Virtually all marine fisheries have shark bycatch, including bottom trawls (for example, for shrimp and cod), gillnets (squid and salmon), demersal (bottom) longlines (Chilean Sea Bass, Greenland Halibut, and Hake), pelagic longlines (Mahi-mahi and Swordfish), and purse seines that use fish aggregating devices (for tunas).

Although this list will vary by location and is incomplete, sharks widely impacted as bycatch include angel sharks, Bonnetheads, dogfish, and catsharks (bottom trawls); Blue Sharks, Salmon Sharks, and juvenile Sandbar and Dusky Sharks (gillnets); Blue, Silky, and Oceanic Whitetip Sharks (pelagic longlines); Cuban Dogfish, Portuguese Dogfish, lantern sharks, and gulper sharks (demersal longlines); and Oceanic Whitetip and Silky Sharks (purse seines).

Even when commercial fishers release sharks, for some species post-release mortality may be high. For example, more than 95 percent of Cuban Dogfish caught on demersal longlines are released alive, but about half soon die. In some cases, indelicately removing the hook from the shark's mouth breaks the lower jaw.

Bycatch can be addressed in several ways. Simply tending the gear more regularly can significantly reduce mortality in some cases. On pelagic longlines, increasing the depth of hooks can reduce bycatch of Silky and Oceanic Whitetip Sharks, which spend most of their time at depths shallower than 330 ft (100 m). Fisheries can be excluded, year-round or temporarily, from areas where sharks and rays congregate or where their populations are depleted. In the US shrimp trawl industry, devices that shunt sea turtles from the nets also exclude larger sharks, for example, Blacknose Sharks. Tests are also underway to develop hooks that repel sharks by jamming their electrosensory systems, but that do not affect target species. One, called SharkGuard, was recently demonstrated to reduce Blue Shark bycatch in trials in a Bluefin Tuna fishery. It is important to note that regulations and incentives for commercial fishers to accept bycatch reduction devices and techniques vary and compliance may be very low without enforcement. It is also important to note that not all fisheries have high bycatch levels in all areas, nor are all the sharks caught as bycatch vulnerable to population depletion as a result—for example, Atlantic Sharpnose Sharks caught in shrimp trawls in the Southeastern United States.

Educating consumers so they can make ethical, sustainable seafood choices that take shark bycatch into account could also play a role, especially in wealthier areas, although getting the information to these consumers has been problematic. More research also needs to be undertaken to identify and implement additional mitigation measures. The window of opportunity is fast closing: human population size is now greater than eight billion, and demand for seafood is expanding.

Captivity and Capture Stress

As a child, observing Sandbar Sharks swimming so elegantly at the New England Aquarium not only changed the way I had considered sharks—as terrifying predators—but also set me on a trajectory to my career as a marine biologist.

While recognizing the immense ethical and environmental questions surrounding capturing, transporting, and maintaining sharks for display, I also know there are benefits, or at least the potential for benefits, of responsible husbandry. These include educating, inspiring, and promoting conservation values and action. It did in my case. Modern shark husbandry also seeks to maintain and breed species of conservation concern, so-called *insurance populations*, as hedges against population decreases in nature.

Keeping sharks in captivity is fairly easy for benthic species like Port Jackson Sharks and Small-spotted Catsharks, which are handily caught, transport well, require only small tanks, are not aggressive, and are not finicky eaters. Many such species will even mate in captivity. For these, however, the *Wow!* factor may be missing, since aquarium visitors prefer large, iconic species over those more diminutive and less thrilling.

On the other end of the spectrum are displays of these iconic, larger sharks, which include Whale Sharks, Bull Sharks, Tiger Sharks, hammerheads, Sand Tigers, Sandbar Sharks, Blacktip Sharks, Silvertip Sharks, Blacktip Reef Sharks, and others. All of these sharks must be captured from the wild and transferred to their destination aquariums, often involving long journeys by truck or even plane.

Whether as bycatch, for display, or even in recreational fishing, capturing a shark sets off a suite of potentially deadly physiological responses collectively known as *capture stress*. These include the release of stress hormones and concomitant build-up of chemical by-products of metabolism (e.g., lactic acid), salt and mineral imbalances, hypoxia (low internal oxygen levels), and even dehydration.

The problems that must be overcome to successfully transport a Whale Shark to the Japanese aquarium in Osaka or the US aquarium in Georgia (as much as 8,000 mi or 12,800 km) are daunting, but moving other larger sharks is no stroll in the garden either. All of the large sharks referred to above are ram ventilators, that is, they swim with their mouths slightly ajar, which allows oxygen-rich seawater to flow over their gills. To compensate for the loss of this water flow during transit, oxygen in the form of superfine bubbles may be pushed into the shark's mouth via a submersible pump. Additionally, to allow the heart to perform its role and circulate blood, some flexion of the posterior part of the shark's body is required to return blood back to the heart. Otherwise, blood may pool in the lower and posterior parts of the body, which is unhealthy. Evidence of the latter is reddening of the underside of the shark due to capillaries rupturing.

Once the shark is settled into its final display tank, which may initially involve separating the newly introduced shark with a barrier from veteran sharks already there, the shark will be closely observed and its feeding and nutritional supplementation closely measured.

Even with advances in the process that allows Whale Sharks, the largest fish in the sea, to be displayed, many species simply are not capable of adjusting to long-term captivity. These include the five species of mackerel sharks (White Shark, Shortfin Mako, etc.), which may overheat and succumb to other aspects of capture stress, as well as Blue Sharks and deep-sea sharks, like the Frilled Shark.

Cartilage

Cartilage is the principal structural material of the shark skeleton and it is the essence of what distinguishes sharks from other vertebrates. Bone, which is heavily mineralized and thus harder than cartilage, has found a home in most living vertebrates, about 74,000 species. The *chondr*- of the class Chondrichthyes, which includes the sharks, skates, rays, and the more obscure chimaeras, means *cartilage*.

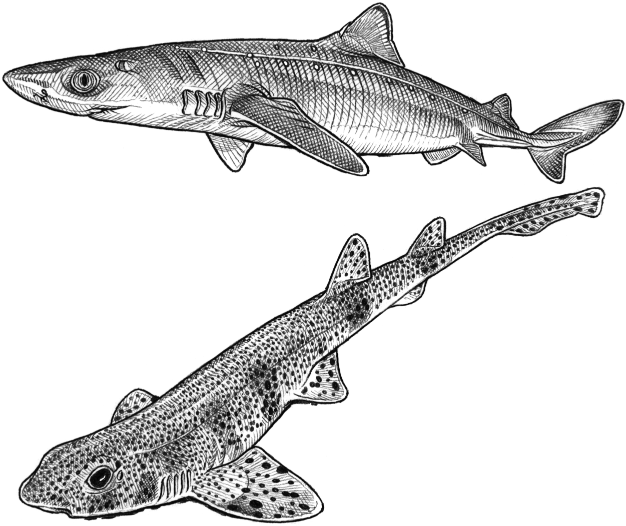
The cartilaginous skeleton of sharks is tough yet lighter and more flexible than bone. It lacks the nerves and blood vessels found in bone. At stress points like the jaw and vertebrae of sharks, the cartilage is strengthened by incorporating calcium in the form of the mineral apatite. Because its crystalline structure is arranged in a pattern resembling a prism, this type of cartilage is known as *prismatic calcified cartilage*. Chemically, cartilage is composed principally of protein and sugar molecules.

In combination with a buoyancy-enhancing, large, oil-filled liver, the lightness of cartilage is a major benefit, since it helps compensate for the shark's heavy, muscle-bound body and its lack of a swim bladder, a gas-filled internal structure found in most bony fishes that allows them to adjust their buoyancy.

Catsharks and Dogfish

The catsharks are the largest taxonomic group of sharks, with more than 150 species. The term "dogfish" refers generally to the approximately 121 species of sharks in the order Squaliformes, but more precisely to the thirty-seven or so species in the family Squalidae. The catsharks and true dogfish ("true" because the common name of some of the catsharks includes the word "dogfish") are separated by over 200 million years, when the two larger groups to which these belong split apart and diverged evolutionarily. Catsharks and true dogfish have some similarities (generally size and diet, for example) but differ in significant life history characteristics. They are lumped together here, to be honest, because of cliches: By discussing them in one instead of numerous entries, I am killing two birds with one stone. And the phrase "cats and dogs" lends itself to having a *catsharks and dogfish* entry.

Catsharks are mostly small (less than 3.3 ft or 1 m). They occupy cold and deep waters worldwide and are among the 40 percent of sharks that are oviparous (egg layers). The group's common name owes to the resemblance of their elongated eyes to those of domestic cats. They have two small dorsal fins positioned far back on the body.



Unless you study deep-sea sharks, you are not likely to cross paths with more than a few catsharks, despite their diversity, and those you see would likely be in marine aquariums or fish markets. One of these is the Small-spotted Catshark, one of the most abundant sharks found in relatively shallow waters in the North Sea, Mediterranean Sea, and nearby. Other shallow-water, more common catsharks include the Chain Dogfish that, despite its name, is not a dogfish, and the Striped Catshark, or Pyjama Shark, found off South Africa and widely displayed in aquariums worldwide.

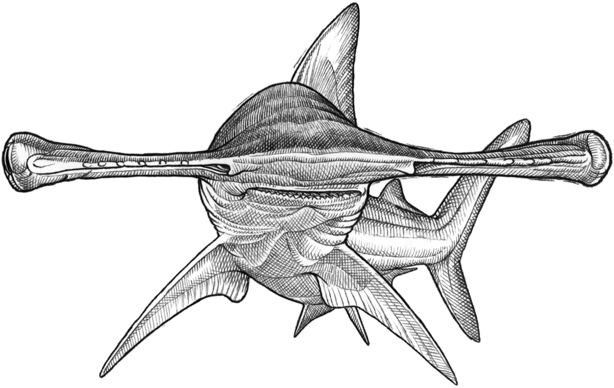
The true dogfish are found worldwide in tropical, temperate, and boreal seas from the intertidal zone to 1,970 ft (600 m) or greater. A key characteristic of dogfish is the absence of the anal fin, the functional significance of which is unknown. Dogfish are cylindrical in cross section, with two dorsal fins each having strong, ungrooved spines, which may be mildly venomous. A recent discovery of Spiny Dogfish in the Thames River after a long absence prompted sensational headlines of "Venomous Shark Found in Thames." Spiracles on the head are large in dogfish, and the dermal denticles make for tough and abrasive skin.

The best-known dogfish is this same Spiny Dogfish (also called the Spurdog or Piked Dogfish). Despite being overfished in the North Atlantic and Mediterranean, it remains plentiful off New Zealand and is still likely among the most abundant shark species. This species has very conservative life history characteristics (few young, late maturity, and roughly a two-year gestation period). Based on these factors and the depletion documented in stock assessments, the International Union for Conservation of Nature lists it as "vulnerable" globally, with a declining trend. Included here because of its relative abundance and conservation story, the Spiny Dogfish is, in fact, the oddity, since it is one of the few coastal members of the family.

Similarities between dogfish and catsharks include diets consisting of small fish and crustaceans and other invertebrates. Both constitute significant bycatch in deep-sea bottom trawl fisheries as well.

Cephalofoil

Odds are the oddest shark you can envision, and one of nature's animal oddballs, is the hammerhead shark (actually, there are nine known species), whose uniquely



shaped head, or *cephalofoil*, has led to these sharks being called *otherworldly*. Two questions immediately come to mind: How did the head evolve? And what functions does it have?

Evolution favors traits that are on balance adaptive, that is, those that in some way help the organism, for example by saving energy or making it a better predator. One idea is that the widened head serves as scaffolding that can more widely distribute the head's sense organs and lead to enhanced sensory abilities, and indeed that has been found to be the case in terms of electroreception and better binocular vision compared to other sharks. When used as a rudder, the cephalofoil also allows greater maneuverability by narrowing the shark's turning radius. Also, hammerheads are known to use their head to pin stingrays to the seabed while they position themselves to bite.

The cephalofoil ranges in size from that of the relatively small Bonnethead to the bizarrely wide head of the Winghead Shark, an Indonesian species whose head is half as wide as its body length.

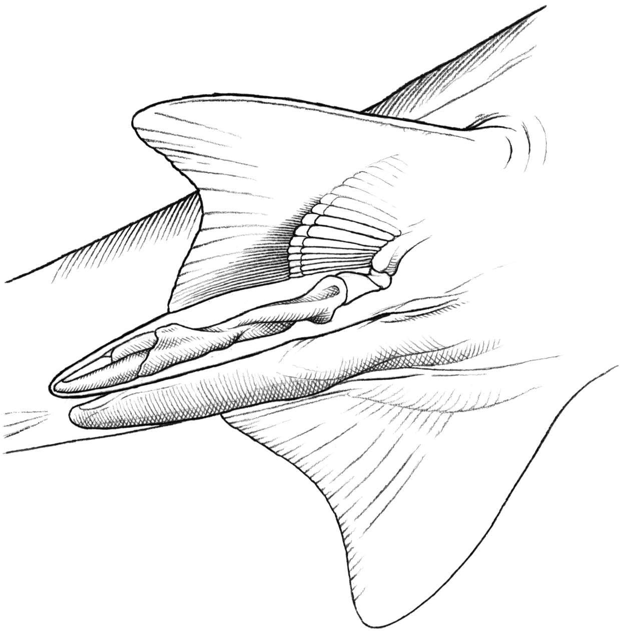
Chondrichthyan Tree of Life

The Chondrichthyan Tree of Life project and website represent an ambitious and ongoing venture to document all known chondrichthyan fishes (sharks, skates, rays, and chimaeras), with range maps, illustrations, and CT scans. The information is organized phylogenetically. The evolutionary relationships depicted on the website are estimated based on DNA sequence data for all of the species from which tissue samples could be collected (about 900 of a possible 1,200 described species so far). The project was spearheaded by shark biologist Gavin Naylor and is a collaboration among scientists with different specializations around the world.

A new addition to the shark trait field is Sharkipedia (not to be confused with the similar title of this book). It advertises itself as an "initiative to make all published biological traits and population trends on sharks, rays, and chimaeras accessible to everyone." Science works better with community-minded contributions like these two examples.

Claspers

All sharks (and skates, rays, and chimaeras) use internal fertilization, as opposed to the female depositing unfertilized eggs in the environment. Transferring the sperm internally while swimming is tricky, which explains in part why internal fertilization is uncommon among the bony fishes. Additionally, females may be unreceptive to the male's attempt at mating, making you wonder



how internal fertilization in sharks survived natural selection's rigorous standards.

The answer to this evolutionary challenge is *claspers*, structures that Aristotle himself observed and named, although he was mistaken in his notion of how they functioned. Also called *mixopterygia*, claspers are rearward tubular modifications of the inner margins of the pelvic fins of male sharks (and a distinguishing feature of chondrichthyan fishes). Aristotle erroneously surmised that the claspers were employed by males to grasp the female while he fertilized eggs externally.

Although the explanation was wrong, the name has endured.

During fertilization, a single clasper is inserted into the cloaca (the common urinary, genital, and anal opening) of the female, after which insemination occurs.

Why two claspers when only one is used at a time? The clasper that is used is rotated ninety degrees or more across the body before insertion. Having two claspers enables access to the female from either side, which comes in handy if multiple males are competing to inseminate the female.

The actual sperm transfer occurs via a groove in the claspers. After the clasper splays open and anchors itself in the cloaca with hooks or spines, or simply enlarges sufficiently to remain in the cloaca, sperm are flushed into the female along with a relatively large volume of seawater that the male had previously imbibed in a specialized siphon sac. After the act, the clasper is disgorged, which may require forceful shaking by the female.

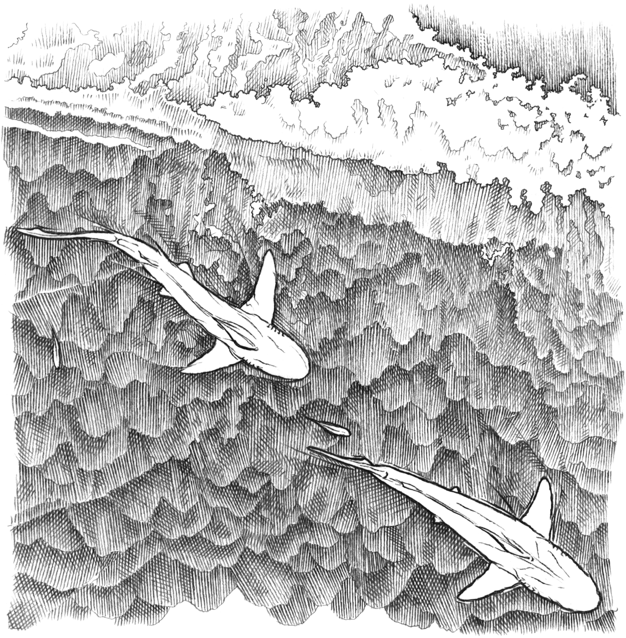
Coastal Sharks

Of all shark habitats, coastal waters are among the most biodiverse. At the same time, because nearly 60 percent of the human population live near the coast, these areas are heavily degraded by pollution and habitat alteration.

Nearly 40 percent of shark species live in the coastal waters of temperate and tropical areas. Many of these areas are characterized by abundant food resources and very high habitat diversity. Coastal habitats include estuaries, kelp forests, seagrass beds, live bottom habitat, and beaches. Here, we focus only on temperate coastal waters (tropical and polar sharks are considered separately).

Estuaries, where freshwater and saltwater meet and intermix, are often found at the mouths of rivers. Today's estuaries are all less than twelve thousand or so years old, resulting from the geologically recent rise of sea level since the last glacial maximum. Their shallow, nutrient-rich waters, along with the intertidal wetlands that line their shores, are some of the most productive ecosystems on Earth. About fifty species of sharks, ranging from neonates (newborns) to adult apex predatory sharks (e.g., Bull Sharks), are found in estuaries. Other sharks commonly found in estuaries include Sandbar Sharks, Lemon Sharks, Blacktip Sharks, Blacknose Sharks, Atlantic Sharpnose Sharks, Pigeye Sharks, Port Jackson Sharks, and Bonnetheads.

In larger estuaries, different shark species may occupy different parts of the system. In Winyah Bay in northeastern South Carolina, one of the largest estuaries on the Atlantic Coast, as many as ten species of sharks in an array of sizes and ages are commonly found in the warmer months. Larger species (greater than 5.7 ft or 1.75 m) include Lemon Sharks, Bull Sharks, Sandbar Sharks, Finetooth Sharks, Spinner Sharks, and Blacktip Sharks. Adults of smaller species, including Atlantic Sharpnose Sharks, Blacknose Sharks, and Bonnetheads, also inhabit the system. Juvenile Sandbar Sharks take advantage of their ability to tolerate the lower salinities, an adaptation that most adult sharks (even Sandbar Sharks) lack, to occupy the middle bay region, where it is much less salty. This juvenile adaptation—tolerance of low salinities—allows them to use the area as a refuge from the predation of most larger sharks.



Of the remaining coastal habitats, the harshest is the zone nearest the beach. Beaches are high-energy, dynamic, unstable environments with coarse sediments, a perfect storm of harsh factors that limit the abundance of both sharks and their prey. Schools of small fish, known as *bait balls*, will attract Blacktip Sharks, Sandbar Sharks, and others near the beach, often creating exciting theatrical displays of huge splashes and charging shark bodies piercing the surface in pursuit of a meal.

Kelp forests, large offshore areas of fast-growing algae that flourish in clear, primarily shallow water, are very productive environments that provide important habitat for a variety of sharks. These include, in different locales, Horn Sharks, Leopard Sharks, Swell Sharks, Pyjama Sharks, Happy Eddie Shysharks, and Broadnose Sevengill Sharks.

Sharks found in other temperate-water coastal ecosystems—for example, on live bottoms—include Spiny Dogfish, Pacific Spiny Dogfish, Leopard Sharks, Dusky Smoothhounds, Tiger Sharks, hammerheads, and a large number of requiem sharks.

Common and Scientific Names

Where I grew up, on the coast of the Southeastern United States, I thought there were only three kinds of sharks: "sand sharks," Blacktips, and hammerheads. To this day, many residents and visitors to the area think similarly. In actuality, the number is two dozen or more, depending on the area. And herein lies the danger of using common names: because the same common name is frequently used for several species, they deny an organism—with its own distinct genes, life history, behavior, and distribution—its earned unique identity, and the consequences from this could be endangering.

In science, *species* refers to organisms that freely breed with each other and that produce viable offspring capable of producing their own offspring at some point. There are currently about 541 distinct species of sharks, although more are likely to be discovered using modern molecular techniques, or as the deep sea is better explored. Each species has a unique two-part scientific name. Almost every species also has one or more common names, even in the same locality. The hammerhead sharks of my youth could have been one of five different species. But we considered them all one species—hammerheads—and blissfully ignored the biodiversity.

Recently, common names for a large number of sharks have been standardized. The accepted common names of the hammerheads of my youth are Bonnethead, Scalloped Hammerhead, Smooth Hammerhead, Great Hammerhead, and Carolina Hammerhead. Note that the first letters are upper case, which is not yet a universal convention—although it should be! (Why do we capitalize the first letters of corporations but disrespect our sharks, trees, and so on?) Also note that, for these sharks, the word "Shark" is not a part of the common name, nor is it for Shortfin Makos, Sand Tigers, and a few others.

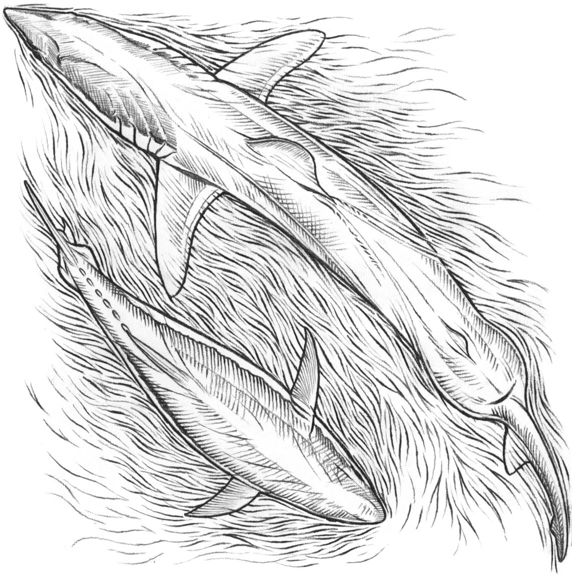
How can using common names endanger sharks? Spiny Dogfish (*Squalus acanthias*) and Dusky Smoothhounds (*Mustelus canis*), discussed earlier in the entry for "Catsharks and Dogfish," overlap in their distribution along the US Atlantic Coast and, to many, resemble each other. Prior to 2002, both were heavily fished and were caught, occasionally in mixed schools, on the same fishing gear. For fishery statistics, which are invaluable to fishery managers and conservation biologists in regulating any fishery, both species were considered in a single category, *dogfish*.

Lest you think classifying them together was innocuous, consider this: The two species are in different superorders (Spiny Dogfish are squalomorphs, and Dusky Smoothhounds galeomorphs), groups that diverged about 210 million years ago. More significantly, their life history characteristics are drastically different. It takes Spiny Dogfish as long as 20 years to mature, after which they give birth to only 4–6 pups every other year, after a two-year (!) gestation period. Smooth Dogfish, aka Dusky Smoothhounds, are at the other extreme. They mature in only three years and have an average of 12 pups annually after a gestation period of 8–9 months. The northwest Atlantic stock of the former species plummeted before fishing was restricted and after a period of rebuilding, mature females and pups have declined again from overfishing. Smooth dogfish also have catch limits and the fishery appears sustainable for now.

One final point: *Carcharodon carcharias* is the White Shark, not the *Great* White Shark. We all know its greatness without that reminder!

Convergent Evolution

Organisms that are not closely related, or perhaps are even in different taxonomic phyla, sometimes have similar anatomical, behavioral, or physiological adaptations. In some of these cases, where ancestors of the different groups lacked the adaptation, these similarities are evidence of *convergent evolution*. Convergent evolution can be thought of as distantly related organisms enhancing their survival in analogous ways. Traits that are the result of convergent evolution are fascinating and they foster a deeper understanding of the traits involved. At the same time, these traits are of little use in understanding an organism's evolutionary history and current relationships. To understand these issues, *homologous* traits—those that result from common ancestry—are required.



There are copious examples of convergent evolution in nature, the most recognizable being the presence of wings among diverse animals such as birds, bees, flying fish, bats, and so on.

The most superlative example of convergent evolution in fishes, including sharks, is the suite of adaptations associated with high-performance swimming and superior predatory abilities among three lineages: the lamnid sharks (e.g., White Shark and Shortfin Mako), the thresher sharks, and about fifteen species of scombrid fishes (tunas). These sharks and tunas are in two taxonomic classes that diverged as long ago as 450 million years.

While studying Shortfin Makos on the Pacific Ocean, I snapped a photo from above of an Albacore tuna and a Shortfin Mako posed next to each other. When the photo was developed (no digital photography then), I was stunned by the similarity of form. Both were heavily muscled, nearly perfectly streamlined oceanic projectiles with superficially similar tails and a broad, flattened, keeled posterior.

The pièce de résistance, though, is the evolution of their regional endothermy, maintaining their internal temperatures above that of their environment, a rare feat among aquatic organisms because water holds a lot of heat and removes it quickly from warmer objects, making it a challenge to be warmer than the water.

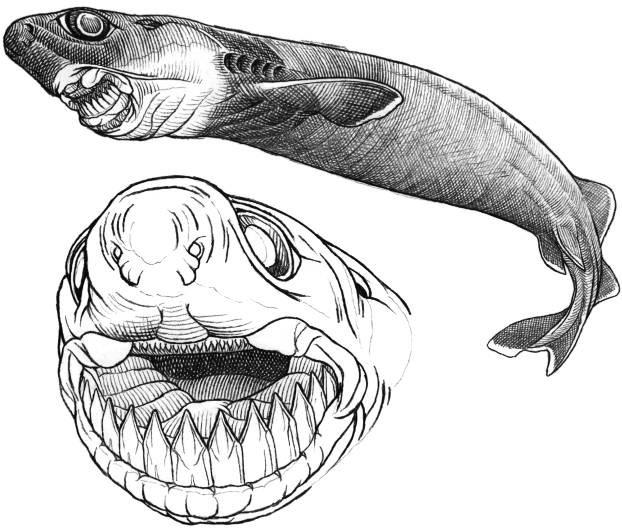
The advantages of endothermy are extreme swimming performance that enables endotherms to be highly mobile and efficient predators, and possibly to move more independently of environmental temperature than other fishes. There is also a cost: feeding the metabolic beast requires more food. But being exceptional predators takes care of that problem!

Cookiecutter Shark

Imagine you are a large, formidable, bony fish or marine mammal (or even a nuclear submarine, see below), fearlessly moving through the ocean's surface waters in the evening. Threats to your existence could come from a bigger or more ferocious predator, but none are present, so you relax and let your guard down. And what luck—lurking just above you is an unsuspecting small fish, a tasty, easy prey for such an impressive predator as you.

Bad move! The small fish is, in fact, subterfuge, a lure to attract you, and you took the bait. It is no fish at all, but actually a darkly pigmented body part that resembles the silhouette of a small fish from below, and its owner is a cigar of a shark, with a disproportionately sized set of razor-sharp, triangular lower jaw incisors and an otherworldly face, at the boundary between silly and diabolical. Were it the subject of a horror film, this shark would be the stuff of nightmares.

When you are close enough to smugly anticipate the ease with which you will catch this poor fish, it engages its supercharger and jets to you, using its powerful caudal fin, to remove a plug of your musculature with a death spiral that operates at near surgical precision.

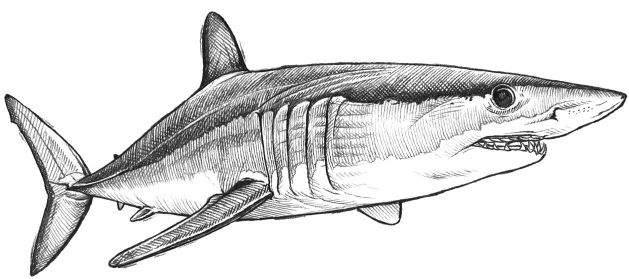


Okay, so I took some liberties with anthropomorphism and hyperbole. But there is such a shark, the Cookiecutter Shark. They are neutrally buoyant vertical migrators, and they have luminous organs that emit light that matches the ambient downwelling light, so the silhouette of the shark disappears from beneath, except for the collar on the underside—the bait that fools many an erstwhile predator.

Cookiecutter Sharks are small (up to 2 ft or 0.6 m). About those nuclear submarines? Yes, Cookiecutter Shark scars have been seen on some rubber parts of these. There are also cases of attacks on people over deep water at night off Hawaii. If Cookiecutter Sharks were common along the shore, I'd rethink evening dips!

Countershading

The name of the game in evolution is survival, and paramount to survival is finding your food and avoiding being someone else's. One common strategy in this game of life employed by sharks and other animals is stealth, and a widely used stealth method is countershading, in which the upper surface is dark and the underside light.



Viewed from below, a countershaded shark blends in with downwelling light. From above, it matches the darkness of the depths.

Numerous sharks (and other species) of the well-lit surface layer are countershaded, as are others in the deeper oceanic twilight zone. Coloration may be from skin pigmentation or bioluminescence. In both cases, a countershaded shark is less conspicuous to both predators (typically bigger sharks) and prey.

Countershading on the Shortfin Mako, with blue on top and white on the underside, is striking. Why would such a high-performance shark, capable of outswimming both predators and prey, require countershading? First, Shortfin Makos, especially juveniles, do indeed have predators, mostly larger sharks. Second, as prodigious as they themselves are as predators, any advantages that make them more successful and save energy in the process will be favored by evolution.

In addition to countershading, sharks employ other strategies, including camouflage, or cryptic coloration. Neonate Nurse Sharks, for example, candidates for the title of *most adorable shark* in anyone's book, have bars and spots that enable them to blend into their shallow water benthic habitats, and thus avoid predators who consider them more tasty than adorable.

CSI: Shark

Among the less attractive activities I have been asked to do is confirming that a wound, typically on a person's arm or leg, is in fact a shark bite. Along the northeast coastline of South Carolina, there are typically several shark bites during the summer, when humans and fast-swimming Blacktip Sharks, thought to be the culprits, coexist in the warm, murky beach shallows. Somehow the news media obtains gruesome photos of some of the wounds and, as the only nearby shark specialist, I invariably find these snaps in my inbox. Inasmuch as shark bites are not my specialty, I limit my assessment to either *yes, it looks like the bite of a shark*, or *no, you can't blame a shark for that one*. Mostly it is the former.

In another book about sharks that I coauthored in 2020, *Shark Biology and Conservation*, I relate a story about an actress in the adult film business who falsely claimed that a shark bit her during a dive. Conveniently for her, the entire episode was filmed—sharks in the water, screams, and then the actress emerging with a bloody but clean laceration. If one of the large sharks in the video had actually bitten her, it would have either removed a sizeable chunk of flesh or left a series of ragged-edge tooth punctures in an arc corresponding to the arched shape of a shark jaw—or both—but it would not have resulted in a clean, straight laceration. This "bite" was most likely self-inflicted with a sharp (but not shark) implement in the opinions of most shark biologists.

What would a trained analyst of shark bites look for, besides puncture marks in an arc? First, the bite radius can give an indication of the size of the shark. Second, the shape of the arc can be diagnostic (e.g., broad or narrow). Third, because teeth can vary among shark species, as well as between the upper and lower jaws of some species, any impressions left by the puncture marks and the spacing between can also be invaluable. Even under the best of situations, because there is no database of shark bite forensics, identifying the kind of shark responsible usually is at best an educated guess, the accuracy of which depends on the investigator's background, experience, and knowledge of local sharks. Having a museum nearby with a collection of shark jaws from local species can help as well.

Shark bite forensics is of interest beyond human bites. Sharks have been known to bite underwater cables and sonar arrays towed behind submarines. Knowing which shark was the culprit in these cases can help to deter the perpetrator from future interactions or mitigate the damage.

Daily Ration

How much does a shark eat in a day? As you might suspect, the answer varies with the species and size. And what you are really asking is, *What is a shark's daily ration?* Since species vary in their weight generally and in different life stages, daily ration is typically reported as the mean percentage of an organism's total weight consumed over a twenty-four-hour period.

Knowing an organism's daily ration is more than merely trivial information. Along with life history characteristics, understanding a shark's ecological role and metabolic needs (amount and kinds of food it must eat to do what a shark does, e.g., swim, breathe, etc.) are critical to determining its conservation status and managing it.

On average, sharks consume between 2 and 3 percent of their body weight per day, a range that varies depending on the energy demands of a specific shark species or life stage and the energy content of the prey.

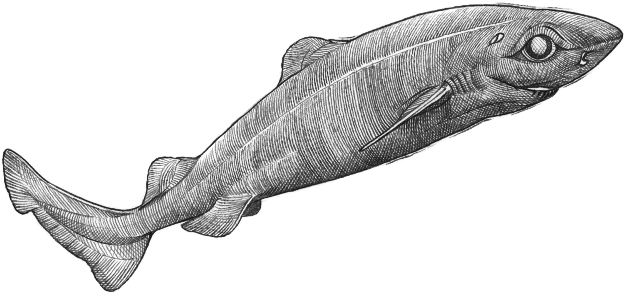
You might expect that an adult Shortfin Mako, the bravura Bugatti of blue water, might have a significantly higher daily ration than less active sharks because of the Mako's need to feed its calorie-hungry metabolic machinery. The data, however, are equivocal, with estimates ranging from 2.2–3.0 percent in one study to greater than 4 percent in another. For an average-sized Shortfin Mako of the Northeastern United States, this translates into about 1,100 lb (500 kg) of bluefish during their half-year residency.

If the unexpected lower estimates are real, the Shortfin Mako's calculated daily ration could reflect higher digestive efficiencies or more calorically dense prey. Alternatively, the data are inexact, since studying the Shortfin Mako is fraught with logistical challenges, as stated in the entry for "Elasmotunatron."

Deep-Sea Sharks

Imagine if nearly half of the planet's bird life lived at altitudes so high that eyeing one was a rare event, and birds thus remained mysteries to the public and scientific communities. Such is the case with deep-sea sharks. That very proportion of shark species inhabit the deep sea, which is generally defined as depths below 660 ft (200 m).

Our lack of scientific understanding of deep-sea sharks is both logistical and economic. Large ships are expensive to operate, costing up to tens of thousands of dollars a day. While submersibles are in wide use in deep-sea industrial applications, only a handful are available for scientific exploration and, you guessed it, these are expensive as well. That leaves the last resort as



commercial fishers, not all of whom are willing or able to share their data.

It should not be surprising that such a large diversity of sharks occupies the deep sea, since it is the largest ecosystem on the planet. In the mesopelagic zone, between 660 ft (200 m) and 3,300 ft (1,000 m), sharks are the dominant predators.

Abundant living space, however, does not necessarily equate to hospitable conditions. The deep sea is cold, dark, and the hydrostatic pressure is high. At 6,500 ft (2,000 m) deep, the pressure is not unlike the entire weight of a moose balancing on your nose. Finally, major sections of the deep sea are food-poor environments. Because the environmental features of the deep sea (pressure, temperature, salinity, and light levels) are similar over wide vertical and horizontal expanses, many shark inhabitants have very broad, sometimes global, distributions.

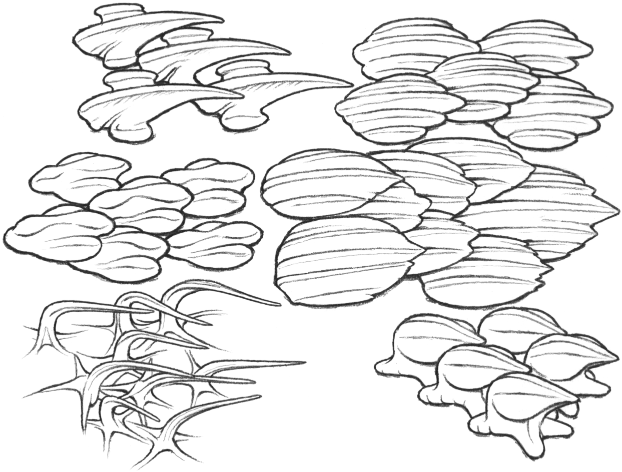
Living in the cold, dark, pressurized, food-poor deep sea environment means evolving adaptations to conserve energy, maintain internal function under extreme conditions, locate prey, avoid being prey yourself, and find mates. These adaptations translate into physical, physiological, and behavioral departures from the fast-swimming, large-bodied, gray coastal shark cousins; deep-sea sharks look different and, in some cases, un-sharklike.

Adaptations among deep-sea sharks to their unique suite of environmental challenges include specialized eyes, photophores (for bioluminescence), lower metabolic rates and activity levels, varieties of teeth that ensure that prey, once captured, do not escape, and year-round breeding.

Sharks of the mesopelagic zone include Cookiecutter Sharks, Goblin Sharks, Frilled Sharks, Gulper Sharks, Dwarf Lantern Sharks, and Cuban Dogfish. Beneath this zone are Portuguese Dogfish and Bluntnose Sixgill Sharks. The depth record for sharks is held by the Portuguese Dogfish, about 12,000 ft (3,700 m), which is noteworthy because at depths below approximately 9,800 ft (3,000 m), the oceans are almost completely devoid of sharks. Explanations for this absence include limited food resources and the inability to synthesize important chemical compounds under the high ambient pressures.

Dermal Denticles

Like bony fishes, the bodies of sharks are covered with scales, specifically *placoid* scales, or *dermal denticles*. These are essentially miniature teeth, with an inner pulp cavity, surrounding layer of dentin (hard, calcified tissue), and a hardened outer layer of enamel. Like their teeth, dermal denticles are shed and replaced, although more slowly.



The scales of bony fishes differ in that they contain mineralized bone and are permanent.

Scales have different functions among sharks, including reducing drag while swimming, protecting against ectoparasites, and safeguarding females from male bites during mating season. Scales vary in size, shape, flexibility, and even coverage in sharks. Bramble Sharks, for example—large, sluggish, poorly known deepwater sharks—have large scales scattered over their body. Spines on the fins of sharks and the whiplike tail of stingrays are modified dermal denticles that are primarily defensive in nature, although in sharks they may have a hydrodynamic function as stabilizers.

The drag-reducing function of the dermal denticles was the inspiration for a full body swimsuit, the Fastskin FSII, developed by Speedo in 2014. Reducing drag, the major force that slows moving objects, is the name of the game in swimming for both sharks and elite competitive swimmers. The Fastskin FSII was marketed as a revolutionary, performance-enhancing body covering that significantly reduced drag. According to Speedo, the fabric channeled water smoothly from front to back along the swimmer's body, in much the same way that the ridges and grooves of a shark's dermal denticles were thought to do. Although the suit produced faster swimming speeds, humans do not swim like sharks, so further investigation of the fabric's mechanism of action is warranted.

Diet

The public perceives that sharks are indiscriminate eaters with insatiable appetites. There is some truth to the former, at least among some species that are opportunistic or generalist predators, but the latter is myth.

Selection of prey often varies on multiple time and space scales. Most sharks are generalists with diverse diets. When prey abundance or choice changes, they can switch prey types. Numerous studies support the conclusion that sharks will consume the most abundant prey available. When we longline for sharks for research, education, and conservation, at times of year when small baitfish like mullet, menhaden, or spot are very abundant, we often catch few or no sharks, when at other times we'd catch ten or more. They forage on the baitfish more so than our bait. Wouldn't you prefer fresh to frozen?

Some shark species specialize in certain prey types. For example, Horn Sharks feed primarily on hardshelled mollusks and crustaceans, Dusky Smoothhounds prefer crabs (especially recently molted crabs—talk about finicky eaters!), Frilled Sharks eat mostly squid, and Bonnetheads selectively devour Blue Crabs.

How do scientists know what sharks eat? Two approaches are most often used: analysis of gut contents and stable chemical isotope ratios. In the former, which is still the most robust method for studying a shark's diet, the stomach contents of dead sharks are removed in the field, preserved or frozen, and then identified in the lab, a meticulous process that might require identifying a species of fish by the presence of a few bone fragments. Flushing the gut contents from the digestive track of living sharks with water, called *stomach lavage*, is also practiced, followed by release of the live shark. *Don't try this at home!*

The second method, analysis of stable isotopes, assumes that *you are what you eat*. All that is needed is a small muscle plug, blood sample, or piece of skin, after which the shark can be released. Analysis of these isotopes can provide information on the shark's trophic level and whether the shark is feeding in a benthic or pelagic food web. A major weakness, however, is not identifying the actual prey species.

Finally, you can infer much about the diet of a shark from the morphology of its jaws and teeth. Sharks like Blacktips and Sandbars have narrow, cusped lower teeth for grasping prey, whereas the upper teeth are slightly wider with lateral, sharper edges that allow them to slice prey into pieces. Bull Sharks have triangular upper teeth for cutting bigger chunks from larger prey. The horn sharks have cusped teeth up front, molariform (flattened) teeth in the back, and hypertrophied jaw muscles for crushing snails, urchins, and crabs.

Many sharks switch their prey as they grow (this is known as *ontogenetic diet shifts*). The Shortfin Mako swallows some of its prey whole (bony fishes and cephalopods, predominantly), but as they age, their teeth become broader and flatter, enabling them to widen their prey options to include organisms too large to swallow whole but from which they can remove a chunk of flesh (e.g., Swordfish, tuna, sharks, sea turtles, and marine mammals).

Finally, no species of shark includes humans as regular menu items, but you knew that already.

Diversity of Sharks

This book has repeatedly referred to the 541 known species of sharks. If we include their close cousins, the batoids and chimaeras, the number rises to around 1,300, or 1.7 percent of known living vertebrates. However, shark taxonomists do not honestly know how many species there are. The number is increasing due to modern molecular techniques that distinguish between species closely resembling each other, as well as increased sampling in the deep sea and remote coastal regions.

Sharks have indeed been successful, but before we shark enthusiasts become smug about their success, consider that the dominant aquatic vertebrates are the approximately 38,000 kinds of bony fishes. Species of catfish are even more numerous: there are about four thousand, which is more than sharks, batoids, and chimaeras combined.

(continued...)