Genetic Tools for Sea Turtle Conservation

By Michael P. Jensen, F. Alberto Abreu-Grobois, Brian M. Shamblin, Kelly R. Stewart, Erin L. LaCasella, Nancy N. FitzSimmons, and Peter H. Dutton

> n tropical and subtropical beaches around the world, female sea turtles have come ashore to lay their eggs for millennia. When the young turtles scurry

down the beach to the ocean, they carry their parents' DNA. If they survive to adulthood, the females return to the same spot to lay their eggs in a process known as natal homing, which was first hypothesized by Archie Carr in 1967. As a result, females nesting in the same region are genetically similar to one another and dissimilar to those in other regions.

Over the past 30 years, genetic tools have helped researchers to understand how sea turtle populations are connected across time and space and have further taught us that the precision of natal homing varies among species and regions. Researchers are learning how demographic, behavioral, and environmental forces shape gene flow among rookeries, plus the implications this information has for identifying appropriate population units for conservation purposes. Rapid advances in genomic technologies and analytic methods have given scientists a means to differentiate among genetically distinct sea turtle groups at increasingly finer scales.

Defining Management Units

Sea turtles have complex life histories; they are long-lived and take decades to reach sexual maturity. Throughout their lives, they occupy widely dispersed oceanic and coastal areas as their ecological needs change. Young turtles from the same nesting beach may end up in distant foraging areas, and foraging areas may host a mix of turtles from widely dispersed rookeries. Addressing such complexity for successful conservation and management is challenging because individual populations need to be identified, evaluated, and monitored across all life stages and habitats. Tagging and satellite telemetry partially address those challenges but can be impractical. Genetics therefore plays a vital role in obtaining reliable, detailed information about sea turtle population structure and behavior.

Natal homing behavior promotes the differentiation of DNA between rookeries, which can help to define genetic stocks or management units (MUs). The MUs are based on significant differences in the distribution of mitochondrial variants (haplotypes) inherited from the mothers or from nuclear DNA (nDNA) alleles inherited from both parents. MUs represent the appropriate scale for monitoring changes in population abundance and assessing threats because individuals lost in one MU are unlikely to be replaced by individuals from another MU. Therefore, the first step in informing effective management decisions is to determine which rookeries to consider as part of a single breeding population and which to consider as separate populations.

A 1992 landmark study led by Brian Bowen provided the first global view of the genetic variation in sea turtles; since then, our understanding of population structure for all sea turtle species has improved enormously. For green turtles, researchers have advanced from 14 MUs in 1992 to more than 76 MUs today (see map on p. 20). Early studies suggested that rookeries less than 500 km (311 mi) apart were not genetically distinct, but more comprehensive sampling continues to reveal more complex patterns of female natal homing and dispersal. We now know that genetic diversity and population structure can vary greatly between species and regions and at unexpectedly fine scales, such as between hawksbill rookeries on either side of Barbados (a distance of 30 km or 19 mi) or green turtle rookeries on opposite sides of a single Florida inlet!

At the same time, olive ridleys nesting in arribadas at Ostional, Costa Rica, are indistinguishable from those nesting at Escobilla, Mexico, more than 1,300 km (808 mi) away. Widespread leatherback turtles are characterized by low genetic diversity globally, and they have fewer rookeries than other marine turtle species. Green turtles, meanwhile, are one of the most globally abundant and widespread of all sea turtles, which is reflected in more MUs (76 and counting) and greater genetic diversity.

A genetic marker is a DNA sequence with a known physical location on the genome. Our use of novel genetic markers improves how well we can detect population structure. Thirty years ago, the first studies about genetic structure in sea turtles used expensive restriction enzymes to cut mitochondrial DNA (mtDNA) and to define haplotypes that were based on gel band patterns, although much of the genetic variation remained hidden. This effort improved with sequencing technology in the late 1970s but was still difficult and expensive; the generation of even short stretches of sequences (approximately 400 base

pairs [bp] at first) was a reason to celebrate! This approach later expanded to approximately 800 bp of the mtDNA control region. More recent work found variation in a hypervariable repeat segment inside the control region that revealed a population structure among Mediterranean green turtle rookeries that was undetectable before.

Now, with sequencing of the entire mitogenome (16,000 bp), a variation that subdivides control region-defined haplotypes into additional variants can be seen. We now know, for instance, that Caribbean green turtles with the 400 bp haplotype CM-A5 represent at least 30 different female family lines, thereby providing even more power for the fine-scale definition of nesting populations.

Making Connections

Once the genetic signature of rookeries has been characterized, the data can be used to determine the origins of turtles sampled far away from the nesting beaches in migratory routes or foraging areas or from live or dead animals impacted by humans. For example, studies show that loggerheads encountered as fishery bycatch in the North Pacific and in foraging grounds off the coast of Baja California, Mexico, all originate from rookeries in Japan. Research on green turtles foraging at Australia's Great Barrier Reef has been used to show how recruitment of juvenile turtles into foraging areas has changed over time and how the changes can be directly linked to reduced hatching success at Raine Island.

Monitoring: Collaborations Are Key

Knowing what proportion of turtles from different MUs is present in shared habitats is vital for conservation planning, because the mortalities in such areas may affect several distant MUs. The power of genetic tools and methods depends on how well sea turtle monitoring can fulfill two key criteria: (a) sampling all or most of the MUs found in shared habitats and (b) ensuring the accuracy of all MU definitions. Such knowledge underscores the importance of continued genetic sampling of all sea turtles wherever they occur, a task that requires global-scale collaboration among a multitude of partners.

Data for several key nesting populations are currently unavailable, too old, or limited by small sample sizes, thereby preventing reliable assessments of MU boundaries. As more laboratories embark on their own sea turtle research, all researchers must strive to work together to develop the highest levels of technical capacity, to create standardized methods, to share research protocols and priorities, and to identify funding so that we can ensure that the most critical conservation challenges are being addressed.

Most importantly, networks among experts must continue to thrive in order to encourage data sharing and to support global marine turtle management and protection efforts. An excellent example of one such network is the Asia–Pacific Marine Turtle Genetics Working Group, which convenes dozens of researchers from across that vast region through frequent workshops and other networking opportunities to enhance in-country capacity for marine turtle genetic studies.



A researcher draws a blood sample from a flatback turtle on Curtis Island, Queensland, Australia. Tools for genetic analysis have both advanced and become vastly cheaper in recent years, making detailed genetic studies much more feasible than before. © Doug Perrine

Ensuring the Future of Stock Identification

Genetic research has come a long way since the cumbersome days of restriction fragment length polymorphism or radioactive staining of microsatellite loci! Only 20 years ago, sequencing the sea turtle genome would have taken 13 years and cost US\$300 million. Today, a complete genome costs as little as US\$1,000 and can be sequenced in a single day on a machine that fits in the palm of a hand. As genetic tools become more affordable, the capacity of researchers to do detailed studies is no longer restricted to a few well-funded laboratories. Highquality reference genomes have been published for green and leatherback turtles (see *SWOT Report*, vol. XVI, pp. 12–13); genomes for all other sea turtle species are expected to be completed within the next two years. Those advances will usher in a new era of whole-genome sequencing and the development of inexpensive assays that will democratize the use of genomics for sea turtle biology and conservation. It will allow us to vastly refine our understanding of sea turtle boundaries and the impacts of threats and to focus sea turtle conservation efforts in targeted ways that were impossible in the not-too-distant past. •

Global Management Units for Sea Turtles

The following maps display global nesting sites and known management units (MUs) for each sea turtle species based on mitochondrial DNA. Individual nesting sites with available genetic information are shown with colored symbols; sites that belong to the same MU share a color. Given the large number of MUs globally, colors may repeat both within and between species maps. Management units can be explored in detail at the SWOT Online Map application (http://seamap.env.duke.edu/swot). Sites that have been sampled but not yet assigned to an existing stock are colored gray. Data for the maps were sourced from the SWOT team and reviewed literature; for complete citations see pp. 53–54.



Loggerhead turtle management units. Of 805 documented nesting sites, 62 rookeries have been genetically sampled, and 26 MUs have been identified. Undersampled regions include the Northeast Indian Ocean.



Green turtle management units. Of 1,568 documented nesting sites, 164 rookeries have been genetically sampled, and 76 MUs have been identified. Undersampled regions include parts of Southeast Asia, the Red Sea, the Northeast Indian Ocean, East Africa, and the East Pacific.



Leatherback turtle management units. Of 889 documented nesting sites, 26 rookeries have been genetically sampled, and nine MUs have been identified. Undersampled regions include parts of Southeast Asia.



Hawksbill turtle management units. Of 1,650 documented nesting sites, 72 rookeries have been genetically sampled, and 30 MUs have been identified. Undersampled regions include West Africa, the Red Sea, the North Indian Ocean, Southeast Asia, and the Southwest Pacific.



Olive ridley turtle management units. Of 494 documented nesting sites, 33 rookeries have been genetically sampled, and 17 MUs have been identified. Undersampled regions include the northeast coast of South America, West India, Pakistan, and Southeast Asia.



Kemp's ridley turtle management units. Of 67 documented nesting sites, nine rookeries have been genetically sampled, and one MU has been identified. Undersampled regions include the Southern Gulf of Mexico.

Legend

Base maps: Ocean Basemap—Esri, DeLorme, GEBCO, and NaturalVue Projection: Eckert IV

Produced in partnership with: Oceanic Society, OBIS-SEAMAP, and the IUCN-MTSG

Flatback turtle management units. Of 225 documented nesting sites, 17 rookeries have been genetically sampled, and seven MUs have been identified. Undersampled regions include Northeast Arnhem Land, Australia.

unsampled sites

- stocks
- Caretta caretta
- Chelonia mydas
- ▲ Dermochelys coriacea
- Eretmochelys imbricata
- + Lepidochelys kempii
- Lepidochelys olivacea
- * Natator depressus

Global Management Units for Sea Turtles Data Citations

The following data sources were used to create the maps of "Global Management Units for Sea Turtles" on pp. 20-21.

LEATHERBACKS

Carreras, C., B. J. Godley, Y. M. León, L. A. Hawkes, et al. 2013. Contextualising the last survivors: Population structure of marine turtles in the Dominican Republic. *PloS ONE* 8 (6): e66037.

Dutton, P. H., B. W. Bowen, D. W. Owens, A. R. Barragan, and S. K. Davis. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *Journal of Zoology* 248 (3): 397–409.

Dutton, P. H., C. Hitipeuw, M. Zein, S. R. Benson, and S. M. Al-Ghais. 2007. Status and genetic structure of nesting populations of leatherback turtles (*Dermochelys coriacea*) in the western Pacific. *Chelonian Conservation and Biology* 6 (1): 47–53.

Dutton, P. H., S. E. Roden, K. R. Stewart, E. LaCasella, et al. 2013. Population stock structure of leatherback turtles (*Dermochelys coriacea*) in the Atlantic revealed using mtDNA and microsatellite markers. *Conservation Genetics* 14 (3): 625–636.

Maslim, A. F., and N. P. Zamani. 2016. Leatherback turtle (*Dermochelys coriacea*) populations in Sumatra: Genetic diversity and connectivity pattern. *Aquaculture*, *Aquarium*, *Conservation and Legislation* 9 (2): 276–283.

Molfetti, É., S. T. Vilaça, J.-Y. Georges, V. Plot, et al. 2013. Recent demographic history and present fine-scale structure in the Northwest Atlantic leatherback (*Dermochelys coriacea*) turtle population. *PLoS ONE* 8 (3): e58061.

Vargas, S. M., F. C. F. Araújo, D. S. Monteiro, S. C. Estima, et al. 2008. Genetic diversity and origin of leatherback turtles (*Dermochelys coriacea*) from the Brazilian coast. *Journal of Heredity* 99 (2): 215–220.

Vargas, S. M., L. S. F. Lins, É. Molfetti, S. Y. W. Ho, et al. 2019. Revisiting the genetic diversity and population structure of the critically endangered leatherback turtles in the South-West Atlantic Ocean: Insights for species conservation. *Journal of the Marine Biological Association of the United Kingdom* 99 (1): 31–41.

FLATBACKS

FitzSimmons, N. N., S. D. Pittard, N. McIntyre, M. P. Jensen, et al. 2020. Phylogeography, genetic stocks, and conservation implications for an Australian endemic marine turtle. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30 (3): 440–460.

HAWKSBILLS

Arantes, L. S., S. M. Vargas, and F. R. dos Santos. 2020. Global phylogeography of the critically endangered hawksbill turtle (*Eretmochelys imbricata*). *Genetics and Molecular Biology* 43 (2): e20190264.

Bass, A. L. 1999. Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the Wider Caribbean: A review and re-analysis. *Chelonian Conservation and Biology* 3 (2): 195–99.

Bass, A. L., D. A. Good, K. A. Bjorndal, J. I. Richardson, et al. 1996. Testing models of female reproductive migratory behavior and population structure in the Caribbean hawksbill turtle, *Eretmochelys imbricata*, with mtDNA sequences. *Molecular Ecology* 5 (3): 321–328.

Bowen, B. W., W. S. Grant, Z. Hillis-Starr, D. J. Shaver, et al. 2007. Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* 16 (1): 49–60. Browne, D. C., J. A. Horrocks, and F. A. Abreu-Grobois. 2010. Population subdivision in hawksbill turtles nesting on Barbados, West Indies, determined from mitochondrial DNA control region sequences. *Conservation Genetics* 11 (4), 1541–1546.

Carreras, C., B. J. Godley, Y. M. León, L. A. Hawkes, et al. 2013. Contextualising the last survivors: Population structure of marine turtles in the Dominican Republic. *PloS ONE* 8 (6): e66037.

Cazabon-Mannette, M., D. Browne, N. Austin, A. Hailey, and J. Horrocks. 2016. Genetic structure of the hawksbill turtle rookery and foraging aggregation in Tobago, West Indies. *Journal of Experimental Marine Biology and Ecology* 485: 94–101.

Díaz-Fernández, R., T. Okayama, T. Uchiyama, E. Carrillo, et al. 1999. Genetic sourcing for the hawksbill turtle, *Eretmochelys imbricata*, in the northern Caribbean region. *Chelonian Conservation and Biology* 3 (2): 296–300.

Gaos, A. R., E. L. LaCasella, L. Kurpita, G. H. Balazs, et al. 2020. Hawaiian hawksbills: A distinct and isolated nesting colony in the central North Pacific Ocean revealed by mitochondrial DNA. *Conservation Genetics* 21 (4): 771–783.

Gaos, A. R., R. L. Lewison, M. J. Liles, V. Gadea, et al. 2016. Hawksbill turtle terra incognita: Conservation genetics of eastern Pacific rookeries. *Ecology and Evolution* 6 (4): 1251–1264.

Hill, J. E., C. M. King, K. R. Stewart, F. V. Paladino, and P. H. Dutton. 2018. Genetic differentiation of hawksbill turtle rookeries on St. Croix, U.S. Virgin Islands. *Chelonian Conservation and Biology* 17 (2): 303–308.

Labastida-Estrada, E., S. Machkour-M'Rabet, P. Díaz-Jaimes, J. R. Cedeño-Vázquez, and Y. Hénaut. 2019. Genetic structure, origin, and connectivity between nesting and foraging areas of hawksbill turtles of the Yucatán Peninsula: A study for conservation and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29 (2): 211–222.

LeRoux, R. A., P. H. Dutton, F. A. Abreu-Grobois, C. J. Lagueux, et al. 2012. Re-examination of population structure and phylogeography of hawksbill turtles in the Wider Caribbean using longer mtDNA sequences. *Journal of Heredity* 103 (6): 806–820.

Levasseur, K. E., S. P. Stapleton, M. C. Fuller, and J. M. Quattro. 2019. Exceptionally high natal homing precision in hawksbill sea turtles to insular rookeries of the Caribbean. *Marine Ecology Progress Series* 620: 155–171.

Monzón-Argüello, C., N. S. Loureiro, C. Delgado, A. Marco, et al. 2011. Príncipe Island hawksbills: Genetic isolation of an eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology* 407 (2): 345–354.

Nishizawa, H., J. Joseph, and Y. K. Chong. 2016. Spatio-temporal patterns of mitochondrial DNA variation in hawksbill turtles (*Eretmochelys imbricata*) in Southeast Asia. Journal of Experimental Marine Biology and Ecology 474: 164–170.

Tabib, M., H. Zolgharnein, M. Mohammadi, M. A. Salari-Aliabadi, et al. 2011. mtDNA Variation of the critically endangered hawksbill turtle (*Eretmochelys imbricata*) nesting on Iranian islands of the Persian Gulf. *Genetics* and Molecular Research 10: 1499–1503.

Trujillo-Arias, N., D. F. Amorocho Llanos, D. López-Alvarez, and L. M. Mejía-Ladino. 2014. Phylogeographic relations of some feeding and nesting of hawksbill turtle rookeries (*Eretmochelys imbricata*) in the Caribbean and Pacific of Colombia. *Bulletin of* Marine and Coastal Research 43 (1): 159–182.

Vargas, S. M., M. P. Jensen, S. Y. W. Ho, A. Mobaraki, et al. 2016. Phylogeography, genetic diversity, and management units of hawksbill turtles in the Indo-Pacific. *Journal of Heredity* 107 (3): 199–213.

Vélez-Zuazo, X., W. D. Ramos, R. P. van Dam, C. E. Díez, et al. 2008. Dispersal, recruitment, and migratory behaviour in a hawksbill sea turtle aggregation. *Molecular Ecology* 17 (3): 839–853.

Vilaça, S. T., P. Lara-Ruiz, M. A. Marcovaldi, L. S. Soares, and F. R. Santos. 2013. Population origin and historical demography in hawksbill (*Eretmochelys imbricata*) feeding and nesting aggregates from Brazil. *Journal of Experimental Marine Biology and Ecology* 446: 334–344.

OLIVE RIDLEYS

Adnyana, W., M. Jayaratha, H. N. Purwanasari, I. N. Wandia, et al. 2020. Post-nesting migration and mitochondrial DNA structures of olive ridley turtles (*Lepidochelys olivacea*) nested on beaches of the Bird's Head of Papua and the Lesser Sunda Regions, Indonesia. *International Journal of Scientific and Research Publications* 10 (7): 809–817.

Bowen, B. W., A. M. Clark, F. A. Abreu-Grobois, A. Chaves, et al. 1998. Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica* 101: 179–189.

Briseño–Dueñas, R., 1998. Variación genética en la región control del ADN mitocondrial de poblaciones de la tortuga golfina (*Lepidochelys olivacea*) en el Pacífico oriental y las implicaciones para su conservación. Master's thesis, Facultad de Ciencias del Mar, Universidad Autónoma de Sinaloa.

Campista León, S., J. A. Beltrán Espinoza, I. Sosa Cornejo, H. Castillo Ureta, et al. 2019. Haplotypic characterization of the olive ridley turtle (*Lepidochelys olivacea*) in northwest Mexico: The northernmost limit of its distribution. *Animal Biodiversity and Conservation* 42 (1): 113–126.

Ferrera, A., A. Formia, C. Ciofi, C. Natali, et al. 2021. Genetic structure of olive ridley sea turtles (*Lepidochelys olivacea*) in Ghana, West Africa. *Journal of Experimental Marine Biology and Ecology* 544: 151614.

Jensen, M. P., C. J. Limpus, S. D. Whiting, M. Guinea, et al. 2013. Defining olive ridley turtle *Lepidochelys olivacea* management units in Australia and assessing the potential impact of mortality in ghost nets. *Endangered Species Research* 21: 241–253.

López-Castro, M. C., and A. Rocha-Olivares. 2005. The panmixia paradigm of eastern Pacific olive ridley turtles revised: Consequences for their conservation and evolutionary biology. *Molecular Ecology* 14 (11): 3325–3334.

Madduppa, H., S. Bahri, A. Taufik, A. T. Ghozali, et al. 2021. Population genetic structure of olive ridley (*Lepidochelys olivacea*) across Indonesian archipelago revealed by mitochondrial DNA: Implication for management. *Regional Studies in Marine Science* 41: 101600.

Plot, V., B. de Thoisy, S. Blanc, L. Kelle, et al. 2012. Reproductive synchrony in a recovering bottlenecked sea turtle population. *Journal of Animal Ecology* 81 (2): 1–11.

Reis, E. C., L. S. Soares, and G. Lôbo-Hajdu. 2009. Evidence of olive ridley mitochondrial genome introgression into loggerhead turtle rookeries of Sergipe, Brazil. *Conservation Genetics* 11 (4): 1587–1591. Rodríguez-Zárate, C. J., A. Rocha-Olivares, and L. B. Beheregaray. 2013. Genetic signature of a recent metapopulation bottleneck in the olive ridley turtle (*Lepidochelys olivacea*) after intensive commercial exploitation in Mexico. *Biological Conservation* 168: 10–18.

Rodríguez-Zárate, C. J., J. Sandoval-Castillo, E. van Sebille, R. G. Keane, et al. 2018. Isolation by environment in the highly mobile olive ridley turtle (*Lepidochelys olivacea*) in the eastern Pacific. *Proceedings of the Royal Society B: Biological Sciences* 285 (1878): 20180264.

Shanker, K., J. Ramadevi, B. C. Choudhury, L. Singh, and R. K. Aggarwal. 2004. Phylogeography of olive ridley turtles (*Lepidochelys olivacea*) on the east coast of India: Implications for conservation theory. *Molecular Ecology* 13: 1899–1909.

Silver-Gorges, I., J. Koval, C. J. Rodríguez-Zárate, F. V. Paladino, and M. Jordan. 2020. Large-scale connectivity, cryptic population structure, and relatedness in eastern Pacific olive ridley sea turtles (*Lepidochelys olivacea*). *Ecology and Evolution* 10 (16): 8688–8704.

Stelfox, M., A. Burian, K. Shanker, A. F. Rees, et al. 2020. Tracing the origin of olive ridley turtles entangled in ghost nets in the Maldives: A phylogeographic assessment of populations at risk. *Biological Conservation* 245: 108499.

KEMP'S RIDLEYS

Frandsen, H. R., D. F. Figueroa, and J. A. George. 2020. Mitochondrial genomes and genetic structure of the Kemp's ridley sea turtle (*Lepidochelys kempii*). *Ecology and Evolution* 10 (1): 249–262.

Frey, A., P. H. Dutton, D. J. Shaver, J. S. Walker, and C. Rubio. 2014. Kemp's ridley *Lepidochelys kempii* nesting abundance in Texas, USA: A novel approach using genetics to improve population census. *Endangered Species Research* 23: 63–71.

Lamont, M. M., N. Moreno, F. Y. Camacho Sánchez, H. H. Acosta Sánchez, et al. 2021. Genetic diversity of immature Kemp's ridley (*Lepidochelys kempii*) sea turtles from the Northern Gulf of Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31 (10): 3003–3010.

GREEN TURTLES

Al-Mohanna, S. Y., A. Y. Al-Zaidan, and P. George. 2014. Green turtles (*Chelonia mydas*) of the northwestern Arabian Gulf, Kuwait: The need for conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 24 (2): 166–178.

Álvarez-Varas, R., N. Rojas-Hernández, M. Heidemeyer, C. Riginos, et al. 2021. Green, yellow, or black? Genetic differentiation and adaptation signatures in a highly migratory marine turtle. *Proceedings of the Royal Society B: Biological Sciences* 288 (1954): 20210754.

Anastácio, R., C. Santos, C. Lopes, H. Moreira, et al. 2014. Reproductive biology and genetic diversity of the green turtle (*Chelonia mydas*) in Vamizi Island, Mozambique. *SpringerPlus* 3: 1–16.

Bagda, E., F. Bardakci, and O. Türkozan. 2012. Lower genetic structuring in mitochondrial DNA than nuclear DNA among the nesting colonies of green turtles (*Chelonia mydas*) in the Mediterranean. *Biochemical Systematics and Ecology* 43: 192–199.

Bjorndal, K. A., A. B. Bolten, L. Moreira, C. Bellini, and M. A. Marcovaldi. 2006. Population structure and diversity of Brazilian green turtle rookeries based on mitochondrial DNA sequences. *Chelonian Conservation and Biology* 5 (2): 262–268. Bjorndal, K. A., A. B. Bolten, and S. Troëng. 2005. Population structure and genetic diversity in green turtles nesting at Tortuguero, Costa Rica, based on mitochondrial DNA control region sequences. *Marine Biology* 147 (6): 1449–1457.

Bourjea, J., S. Lapègue, L. Gagnevin, D. Broderick, et al. 2007. Phylogeography of the green yurtle, *Chelonia mydas*, in the Southwest Indian Ocean. *Molecular Ecology* 16 (1): 175–186.

Bourjea, J., J. A. Mortimer, J. Garnier, G. Okemwa, et al. 2015. Population structure enhances perspectives on regional management of the western Indian Ocean green turtle. *Conservation Genetics* 16 (5): 1069–1083.

Bowen, B. W., A. B. Meylan, J. P. Ross, C. J. Limpus, et al. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution*: 46 (4): 865–881.

Bradshaw, P. J., A. C. Broderick, C. Carreras, W. Fuller, et al. 2018. Defining conservation units with enhanced molecular tools to reveal fine scale structuring among Mediterranean green turtle rookeries. *Biological Conservation* 222: 253–260.

Chassin-Noria, O., F. A. Abreu-Grobois, P. H. Dutton, and K. Oyama. 2004. Conservation genetics of the East Pacific green turtle (*Chelonia mydas*) in Michoacán, Mexico. *Genetica* 121: 195–206.

Cheng, I.-J., P. H. Dutton, C.-L. Chen, H.-C. Chen, et al. 2008. Comparison of the genetics and nesting ecology of two green turtle rookeries. *Journal of Zoology* 276 (4): 375–384.

Dethmers, K. E. M., D. Broderick, C. Moritz, N. N. FitzSimmons, et al. 2006. The genetic structure of Australasian green turtles (*Chelonia mydas*): Exploring the geographical scale of genetic exchange. *Molecular Ecology* 15 (13): 3931–3946.

Dutton, P. H., M. P. Jensen, A. Frey, E. LaCasella, et al. 2014. Population structure and phylogeography reveal pathways of colonization by a migratory marine reptile (*Chelonia mydas*) in the central and eastern Pacific. *Ecology and Evolution* 4 (22): 4317–4331.

Dutton, P. H., M. P. Jensen, K. Frutchey, A. Frey, et al. 2014. Genetic stock structure of green turtle (*Chelonia mydas*) nesting populations across the Pacific Islands. *Pacific Science* 68 (4): 451–464.

Encalada, S. E., P. N. Lahanas, K. A. Bjorndal, A. B. Bolten, et al. 1996. Phylogeography and population structure of the Atlantic and Mediterranean green turtle *Chelonia mydas*: A mitochondrial DNA control region sequence assessment. *Molecular Ecology* 5 (4): 473–483.

Formia, A., A. C. Broderick, F. Glen, B. J. Godley, et al. 2007. Genetic composition of the Ascension Island green turtle rookery based on mitochondrial DNA: Implications for sampling and diversity. *Endangered Species Research* 3: 145–158.

Formia, A., B. J. Godley, J.-F. Dontaine, and M. W. Bruford. 2006. Mitochondrial DNA diversity and phylogeography of endangered green turtle (*Chelonia mydas*) populations in Africa. Conservation Genetics 7: 353-369.

Hamabata, T., N. Kamezaki, and T. Hikida. 2014. Genetic structure of green turtle (*Chelonia mydas*) peripheral populations nesting in the northwestern Pacific rookeries: Evidence for northern refugia and postglacial colonization. *Marine Biology* 161 (3): 495–507.

Hamabata, T., S. Nishida, N. I. Kamezaki, and H. Koike. 2009. Genetic structure of populations of the green turtle (*Chelonia mydas*) in Japan using mtDNA control region sequences. Bulletin of the Graduate School of Social and Cultural Studies, Kyushu University 15: 35–50.

Jensen, M. P., I. P. Bell, C. J. Limpus, M. Hamann, et al. 2016. Spatial and temporal genetic variation among size classes of green turtles (*Chelonia mydas*) provides information on oceanic dispersal and population dynamics. *Marine Ecology Progress Series* 543: 241–256.

Jordão, J. C., A. C. V. Bonioli, L. F. de Almedina-Toledo, K. Bilo, et al. 2017. Mixed-stock analysis in green turtles *Chelonia mydas*: mtDNA decipher current connections among West Atlantic populations. *Mitochondrial DNA Part A* 28 (2): 197–207.

Joseph, J., and H. Nishizawa. 2016. Genetic structure and diversity of green turtles (*Chelonia mydas*) from two rookeries in the South China Sea. Journal of Sustainability Science and Management 1: 41–47.

Lahanas, P. N., M. M. Miyamoto, K. A. Bjorndal, and A. B. Bolten. 1994. Molecular evolution and population genetics of Greater Caribbean green turtles (*Chelonia mydas*) as inferred from mitochondrial DNA control region sequences. *Genetica* 94 (1): 57–66.

Nishizawa, H., O. Abe, J. Okuyama, M. Kobayashi, and N. Arai. 2011. Population genetic structure and implications for natal philopatry of nesting green turtles *Chelonia mydas* in the Yaeyama Islands, Japan. *Endangered Species Research* 14 (2): 141–148.

Reece, J. S., A. Alansari, H. M. Kalkvik, A. Alkindi, et al. 2016. A survey of the genetic diversity of the loggerhead and green turtles of the Sultanate of Oman. *Bulletin of the Florida Museum of Natural History* 54: 104–117.

Ruíz-Urquiola, A., F. B. Riverón-Giró, E. Pérez-Bermúdez, F. A. Abreu-Grobois, et al. 2010. Population genetic structure of Greater Caribbean green turtles (*Chelonia mydas*) based on mitochondrial DNA sequences, with an emphasis on rookeries from southwestern Cuba. *Revista de Investigaciones Marinas* 31 (1): 33–52.

Shamblin, B. M., D. A. Bagley, L. M. Ehrhart, N. A. Desjardin, et al. 2015. Genetic structure of Florida green turtle rookeries as indicated by mitochondrial DNA control region sequences. *Conservation Genetics* 16 (3): 673–685.

Shamblin, B. M., K. A. Bjorndal, A. B. Bolten, Z. M. Hillis-Starr, et al. 2012. Mitogenomic sequences better resolve stock structure of southern Greater Caribbean green turtle rookeries. *Molecular Ecology* 21 (10): 2330–2340.

Shamblin, B. M., P. H. Dutton, D. J. Shaver, D. A. Bagley, et al. 2017. Mexican origins for the Texas green turtle foraging aggregation: A cautionary tale of incomplete baselines and poor marker resolution. *Journal of Experimental Marine Biology and Ecology* 488: 111–120.

Shamblin, B. M., K. M. Hart, K. J. Martin, S. A. Ceriani, et al. 2020. Green turtle mitochondrial microsatellites indicate finer-scale natal homing to isolated islands than to continental nesting sites. *Marine Ecology Progress Series* 643: 159–171.

Song, J., B. Lin, Y. Jia, P. H. Dutton, et al. 2022. New management unit for conservation of the endangered green turtle *Chelonia mydas* at the Xisha (Paracel) Islands, South China Sea. *Endangered Species Research* 47: 145–154.

Tikochinski, Y., P. Bradshaw, A. Mastrogiacomo, A. Broderick, et al. 2018. Mitochondrial DNA short tandem repeats unveil hidden population structuring and migration routes of an endangered marine turtle. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28 (4): 788–797.

Yang, W., Y. Wang, and M. Chen. 2015. Genetic structure and diversity of green sea turtle (*Chelonia mydas*) from South China Sea inferred by mtDNA control region sequence. *Biochemical Systematics and Ecology* 60: 95–98.

LOGGERHEADS

Bowen, B. W., N. Kamezaki, C. J. Limpus, G. R. Hughes, et al. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* 48 (6): 1820–1828.

Bowen, B. W., A. L. Bass, S.-M. Chow, M. Bostrom, et al. 2004. Natal homing in juvenile loggerhead turtles (*Caretta caretta*). *Molecular Ecology* 13 (12): 3797–3808.

Boyle, M. C., N. N. FitzSimmons, C. J. Limpus, S. Kelez, et al. 2009. Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proceedings of the Royal Society B: Biological Sciences* 276 (1664): 1993–1999.

Carreras C., M. Pascual, L. Cardona, A. Aguilar, et al. 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. *Conservation Genetics* 8 (4): 761–775.

Chaieb, O., A. El Oauer, F. Maffucci, M. N. Bradai, et al. 2010. Genetic survey of loggerhead turtle *Caretta caretta* nesting population in Tunisia. *Marine Biodiversity Records* 3: e20.

Clusa, M., C. Carreras, M. Pascual, A. Demetropoulos, et al. 2013. Mitochondrial DNA reveals Pleistocenic colonization of the Mediterranean by loggerhead turtles (*Caretta caretta*). Journal of Experimental Biology and Ecology 439: 15–24.

FitzSimmons, N. N., C. Moritz, C. J. Limpus, J. D. Miller, et al. 1996. Comparative genetic structure of green, loggerhead, and flatback populations in Australia based on variable mtDNA and nDNA regions. In B. W. Bowen and W. N. Witzell (eds.), *Proceedings of the International Symposium on Sea Turtle Conservation Genetics*, 25–32. NOAA Technical Memorandum NMFS-SEFSC-396, National Oceanic and Atmospheric Administration, Washington, D.C.

Garofalo, L., T. Mingozzi, A. Micó, and A. Novelletto 2009. Loggerhead turtle (*Caretta caretta*) matrilines in the Mediterranean: Further evidence of genetic diversity and connectivity. *Marine Biology* 156 (10): 2085–2095.

Hatase, H., M. Kinoshita, T. Bando, N. Kamezaki,

et al. 2002. Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: Bottlenecks on the Pacific population. *Marine Biology* 141 (2): 299–305.

Matsuzawa, Y., N. Kamezaki, T. Ishihara, K. Omuta, et al. 2016. Fine scale genetic population structure of loggerhead turtles in the Northwest Pacific. *Endangered Species Research* 30 (1): 83–93.

Monzón-Argüello, C., C. Rico, E. Naro-Maciel, N. Varo-Cruz, et al. 2010. Population structure and conservation implications for the loggerhead sea turtle of the Cape Verde Islands. *Conservation Genetics* 11 (5): 1871–1884.

Reis, E. C., L. S. Soares, S. M. Vargas, F. R. Santos, et al. 2010. Genetic composition, population structure, and phylogeography of the loggerhead sea turtle: Colonization hypothesis for the Brazilian rookeries. *Conservation Genetics* 11 (4): 1467–1477.

Ruíz-Urquiola, A., M. Vega, F. B. Riverón, F. A. Abreu-Grobois, et al. 2008. Estructura genética de poblaciones de *Caretta caretta* en el Gran Caribe y la costa Atlántica de Estados Unidos, con enfasis en colonias de anidación del suroeste cubano. *Revistas de Investigación Marina* 29: 151–160.

Saied, A., F. Maffucci, S. Hochscheid, S. Dryag, et al. 2012. Loggerhead turtles nesting in Libya: An important management unit for the Mediterranean stock. *Marine Ecology Progress Series* 450: 207–218.

Shamblin, B. M., M. G. Dodd, D. A. Bagley, L. M. Ehrhart, et al. 2011. Genetic structure of the southeastern United States loggerhead turtle nesting aggregation: Evidence of additional structure within the peninsular Florida recovery unit. *Marine Biology* 158 (3): 1–17.

Shamblin, B. M., A. B. Bolten, K. A. Bjorndal, P. H. Dutton, et al. 2012. Expanded mitochondrial control region sequences increase resolution of stock structure among North Atlantic loggerhead turtle rookeries. *Marine Ecology Progress Series* 469: 145–160.

Shamblin, B. M., A. B. Bolten, F. A. Abreu-Grobois, K. B. Bjorndal, et al. 2014. Geographic patterns of genetic variation in a broadly distributed marine vertebrate: New insights into loggerhead turtle stock structure from expanded mitochondrial DNA sequences. *PLoS ONE* 9 (1): e85956.

Watanabe, K. K., H. Hatase, M. Kinoshita, K. Omuta, et al. 2011. Populations structure of the loggerhead turtle, *Caretta caretta*, a large marine carnivore that exhibits alternative foraging behaviors. *Marine Ecology Progress Series* 424: 273–283.

Yılmaz, C., O. Türkozan, and F. Bardakçı. 2011. Genetic structure of loggerhead turtle (*Caretta caretta*) populations in Turkey. *Biochemical Systematics and Ecology* 39 (4–6): 266–276.