Navigating Our Way to Solutions in Marine Conservation

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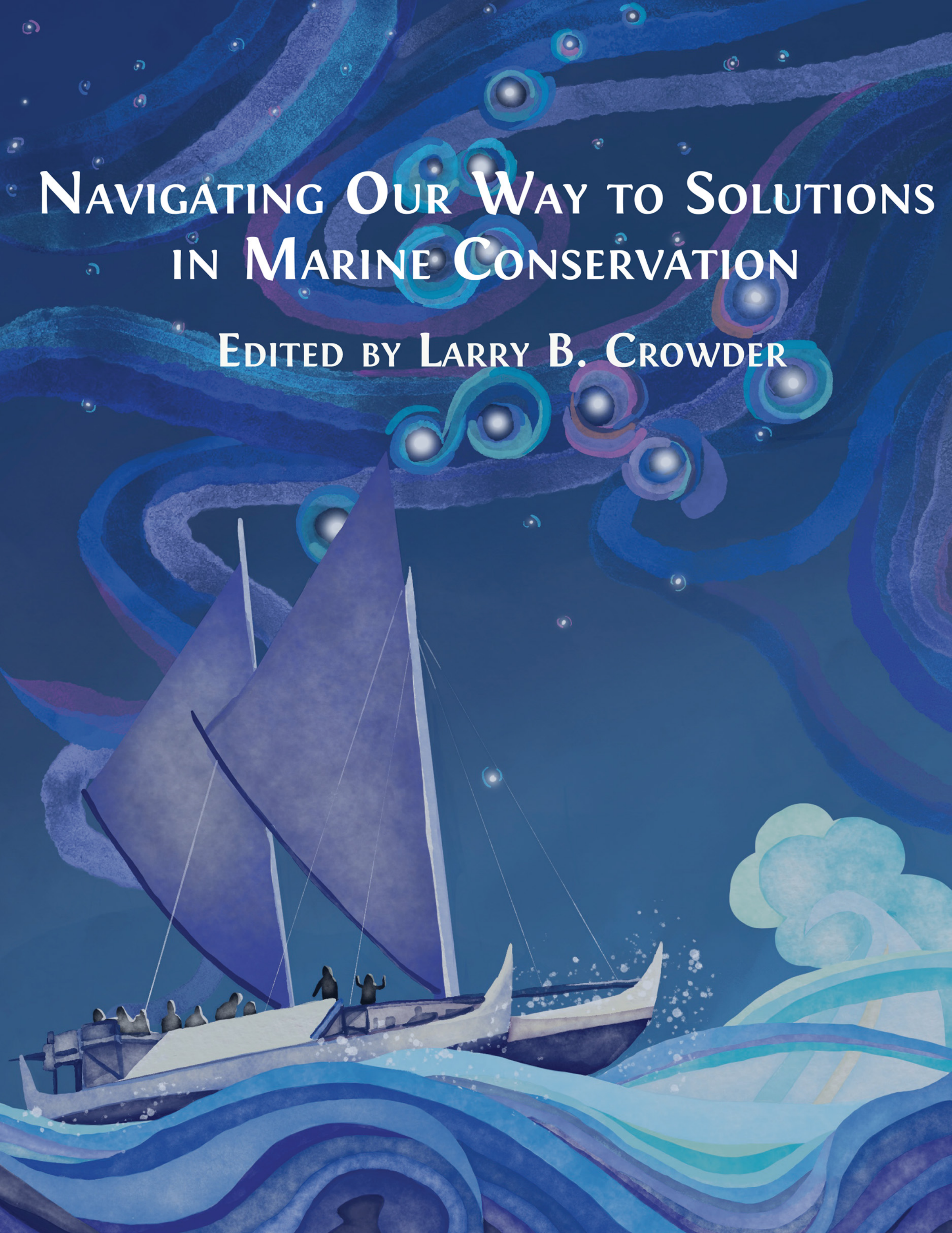

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4. New approaches to conserving endangered sea turtles

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In 1996, marine biologist Wallace J. Nichols and colleagues released a female loggerhead sea turtle (*Caretta caretta*) named Adelita off the Pacific coast of Baja California, Mexico (Resendiz et al., 1998; Nichols et al., 2000). After spending most of her adult life in captivity it was hoped that Adelita, outfitted with a satellite tracking device, would provide insight into the at-sea portion of a sea turtle's life history for which little was known (Carr, 1980). For decades, aggregations of juvenile loggerheads were known to feed along the coast of Baja California Sur, but scientists were unable to locate their nesting beaches anywhere in the region. The vastness and sheer complexity of the ocean made it difficult to monitor sea turtle movements beyond the coastal zone, causing much of their life history between the time they disappeared into the ocean upon hatching to re-emerging as adults, to remain one of the greatest mysteries in sea turtle conservation biology. For Adelita, where she might go and how far she might swim was unknown, but it was hoped that this relatively new satellite tagging technology might provide a peek into her oceanic world. However, no one expected Adelita's journey to completely change the course of sea turtle ecology.

After traveling over 11,500km (7,145 miles) in 368 days, Adelita reached the coast of Japan and became the first ever animal to be tracked swimming across an entire ocean basin (Nichols et al., 2000; Seminoff et al., 2018). Her remarkable journey captivated international audiences and provided scientists with an understanding of basin-wide population connectivity that up until then seemed unimaginable (see Adelita's tracks on seaturtle.org and learn about her story here).[2] Since then, the combination of satellite tracking and genetic analyses have confirmed the North Pacific loggerhead sea turtle as one distinct population, with all individuals originating from Japan and dispersing across the entire North Pacific Ocean as juveniles, only to return home upon maturity—a level of population connectivity that would be impossible to understand without the mighty Adelita guiding the way.

Today, sea turtles are some of the most well-tracked species in our world's ocean, and the ability to study their life at sea has greatly complemented the rich history of scientific research and conservation efforts that, until the last 25 years, have primarily focused on land (i.e., adult nesting females, embryos, and hatchlings). Together, these efforts have fundamentally advanced our understanding of sea turtle biology and conservation, but for an elusive animal that spends more than 99% of their lifespan in the ocean, a more complete picture has been necessary to fill the critical gaps across their understudied oceanic life history stages. This is especially true given concerns over the global rates of decline for many populations and the challenging suite of pressures individuals must navigate during their time at sea (e.g., fisheries interactions, pollution, and climate change).

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Traditional methods of studying sea turtle movement ecology relied on information gathered from nesting beaches, survey data, and fisheries catch and observation data. For this reason, we have long known their geographic distributions, but as a highly migratory species, our ability to understand where they go upon leaving their natal beaches and how they get there has remained one of the most arduous challenges in marine science. With emerging and innovative technologies, researchers have been able to peer into the oceanic phase like never before, extracting new insights across these knowledge gaps in sea turtle biology and conservation (reviewed in Dutton et al., 2019; Maxwell et al., 2019). Given the at-sea stage represents the longest part of their life history and the most sensitive to population growth and recovery (Crouse et al., 1987), it is important to review what we have learned about this historically under-studied phase. Specifically, we asked: What technologies and applications are we now using to expand our knowledge and how have these tools advanced our approach to successful sea turtle conservation and research during their time at sea?

Here we review several new directions and research advancements that have been transformative to our understanding of the at-sea phase for sea turtles. First, we highlight some of the emerging innovations in technology and monitoring capabilities employed to study this cryptic phase. We then discuss the application of these tools in the development of diverse conservation and mitigation approaches, across a range of in-water threats. Finally, we address some of the challenges and limitations that persist, and the future directions to ensure the successful protection and management of these vulnerable species.

Innovations: Advancements in technology and monitoring capabilities

Tagging technology and biologging capabilities

The advent of satellite telemetry in the 1980s was a breakthrough in the study of animal movement, and sea turtles were some of the first ocean migrants to be tracked. Such technologies were pivotal in taking marine turtle research from land to sea, addressing key ecological questions, and breaking down some of the greatest barriers to understanding the oceanic phase, including long-distance migration, behavior, and population connectivity (e.g., Luschi et al., 1998, 2007; Hays et al., 2004; McClellan and Read, 2007; Dodge et al., 2014; and see references within Supplemental Bibliography).

In the past few decades, the number and scope of sea turtle tracking studies have increased exponentially (*see* Godley et al., 2008; Hart and Hyrenbach, 2009; Hays and Hawkes, 2018). Tagging technologies have now been deployed on every species and stage of sea turtle, with state-of-the-art developments that reduce some of the inherent biases and limitations that persisted with early tagging studies (e.g., skewed representations by geography and age-stage, and limited battery longevity). While challenges still exist in animal telemetry (including tag cost and data capture, reviewed in Hazen et al. (2012) and Harcourt et al. (2019)), the sheer volume, and application to sea turtle research, is now more robust and reliable than ever before (Hays and Hawkes, 2018). Sophisticated designs in electronic tags now allow for multi-year (e.g., Shillinger et al., 2008; Briscoe et al., 2016a), multi-population (Bailey et al., 2012; Fossette et al., 2014), and multispecies tracking studies (Shimada et al., 2016; Lamont and Iverson 2018; and see Supplemental Bibliography). Time-depth recorders, acoustic transmitters, and animal-borne videos can reveal fine-scale movements and behaviors in relation to foraging ecology and diving behavior (Seminoff et al., 2006; Chevis et al., 2017; Tyson et al., 2017; Hardin and Fuentes, 2021). Equally fascinating, satellite biologgers outfitted with autonomous sensors have transformed animals into physical oceanographers, collecting a suite of environmental variables, especially from regions otherwise difficult to sample (Doi et al., 2019; Harcourt et al., 2019; Bousquet et al., 2020). Most recently, the miniaturization of tagging devices has allowed researchers to follow the earliest portion of the at-sea period, with studies deploying tiny acoustic (Thums et al., 2013; Scott et al. 2014a; Hoover et al., 2017) and solar-powered (Mansfield et al., 2014, 2021) trackers attached to the shells of neonate sea turtles as small as 11cm carapace length during the 'lost years' (Hays and Hawkes, 2018). Once thought impossible, these technologies have provided empirical evidence into every stage in a turtle's life history, fundamentally shifting the paradigm of sea turtle research from land to sea.

Coupling environmental data, ocean physics, and computer simulations to simulate sea turtle movements and strandings

In recent years, the coupling of environmental datasets with sea turtle tracks has played a significant role in understanding oceanic distribution and habitat preferences in relation to a suite of biotic and abiotic processes (e.g., Coles and Musick, 2000; Polovina et al., 2000; Gaspar et al., 2006; Hawkes et al., 2007; and see Supplemental Bibliography). For example, species distribution models (SDMs) are now common tools used to explore mechanistic and correlative linkages between an animal and its environment across a geographic space (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009; Melo-Merino et al., 2020). State-space models allow researchers to estimate biologically relevant parameters with satellite telemetry (Jonsen et al., 2007). Such applications employ a wide range of statistical and machine learning techniques to understand, predict, and manage a species in a changing environment, and there is now a wealth of detailed literature in this field (e.g., Guisan and Thuiller, 2005; Aarts et al., 2008; Robinson et al., 2017). For sea turtles, some examples of habitat characterization include identification of high use areas under contemporary conditions and prey landscapes (e.g., Witt et al., 2007; Fossette et al., 2010; Mencacci et al., 2010), exploration of distributional shifts under changing oceanic and atmospheric conditions (e.g., Saba et al., 2008; Willis-Norton et al., 2015; Patel et al., 2021), and most importantly, serving as mitigation tools for effective conservation and management (Maxwell et al., 2011; Scott et al., 2012; Roe et al., 2014; Howell et al., 2015; Smith et al., 2021).

In addition to using satellite-derived and *in situ* environmental measurements, more sophisticated particle tracking, and numerical models, are now used to simulate the transport and spatial distribution of hatchlings, and subsequently juveniles, in relation to ocean currents. Demographic, behavioral, and observational turtle data can be combined with ocean circulation models to provide transport predictions (forecasts and hindcasts), simulating such scenarios oceanic-stage survival (e.g., Shillinger et al., 2012a; Putman et al., 2013; Chambault et al., 2021), dispersal pathways (Gaspar et al., 2012; Briscoe et al., 2016b; Lalire and Gaspar, 2019; DuBois et al., 2021), and neonate drift experiences that may ultimately drive population dynamics and shape the ontogeny of migratory routes as adults (Hays et al., 2010; Scott et al., 2014b; Ascani et al., 2016; and see Supplemental Bibliography).

Sea turtle stranding events can provide unique opportunities to study drivers of at-sea turtle mortality. Sea turtles that are found injured or ill on beaches, or floating at-sea, are considered 'stranded' and often recorded and necropsied by regional standing networks. Stranding data can provide critical information around potential causes of sea turtle mortality and their spatio-temporal trends (Chaloupka et al., 2008; Casale et al., 2010; Koch et al., 2013; Monteiro et al., 2016). Importantly, new efforts to combine stranding records with oceanographic models can further help illuminate drivers of mortality through a deeper understanding of the oceanic transport of dead sea turtle carcasses (Hart et al., 2006; Santos et al., 2018a; Liu et al., 2019). These approaches simulate the movements of carcasses using methods such as ocean circulation models and virtual particle tracking tools to determine where sea turtles might have been after death, and prior to washing ashore.

In addition to using virtual particle tracking tools, various studies have also used drifter experiments in the field to better parameterize surface movements of floating sea turtle carcasses. Surface drifter experiments, aimed at improving our understanding of carcass drift, have been deployed with different objects such as individually marked oranges (Mancini et al., 2012; Koch et al., 2013), drift bottles (Hart et al., 2006), bucket drifters (Santos et al., 2018b), standard surface drifters (Liu et al., 2019), wooden sea turtle models (Santos et al., 2018b; Cook et al., 2021), and even actual sea turtle carcasses (Santos et al., 2018b; Cook et al., 2021). Studies that have used actual sea turtle carcasses have used both reconstructed sea turtle drifters made from cadavers and insulating foam to ensure positive buoyancy (Santos et al., 2018b), and also intact bloated sea turtle carcasses to allow for the incorporation of natural decomposition and scavenging (Reneker et al., 2018; Cook et al., 2021). Such field research can improve our ability to use oceanographic models to simulate sea turtle carcass drift prior to beached stranding events. Importantly, the ability to backtrack the drift movements of stranded carcasses can allow us to better pinpoint where mortality may have occurred, which can help scientists determine what might have caused this mortality in the first place.

Advanced data collection and computation

Innovations in animal-based telemetry and animal-borne imaging techniques have rapidly advanced our understanding of animal movement and behavior (see Dutton et al. (2019) for examples), but their expense and requisite physical contact can be limiting factors in the data collection process (Hanna et al., 2021). The integration of uncrewed instrumentation, novel computational approaches, and citizen science participation, now offers new ways to collect information, providing alternative, cost-effective, and contactless monitoring and threat assessment, both above and below the water's surface. For example, high-tech advancements in unmanned aerial vehicles (UAVs, commonly known as drones) now provide efficient, cost-effective ways of obtaining population estimates using aerial imagery and photogrammetry (3D models) to collect a suite of information from hard to monitor, free ranging individuals (Varela et al., 2019; Varela and Rees, 2020). In addition to UAVs, the use of submersible cameras and autonomous underwater vehicles have become increasingly common tools to monitor wildlife in the past decade, due to their ability to provide high resolution information and offer an alternative to common in-water and aerial surveys (e.g., boat-based, manned aircraft, or SCUBA and snorkeling surveys) (Rees et al., 2018). Sightings and information provided by citizen-scientists have also enabled researchers to collect constant streams of data in the form of descriptions, web maps, and smartphone 'apps' (Baumbach et al., 2019; Hanna et al., 2021). Together, such forms of data collection have helped to bridge the gap for researchers, especially for hard-to-reach habitats or when individuals are hard to find (Rees et al., 2018). Given their low cost and practicality of use, especially under limited funding, such advanced monitoring platforms have provided new opportunities for remote observation and surveillance. For sea turtles, some applications of these approaches include in-water density and abundance estimates (e.g., Sykora-Bodie et al., 2017; Mello-Fonseca et al., 2021), foraging behavior (Letessier et al., 2014; Patel et al., 2016), courtship and mating interactions (Bevan et al., 2016; Papafitsoros et al., 2022), and uncovering more unique behaviors, such as the use of fish cleaning stations during breeding periods (Schofield et al., 2017).

Another rapidly developing field combines the use of drones with artificial intelligence, for near real-time detection of animals (Varela and Rees, 2020). Computer vision and image recognition techniques such as Convolutional Neural Networks (CNNs), a prominent type of deep learning classifier, have been used to detect and classify sea turtles on land and in water (Badawy and Direkoglu, 2019). Maki et al. (2020) combined drones with CNNs, as a form of tagless tracking of individuals with multibeam sonar imagery, and Gray et al. (2019) used neural networks and drone images to gain population-level insights, detecting and enumerating olive ridley sea turtles (*Lepidochelys olivacea*) in the coastal waters of Ostional, Costa Rica during a mass-nesting event.

Such advanced detection techniques have not only transformed our monitoring and detection capabilities of sea turtles in their marine environment, but they have also enabled the exploration of a wide range of research questions in relation to critical habitat use, behavior, and population-level estimates that have been inherently too difficult to access. Importantly, when paired with other datasets, these approaches can provide a new level of understanding of threats, such as fishing activity. Drones and object-based detection algorithms have been used to reveal sea turtle behavior in relation to fishing gear (Reavis et al., 2021), and to detect fishing vessel interactions (Varela and Rees, 2020) and illegal fishing practices (Zendejas, 2013) for effective enforcement bycatch regulations.

Understanding neonate survival from land to sea

While much of the focus has been on the juvenile and later stages at-sea, methodological advances have also allowed for new and innovative ways to better understand sea turtle behavior during the critical 24 hours after emerging from nests. Known as the frenzy period, newly hatched sea turtles will scramble across the beach and then start their long and dangerous swim to offshore habitats. Hatchlings face several threats throughout these early days, including predation risks on land that depend on how quickly they can run along the exposed beach and safely disappear into the darkness of the oceans. These animals can be disrupted by artificial lighting in urban areas, disorienting them and making their path towards the open sea more challenging. As coastal areas become increasingly urbanized and developed, assessing energy usage during this time of potential disorientation has been important for understanding its impact on animal survival. Survival during the high energy frenzy period can depend on swimming performance. Mortality rate from predation is high during these hours, and one of the factors that hatchlings rely on to evade predators is their speed. Importantly, the additional energy used from crawling unnecessary distances from lighting disorientation can negatively impact their offshore swim and decrease their overall survival rate.

To study energy use, as hatchlings made their way from land to sea, researchers sought to measure oxygen consumption during crawling and swimming phases. In the first study of its kind, Pankaew and Milton (2018) constructed tiny treadmills from modified belt sanders and placed them within airtight respiratory chambers. Hatchlings were placed on the treadmills and monitored throughout their movement and rest periods. These frenzy crawl trials were coupled with swim trials, and energy consumption was calculated during both crawl and swim periods to mimic frenzy period conditions. Videos of these trials can be seen on National Geographic's Youtube[3] channel and Florida Atlantic's Youtube[4] channel. Although the researchers ultimately found that the longer distances during disorientation crawling did not appear to affect swim performance, they note that disorientation can still negatively impact hatchlings by more rapidly depleting the limited energy stores that the animals rely on in the upcoming days. While constructed treadmills have been used in other animal studies (e.g., Rubin and Mickle, 1982), this is the first study of its kind to apply these methods to sea turtles. Coupled with the aforementioned neonate tagging technologies (Mansfield et al., 2021), these studies provide some of the earliest insights into movement and survival at the very outset of their 'lost years' journey.

Development of novel genetic and molecular techniques

At the molecular level, rapid advances in laboratory technology, combined with decreasing per-unit-costs for sample analysis, are opening new avenues for sea turtle research. Samples collected from wild animals (i.e., skin, blood, and bone from recovered caracasses), and even older, historical samples stored in archives, are being used in new, and more widespread ways, to inform conservationists and population managers about stock structure, foraging and nesting habitat connectedness, habitat movement patterns, responses to stressors including fishing, pollution and climate change, and more. The ever-expanding field of genomics - guided by the recently published whole genomes of several sea turtle species - is beginning to illuminate many aspects of sea turtle biology and ecology (e.g., Komoroske et al., 2017; Mayne et al., 2022; Bentley et al., 2023). Further, genetic 'tagging' and chemical 'tracing' techniques are illuminating sea turtle populations and habitat connectedness. For example, genetic and chemical analyses of sea turtle tissues can serve as forensic tracking methodologies to explore foraging dichotomies associated with differential habitat use (McClellan et al., 2010; Zbinden et al., 2011; Ceriani et al., 2012), geographic origin of foragers at the population level (Vander Zanden et al., 2015), ontogenetic recruitment (Turner Tomaszewicz et al., 2016; Ramirez et al., 2019), and habitat use patterns and

3 https://www.youtube.com/watch?v=XtjF5dIedhI
4 https://www.youtube.com/watch?v=itkAuPubbxI&t=19s

residency duration, useful for informing bycatch reduction and prioritizing habitats for conservation (Turner Tomaszewicz et al., 2015; and see Supplemental Bibliography).

Genomic applications for at-sea life stages

Genetic tagging has become a valuable tool for conservation of sea turtles for several reasons, ranging from understanding habitat connectivity between foraging and nesting areas, to establishing phylogeography and stock structure (see full review in Komoroske et al., 2017). Emerging genomic techniques, and the studies that follow, will continue to elucidate the 'how' and 'why' of sea turtles' population ecology (e.g., Shirtika et al., 2022; Bently et al., 2023). Specifically important for turtles in the high seas, genetic analysis informs managers of the origins of sea turtles captured as bycatch during fishing activities. The relatively simple process of collecting skin (or other tissues) from bycaught turtles can reveal which populations and stocks are being most affected by specific fishery types in specific ocean regions, allowing for a more targeted approach for conservation efforts. This is done by first having individual nesting subpopulations characterized by unique haplotypes (mitochondrial DNA, mtDNA) and defining management units (Wallace et al., 2010; Dutton et al., 2014; Komoroske et al., 2017). For example, Stewart et al. (2016) identified source populations for leatherback sea turtles bycaught during pelagic longline fishing throughout the Western North Atlantic. This study used many-to-many mixed-stock analysis to reveal an unexpectedly disproportionate number of leatherbacks from Costa Rica being caught in longline fisheries in the Gulf of Mexico. Ongoing observer and at-sea monitoring in cooperation with fisheries allow for the collection of these samples for genetic analysis, which ultimately helps guide policy for bycatch reduction. A similar approach was also used by Stewart et al. (2019) to conduct mtDNA and mixed stock analysis on samples collected from 850 loggerhead turtles bycaught across the Western North Atlantic over a 14 year period. The study identified which distinct management units of loggerheads were most affected by different fishing efforts and revealed size-structured differences in bycatch rates in distinct spatial regions. Most recently, such applications have been used to address and reduce illegal poaching and trade of products made from protected species, including sea turtles (e.g., hawksbill carapace shell, LaCasella et al., 2021).

Using chemical tracers

As with the explosion in genomic studies, the past decade has seen a great increase in studies utilizing various chemical and biogeochemical tools for ecological, conservation, and management research of sea turtles. Methods include: stable isotope analysis, trace element analysis, contaminant concentrations, and even hormone levels. Stable isotope analysis – both bulk and compound specific amino acids – have been applied on all sea turtle species, to address several biological and conservational questions (Haywood et al., 2019). Analysis of stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) of a variety of sea turtle tissues have been widely applied to study turtle foraging behavior and trophic position (Jones and Seminoff, 2013), connectedness among different habitats (Avens et al., 2021) and populations (Figgener et al., 2019), timing of ontogenetic shifts (Reich et al., 2007) and even inform survivorship as determined by residency time (Turner Tomaszewicz et al., 2017), with many opportunities for future studies (Pearson et al., 2017).

As studies strive to collect and process samples with consistent methods, comparisons among studies are beginning to illuminate not just ocean-basin differences in baseline stable isotope (SI) ratios (Wallace et al., 2006) and sea turtles as region-specific consumers (Seminoff et al., 2012), but also subtle differences in foraging and habitat use of juveniles vs. adults, and foraging behavior, such as specialized foragers in groups that were assumed to be generalists (Vander Zanden et al., 2010). As more studies utilize stable isotope analysis as a powerful tool, the abundant SI data generated makes the creation of large-scale isotope mapping, or 'isoscapes' possible (Graham et al., 2010; McMahon et al., 2013) when care is taken to specify distinct regions being mapped or specific sea turtle populations and tissues being used (Ceriani et al., 2014; Turner Tomaszewicz et al., 2017; Haywood et al., 2020). For example Hatase et al. (2013) identified that North Pacific loggerheads from the same nesting sites had two different foraging behaviors, with smaller turtles foraging in oceanic habitats, and larger turtles feeding in neritic habitats, and that these differences likely affect the fitness and spatial risk of the different groups - an important factor in tracking population abundance trends. Using both bulk and compound specific amino acid analysis of stable nitrogen isotopes, together with satellite telemetry, Seminoff et al. (2012) revealed that the endangered Pacific leatherbacks nesting in Indonesia have split migratory strategies - some remaining in the Western Pacific to forage, while others traversed the entire ocean basin to forage in the Eastern Pacific. The application of biogeochemical analysis to address questions about the ecology and behavior of sea turtles when they are in remote oceanic locations – indeed, where they spend the most of their time – has been especially valuable. Continued studies that build upon lessons learned, and combine different techniques, will be extraordinary in how they further our understanding of the oceanic phases of sea turtles.

A recent example of a study that combined molecular lab techniques (skeletochronology with stable isotope analysis (Turner Tomaszewicz et al., 2017), land-based headstarting and in-water satellite tagging with remotely sensed satellite data (Briscoe et al., 2016a), sample recovery from beach surveys (Peckham et al., 2008), and aerial surveys (Seminoff et al., 2014; Eguchi et al., 2018)), was Briscoe et al. (2021). This hugely collaborative effort pooled together results about North Pacific loggerhead turtles, to propose that the mechanism behind movements between the Central North Pacific and the Eastern Pacific (including bycatch regions near southern California, US, and Baja California, Mexico) may be facilitated by a dynamic thermal corridor between the two ocean regions, the frequency of which may vary with ocean climate (El Nino-La Nina) and anomalous oceanographic conditions (such as the 'blob' and other marine heatwaves), becoming more common (Oliver et al., 2021; Samhouri et al., 2021).

Evolving molecular techniques

The continued expansion of molecular tools like genetic tagging and chemical tracing, will open the door for new combinations of multi-pronged approaches to study sea turtles at sea (and on land). As these tools become more widely applied and novel laboratory techniques advance, continued monitoring and sampling effort will facilitate further understanding of the life history and ecology of sea turtles (and other marine megavertebrates). One example is the utility of combining SI and chemical analysis with hormone analysis to better assess health, nutrition, stress and reproduction (Fleming et al., 2018); estimate population sex-ratios using blood hormones (Jensen et al., 2018); assess stress-related responses to fishery bycatch and cold-stun events (e.g., Hoopes et al., 2000; Hunt et al., 2016); and analyze pollution in distinct habitats using fatty acids, contaminant concentrations, and trace elements (Ramirez et al., 2019; Avens et al., 2021; Shaw et al., 2021).

Another rapidly evolving method that can be used to monitor species is environmental DNA (eDNA), which can be used to detect the presence of animals through the cellular material they deposit (Thomsen and Willerslev, 2015). Species expel DNA into the environment from various sources, such as through the shedding of skin cells, urine, and saliva, which can be sampled and detected using molecular techniques. Emerging eDNA capabilities allow for the non-invasive detection of aquatic organisms through DNA identification in water samples. Eliminating the need to manually capture, collect, or otherwise physically observe live animals to document their presence, eDNA has great potential for use in biodiversity monitoring (Thomsen and Willerslev, 2015). Animal detection and assessments of species distribution is often a critical first step for conservation efforts, and eDNA can be particularly useful for collecting data on endangered species where physical detection can be difficult. The popularity of eDNA as an emerging tool has increased since it was successfully used in 2008 to detect the presence of the invasive American Bullfrog in French wetlands (Ficetola et al., 2008). eDNA techniques have since been used in marine environments, successfully detecting harbor porpoises (Foote et al., 2012), orcas (Baker et al., 2018), and sharks (Boussarie et al., 2018).

A limited number of studies have applied eDNA to aquatic reptiles (Roussel et al., 2015), and only in recent years have eDNA methods been studied in sea turtles. Kelly et al. (2014a) used eDNA to detect the presence of green sea turtles (*Chelonia mydas*) within a mesocosm community, although the study site was a non-natural tank environment. Harper et al. (2020) used the technique to successfully track greens in a Californian estuary, demonstrating the potential to use these methods to assess sea turtle presence in the wild, without animal capture. The ability to use eDNA to detect organisms directly from the environment can fundamentally transform ecological monitoring and management. eDNA can replace labor intensive and time-consuming conventional methods, to assess species richness and abundance more rapidly, as well as on a much wider and more comprehensive scale (Deiner et al., 2017). In the case of endangered species, such as sea turtles, the ability to conduct cost-efficient and non-invasive biodiversity assessments through eDNA can allow for improved estimates of species distribution and facilitate targeted policy and management efforts (Kelly et al., 2014b; Thomsen and Willerslev, 2015).

Understanding at-sea threats and applications for conservation

Plastic ingestion threats

From viral videos of a sea turtle with a straw wedged up its nose (Robinson et al., 2015) to provocative images of decomposing carcasses with stomachs full of trash, attention on the impacts of pollution on the marine environment, and its effects on sea turtles (Santos and Crowder, 2021), has grown in recent years. Hazardous debris can include parts of fishing gear, such as nets, lines, and ropes, as well as anthropogenic items including plastic bags, tar, styrofoam, and glass. These materials can entangle sea turtles, preventing them from diving to feed or surfacing to breathe. Sea turtles may also ingest debris, which can obstruct their throats or accumulate and affect their digestive systems.

Sea turtles around the world have been noted to ingest plastic debris (Schuyler et al., 2014). Globally, more than half of all sea turtles have been estimated to have ingested plastics, although rates can vary among regions and species (Schuyler et al., 2016). Plastic debris has been found ingested by sea turtles of all life stages, from post-hatchlings to adults (Witherington, 2002; Digka et al., 2020). Oceanic-stage turtles are among those most at-risk to plastic debris ingestion, with the highest regions of risk including the east coasts of the USA, Australia, and South Africa, as well as within waters of the East Indian Ocean, and Southeast Asia (Schuyler et al., 2016). In a study of stranded sea turtles in Australia, Schuyler et al. (2012) found that benthic sea turtles have a stronger selection for clear, soft plastic, while pelagic turtles were less selective but tended to consume more rubber items, such as balloons (Schuyler et al., 2012). Ingestion may also vary by feeding preferences; carnivorous sea turtles have been found to be less likely to ingest debris compared to herbivores and omnivores (Schuyler et al., 2014; Rizzi et al., 2019).

Plastic debris ingestion can have both sublethal and lethal impacts on sea turtles (McCauley and Bjorndal, 1999). Higher concentrations of ingested plastic have been linked to higher probability of mortality, with Wilcox et al. (2018) reporting that 14 pieces of plastic in a sea turtle's gut leads to a 50% probability of mortality. Santos et al. (2015) found that less than one gram of ingested debris can kill juvenile turtles. Even when not lethal, ingested debris may impact sea turtles in other ways, such as reducing swimming capacity, or making turtles more susceptible to bycatch. Sublethal effects of debris ingestion include reduced nutrient gains through dietary dilution (McCauley and Bjorndal, 1999).

Land-based plastics have been found to account for most ingested debris found within sea turtles (Schuyler et al., 2014) and other marine animals (Boerger et al., 2010; Codina-García et al., 2013; De Stephanis et al., 2013). With over 4-12 million tons of plastic estimated to enter the oceans each year (Jambeck et al., 2015), and this significantly increasing (Ostle et al., 2019), plastic pollution is a critical problem that is not going away anytime soon. Better understanding its impacts on sea turtles and their habitats, as well as large-scale solutions to minimize plastic discharge into marine environments, will be important avenues for future research.

Bycatch threats and reduction technologies

Fisheries bycatch is one of the most significant threats to sea turtles around the world (Spotila et al., 2000; Wallace et al., 2013; Lewison et al., 2014; Patel et al., 2021). Accidental engagement in fishing gear, known as bycatch, kills thousands of sea turtles every year (Lewison et al., 2004; Finkbeiner et al., 2011). Various bycatch reduction technologies have been developed to limit the impact of fishing activity on sea turtles. Most efforts have focused on the use of turtle excluder devices in trawl nets (Crowder et al., 1994; Jenkins, 2012) and circle hooks in longlines (Gilman et al., 2006; Pacheco et al., 2011), but more recently gear modifications have been developed for gillnets. Gillnets are used in coastal waters worldwide and engagement in gillnets can be a large source of mortality for sea turtles (Gilman et al., 2010), yet bycatch reduction strategies have been difficult to develop (Žydelis et al., 2013).

Studies suggest that visual cues may be one promising avenue that can be used to alleviate gillnet entanglement with various bycaught species, including sea turtles (Martin and Crawford, 2015). Sea turtles rely on visual cues when foraging (Constantino and Salmon, 2003), and thus illuminating gillnets may be one way to alert the animals of their presence. Equipping gillnets with light-emitting diodes (LEDs) or chemical lightsticks have both been shown to reduce the number of sea turtle and gillnet interactions, without negatively impacting overall catch rates of the target species (Wang et al., 2010; Bielli et al., 2020; Senko et al., 2022). Importantly, other commonly bycaught species, such as seabirds and marine mammals, also rely strongly on visual cues (Schakner and Blumstein, 2013; Martin and Crawford, 2015). Therefore, there is potential for net illumination to be used as a multi-taxa bycatch reduction tool, with species-specific conservation benefits beyond just sea turtles. In addition, researchers are currently building and assessing the use of solar-powered LEDs, which will help reduce battery cost and waste as well as provide a more environmentally friendly option (Senko et al., 2020).

Decision-support tools and dynamic management approaches

With a greater understanding of critical habitats and oceanic movements, efforts to mitigate overlap between fisheries activities and sea turtles is a significant priority. But a key challenge to fisheries management is understanding and planning for species interactions in a dynamic environment (Lewison et al., 2015; Maxwell et al., 2015). This is especially true for highly migratory sea turtles that exploit multiple oceanic habitats across global boundaries.

New approaches to ocean management have begun to incorporate the shifting nature of the ocean, its users, and its inhabitants based on the integration of new biological, environmental, or socioeconomic conditions in near real time (Maxwell et al., 2015; Hazen et al., 2018). 'Dynamic management' approaches are reviewed in detail by Hazen et al. (Chapter 13) and demonstrate great potential as fully operational, data-driven decision-support tools for bycatch avoidance and marine resource management in ways that traditional static spatial management objectives may fall short. For example, TurtleWatch[5] is a tool derived from sea turtle-temperature affinities and uses up-to-date information about the location of thermal habitat to reduce interactions between U.S. Hawaii longline fishers, and sea turtles (Howell et al., 2008; Howell et al., 2015).

Multispecies tools such as EcoCast[6] provide daily predictions to fishers for both target (swordfish, *Xiphias gladius*) and non-target species (leatherback sea turtles, *Dermochelys coriacea*, California sea lions, *Zalophus*

5 https://www.fisheries.noaa.gov/resource/map/turtlewatch
6 https://coastwatch.pfeg.noaa.gov/ecocast/about.html

californianus, and blue sharks, *Prionace glauca*) (Hazen et al., 2018; Welch et al., 2019a) along the U.S. West Coast. Given that species-environment associations predictably change over daily, seasonal, and interannual scales, these tools allow decision-makers to frequently and automatically adjust management approaches in near-real time. However, the built-in flexibility also ensures that these tools are capable of delivering proactive, climate-ready solutions, as species-environment relationships change or break down, and as new threats emerge under anomalous environmental conditions (e.g., NOAA's TOTAL[7] tool, Welch et al. (2019b); also see Hazen et al. (Chapter 13), 2018; Hobday et al., 2018).[8]

Climate impacts and a changing ocean

Warming oceanic temperatures and more frequent marine heat waves are expected to cause unprecedented challenges for marine species (McHenry et al., 2019). As a wide-ranging species that is both circumglobally distributed and highly susceptible to environmental variability (Wallace et al., 2010), the impact of climate change is a forefront issue that touches every age and stage of their life cycle (see Patrício et al., 2021).

An emerging volume of research has observed and predicted impacts of climate change on sea turtles, although for practical and accessibility reasons, most of these studies have focused on the terrestrial life history phase (Witt et al., 2010; Patrício et al., 2021). From these extraordinary efforts, we now understand the direct and indirect effects of climate variables, particularly those associated with air, sand, and ocean temperatures, increased rainfall and storm intensity, and sea level rise, on sex ratios, hatchling success and morphology, nesting phenology and habitat, and reproductive success, to name a few (Hawkes et al., 2009; Poloczanska et al., 2009; Witt et al., 2010; Saba et al., 2012; Patel et al., 2021; Patrício et al., 2021). These studies provide more detailed reviews of impacts than we can cover in this chapter, with key insights by species, habitat, geographical region, and threat, highlighting key priorities for future research and management, and emphasizing the critical gaps that remain in our ability to fully understand the impacts experienced at-sea. Optimal temperature ranges are known to vary among species, but warming temperatures and changing ocean circulation patterns are projected to induce shifts in at-sea movements and distributions, with implications across ontogenetic stages and habitats (Poloczanska et al., 2009; Patrício et al., 2021). Climate-forced changes to productivity and prey availability may shift, altering species' habitat, distribution, reproductive patterns, growth rates, and recruitment (Poloczanska et al., 2009; Ascani et al., 2016; Stubbs et al., 2020). More frequent bouts of anomalous environmental conditions may influence migratory corridors and habitat connectivity, leading to the development of ecological bridges or barriers, connecting or disconnecting animals to preferred habitats under varying ocean conditions (Briscoe et al., 2017). Such changes (whether temporary or permanent) will have lasting effects on population management.

Lesser studied but equally important concerns include resilience against infectious diseases and pathogens, as it is unknown how such stressors may be altered in a warming environment (Harvell et al., 2009; Tracy et al., 2019). The full breadth and depth of climate-related threats are yet to be understood, and despite significant technological and analytical advances, there is still a great need for information across this cryptic at-sea stage. With varying degrees of vulnerability, adaptability, and life history characteristics, resilience to climate change and other stressors (human and environmental) may be easier for some populations than others, but all will require dynamic approaches to successfully manage for the future (Maxwell et al., 2020). Marine turtles have weathered 120 million years and multiple climate change events, but never at such an unprecedented rate of change (IPCC, 2021; Patrício et al., 2021). As global environmental conditions are expected to become more extreme, the implications are significant. Understanding the opportunities for mitigation and intervention on land and at sea is an essential element to the conservation of these charismatic species.

7 https://coastwatch.pfeg.noaa.gov/loggerheads/
8 https://coastwatch.pfeg.noaa.gov/loggerheads/

Limitations

The utilization of these novel methodologies has enabled us to effectively navigate numerous conservation and management challenges inherent to the at-sea stage (Robinson et al., 2023), however there remain several limitations. Although advancement of tagging technologies have allowed for a deeper understanding of the movements and behavior of marine turtles (see Godley et al., 2008; Hays, 2008; Hart and Hyrenbach, 2009; Hussey et al., 2015; Hays and Hawkes, 2018) data gaps still remain, given that most tracking technologies are unable to span the length of life history stages (Hazen et al., 2012; Shillinger et al., 2012b). Logistical challenges and limited access to sea turtles at-sea tends to hinder research efforts of life history characteristics during these life stages, in comparison to when they are in nearshore environments (Hamann et al., 2010). The issue of data availability and data sharing remains a pervasive limitation, given the importance of continued and improved conservation and monitoring efforts (Jeffers and Godley, 2016; Mazaris et al., 2017; Wildermann et al., 2018; Hays et al., 2019; Godley et al., 2020). This is especially true when only a small proportion of animals tend to be tracked, often representing only a fraction of the whole population (Hays and Hawkes, 2018). Although research interest in sea turtles has increased substantially over time (Hamann et al., 2010; Rees et al., 2016), some sea turtle populations tend to be more well-studied than others. In particular, there is a highlighted need to increase scientific understanding on immature leatherback and hawksbill populations, as well as studies on all marine turtle species across the Indian, South Pacific, and South Atlantic Oceans (Wildermann et al., 2018).

Efforts to advance sea turtle knowledge can also be impacted by limited support. Lack of resources, including funding, has been identified as a significant individual barrier hindering research in this field, particularly for experts working in the Atlantic and Mediterranean regions (Wildermann et al., 2018). This is especially true with some of the more advanced technologies and techniques (e.g., equipment, data accessibility and storage, and analytical expertise), which require expendable budgets and specific skill sets. For example, satellite tracking data remains very expensive and difficult to obtain (Hays and Hawkes, 2018), and complex analyses in machine learning and artificial intelligence require a specific level of expertise. There should be targeted attempts to extend access to such technologies and methodologies, distributing resources to the less well funded nations and regions. In instances where data is limited, local ecological knowledge (LEK) can be used to uncover historical trends (Beaudreau and Levin, 2014; Lee et al., 2019) and document baseline data that cannot be acquired solely through natural science methods (Mukherjee et al., 2018; Mason et al., 2019). LEK has been used to produce data to better understand the population trends of Eastern Pacific greens (Early-Capistrán et al., 2020) as well as to support the identification of sea turtle nesting beaches in Panama (Flores et al., 2021). Active and meaningful integration of LEK alongside Western methods of scientific research can facilitate a more holistic view of sea turtle biology. It can also aid in ensuring management decisions are attuned to the cultural and socioeconomic needs of the local communities that sea turtles belong to, maximizing conservation benefits for both humans and animals alike.

Conclusions

In a changing ocean, the utilization of diverse approaches to species conservation in marine management is essential. For many marine species, including sea turtles, transformative advances in technology and monitoring capabilities have bolstered our ability to observe, learn, and protect individuals and their habitats. In this chapter, we reviewed new and emerging research directions that have deepened our ability to study sea turtles during their critical at-sea phases. The studies cited in this chapter are by no means exhaustive, but serve as examples of the rapid pace of scientific discovery in sea turtle biology and conservation. Here, we highlight how several advancements, including innovative approaches in animal telemetry, genetic and molecular technologies, automated data collection, and computation modeling, have been used to address some knowledge gaps in sea turtle habitat, movement, and behavior at sea. In addition to studying sea turtle behavior and movement, these tools also can be used to inform the development of conservation and management approaches. Despite some of the challenges and limitations that still exist with studying these elusive animals, these applications have provided promising new directions for the long-term sustainability of sea turtle populations around the globe.

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Innovations: Advancements in Technology & Monitoring Capabilities

Tagging technology and biologging capabilities

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