SPECIAL FEATURE

WHAT'S HOLDING BACK the Leatherback?

By Bryan P. Wallace

We've all heard many words to describe *Dermochelys coriacea*. Superlative. Ancient. Enormous. Beautiful. I'll add another one that I think describes them well: weird. They have weird physiology: They can stay warm in frigid waters and avoid overheating in tropical waters, and they can dive more than a kilometer (3,280 feet) deep. We don't really know what they do down there. They lay weird eggs that are not even eggs—shelled albumen gobs containing no yolk that serve no apparent purpose (and we've looked for one). They have weird semi-bony shells. They grow to huge sizes, and they thermoregulate and migrate across ocean basins while eating *only jellyfish*, for goodness' sake! What if we have underestimated their weirdness when trying to assess and understand their population status?

Lots of Data, but Little Clarity

If we don't know where we are and where we've been, it's hard to know where we might be going. This is true for many things, including the status of sea turtle populations, and especially for the status of leatherback populations. Decades of effort by hundreds of researchers and volunteers on nesting beaches, in the water, and even via satellite-relayed movements and oceanographic conditions, have yielded mountains of data about sea turtles and how they live.

Yet despite all the knowledge we have gained, we're still unable to understand the leatherback population trends we see or understand why we haven't seen recovery after decades of conservation effort. In part, this paradox is rooted in a history of assessing leatherback status in ways that are fraught with inconsistencies. Flawed assumptions about how to go from a snapshot in time and space to a full global picture, which beaches to include, and more have confounded efforts to get a complete picture about how leatherbacks are doing. On multiple occasions,

AT LEFT: A Leatherback sea turtle feeds on a pyrosome off the Azores in the North Atlantic Ocean. © Brian Skerry; **PREVIOUS SPREAD:** A leatherback hatchling swims away from shore after leaving the beach. After decades of research, there are still many unanswered questions about the leatherback's conservation status. © Ben J. Hicks / benjhicks.com researchers have sounded the alarm that leatherbacks are in decline, but each time uncertainties have remained about the underlying dynamics of the situation and about what those dynamics might mean for the future.

The Challenge of Understanding the Past

Nearly 30 years ago, in 1996, Jim Spotila and coauthors asked the question "Are leatherbacks going extinct?" After they compiled data, rough estimates, and personal communications from researchers around the world, their analysis indicated that several populations were indeed declining, especially those in the Pacific Ocean, and that global leatherback abundance had declined from 115,000 to 34,500 adult females. A few years later, in 2000, the IUCN Marine Turtle Specialist Group concluded in a Red List assessment that the global leatherback population deserved critically endangered status, a listing that was again largely driven by the rapidly declining East Pacific and peninsular Malaysia populations. In fact, by the early 2000s, the once large leatherback population in Terengganu, Malaysia, was extinct. Seems pretty bad, right?

As with any trend, however, its accuracy depends on the source information. Both the Spotila et al. and Red List assessments used a baseline population estimate of 115,000 adult female leatherbacks worldwide, published in 1982 by Peter Pritchard—more than *80,000* of which were in the eastern Pacific alone. This 1982 estimate was itself an enormous increase over a much more modest population estimate by the same author in 1971 of 29,000–40,000 females globally, with approximately 8,000 in the eastern Pacific. This massive change was based on a two-day aerial survey that was of leatherback nesting in three Mexican states and was undertaken in 1980, which stimulated a vast extrapolation of existing (largely anecdotal) nesting abundance values, many of which had been conveyed to authors personally and without information about monitoring effort.

Until recently, this type of reporting—personal communications, second-hand information, and a lack of consistent monitoring or data analysis underpinning back-of-envelope calculations—was the norm. The Spotila et al. paper and the Red List assessment had simply adopted the 115,000 number because it was the best available science at the time. However, several researchers have noted that Pritchard's numbers are almost certainly overestimates for the reasons mentioned previously. Further, no estimates before or since have landed global leatherback numbers in the same order of magnitude as Pritchard's 1982 tally, even as more and more beaches have been included with improved monitoring, reporting, and collaboration over time. So does this mean that leatherbacks were *not* actually declining toward extinction globally?

Status Improves—or Does It?

Since those days, we've learned much more about leatherbacks and gained data from significant beaches in parts of the world that had been overlooked or unmonitored when the early assessments were done. In 2013, the leatherback status on the Red List was updated by evaluating nesting turtle abundance data through 2010 from many of the same places included in Spotila et al.'s paper, plus many more locations. This updated Red List assessment confirmed the critically endangered status of the West and East Pacific leatherback subpopulations (also called *regional management units*, or RMUs) while highlighting that the Northwest Atlantic RMU was abundant and stable, if not increasing. Further, the Southeast Atlantic RMU appeared to be at least as abundant—though with an undetermined trend—as the Northwest Atlantic RMU. But with the apparently robust Northwest Atlantic RMU included, the global status looked better than it had two decades prior. The global Red List assessment improved from critically endangered in 2000 to vulnerable in 2013. Finally, some good news!

Some apparent improvements in status were due to differences in which rookeries were included in the various analyses. For example, Pritchard's aerial survey–based estimates of global population size did not include the large rookeries of Trinidad and Tobago in the Wider Caribbean Region nor Gabon on the West African coast, and Spotila et al.'s estimates of those rookeries were far lower than those used in the updated Red List assessment. In fact, in his first global assessment in 1971, Pritchard mentioned that only one or two leatherbacks nested nightly in northeastern Trinidad, and Spotila reported about 200 females per year in 1996, whereas now it's normal to see hundreds *per night* during the peak nesting season. Similarly, while Pritchard asserted in 1971 that "a moderate amount of nesting" probably occurred in West Africa, by 1996, Spotila reported fewer than 5,000 females per year there. But by 2010, estimates of leatherback abundance were an order of magnitude higher.

Maybe leatherbacks really had increased in several places—and globally. Even after one accounted for discrepancies among different assessments, it seemed that things might be looking up for leatherbacks in some places and that there were more leatherbacks in the world than we had previously known. Those findings also gave much-needed hope for a brighter future in places where leatherbacks had declined and not yet recovered, such as the eastern Pacific.

More Populations in Decline

Just a few years after the updated 2013 Red List assessment was published, nervous whispers that leatherbacks actually might be in *decline* in parts of the Wider Caribbean rose to a chorus of concern, prompting a regional analysis of nest abundance trends, with data through 2017 amassed by the Wider Caribbean Sea Turtle Conservation Network. This analysis showed that annual numbers of leatherback nests had dropped on almost every nesting beach examined, producing a regionwide negative trend that accelerated in the most recent decade analyzed. For example, leatherback abundance in French Guiana—considered for decades to be robust and stable—had declined from tens of thousands of nests per year in the 1990s to a few hundred per year by 2017. The Red List status for the Northwest Atlantic RMU was updated with those new data in 2019, changing the status from least concern to endangered.

To make matters worse, soon after this Northwest Atlantic status update, a new global assessment of leatherback status delivered more bad news. In a comprehensive evaluation of abundance and trends from all leatherback RMUs through the year 2020, the U.S. National Oceanic and Atmospheric Administration biological review team confirmed the dire status of the Pacific RMUs and the Northwest Atlantic RMU. The team also revealed that the Southeast Atlantic RMU—thought to be the most abundant on the planet just 10 years earlier—was actually in decline. Other RMUs (Southwest Indian Ocean, Southwest Atlantic Ocean) are relatively small and geographically restricted, making them susceptible to declines as well, if the right threats were to come along.

Leatherbacks Are Weirdly Unique and Uniquely at Risk

Today, looking back on all the status assessments since the 1970s and accounting for their associated caveats, the global leatherback population trend does indeed appear to be downward. So maybe it's time to ask the question posed by earlier researchers: Are leatherbacks going extinct? Like, for real this time?

To be clear, I consider myself an optimistic realist about sea turtle status. I tend to think that the extinction of any species—particularly at a global scale—is highly unlikely. After all, sea turtles survived the asteroid that took out most of life on Earth (including their non-avian dinosaur cousins), not to mention shifting continents and climate ups and downs over millennia. And despite everything we've thrown at them in the past few centuries—and it has been a *lot*—sea turtle populations seem to be hanging on everywhere and even bouncing back in some places. The drumbeat of good news for sea turtles appears to be getting louder, a testament to the incredible conservation efforts performed by so many people in so many places. To me, the trends underscore turtles' resilience in the face of adversity, especially with sustained help from humans. Slow and steady just might win the race after all.

But leatherbacks do not seem to show the same resilience as other sea turtle species, at least not in the past five decades. Why are they doing so poorly? When are they going to recover? *Are* they going to recover? Threats to leatherback survival have been well-documented in many places. Chief among them have been human consumption of eggs and meat and incidental mortality in fishing gear. But something else might be compounding the negative effects of high mortality and low recruitment. Something else might be holding back the leatherback.

Perhaps that something is heightened sensitivity of the species to fluctuations in the marine environments the turtles depend on to survive and thrive. Like those of all animals, leatherback populations are driven by environmental ups and downs. Research in the early 2000s showed that eastern Pacific leatherbacks encountered much less predictable, much less favorable oceanographic conditions than did their Northwest Atlantic counterparts, making them smaller and more vulnerable to threats (see *SWOT Report*, vol. IV, pp. 8–11). This change caused divergent population trajectories between the two RMUs. Might the same one-two punch of poor ocean conditions and threats now be knocking down the Northwest Atlantic and other RMUs as well? Maybe we have underestimated the unique—and uniquely weird—sensitivity of the species to environmental conditions.

A leatherback takes a deep breath while nesting at Grande Riviere on the northern coast of Trinidad. © Tui De Roy / Roving Tortoise Photos

Digging further into available data might provide some clues. Mark-recapture analyses of flipper tags and microchips on individual leatherbacks can reveal how long leatherbacks take to return to beaches between nesting seasons and can shed light on the probability that leatherbacks survive from one season to the next. In declining populations like Pacific Mexico, Pacific Costa Rica, and French Guiana, adult female survival rates (lower than 80 percent per year) are indeed much lower than they should be for long-lived vertebrate populations with stable trends (typically above 90 percent per year), thereby pointing to high adult mortality. However, those analyses have also revealed an interesting and often overlooked phenomenon: the surprising prevalence of so-called *transient turtles*—turtles that are tagged in one season and then never seen again.

Transients are common in animal population biology and are usually explained as individuals that are merely "passing through" a study area, rather than long-term residents. However, given robust coverage of leatherback nesting in most regions, the proportion of these one-and-done nesters is much higher than expected in multiple populations. For example, of roughly 8,000 turtles tagged across 30 years in Mexico and Costa Rica, perhaps 30 percent were tagged in one season and never seen again, and adult female survival probability was quite low—less than 80 percent per year. Similarly, in French Guiana, the high number of one-and-done turtles strongly influenced survival rates, which were also less than 80 percent per year.

Why would there be so many transients, and how might this be a clue to what is happening with leatherback populations globally? Let's assume that a turtle receiving her first tags at a long-term monitoring project is a newly reproductive adult. Given what we know about sea turtles' site fidelity, we should expect to see her again in another nesting season. So, if she does not return, it is possible that she has been unable to find the food resources she needs to remigrate and reproduce. Perhaps this just means that she needs a prolonged remigration interval to gather what she needs. Maybe some turtles are swimming around for 10 years or more trying to accumulate enough fat stores to make the return trip. In fact, this is exactly what researchers in Australia have observed in green turtles tagged on nesting beaches and recaptured in foraging areas without being resighted on beaches over prolonged periods.

Or maybe the cost of being a reproductive adult is just harder on the neophytes. It's a huge physiological shift from being a juvenile to actually "adulting," which for a leatherback requires migrating across oceans to make and lay 30 kilograms of eggs each nesting season. This shift is particularly costly if neophytes haven't honed their foraging and migration skills like older, more experienced turtles. Maybe this physiological cost is simply too high for many new adults, resulting in proportionally higher mortality in this age class compared to older remigrants.

The large number of one-and-done leatherbacks across multiple populations suggests that, in general, leatherbacks might just be more sensitive to environmental conditions than we appreciate. For example, according to tag return data, female leatherbacks in French Guiana are expected to reproduce no more than three times in their entire lives. Normal sea turtle life history assumes reproduction occurs every few years over multiple decades to compensate for high mortality of eggs, hatchlings, and juveniles. In comparison, the oddly brief reproductive lifespan of leatherbacks makes them more like salmon than sea turtles.

The possibility of environmental sensitivity becomes more intriguing when we look beyond the data from recent monitoring programs. For example, elder residents in communities of Pacific Costa Rica have recounted how, in the 1960s, very few leatherbacks were on the very beaches that by the 1980s were crawling with so many turtles that locals referred to these behemoths as "ants." Colleagues in Mexico confirmed that elders there recalled similar patterns—not many leatherbacks in the 1960s, but tons by the 1980s.

What if the historical absence (or comparatively low abundance) of rookeries we now know to be highly abundant (for instance, Trinidad and Gabon) suggests that those patterns also occurred elsewhere in the world? The smaller numbers of leatherbacks were probably not due to human threats; it seems that there simply were not many leatherbacks around at the time of the early global assessments. Perhaps presciently, Pritchard wrote in 1971 that "there is no evidence that present numbers are yet substantially reduced from primordial, equilibrium population levels." Is it possible that historical leatherback abundance has fluctuated over time, often without *human* intervention?

A Future for Leatherbacks

Despite all our data—and all our supposed knowledge of how populations work—perhaps the forces truly driving leatherback population dynamics or limiting their recovery are mainly environmental in nature. This hypothesis contends that the rapid increase in leatherback numbers in the 1970s and 1980s in the eastern Pacific (perhaps later in other regions) would have been due to long-term cycles in environmental conditions that favored leatherback growth, recruitment, survival, and reproductive output for a period.

On the flip side, when times get tough, leatherback fecundity might be significantly depressed, slowing population growth and making them less resilient to threats. Maybe this boom and bust cycle characterizes leatherback population dynamics over long time periods and perhaps more so than other sea turtle species. Of course, human-caused mortality from commercial egg harvesting and fisheries bycatch is sufficient to reduce turtle numbers on its own, regardless of environmental conditions. But if unsustainably high mortality is coupled with unfavorable environments, this is a recipe for disaster for leatherbacks.

But there is a positive side to this paradigm: With effective threat reduction and favorable environmental conditions, leatherbacks *should* recover eventually. Their numbers apparently increased on their own many decades ago, and they have contracted and expanded globally with the wax and wane of glaciers over geological time. Though there isn't much we can do to produce more reliable food sources for leatherbacks, there is a *lot* we can do to bolster resilience in leatherback populations through effective conservation efforts.

Fortunately, people are rising to the challenges by reorganizing and redoubling efforts to reduce threats that leatherback populations currently face. In the eastern Pacific, the Eastern Pacific Leatherback Conservation Network (*Red Laúd OPO* in Spanish) is coordinating and supporting members' efforts everywhere they need to happen, whether on beaches or on boats or in conference rooms. In the Wider Caribbean, a hot-off-the-press regional action plan developed by key actors across the region highlights priority actions that must be implemented to promote leatherback recovery. And a tri-national plan involving Indonesia, Papua New Guinea, and Solomon Islands is in place to promote West Pacific leatherback conservation. There are many comparable examples in other parts of the world.

Good conservation is a long, hard slog that involves long-term collaborations among multiple stakeholders to implement the best possible interventions. And we have lots of examples of effective, long-term conservation providing positive results for sea turtles. Despite all the bad news, our conservation efforts will work in the long run—especially when Mother Nature lends her hand by providing leatherback-friendly ocean conditions. This is not the first time people have thought leatherbacks were headed toward extinction, and each time, there was more to the story. This time will be no exception.

So let's keep slogging. •

SWOT FEATURE MAPS

Welcome to Planet Leatherback

By Bryan P. Wallace, Helen Bailey, Scott R. Benson, Kara Dodge, Peter H. Dutton, Karen L. Eckert, Sabrina Fossette, Michael C. James, Milagros López-Mendilaharsu, Nathan J. Robinson, Kartik Shanker, George L. Shillinger, Adhith Swaminathan, Manjula Tiwari, and Matthew Witt

The first *SWOT Report* maps in 2006 showed the global distribution of leatherback nesting, but they did not attempt to draw lines around the species' distribution across our blue planet. So what more can nearly 20 years of additional data—including hundreds of satellite tracks and tens of thousands of nests counted—tell us? As you'll see in the

A leatherback dives in the clear waters of Maluku, Indonesia. Leatherbacks inhabit vast oceanic ranges—more so than any other turtle species—as evident in the maps on pp. 27–29. © Jason Isley / Scubazoo updated maps in the pages of this 18th volume of *SWOT Report* (pp. 27–29), the more beaches we walk and the more turtles we tag and track, the more we see that leatherbacks really are ... everywhere.

In fact, instead of describing where leatherbacks are, perhaps it is more appropriate to ask where they *aren't*. We've got just the map for that: the funky, Antarctica-focused telemetry map on p. 27 provides a novel perspective of the world's one big, interconnected ocean that is centered around the one place that leatherbacks are apparently absent. The South Pole seems to be encircled in an anti-leatherback force field, successfully repelling any attempt by these otherwise intrepid explorers. Similarly, a leatherback-free zone fringes the frigid waters ringing the North Pole. Although their ability to stay warm in cold waters while chowing down on jellyfish is well known, even mighty leatherbacks cannot withstand icy polar seas.

Apart from those gaps, leatherbacks are truly circumglobal—more so than any other sea turtle species. Leatherbacks regularly travel back and forth between the tropics and subpolar latitudes, connecting distant ocean areas in a way very few species ever have in Earth's history. For example, nearly 100 leatherbacks tracked from Papua Barat, Indonesia, and the U.S. West Coast over the past couple of decades show epic trans-Pacific migrations between breeding areas in warm near-equatorial waters in the west and feeding areas in the cold, foggy California Current in the east, several thousand miles apart. Meanwhile, other turtles from this nesting population take different paths into the South China Sea, to oceanic convergence areas north of Hawaii, and even as far afield as Tasmania and New Zealand. Overall, the North Pacific Ocean in the maps on pp. 27–29 seems to feature more cells that have hosted leatherback action at some point than empty blue spaces.

In the South Atlantic, movements of leatherbacks from three different regional management units (RMUs, see pp. 12–15) connect the South American and African continents, stretching like chewing gum between what was once a single landmass in the southern hemisphere. Leatherbacks in the Northwest Atlantic are known to use the entire basin—from the Caribbean to Newfoundland to Mauritania to the Mediterranean—moving from bloom to bloom of ephemeral jellyfish prey like waterborne butterflies foraging among flower patches in the summer.

Recent data from the Indian Ocean provide a new flavor of the well-established leatherback recipe for long-distance movements connecting far-reaching corners of ocean basins. Instead of all following a shared trajectory, leatherbacks leaving nesting areas in the Andaman Islands in the northeastern Indian Ocean initially travel south and spread out in two directions—mainly southwest toward the eastern coast of Africa and southeast toward the northwestern coast of Australia and the Timor Sea—providing a near mirror image of the diverse navigations of West Pacific turtles from Indonesia, Papua New Guinea, and the Solomon Islands.

Although leatherback movement data paint with a broad brush across the blue ocean canvas, they paint thinly. Compared with other species, leatherbacks lack obvious hotspots where many of them tend to hang out. Most grid cells across the ocean have at least a few leatherback locations, but very few cells have high concentrations of location data—with a few notable exceptions near nesting beaches and places like New England, U.S.A., and Nova Scotia, Canada. Eastern Pacific leatherbacks represent this pattern well. More than 50 turtles tracked from nesting beaches in Mexico and Costa Rica over two decades showed a persistent migration stretching southwest through the Galápagos Islands before fanning out in the southeastern Pacific, their migratory corridor dissolving into the open ocean. Tracks from large juveniles and adults tagged in feeding areas off the coasts of Peru and Mexico have shown similar divergence.

Mapped telemetry data help us visualize where turtles go so that we can whittle down the vast expanse of Planet Ocean to, theoretically, more manageable areas of importance for turtles. With our surreptitiously attached our trackers, turtles themselves unwittingly disclose to us where they are in the world with each connection between transmitter and satellite. Using the rich but imperfect information we obtain through these spy games, we become *Dermochelys* detectives, trying to unravel mysteries about leatherback behaviors and hangouts we rarely—if ever—see for ourselves.

But as much as we've learned about leatherback movements and habitat use thanks to the bewildering evolution of remote tracking technology, we grudgingly recognize that these fancy tools provide only brief and biased snapshots of what turtles really do and—most importantly—why they do these things. Transmitters typically last a few months, with best-case scenarios pushing a year or slightly more; yet improvements in design and miniaturization are enabling the tracking of smaller turtles, even yearling juveniles. In addition, the majority of data shown in the maps on pp. 27–29 and described in the data citations on pp. 52–53 (which does not reflect all the global tracking data for this species) come from adult females leaving their nesting beaches in search of food in far-off waters. The movements of males, smaller juveniles, and hatchlings remain largely invisible to our lens, although genetic and oceanographic modeling tools have begun to shed some light on these missing pieces. Perhaps a more complete map that accounted for those caveats would leave no patch of open ocean between the Arctic and Antarctic untouched by a leatherback flipper.

Though leatherbacks dare to swim in waters inhospitable to their cheloniid cousins, their nesting sites are still constrained to low latitudes where favorable nest conditions exist, just like those of other sea turtles. As recently as a decade ago, the Northwest and Southeast Atlantic leatherback RMUs appeared to be abundant and stable, buoying hope for leatherbacks globally amid consistently bad news from the West and East Pacific RMUs.

Although there are fewer leatherbacks now than when we started counting, the good news is that leatherbacks are persisting almost everywhere, and our increased understanding of how they move through the oceans makes us better equipped to protect them. However, most leatherback populations are not increasing in abundance, and few are sufficiently large to withstand significant threats. So wherever we work, let's keep discovering and sharing details about where leatherbacks are and what they're doing there. If we do, the version of the leatherback map that one day appears in *SWOT Report*, volume XXXVIII, will provide an improved and hopeful view of Planet Leatherback. ●

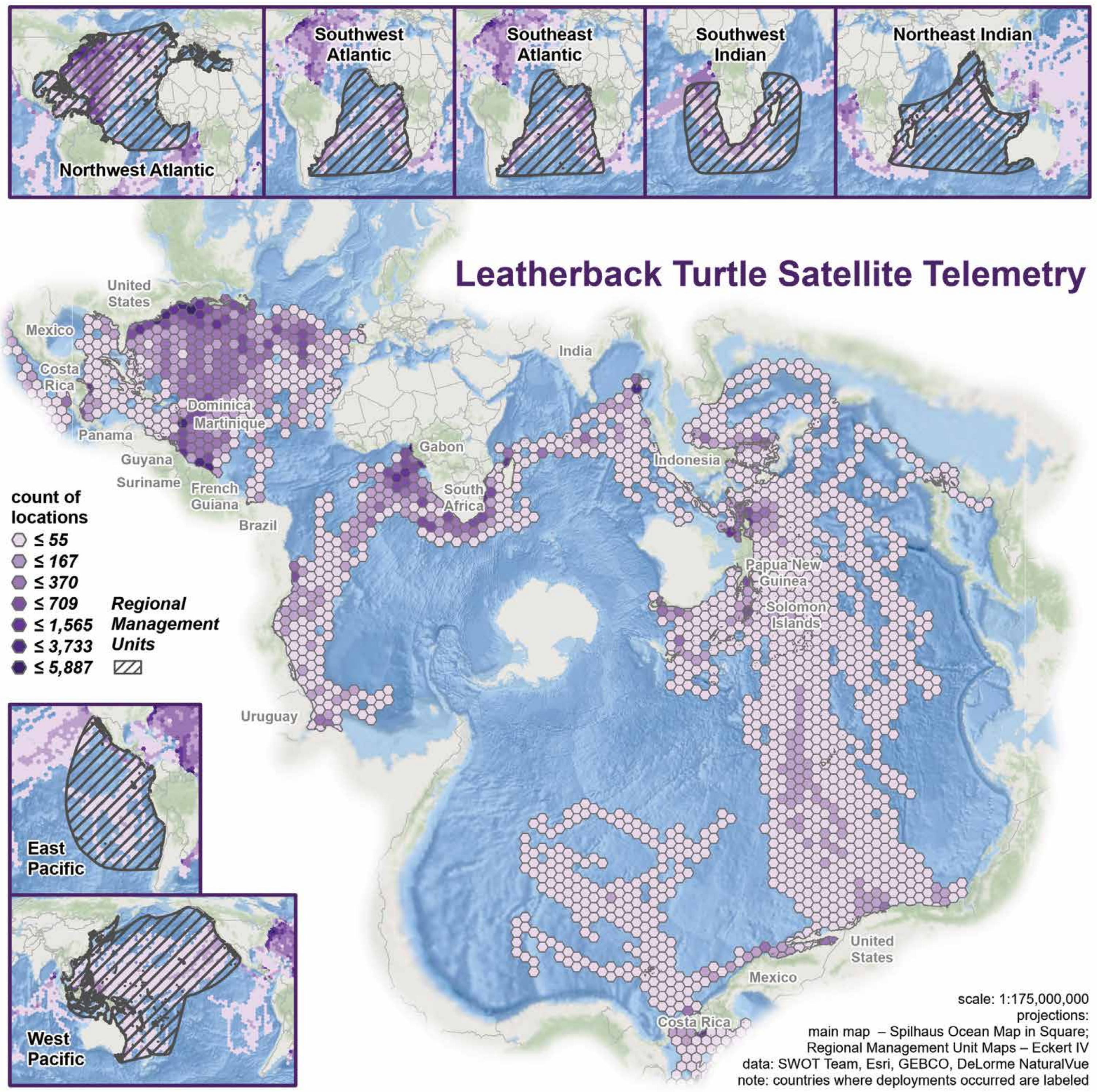
GLOBAL BIOGEOGRAPHY OF LEATHERBACK SEA TURTLES

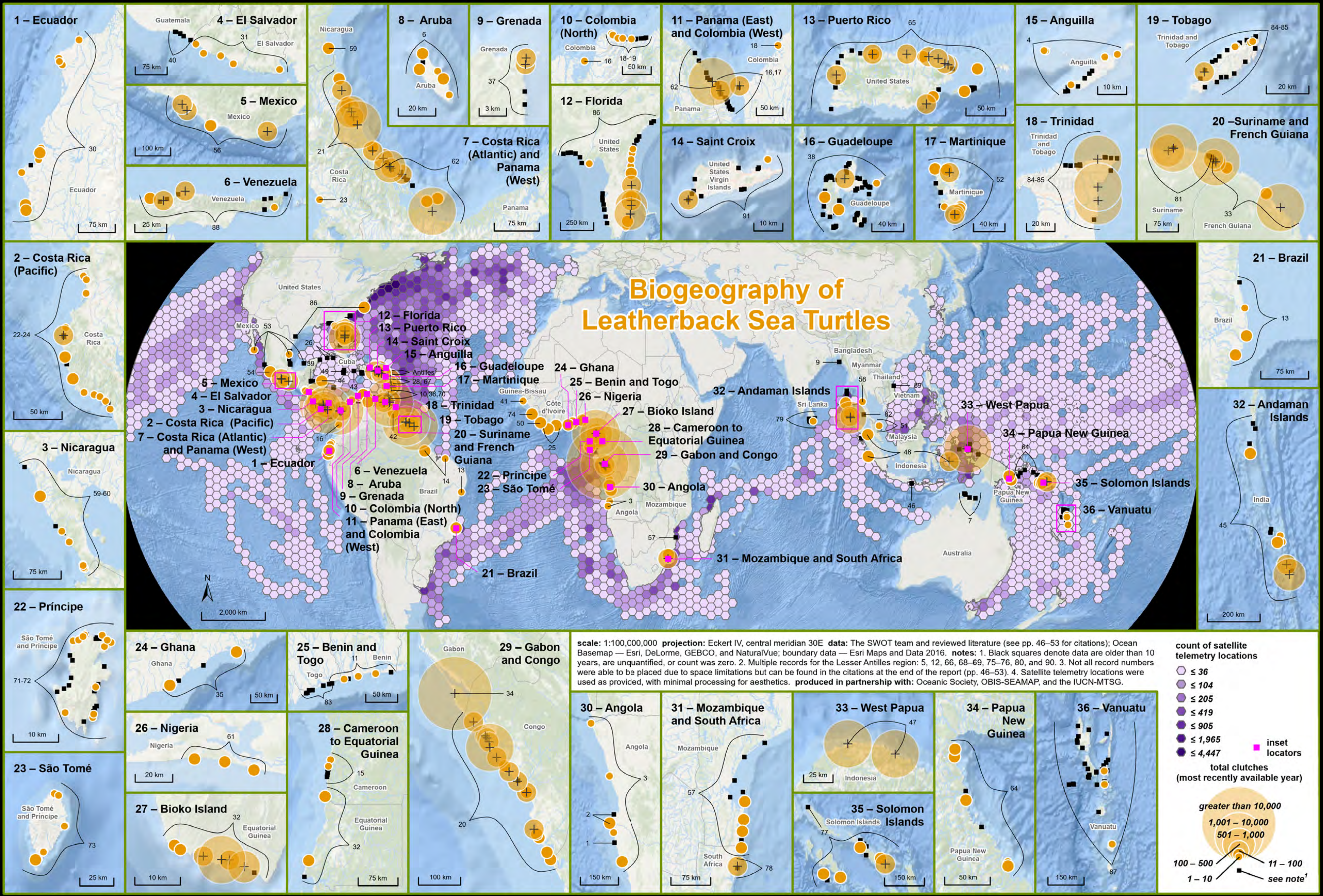
The maps below and on pp. 28–29 display available nesting and satellite telemetry data for leatherback sea turtles. The data include 988 nesting sites and 321 satellite tags, compiled through a literature review and provided directly to SWOT by data contributors worldwide. For metadata and information about data sources, see the data citations on pp. 46–53.

Nesting sites are represented by orange dots scaled according to their relative nesting abundance in the most recent year for which data are available. Black squares represent nesting sites for which data are older than 10 years, data are unquantified, or the nest count for the most recent year was given as zero. For the purposes of uniformity, all types of nesting counts (e.g., number of nesting females, number of crawls) were converted to number of clutches as needed. Conversion factors ranged from 4.1 to 6.4 clutches per female and 0.75 to 0.9 crawls per clutch.

Satellite telemetry data are represented as polygons that are colored according to the number of locations within each hexagon. Darker colors represent a higher number of locations, which can indicate that a high number of tracked turtles were present in that location or that turtles spent a lot of time in that location. Telemetry data are displayed as given by the providers, with minimal processing to remove locations on land and visual outliers, and represent almost 150,000 animal locations. Some tracks are raw Argos or GPS locations, whereas others have been more extensively filtered or modeled.

We are grateful to all of the data contributors and projects that participated in this effort. For details, please see the complete data citations on pp. 46–53.





scale: 1:100,000,000 **projection:** Eckert IV, central meridian 30E **data:** The SWOT team and reviewed literature (see pp. 46–53 for citations); Ocean Basemap — Esri, DeLorme, GEBCO, and NaturalVue; boundary data — Esri Maps and Data 2016. **notes:** 1. Black squares denote data are older than 10 years, are unquantified, or count was zero. 2. Multiple records for the Lesser Antilles region: 5, 12, 66, 68–69, 75–76, 80, and 90. 3. Not all record numbers were able to be placed due to space limitations but can be found in the citations at the end of the report (pp. 46–53). 4. Satellite telemetry locations were used as provided, with minimal processing for aesthetics. **produced in partnership with:** Oceanic Society, OBIS-SEAMAP, and the IUCN-MTSG.