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WHY HEALTHY OCEANS NEED SEA TURTLES: THE IMPORTANCE OF SEA TURTLES TO MARINE ECOSYSTEMS

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PHOTO MICHAEL STUBBLEFIELD

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EXECUTIVE SUMMARY

Sea turtles have played vital roles in maintaining the health of the world's oceans for more than 100 million years. These roles range from maintaining productive coral reef ecosystems to transporting essential nutrients from the oceans to beaches and coastal dunes.

Major changes have occurred in the oceans because sea turtles have been virtually eliminated from many areas of the globe. Commercial fishing, loss of nesting habitat and climate change are among the human-caused threats pushing sea turtles towards extinction. As sea turtle populations decline, so does their ability to fulfill vital functions in ocean ecosystems.

Our oceans are unhealthy and under significant threat from overfishing, pollution and climate change. It is time for us to protect sea turtles and rebuild their populations to healthy levels as a vital step in ensuring healthy and resilient oceans for the future.

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U.S. SEA TURTLES

Seven species of sea turtles swim in the world's oceans: flatback (*Natator depressus*), green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), Kemp's ridley (*Lepidochelys kempii*), leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*). Every species except for the flatback inhabits U.S. waters and was listed as endangered or threatened under the Endangered Species Act (ESA) more than 30 years ago. Despite associated protection measures, no sea turtle species has recovered enough to be removed from the ESA and some populations continue to decline.

Green Sea Turtles

ENDANGERED/THREATENED

Florida & Mexico Breeding Colony/All other areas



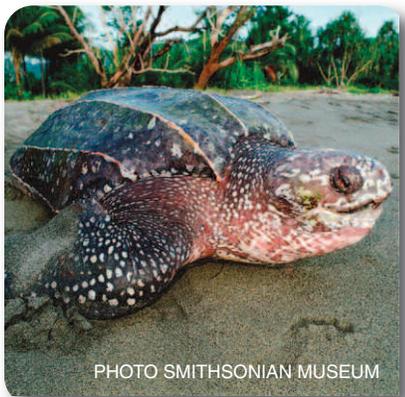
Hawksbill Sea Turtles

ENDANGERED



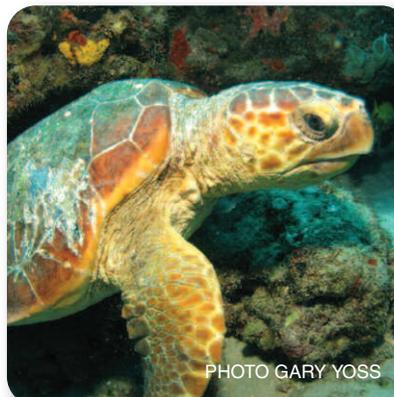
Kemp's Ridley Sea Turtles

ENDANGERED



Leatherback Sea Turtles

ENDANGERED



Loggerhead Sea Turtles

THREATENED



Olive Ridley Sea Turtles

ENDANGERED/THREATENED
Mexico Breeding Colony/All other areas

IMPORTANCE OF SEA TURTLES TO HEALTHY OCEANS

Humans have caused sea turtle populations to decline significantly all over the world.¹ Initially, direct fishing for sea turtles was the main reason for population declines. Today, other threats, including injury or death in commercial fisheries, habitat degradation and climate change top the list.² The resulting population declines have reduced the species' ability to fulfill their roles in maintaining healthy marine ecosystems.³

Because large sea turtle population declines occurred centuries ago, we lack a proper perspective or a reliable baseline against which to compare their current state.⁴ Due to the lack of historic information, some of the past ecological functions of sea turtles during periods of great abundance have certainly been forgotten.⁵

Although we cannot now fully understand the roles sea turtles played centuries ago, it is important that we discover as much as possible. Better understanding of these roles will allow us to determine what structure and functions were lost in the ocean ecosystems, the environmental effects of remaining populations, and management and conservation measures required for sea turtles to reach historic levels—and the improvements in ecosystem health that could result from restored sea turtle populations.⁶

What we do know is that sea turtles—even at diminished population levels—play an important role in ocean ecosystems by maintaining healthy seagrass beds and coral reefs, providing key habitat for other marine life, helping to balance marine food webs and facilitating nutrient cycling from water to land.

Sea turtles — even at diminished population levels — play an important role in ocean ecosystems.



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MAINTAINING HABITAT



Impact of Green Sea Turtles on Seagrass Beds

Green sea turtles, one of the few large species of herbivores that eat seagrass, help to maintain healthy seagrass beds. When green sea turtles graze, they increase the productivity and nutrient content of seagrass blades.^{7,8} Without constant grazing, seagrass beds become overgrown and obstruct currents, shade the bottom, begin to decompose and provide suitable habitat for the growth of slime molds.^{9,10} Older portions of seagrass beds tend to be overgrown with microorganisms, algae, invertebrates and fungi.¹¹

Sea turtles forage on seagrass just a few centimeters from the bottom of the blades, allowing older, upper portions of the blades to float away.^{12,13} As the turtles crop and re-crop the same plot, seagrass blades are removed from the area rather than accumulating on the bottom. This results in a 15-fold decrease in the supply of nitrogen to seagrass roots, which impacts plant species, nutrient cycling, animal densities and predator-prey relations.¹⁴ As seen in the Caribbean, the decline of green sea turtles can result in a loss of productivity in the food web – including commercially exploited reef fish – decreasing the amount of protein-rich food available for people.¹⁵

Florida Bay and the Gulf of Mexico are two excellent examples of the importance of green sea turtles on the health of seagrass beds. The die-off of seagrass in these areas during the 1980s has been directly linked to the ecological extinction of greens.¹⁶

PHOTO TIM CALVER

When green sea turtles graze, they increase the productivity and nutrient content of seagrass blades.



PHOTO GARY YOSS

Hawksbills allow other species, such as coral, to colonize and grow by removing sponges from reefs.



Impact of Hawksbill Sea Turtles on Coral Reefs

Equipped with beak-like mouths, hawksbill sea turtles forage on a variety of marine sponges. By doing this, they change the species composition and distribution of sponges in coral reef ecosystems.¹⁷ Sponges compete aggressively for space with reef-building corals. By removing sponges from reefs, hawksbills allow other species, such as coral, to colonize and grow.^{18,19} Without hawksbills, sponges are likely to dominate reef communities, further limiting the growth of corals and modifying the very structure of coral reef ecosystems.²⁰

The physical and chemical defenses of sponges prevent most fish and marine mammals from eating them.²¹ As hawksbills rip sponges apart during feeding,



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they expose food to marine species typically unable to penetrate the sponge's exterior, making sponges more vulnerable to predators.^{22,23} Through their selective foraging behavior, hawksbills impact the overall diversity of reef communities.²⁴



PHOTO CARLOS SUAREZ



Benefit of Sea Turtles to Beach Dunes

Sea turtle eggs directly and indirectly affect the vegetation, species distribution and stability of sandy shorelines. By supplying a concentrated source of high-quality nutrients, sea turtles improve their nesting beaches.²⁵ Limited nutrients in dune ecosystems, such as nitrogen, phosphorus and potassium, are partially provided to the ecosystem by unhatched sea turtle eggs. These vital nutrients allow for the continued growth of vegetation and subsequent stabilization of beach dunes.²⁶ Plant growth not only helps to stabilize the shoreline, but also provides food for a variety of plant eating animals and therefore can influence species distribution.²⁷ Sea turtle eggs also provide a food source for many predators, which in turn redistribute nutrients among dunes through their feces.²⁸ These nutrients aid the growth of vegetation and stabilization of the dunes. By contributing nutrients to beach ecosystems, sea turtles help to stabilize dunes, and therefore their own nesting habitat.²⁹

Sea turtles improve their nesting beaches by supplying a concentrated source of high-quality nutrients.



PHOTO DREW HAWKINS

PHOTO MICHELLE FABIE



MAINTAINING A BALANCED FOOD WEB



Sea Turtles and Jellyfish

Leatherbacks, the largest of the sea turtles, travel the farthest of any sea turtle species and have wide ranging effects on the ocean ecosystem. Surprisingly, leatherbacks get their energy and nutritional needs from a small, gelatinous source—jellyfish.³⁰ Growing up to 9 feet in length and migrating across entire oceans, leatherbacks rely on large concentrations of jellyfish to satisfy their appetites.³¹ They have been known to consume up to 440 pounds of jellyfish – nearly the weight of an adult African lion– each day.^{32,33}

As significant consumers of jellyfish globally, leatherbacks play a pivotal ecological role as a top jellyfish predator.³⁴ Declines in leatherback turtle populations along with declines in other key predators, such as some commercially valuable fish species, could have repercussions for jellyfish population control.³⁵

This is of particular concern since, as a result of overfishing of many finfish populations, jellyfish are gradually replacing once-abundant fish species.³⁶



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Declining fish stocks leave jellyfish with less competition for food, resulting in proliferation of jellyfish around the world.³⁷ The increase in jellyfish is already proving detrimental to the recovery of fish stocks since jellyfish prey on fish eggs and larvae.^{38,39} Fewer fish result in more jellyfish, which means even fewer fish in the future. Because leatherbacks consume large amounts of jellyfish, declines in leatherbacks could further shift species dominance from fish to jellyfish.

Other sea turtle species, including loggerhead and green sea turtles, also consume jellyfish.

Leatherbacks get their energy and nutritional needs from jellyfish.





Sea Turtles Provide Food for Fish

By carrying around barnacles, algae and other similar organisms known as epibionts, sea turtles provide a food source for fish and shrimp. Other organisms, such as sheepshead bream,⁴⁰ wrasse,⁴¹ angelfish and barber pole shrimp,⁴² establish “cleaning stations” for sea turtles to visit. With outstretched limbs and a raised head, sea turtles expose their bodies, offering a meal to eager fish and shrimp.⁴³ This behavior not only feeds smaller organisms, but also benefits sea turtles by reducing drag and keeping their skin and shells clean.⁴⁴ Schools of fish can be seen cleaning sea turtles while they sleep or even following aggregations of sea turtles in transit.⁴⁵ Some species obtain their diet strictly from epibionts found on sea turtles.⁴⁶ Without this food source, certain species of fish and shrimp might be forced to develop other, less successful methods for obtaining food.

All sea turtle species are also prey, providing food for other animals both on shore and at sea.

All sea turtle species are also prey, providing food for other animals, both on shore and at sea. Like many marine organisms, sea turtles are most vulnerable to predation as eggs, hatchlings and juveniles. A long list of terrestrial animals – ants, crabs, rats, raccoons, foxes, coyotes, feral cats, dogs, mongoose and vultures – are known to dig up unhatched nests. The eggs provide a nutrient-rich source of food for these predators. As hatchlings emerge from the nest, they provide another feeding opportunity for natural predators, which includes a variety of seabirds. While most seabirds are daytime predators, species such as the night heron actually listen for hatchlings emerging from nests.⁴⁷ If the hatchlings make it to the water, they face continued predation from seabirds with an aerial view of the tiny turtles as they float near the surface.⁴⁸ Reef fish, such as grouper and jacks, are also common predators of both hatchlings and juvenile sea turtles.⁴⁹ In fact, one study of green sea turtles in Australia showed that up to 97 percent of hatchlings are eaten within the first hour of entering the water.⁵⁰ Clearly, hatchlings provide a significant source of protein for nearshore predatory fish. As sea turtles grow, the risk of predation decreases.⁵¹ Adult sea turtles have very few natural predators other than killer whales and sharks. Tiger sharks are known to prey upon green sea turtles and great whites have been documented preying on both green and loggerhead sea turtles.^{52,53}

NUTRIENT CYCLING



PHOTO GARY YOSS



Loggerheads Benefit Ocean Floor Ecosystems

Loggerheads are equipped with powerful jaws to feed on hard-shelled prey, such as crustaceans. This allows them to reduce the shells of their prey into fragments that are either discarded on site or further away in the form of feces.⁵⁴ By breaking up the shells while foraging, loggerheads increase the rate at which the shells disintegrate⁵⁵ and increase the rate of nutrient recycling in benthic or ocean bottom ecosystems.

Loggerheads also find prey by clearing away sand to expose their next meal.⁵⁶ As they glide along the sea

floor in search of food, loggerheads create trails in the sediment.⁵⁷ This foraging behavior is important for both loggerheads and the habitat.⁵⁸ The loggerheads trails affect the compaction, aeration and nutrient distribution of the sediment,⁵⁹ as well as the species diversity and dynamics of the benthic ecosystem.⁶⁰ When foraging, loggerheads naturally alter the ocean bottom and benefit the underwater community.



Sea Turtles Improve Nesting Beaches

Female migrations from foraging grounds to nesting beaches are ecologically significant journeys.⁶¹ When females lay their eggs on sandy shorelines, they introduce nutrients and energy from distant and dispersed foraging grounds into relatively small and nutrient-poor beaches.^{62,63} One of the longest and most impressive examples of this transfer of nutrients is by leatherbacks, which feed on jellyfish near the Arctic circle and nest on tropical beaches.^{64,65}

Sea turtle eggs have four possible fates, each with its own energy path: 1) the eggs hatch and most of the nutrients return to the sea as hatchlings, leaving some nutrients on the beach in the form of eggshells and embryonic fluid; 2) the eggs fail to hatch, allowing nutrients to enter the detrital food chain; 3) the eggs are consumed by predators; or 4) the eggs are penetrated by roots, enabling

plants to absorb the nutrients.⁶⁶ In addition, nesting and the emergence of hatchlings bring egg matter and nest organisms to the surface.⁶⁷ These processes help disperse nutrients to small organisms in beach sand.⁶⁸ Consequently, the presence of turtle eggs drives community dynamics on nesting beaches.⁶⁹



PHOTO CORY WILSON

PROVIDING HABITAT

Many marine organisms rely on sea turtles as a place to call home. These small creatures called “epibionts” attach themselves to solid surfaces in the ocean such as floating debris and sea turtle shells. Loggerheads play host to the largest and most diverse communities of epibionts.⁷⁰ In fact, more than 100 different species have been identified on loggerhead shells.⁷¹

Compared to floating debris, sea turtles provide increased survival rates,⁷² enhanced foraging⁷³ and wider dispersal for attached epibionts.⁷⁴ For example, Columbus crabs (*Planes minutus*) found on loggerheads tend to be larger in size and have higher proportions of female crabs with brooding eggs than those attached to debris.⁷⁵ Furthermore, Columbus crabs found on loggerheads are more successful foragers with a diverse diet, while crabs found on debris mainly consume algae.⁷⁶ Columbus crabs feed on other epibionts found on loggerhead shells, particles from the loggerhead’s captured prey and the shedding skin and feces of loggerheads.⁷⁷ Sea turtles clearly provide numerous benefits to the epibionts they host.

Sea turtles also help to structure their marine habitats through the dispersal of epibionts.⁷⁸ Organisms such as plants and crustaceans are transported to and from reefs, seagrass beds and the open ocean.⁷⁹ The greatest illustration of sea turtles’ impact on dispersal is seen in the range of the coronulid barnacle (*Chelonibia testudinaria*), the most common sea turtle epibiont.⁸⁰ At any particular time, 94 percent of nesting loggerheads host at least one species of barnacle.⁸¹



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PHOTO KIM BASSOS-HULL

The loggerhead's transatlantic migration to the Mediterranean is believed to play a key role in expanding the barnacle's range and genetic diversity.⁸² Species associated with a host, such as sea turtles, are important to generating and maintaining diversity throughout the world's oceans.⁸³ Continued loss of loggerheads and other sea turtle species means a decrease in available substrate for the growth and livelihood of such marine diversity.⁸⁴

In the open ocean, miles from shore, sea turtles offer an oasis to fish and seabirds. Similar to floating debris, sea turtles can be used as a place to rest, a foraging ground and even a safe haven from potential predators. Of all the sea turtle species, olive ridleys are most frequently associated with seabirds, particularly in the Eastern Tropical Pacific.⁸⁵ As they surface to bask in the sun, olive ridleys expose the center of their shell and create a platform for seabirds to perch.⁸⁶ Some seabirds take advantage of this opportunity to roost if their feathers are

Sea turtles offer an oasis to fish and seabirds in the open ocean.

not extremely water-resistant.⁸⁷ By perching on sea turtles, seabirds that would otherwise be vulnerable to attack, find refuge from sharks.⁸⁸ Small baitfish also use sea turtles for protection, by forming tight schools beneath the turtle's body.⁸⁹ These schools of fish then provide a food source for resting seabirds.⁹⁰ Some seabirds occasionally feed on epibionts inhabiting the sea turtle's shell.⁹¹ By offering a location to roost, feast and hide, sea turtles represent an important resource for birds and fish at sea.⁹²



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THE RISK OF ECOLOGICAL EXTINCTION

Sea turtles clearly play important roles in marine ecosystems. Each sea turtle species uniquely affects the diversity, habitat and functionality of its environment. Whether by grazing on seagrass, controlling sponge distribution, feasting on jellyfish, transporting nutrients or supporting other marine life, sea turtles play vital roles in maintaining the health of the oceans.

Unfortunately, over the past few centuries, sea turtle populations have experienced significant declines. Before a species goes physically extinct, it can become ecologically extinct. Ecological extinction, which occurs when the number of individuals in a species becomes so small that it is unable to perform its ecological role, happened to green sea turtles in the Caribbean. At the time of Columbus' voyages to the Caribbean, sea turtles were so abundant that vessels that had lost their way could follow the noise of sea turtles swimming along their migration route and find their way to the Cayman Islands.⁹³ Current estimates of Caribbean sea turtle populations at that time range from 33 million to 660 million.⁹⁴ Greens in the Caribbean consumed such large amounts of seagrass, sponges and jellyfish that their virtual ecological extinction resulted in major changes in the structure and function of the marine ecosystem.⁹⁵

Sea turtle populations around the world have dwindled in recent centuries and in many places, continue to decline. For some populations, there is risk not only of ecological extinction, but of physical extinction as well. In the words of Aldo Leopold, one of the most influential conservation thinkers of the 20th century, "To keep every cog and wheel is the first precaution of intelligent tinkering."⁹⁶ Applying this principle to the oceans, quite simply, we need to keep all of the species. Natural resource managers are moving towards an "ecosystem approach" to managing the oceans. The first step in taking an ecosystem approach is to ensure the survival of the key components of the ecosystems, which unequivocally must include sea turtles. The next step is to ensure their populations actually recover. Increased populations of sea turtles are a key step in restoring the balance among ocean species, an essential step toward restoring healthy ocean ecosystems.

Some populations of sea turtles risk not only ecological extinction, but physical extinction.

CONCLUSIONS

As sea turtle populations decline, so does their ability to perform vital roles in maintaining the health of the world's oceans. Death and injury in commercial fisheries, loss of important habitat, pollution and climate change are among the many human-caused threats pushing sea turtles towards extinction. More proactive conservation measures are needed to protect sea turtles and rebuild their populations to healthy levels so they can fulfill the full extent of their historic roles in ocean ecosystems. At historic levels, sea turtles will help restore the health of our oceans and make them more resilient to future threats.

The following actions must be taken to protect and restore sea turtle populations:

- *Reduce sea turtle interactions and mortalities in commercial fisheries*
- *Protect key habitat areas on land and in the water*
- *Pass comprehensive legislation that establishes a system to protect and restore sea turtle populations*



PHOTO JACOB TUTTLE



REFERENCES

- ¹ R Bjorndal, K.A. and Jackson, J.B.C. 2003. Roles of sea turtles in marine ecosystems: Reconstructing the past. In Lutz, P.L., Musick, J.A. and Wyneken, J. (Eds.) *The Biology of Sea Turtles Volume II*. CRC Press, Boca Raton, Florida (USA). Pp. 259-273.
- ² Bjorndal, K.A., Jackson, J.B.C. 2003.
- ³ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁴ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁵ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁶ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁷ Bjorndal, K.A. 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Marine Biology* 56: 147-154.
- ⁸ Thayer, G.W., Bjorndal K.A., Ogden, J.C., Williams, S.L., Ziemann, J.C. 1984. Role of larger herbivores in seagrass communities: Functional ecology of seagrass ecosystems: A perspective on plant-animal interactions. *Estuaries* 7(4): 351-376.
- ⁹ Ziemann, J.C., Fourqurean, J.W., and Frankovich, T.A. 1999. Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of turtle grass, *Thalassia tertudinum*. *Estuaries* 22(2B): 460-470.
- ¹⁰ Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293(5530): 29-637.
- ¹¹ Jackson, J.B.C. 2001. What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences of the United States of America* 98 (10): 5411-5418.
- ¹² Bjorndal, K.A. 1980.
- ¹³ Thayer, G.W., et al. 1984.
- ¹⁴ Thayer, G.W. et al. 1984; Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16: S23-S32.
- ¹⁵ McClenachan, L., Jackson, J.B.C., and Newman, M.J.H. 2006. Conservation implications of historic sea turtle nesting beach loss. *Frontiers in Ecology and the Environment* 4(6): 290-296.
- ¹⁶ Jackson, J.B.C. 2001.
- ¹⁷ Meylan, A. 1988. Spongivory in hawksbill turtles: A diet of glass. *Science* 239(4838): 393-395.
- ¹⁸ Meylan, A. 1988.
- ¹⁹ Leon, Y.M. and Bjorndal, K.A. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progress Series* 245: 249-258.
- ²⁰ Leon, Y.M., Bjorndal, K.A.. 2002.
- ²¹ Leon, Y.M., Bjorndal, K.A.. 2002.
- ²² Meylan, A. 1988.
- ²³ Leon, Y.M., Bjorndal, K.A.. 2002.
- ²⁴ Meylan, A. 1988.
- ²⁵ Bouchard, S.S. and Bjorndal, K.A. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* 81: 2305-2313.
- ²⁶ Hannan, L.B., Roth, J.D., Ehrhart, L.M., and Weishampel, J.F. 2007. Dune vegetation fertilization by nesting sea turtles. *Ecology* 88(4): 1053-1058.
- ²⁷ Bouchard, S.S., Bjorndal, K.A. 2000.
- ²⁸ Bouchard, S.S., Bjorndal, K.A. 2000.
- ²⁹ Bouchard, S.S., Bjorndal, K.A. 2000.
- ³⁰ Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., and Hays, G.C. 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87(8): 1967-1972.
- ³¹ Houghton, J.D.R., et al. 2006.
- ³² Houghton, J.D.R., et al. 2006.
- ³³ Duron-Dufrenne, M. 1987. Premier suivi par satellite en Atlantique d'une tortue Luth *Deremochelys coriacea*. *Comptes Rendue Academie des Sciences Paris Ser.III*, 304: 399-402.
- ³⁴ Gibbons, M.J. and Richardson, A.J. 2009. Patterns of jellyfish abundance in the North Atlantic. *Hydrobiologia* 616:51-65.
- ³⁵ Purcell, J.E., Shin-ichi, U., Wen-Tseng, L. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. *Mar. Ecol. Prog. Ser.* 350: 153-174.
- ³⁶ Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C.A.J., Coetzee, J., Heywood, B.G., Brierley, A.S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* 16(13): R492-R493.
- ³⁷ Lynam, C.P., et al. 2006.
- ³⁸ Purcell, J.E. and Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. *Hydrobiologia* 451: 27-44.
- ³⁹ Lynam, C.P., et al. 2006.
- ⁴⁰ Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C. 2006. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research* 2: 71-79.
- ⁴¹ Losey, G.S., Balazs, G.H., Privitera, L.A. 1994. Cleaning symbiosis between the wrasse, *Thalassoma duperry*, and the green turtle, *Chelonia mydas*. *Copeia* 5: 684-690.
- ⁴² Sazima, I., Grossman, A., Sazima, C. 2004. Hawksbill turtles visit mustached barbers: cleaning symbiosis between *Eretmochelys imbricata* and the shrimp, *Stenopus hispidus*. *Biota Neotropica* 4(1): 1-6.
- ⁴³ Schofield, G., et al. 2006.
- ⁴⁴ Losey, G.S., et al. 1994.
- ⁴⁵ Schofield, G., et al. 2006.
- ⁴⁶ Losey, G.S., et al. 1994.
- ⁴⁷ Gulko, D.A. and Eckert, K.L. 2004. *Sea Turtles: An Ecological Guide*. Mutual Publishing, Honolulu, HI. 128 pp.
- ⁴⁸ Gulko, D.A. and Eckert, K.L. 2004.

- ⁴⁹ Gulko, D.A. and Eckert, K.L. 2004.
- ⁵⁰ Gyuris, E. 1994. The rate of predation by fishes on hatchlings of the green turtle (*Chelonia mydas*). *Coral Reefs* 13:137-144.
- ⁵¹ Musick, J.A. and Limpus, C.J. 1997. Habitat utilization and migration in juvenile sea turtles. In: P. L. Lutz & J. A. Musick (Eds). *The Biology of Sea Turtles*. CRC Press, Boca Raton. pp. 137-163.
- ⁵² Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thompson, J., Bejder, L. 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology* 76(5):837-844.
- ⁵³ Fergusson, I. K., Compagno, L. J. V., Marks, M. A. 2000. Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as stomach contents. *Environmental Biology of Fishes* 58(4): 447-453.
- ⁵⁴ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁵⁵ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁵⁶ Preen, A. R. 1996. Infaunal mining: A novel foraging method of loggerhead turtles. *Journal of Herpetology* 30(1): 94-96.
- ⁵⁷ Preen, A.R. 1996.
- ⁵⁸ Preen, A.R. 1996.
- ⁵⁹ Bjorndal, K.A., Jackson, J.B.C. 2003.
- ⁶⁰ Preen, A.R. 1996. Bjorndal, K. A. and Jackson, J.B.C. 2003. Roles of sea turtles in marine ecosystems: Reconstructing the past. In Lutz, P.L., Musick, J.A. and Wyneken, J. (Eds.) *The Biology of Sea Turtles Volume II*. CRC Press, Boca Raton, Florida (USA). Pp. 259-273.
- ⁶¹ Bjorndal, K.A. 2003. Roles of loggerhead sea turtles in marine environments. In Bolten, A.B. and Witherington, B.E. (Eds.) *Loggerhead Sea Turtles*. Smithsonian Institution Press, Washington, DC. Pp. 235-254.
- ⁶² Bouchard, S.S., Bjorndal, K.A. 2000.
- ⁶³ Meylan, A., Schroeder, B., Mosier, A. 1995. Marine turtle nesting activity in the state of Florida, 1979–1992. *Florida Marine Research Publication Number* 52.
- ⁶⁴ Bouchard, S.S., Bjorndal, K.A. 2000.
- ⁶⁵ Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. In Lutz, P.L. and Musick, J.A. (Eds.) *The Biology of Sea Turtles*. CRC Press, Boca Raton, Florida, USA. Pp. 199–232.
- ⁶⁶ Bouchard, S.S., Bjorndal, K.A. 2000.
- ⁶⁷ Madden, D., Ballesteros, J., Calvo, C., Carlos, R., Christians, E., Madden, E. 2008. Sea turtle nesting as a process influencing a sandy beach ecosystem. *Biotropica* 40(6): 758-765.
- ⁶⁸ Madden, D., et al. 2008.
- ⁶⁹ Madden, D., et al. 2008.
- ⁷⁰ Frick, M.G., Williams, K.L., Veljacic, D., Pierrard, L., Jackson, J.A., and Knight, S.E. 2000. Newly documented epibiont species from nesting loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. *Marine Turtle Newsletter* 88: 3-5.
- ⁷¹ Pfaller, J.B., Bjorndal, K.A., Reich, K.J., Williams, K.L., Frick, M.G. 2006. Distribution patterns of epibionts on the carapace of loggerhead turtles, *Caretta caretta*. *Biodiversity Records*: 1-4.
- ⁷² Dellinger, T., Davenport, J., Wirtz, P. 1997. Comparisons of social structure of Columbus crabs living on loggerhead sea turtles and inanimate flotsam. *Journal of the Marine Biological Association of the United Kingdom* 77(1): 185-194.
- ⁷³ Frick, M.G., Williams, K.L., Bolten, A.B., Bjorndal, K.A., Martins, H.R. 2004. Diet and fecundity of Columbus crabs, *Planes minutus*, associated with oceanic-stage loggerhead sea turtles, *Caretta caretta*, and inanimate flotsam. *Journal of Crustacean Biology* 24(2): 350-355.
- ⁷⁴ Rawson, P.D., Macnamee, R., Frick, M.G., Williams, K.L. 2003. Phylogeography of the coronulid barnacle, *Chelonibia testudinaria*, from loggerhead sea turtles, *Caretta caretta*. *Molecular Ecology* 12: 2697-2706.
- ⁷⁵ Dellinger, J.B., Davenport, J., Wirtz, P. 1997.
- ⁷⁶ Frick, M.G., et al. 2004.
- ⁷⁷ Frick, M.G., et al. 2004.
- ⁷⁸ Frick, M.G., Mason, P.A., Williams, K.L., Andrews, K., Gerstung, H. 2003. Epibionts of hawksbill turtles in a Caribbean nesting ground: A potentially unique association with snapping shrimp (Crustacea: Alpheidae). *Marine Turtle Newsletter* 99: 8-11.
- ⁷⁹ Frick, M.G. et al. 2003.
- ⁸⁰ Rawson, P.D. et al. 2003.
- ⁸¹ Rawson, P.D. et al. 2003.
- ⁸² Rawson, P.D. et al. 2003.
- ⁸³ Rawson, P.D. et al. 2003.
- ⁸⁴ Bjorndal, K.A. 2003.
- ⁸⁵ Pitman, R.L. 1993. Seabird associations with marine turtles in the eastern Pacific Ocean. *Colonial Waterbirds* 16(2): 194-201.
- ⁸⁶ Pitman, R.L. 1993.
- ⁸⁷ Pitman, R.L. 1993.
- ⁸⁸ Pitman, R.L. 1993.
- ⁸⁹ Pitman, R.L. 1993.
- ⁹⁰ Pitman, R.L. 1993.
- ⁹¹ Pitman, R.L. 1993.
- ⁹² Pitman, R.L. 1993.
- ⁹³ King, F.W. 1982. Historical review of the decline of the green turtle and the hawksbill. In Bjorndal, K.A. (Ed.) *Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, D.C. Pp. 183-188.
- ⁹⁴ Jackson, J.B.C. 1997.
- ⁹⁵ Bjorndal, K. A. and J. B. C. Jackson. 2003.
- ⁹⁶ Leopold, A. 1993. *Round River*. Oxford University Press, New York. Pp. 145-146.

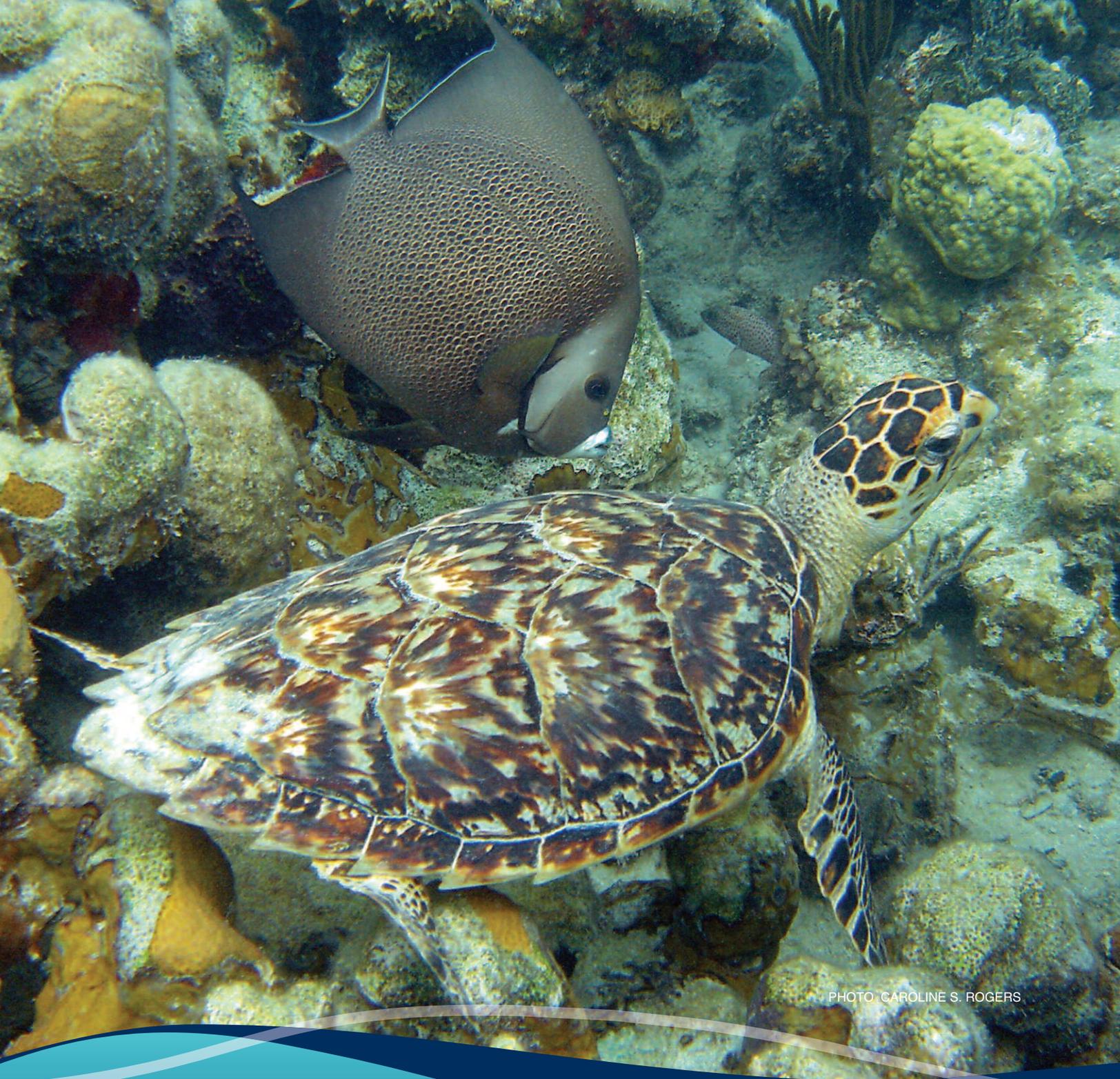


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