annual survival of nesting adults was only 0.7 (it needs to be over 0.9 to achieve a stabilisation of the population, which decreased annually by 15%. Without much enhanced conservation on beaches and at sea this population will be extinct decades before 2100.

Tourism, particularly international tourism, was negligible in 1950 but has risen exponentially since, so that by 1980 there were 250 million annual tourist arrivals per year, by 2000 there were about 600 million and by 2018 it had reached 1.4 billion (Davenport and Davenport 2006; <https://www.unwto.org/global/press-release/2019-01-21/international-tourist-arrivals-reach-14-billion-two-years-ahead-forecasts>). Much of this tourism is beach-based, so global pressure from entrepreneurs and the tourism industry to develop turtle nesting beaches is unrelenting. For example, since 1987, the Mediterranean Association to Save the Sea Turtles has been trying to ensure that national and international laws are enforced to protect the largest loggerhead nesting site at Zakynthos, Greece as well as other sites in Greece and Turkey. They currently report (<https://medasset.org/portfolio-item/zakynthos-the-most-important-nesting-area-in-the-mediterranean/>) that illegal activities including construction, beach horse riding, extension of beach furniture and near-shore fishing persist at Zakynthos nearly four decades later because existing laws are unenforced.

The climate emergency is mainly caused by anthropogenic emissions of CO₂ and methane, which cause environmental temperatures to rise. These rises increase storminess, and cause rises in sea levels. The 'Keeling Curve' of CO₂ readings (422ppm in December 2023) recorded in Hawaii is still accelerating, currently rising at about 3ppm per annum (<https://gml.noaa.gov/ccgg/trends/>). Global air temperatures are likely to rise to at least 2°C above preindustrial levels (IPCC 2023) by 2100 unless deep emission reductions that are far beyond those currently envisaged, are accomplished before 2050. Such a temperature rise will directly impact turtle breeding success but will also cause the death of 99% of coral reefs (Setter *et al.* 2022) well before 2100, removing vital foraging habitats, especially those associated with hawksbills, which have already been much depleted by wildlife crime.

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