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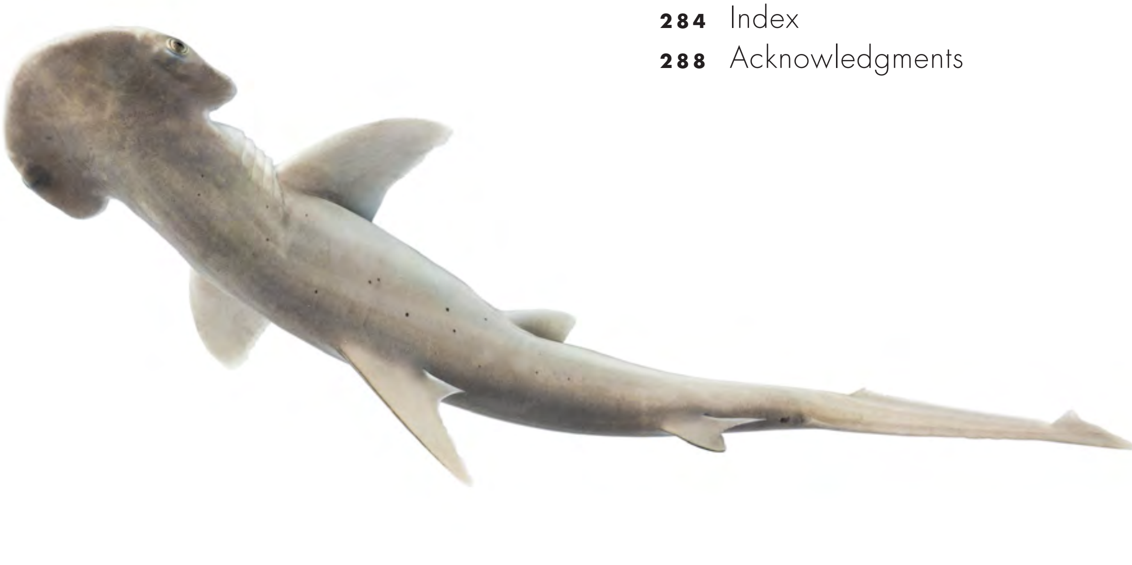


GINGLYMOSTOMA CIRRATUM

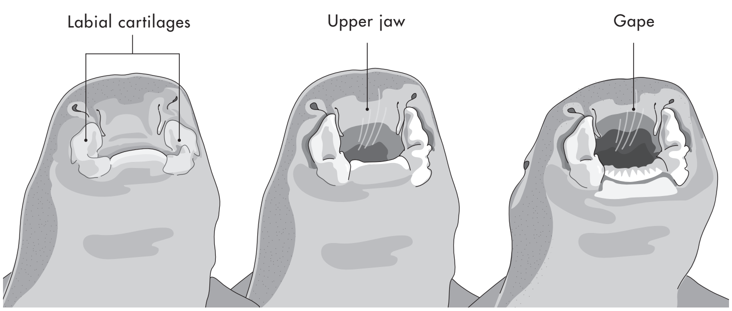
Nurse Shark

Bottom-dwelling suction feeder

SCIENTIFIC NAME	*Ginglymostoma cirratum*
FAMILY	Ginglymostomatidae
NOTABLE FEATURE	Nasal barbels; first dorsal fin above, or posterior to, pelvic fins
LENGTH	10 ft (3 m)
TROPHIC LEVEL	Nocturnal mesopredator of small fishes and invertebrates

The Nurse Shark is a nocturnal species, so if you've seen one in an aquarium or in the wild, chances are it was motionless, perhaps under a ledge. You may have heard the notion that sharks must continually swim or they will die, in part because they are incapable of pumping water over their gills if not in motion. While this perception is true for many of the more familiar shark species (which would also sink if not moving), benthic sharks and some others are indeed capable of pumping water to irrigate and oxygenate their gills.

The Nurse Shark (not to be confused with the Australian Grey Nurse Shark, *Carcharias taurus*, which is a member of another family) is an inshore benthic (bottom-associated) species that grows to about 10 ft (3 m) in length. It is widely distributed in tropical and subtropical coastal ecosystems. The species is remarkable in that it has extremely powerful jaw musculature, which it uses to suction feed on a diet of mainly small fish, crustaceans, and mollusks. If a hungry Nurse Shark encounters a Queen Conch (*Aliger gigas*), a large snail with a thick shell that deters most predators from the notion of crushing it, the shark positions its mouth over the snail's shell opening and applies suction strong enough to extract and inhale the soft animal from its protective shell—an act that you would be incapable of achieving with your hands. It then proceeds to macerate the snail through a series of bite-and-spit maneuvers that result in a sufficiently softened, bite-sized morsel that is suitable for swallowing.



Highly evolved feeding technique
Underside of the head of a Nurse Shark expanding the space inside its mouth. Doing this creates suction, which it uses when foraging. From left: the mouth is closed prior to feeding; the lower jaw drops and the labial cartilages protrude; maximum suction is created as the gape expands.

→ A Nurse Shark on a coral reef, Saba, Caribbean. The Nurse Shark is durophagous (eats hard-bodied prey) and uses a suck, crush, spit, and repeat mode of feeding. If provoked, it can attach itself to a person and may be nearly impossible to dislodge.

CEPHALOSCYLLIUM VENTRIOSUM

Swell Shark

Shark water balloon

SCIENTIFIC NAME	*Cephaloscyllium ventriosum*
FAMILY	Scyliorhinidae
NOTABLE FEATURE	Flattened head with short snout, spotted body with dark saddles
LENGTH	3.3 ft (1 m)
TROPHIC LEVEL	Nocturnal mesopredator of small fishes and invertebrates

The relatively small Swell Shark (it reaches 3 ft/1 m in length) is not an apex predator, and in fact is named for its predator-avoidance behavior. This sees it making a water balloon out of its body by actively and quickly swallowing seawater to inflate itself. It may also grab its own tail while it doubles in size, making it more difficult for smaller predators to bite. If the shark expands while under a ledge, it is capable of wedging itself there such that it cannot be dislodged. This ability to swallow water and increase in size is unique among the sharks. If a predator does eat a Swell Shark, it may be disappointed by the weakly muscled body of its chosen meal.

Another fascinating adaptation of the Swell Shark, along with its relative the Chain Catshark (*Scyliorhinus retifer*), is that it can glow, or biofluoresce, reflecting bright colors when exposed to certain light. This differs from bioluminescence, which is actual biological light production, as seen in lantern sharks (page 78). However, in both cases the species apparently exhibit a unique pattern of fluorescence or luminescence that could allow them to communicate with other individuals, attract prey, or perhaps camouflage themselves.

Swell Sharks live exclusively in the eastern Pacific Ocean in relatively shallow water (typically at depths of less than 130 ft/40 m). They belong to the family of sharks called cat sharks, which are oviparous (egg-layers). The female Swell Shark produces egg cases with long tendrils, which become wrapped around kelp to hold the egg case in place for the 12 months or so it takes the pup to develop and hatch.

→ A Swell Shark off the California coast. The species belies the reputation of sharks as fearsome, as it is known for its predator-avoidance behavior more so than its predatory prowess.

SPHYRNA MOKARRAN

Great Hammerhead

Uniquely adapted head

SCIENTIFIC NAME	*Sphyrna mokarran*
FAMILY	Sphyrnidae
NOTABLE FEATURE	Cephalofoil (head) with straight anterior margin, high first dorsal fin
LENGTH	16 ft (5 m)
TROPHIC LEVEL	Top predator of bony fishes, sharks, and batoids

If any sharks could be considered otherworldly, the hammerheads certainly fit that category. Among the members of the hammerhead family (Sphyrnidae), the most iconic is the Great Hammerhead. Hammerheads are named for their laterally expanded heads, which are called cephalofoils, in recognition of their resemblance to airfoils (airplane wings) and the perception that they provide lift to the shark in the same way wings do for an airplane. The head owes its odd shape to expanded lateral cartilage underneath the skin.

→ A Great Hammerhead highlighted against a colorful Caribbean sky. Their unique head, called a cephalofoil, may confer advantages in the areas of swimming, maneuverability, and locating and handling prey.

For such an odd and unique shape like the cephalofoil to evolve and be retained in a group of sharks, it must have some overarching adaptive value—in other words, it must help the shark survive in its environment. Determining exactly how this feature confers some advantage to its owner is not an easy task, but it seems the widened head serves as scaffolding that can distribute the head's sense organs over a wider distance. For example, researchers have shown that hammerheads have a wider surface for electroreception and better binocular vision compared to other sharks. The cephalofoil also makes the shark more maneuverable by narrowing its turning radius, but this comes at a cost as the large head also provides lift to the front of the shark. This lift is balanced by having relatively small pectoral fins and an elongated upper lobe to the caudal fin. Finally, hammerheads have been observed pinning down one of their favorite foods, stingrays, to the seabed with their head while they maneuver to bite the prey.

The Great Hammerhead inhabits tropical and warm-temperate seas from the surface to a depth of 900 ft (275 m), and can grow to more than 16 ft (5 m) in length. It produces live offspring that are nourished through an umbilical connection to the mother during development, analogous to placental birth in mammals.

CETORHINUS MAXIMUS

Basking Shark

Gentle giant

SCIENTIFIC NAME	*Cetorhinus maximus*
FAMILY	Cetorhinidae
NOTABLE FEATURE	Large gill slits, conical snout, caudal keels, small teeth, huge mouth
LENGTH	40 ft (12 m)
TROPHIC LEVEL	Planktivorous

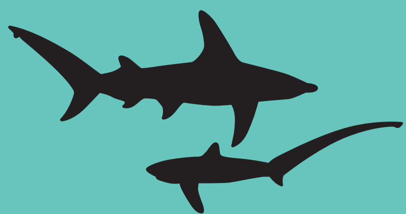
The Basking Shark is second only to the Whale Shark (*Rhincodon typus*; page 144) in the list of the world's largest sharks, but it takes no back seat when it comes to having the largest mouth—its gape can exceed 3 ft (1 m) in width. A shark that can reach 40 ft (12 m) in length and be equipped with a huge mouth could be terrifying, but this giant is actually one of only three species of shark that feed on plankton, and that huge mouth has only a few rows of tiny hooked teeth.

Named after their tendency to "bask" on the ocean surface, Basking Sharks feed actively near the surface, moving through dense patches of zooplankton with their mouth open. Huge volumes of water (and plankton) pass through their gill rakers, which sieve out the plankton and allow the water to exit through extremely large gill slits. Although Basking Sharks are referred to as coastal–pelagic inhabitants of cool-temperate oceans, they have been documented migrating thousands of miles following patches of zooplankton. Some individuals have even been tracked traveling from Massachusetts in the United States to Brazil. Researchers have also discovered that Basking Sharks don't always remain near the ocean's surface, and have tracked them diving to depths of more than 3,000 ft (900 m).

Reproduction in Basking Sharks is similar to that of the Shortfin Mako (*Isurus oxyrinchus*; page 74), with developing embryos relying on unfertilized eggs for nourishment. Basking Shark pups are believed to be 5–6 ft (1.5–1.8 m) long at birth, making them likely the largest of all shark neonates.

Basking Sharks were heavily hunted for their meat, livers (which are rich in oil), fins, and even their skin, for use as a leather called shagreen. As a result, their numbers dropped dramatically and harvest and trade of the species is now heavily restricted in many countries.

→ A Basking Shark in full filter-feeding mode, with plankton-laden water moving into its prodigious gape and exiting its huge gill slits. Staying afloat at the surface while foraging is facilitated by a deceptively fast swimming speed (about 3 ft, or 1 m, per second) and a large, buoyant liver comprising as much as 25 percent of its body weight.



ADAPTATIONS OF SHARKS

Shark anatomy

Like tuna, salmon, and minnows, sharks are fish: aquatic vertebrates with gills for respiration and fins for swimming. As discussed in the previous chapter, sharks and their relatives are distinguished externally from the other major group of fishes, the bony fishes, by having 5–7 external gill slits and an asymmetrical caudal fin. Other external characteristics, however, are similar to those of bony fishes.

SHARK FINS

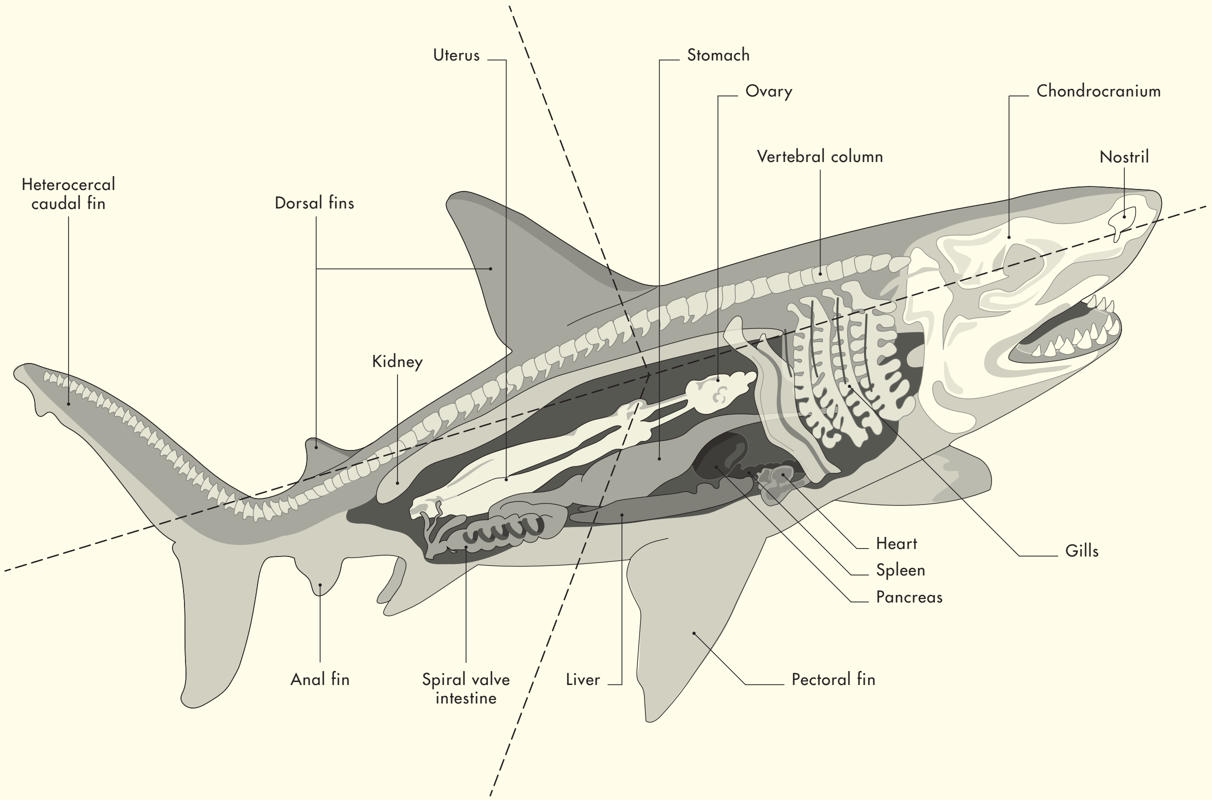
Sharks have two sets of paired fins, the more forward pectorals and the more posterior pelvics. They also have median fins along the body's midline. These include either one or two dorsal fins, which may have spines on their leading edge, and, in most groups, an anal fin. Some groups—for example, the cow sharks—have lost a dorsal fin through evolution and have only one. Fins serve a variety of functions in sharks, not all of which are apparent and not all of which are the same in every species. What shark biologists do know about the roles of fins comes mainly from a limited number of studies on inanimate models and a few smaller species capable of living in captivity. The latter include the Leopard Shark (*Triakis semifasciata*), Spiny Dogfish (*Squalus acanthias*; page 264), and Whitespotted Bamboo Shark (*Chiloscyllium plagiosum*; page 238), none of which is broadly representative of the wide range of lifestyles of sharks.

One major role fins play is to stabilize the shark when it is in motion, preventing it from rolling (spinning in a circle along the long axis of the body), yawing (moving from side to side), and pitching (moving up and down). The dorsal fins and, to a lesser degree, the anal fin, serve primarily as keels. The pectoral fins control pitch and roll, and possibly yaw, and the pelvic fins also play a role in pitch control.

Fins are also important for maneuverability in sharks. No shark is capable of swimming backward in the way that bony fishes can (dragging a shark backward with a boat, as some fishers are known to do, damages its gills and is often fatal). However, some benthic species such as the Epaulette Shark (*Hemiscyllium ocellatum*) can move backward when in contact with the substrate. While their main propulsion for swimming comes from the caudal fin,

OTHER ANATOMICAL ADAPTATIONS

Since all sharks use internal fertilization, males have paired claspers on the inner margins of their pelvic fins (page 26). Inside the shark is the standard suite of vertebrate organs. A four-chambered heart rests inside the pericardial cavity, near the anterior of the shark. In the abdominal cavity are the organs of digestion and reproduction, the liver being the largest of these. In addition to its central role in metabolism, this oil-filled organ adds buoyancy that compensates for the heavy musculature of most sharks.



Selected internal anatomical features of a typical female shark

The heart, located slightly behind the gills, pumps blood to the gills, before being distributed to the rest of the body. Food enters the mouth, then traverses the various parts of the digestive tract, including the esophagus, stomach, and spiral valve intestine, before waste is eliminated at the cloaca. The liver, the largest organ in the shark, lies under the digestive organs.

← Two Scalloped Hammerheads (*Sphyrna lewini*) swimming in the Red Sea off Egypt.

Epaulette Sharks can crawl along the seafloor and even when emerged between tide pools, using their pelvic and pectoral fins. Skates are also capable of crawling on the seafloor using modifications of their pelvic fins, a phenomenon known as punting. Could these adaptations signify an unrecognized evolutionary trend that may have led to the development of limbs among vertebrates? Unfortunately, no. While limbs indeed developed from fins, it is the lobe-finned fishes, with living relatives that include the lungfishes and coelacanths, that are responsible for the emergence of limbs.

Although the fins of sharks have evolved to become less rigid, they are still stiffer than those of bony fishes. This stiffness, plus the limited flexibility of a shark's vertebral column and the tightness of its skin, limits how tightly some species can turn. That said, species such as juvenile Scalloped Hammerheads (*Sphyrna lewini*), Lemon Sharks (*Negaprion brevirostris*; page 230), and Bluntnose Sixgill Sharks (*Hexanchus griseus*; page 38) are all flexible enough to bite their own tails.

THE SHARK HEAD

The head of sharks houses the sensory organs, including eyes, nostrils, external ear openings (yes, sharks have ears!), and a series of gel-filled pores called ampullae of Lorenzini (page 26). Together with the lateral line, which runs the length of the body on both flanks, these senses enable sharks to interpret their surroundings and respond appropriately. Specifically, they help them detect prey, predators, members of the same species (including potential mates), other organisms, and objects that may be obstacles. They also help sharks orient themselves and even migrate. Benthic and other sharks (such as the dogfishes) have paired, bilateral openings behind the eyes called spiracles (actually modified gill arches) that connect the mouth to the water environment and allow the gills to be irrigated with seawater when the mouth is closed.

↑ A Scalloped Hammerhead amidst a school of fish in waters off Australia.

↖ A Triton Epaulette Shark (*Hemiscyllium henryi*) in the Indo-Pacific Ocean near West Papua, Indonesia. Epaulette sharks live in shallow reef habitats and often crawl on the bottom and even over emergent rocks and coral.

→ A pair of Lemon Sharks (*Negaprion brevirostris*) skim the surface of the water in a synchronous dance off Grand Bahama. Their lateral lines and other senses enable these coordinated movements at close distances.

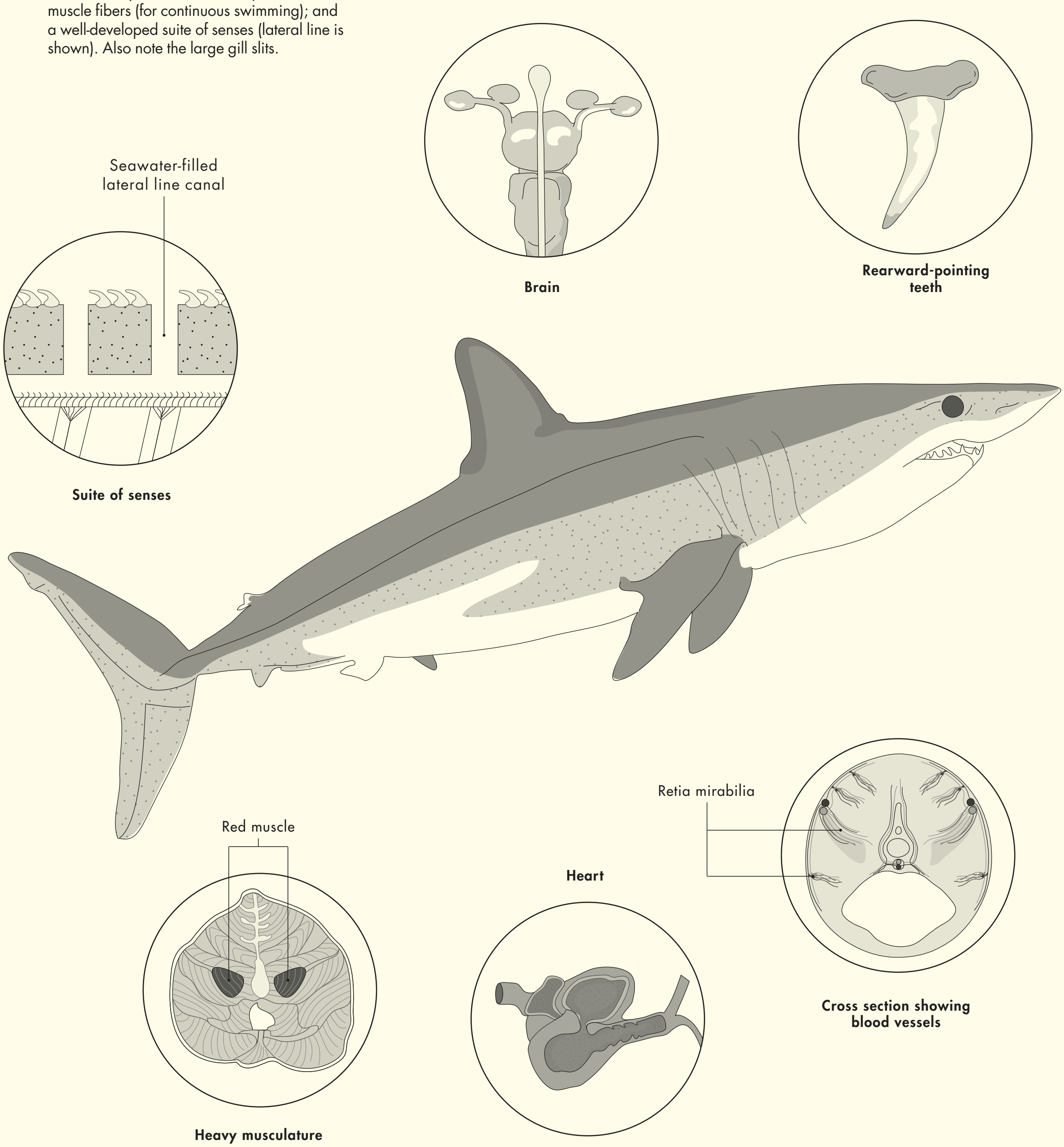
The most magnificent fish in the sea

Some of the most fascinating aspects of shark biology are the adaptations that make them such superlative predators. Adaptations refer to aspects of an organism's anatomy, physiology, and behavior that help it survive in its environment and that are hereditary. The Velvet Belly Lanternshark (*Etmopterus spinax*; page 78), for example, uses bioluminescence on its ventral side as a form of counterillumination so that it is hidden from potential predators beneath it. In sharks, paramount among these is their superior ability to locate their prey and catch it, such as the use of sensory barbels and the elongated, blade-like toothed rostrum of the Sixgill Sawshark (*Pliotrema warreni*).

BUILT TO HUNT

A candidate for paragon of predatory sharks, the ultimate marine predator, is the Shortfin Mako (*Isurus oxyrinchus*; page 74). This species is a blue-water shark, meaning that it lives in the open ocean, with its vast spaces and relative low abundance of prey. The Shortfin Mako has an array of senses, as well as a large brain for collecting and processing sensory information. Once prey—say a Bigeye Tuna (*Thunnus obesus*)—is located, the mako's streamlined body enables it to glide smoothly and stealthily through the water to reach it. To help avoid detection by its prey as it approaches, the shark has countershading, with blue on top and white on the underside. This allows it to blend into both the downwelling surface light when it is viewed from below, and the deep-blue darkness when viewed from above.

← A Shortfin Mako (*Isurus oxyrinchus*) escapes its watery confines to feed on a piece of bait near Cape Point, South Africa. Its large eyes, ampullae of Lorenzini (pores on the snout), and nostrils all play roles in its superior prey-finding ability.



The makings of a high-performance predator

Characteristics that contribute to the predatory prowess of the Shortfin Mako. Clockwise from the top: a relatively large brain; rearward-pointing dagger-shaped teeth; networks of intermingled blood vessels known as retia mirabilia that work to conserve heat and thus warm the body; a heart larger than that of most other comparatively sized sharks; heavy musculature with prominent red muscle fibers (for continuous swimming); and a well-developed suite of senses (lateral line is shown). Also note the large gill slits.

On the Shortfin Mako's approach, its crescent-shaped caudal fin provides the optimal combination of constant thrust and acceleration. And its huge gill slits hide a very large set of gills, which capture essential oxygen from seawater for the body's high-performance aerobic metabolic engine. Once the prey is captured, it will likely be swallowed whole, its escape thwarted by the backward-pointing teeth of the Shortfin Mako's impressive jaw.

METABOLIC ADAPTATIONS

Underlying the Shortfin Mako's adaptations for predation is an additional and extremely unusual feature for a fish: the ability to keep its body warmer than the surrounding water. Most cartilaginous and bony fishes are ectotherms, meaning that their internal body temperature is the same as the environment's. The thermal properties of water make it extremely difficult for aquatic animals to retain their body heat, which is why an air temperature of 70°F (21°C) feels comfortable to us, but water of the same temperature is considered dangerous and will lead to hypothermia in as few as three hours because it draws away your body's heat. Marine mammals successfully keep warmer than the water in which they reside using blubber and fur, neither of which is available to fishes. Fishes are further disadvantaged: their body heat is readily lost to the water when their blood traverses their thin-walled gills to obtain oxygen.

Two groups of fishes—the five species of mackerel sharks (which include both species of mako, White Shark (*Carcharodon carcharias*; page 106), Porbeagle (*Lamna nasus*; page 110), and Salmon Shark (*Lamna ditropis*; page 136), as well as the tunas and members of five other fish families—have evolved specializations to retain some of the heat that would

← A Shortfin Mako in its splendorous entirety, a high performance beast of a shark as magnificent as it is deadly to its prey.

otherwise be lost to their environment. They do so using an elegant engineering principle called countercurrent exchange. In simple terms, the blood that is warmed by heat generated by muscles deep in the body as they work to propel the shark moves in a series of vessels that run straight from the interior near the backbone to the surface. These vessels are juxtaposed with other blood vessels that carry cooler blood from near the outermost parts of the shark straight back to the interior. As the warmed blood moves adjacent to the cooled blood, the heat is transferred from the former to the latter, trapping it inside the shark's body. Through this adaptation, a Shortfin Mako's body temperature can be elevated by as much as 14°F (8°C) over that of its environment.

This metabolic machinery, combined with a high-performance cardiovascular system, enables the Shortfin Mako to have more powerful muscles and thus swim faster. A warm body also allows it to move more independently of seawater temperature than ectothermic sharks, and it improves the acuity of the shark's senses, in part by speeding up the nerve impulses from the sense organ to the central nervous system, where the sensory signal is also processed faster.

Alas, there is no such thing as a free lunch, and maintaining a warm body in seawater comes at a cost. The metabolic furnace that provides the surplus of heat—specifically the muscles—must be fed constantly. But we're talking about a magnificent, super-efficient beast of a fish here, so eating up to 4 percent of its body weight each day is not a chore.

Behind the myth of shark senses

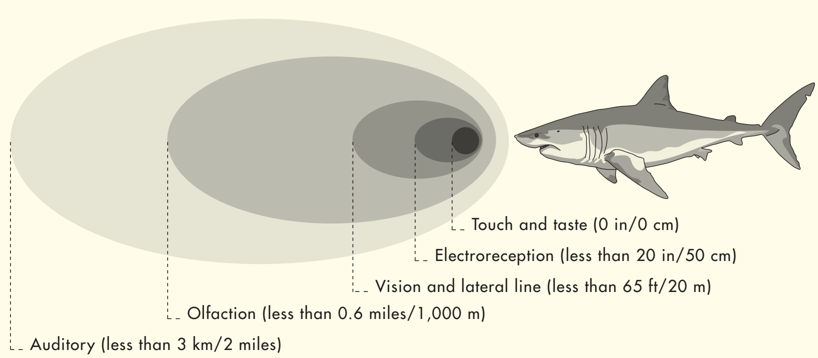
You may have heard sharks being referred to as "swimming noses," a reference to their superior sense of smell. Like many assertions about sharks, there is both truth and myth in this statement. The nose of sharks—paired nostrils on the underside of their snout—is sensitive to smells associated with certain chemicals at relatively low concentrations, such as proteins emanating from a wounded fish. Two caveats about shark smell are in order here: first, in most cases a shark's sense of smell is no more acute than that of an ecologically similar bony fish; and second, smell is only part of the shark's sensory repertoire, and its senses exist in a hierarchy.

THE SENSITIVE TYPE

The ocean is full of sensory information. A shark may use some of this information to find prey, avoid predators, find a mate, avoid unhealthy environments, navigate around obstacles, or even migrate over great distances.

Let's consider locating prey—in this example, an injured fish that has escaped from another predator or that was speared by a diver. Sharks are most sensitive to irregular, low-frequency sounds, such as those emitted by a struggling fish. These sounds might register in the inner ears of a shark as much as 2 miles (3 km) distant. As the shark orients to and swims toward these sounds, it might pick up the scent trail from the bits of tissue and fluid emanating from the wounded fish about 1,000 yd (1 km) away, providing it is downstream of the prey. As the shark swims in and out of the odor corridor, it detects the strongest scent and moves in that direction. Then, when it has closed the distance between itself and the targeted prey to about 65 ft (20 m), and assuming the water is clear, it may use its vision to locate the prey. This is fortunate, since smell and sound can be confusing sensory signals close to the prey.

← A Sand Tiger (*Carcharias taurus*) noses its way through a massive baitball of tiny fish off the coast of North Carolina. These baitballs sometimes conceal the sharks in their midst and provide a measure of stealth to the predator.



Hierarchy of a shark's sensory system

An overview of the senses used by a shark to locate prey based on distance from the stimulus (sound, smell, water movement, sight, bioelectrical field, and taste).

← A White Shark (*Carcharodon carcharias*) feasts on a marine mammal carcass, a fortuitous find that provides high-quality nutrition to feed the shark's demanding metabolic machinery. The shark's eyes have reflexively rolled back, exposing the white, tough, fibrous protective sclera.

→ Two juvenile Port Jackson Sharks (*Heterodontus portusjacksoni*), a horn shark common in southern Australia. Should a predator such as an angel shark (*Squatina*) conclude that one would make a delicious snack, it should think again: the stout spines on the dorsal fins make all nine species of horn sharks unpalatable, even dangerous, to most predators.

The aromas of a great restaurant and the clinking and sizzling sounds emanating from its kitchen may draw you inside, but once there, these signals alone won't guide you to the source of the food.

Vision will take a shark to within 1.5 ft (50 cm) of the prey, and its lateral line will also detect the struggling fish. But the sensory environment can still be confusing at close distances, especially when the shark opens its mouth immediately in front of the prey. At that point, movement of its head may enlarge its natural blind spot or, in many sharks, protective eyelids called nictitating membranes rise to cover the eyes. In White Sharks, the entire eye rolls 180 degrees in the socket, exposing the whites. Again, sharks have this situation covered, since their ampullae of Lorenzini, a series of gel-filled pores on shark heads (page 26), detect the minute electrical field of the hapless prey, and gulp, it is history.

What happens if the shark makes a mistake and the prey's tissues are poisonous? Sharks have this situation well in hand too, since taste buds lining their mouth sample the fish and can instantaneously decide if the prey is suitable. If not, it is rejected. These taste buds may account for bite-and-release shark interactions where, say, a Blacktip Shark (*Carcharhinus limbatus*) mistakes a swimmer's feet for a swimming fish, only to be informed by its own taste buds to release and move on.

HEARTLESS HUNTERS?

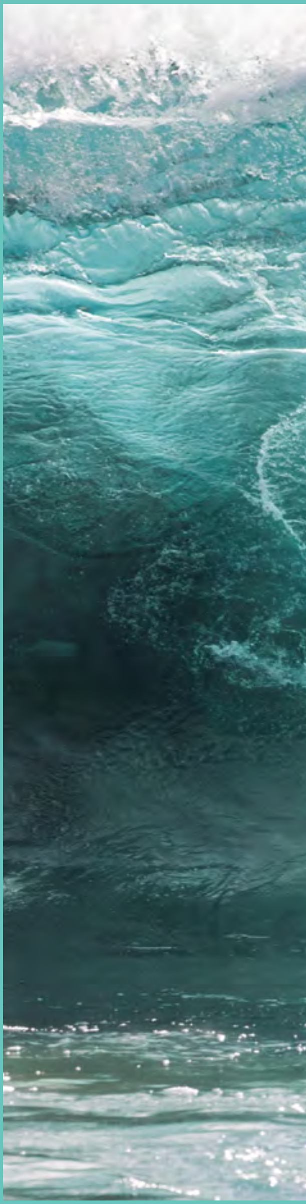
It is true that the heart of sharks, as well as bony fishes, is quite small compared to that of mammals. Our heart weighs about 0.7 percent of our total body weight, whereas the heart of a shark weighs from about 0.1 percent of its body weight (Horn Shark, *Heterodontus francisci*) to more than double that for a Shortfin Mako or White Shark. A human's heart weighs about 2.5 times that of the White Shark.

The heart's function is to pump blood to a series of vessels that distribute the blood to the parts of the body where it is needed most at any particular time. The relative size of the heart correlates most directly with an animal's activity level and metabolic rate—

in other words, how quickly it uses energy and how much energy it uses (typically measured by the rate of oxygen consumption). The more sedentary Port Jackson Shark (*Heterodontus portusjacksoni*; page 76), which typically rests during daylight hours on the seafloor and moves episodically and slowly at night, requires a smaller heart than sharks at the other end of the metabolic spectrum, such as the Shortfin Mako.

Two other features distinguish the shark heart from that of other vertebrates, including bony fishes. First, the shark heart lies within a capacious pericardium that has relatively inflexible walls (our pericardium, in contrast, envelops the heart more tightly and is flexible). When the largest and most muscular of the shark's four cardiac chambers contracts, the pericardial walls resist moving in, and suction is developed within the pericardial space (according to basic physics, if the volume in a fixed space declines, so must the pressure). This suction pulls blood back into the heart from the posterior. Cardiac suction occurs in all vertebrates, but not to the extent that it does in sharks.

The second distinguishing feature of the shark heart is the presence of a pressure-relief valve in the wall of the pericardium. Only a few oddball fish have this adaptation, which allows the heart to expand when it needs to pump more blood by squirting some of the pericardial fluid into the abdominal cavity. And this adaptation helps prevent some sharks from dying when the heart is injured, an example being when a Port Jackson Shark eats a sea urchin and one or more of its spines pierce the shark's heart and cause it to bleed. Without a way to vent the blood in such a situation, pressure in the pericardium would increase and likely kill the shark. In another example, one of the authors caught a perfectly healthy Tiger Shark (*Galeocerdo cuvier*; page 232) with a 4 in-long (10 cm) catfish spine sticking out from its pericardium. The shark had eaten the catfish and the spine had passed from its esophagus into the pericardium, presumably through part of the heart, and then eventually worked its way out.

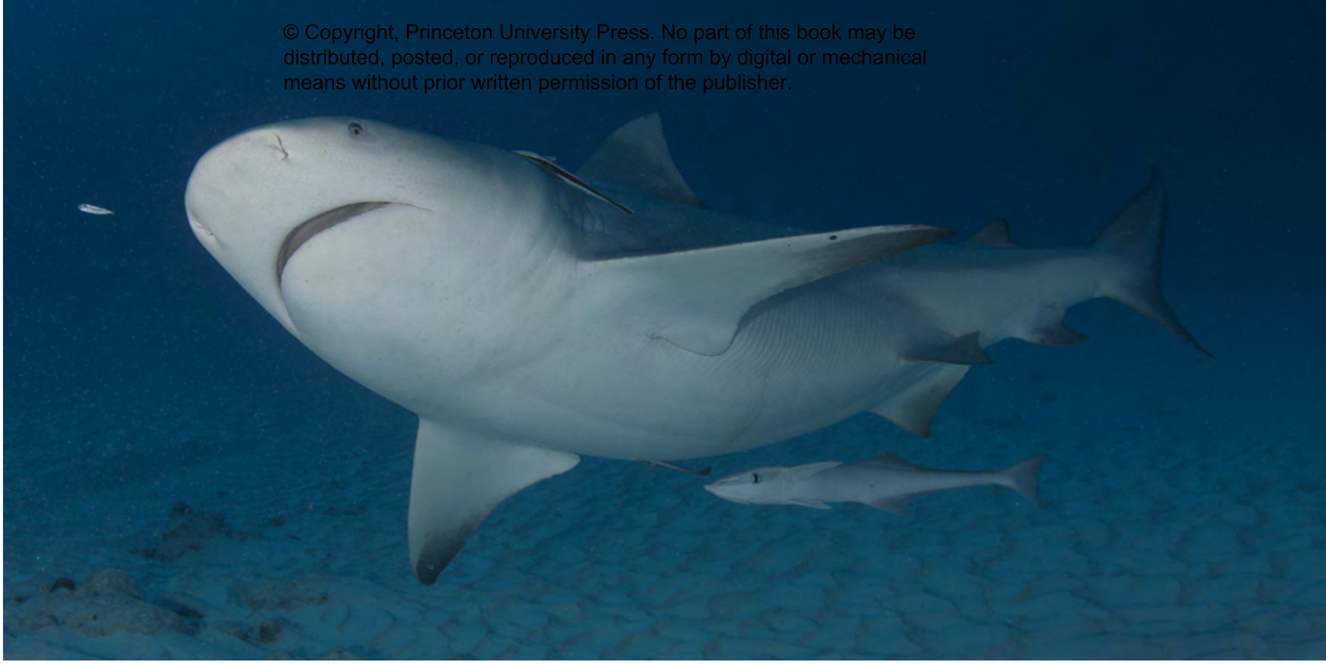


↑ A Blacktip Reef Shark (*Carcharhinus melanopterus*) in Maldives. This species is a common mesopredator on shallow Indo-Pacific reefs; its fins appear to have been dipped in India ink. It is often confused with its larger cousin, the Blacktip Shark (*C. limbatus*).

↗ Mesmerizing photo of sharks feeding on a bait ball in the breaking ocean waves off Carnarvon, Western Australia.

Unparalleled reproductive adaptations

The suite of shark adaptations related to reproduction will likely far exceed your expectations. They range from the novel mechanism males use to internally fertilize the females' eggs, to the incredible array of modes females employ to nourish their embryos.



SEXUAL DIMORPHISM

Thoughts of sexual dimorphism, or differences in appearance between males and females, likely conjure up images of birds with starkly different plumages (for example, the showy tail feathers of the peacock versus the drab coloration of the peahen) or the presence of large antlers in bull Elk (*Cervus canadensis*) and Moose (*Alces alces*) compared to the antlerless cows. Sharks also show marked dimorphism between the sexes, the most obvious being size dimorphism, with females often being much large than males. These differences are most extreme in species that give birth to live young, since the female must carry the offspring, and are less so in species that lay eggs.

↑ A pregnant Bull Shark (*Carcharhinus leucas*) off Playa Del Carmen, Mexico. Up to 13 offspring are born after 12-months' gestation.

← Nurse Sharks' (*Ginglymostoma cirratum*) courtship in the shallows. A male has grasped the pectoral fin of the female, which may be followed by mating. Shark biologists Wes Pratt and Jeff Carrier were the first to describe social structure and mating behavior in the species.

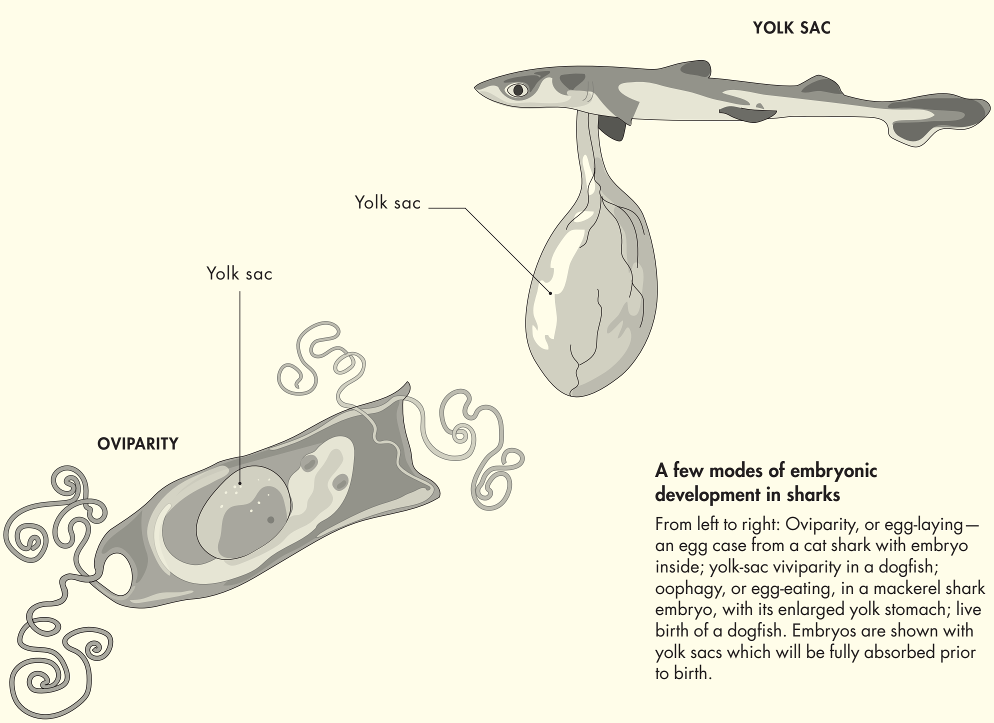
The most obvious sexually dimorphic feature in sharks are the claspers mentioned earlier. These tubular extensions of the pelvic fins, stiffened by calcified cartilage, are present only in males and provide the mechanism for transferring sperm into the female for egg fertilization. Males have two claspers, but only one is inserted into the female's cloaca during mating (which one depends on the position of the male relative to the female). Nerves stimulate the clasper to rotate forward, and once it is inserted, the end splays open, anchoring it into the female during mating. Depending on the species, the splayed clasper may display a variety of hooks, spikes, or lobes to assist in anchoring.

Sharks have other sexually dimorphic characteristics related to the mating process itself. Males often bite the fins or flanks of the female during copulation, causing visible mating wounds. To combat this, female sharks typically have thicker skin than males. For example, the skin on the flank of a female Blue Shark (*Prionace glauca*; page 138) is three times as thick as the male's. Smooth-hounds and other sharks that feed mostly on invertebrates often have flattened teeth for crushing prey. But males in these species have pointed cusps on their teeth, to assist in holding onto the female during mating.

MODES OF EMBRYONIC DEVELOPMENT

Once mating has taken place and the eggs have been fertilized, female sharks employ more modes of nourishing their embryos than any other animal group. Whereas birds and amphibians use only one mode of embryonic development (egg-laying) and mammals employ a mere two (placental live birth and a few egg-layers), there are as many as 10 modes in sharks. In all vertebrates, the yolky part of the egg forms a yolk sac that is attached to the embryo's digestive tract and provides its primary source of nourishment, at least during early development. However, in sharks the many modes of embryonic nourishment exist on a spectrum, from species that get nourishment only from the yolk sac (lecithotrophy, or yolk-feeding) to those that get a significant amount of energy directly from the mother (matrotrophy, or mother-feeding). Cat sharks and horn sharks are egg-layers. In these species the fertilized egg is enveloped in a horny casing that is expelled from the mother and most development occurs outside of the mother using only the attached yolk sac for nourishment. Once the yolk is depleted, the baby shark breaks free of its egg capsule.

All other shark species have some form of live birth. Sharks have paired uteri and, in most, embryo development in both. Sawsharks, angel sharks, cow

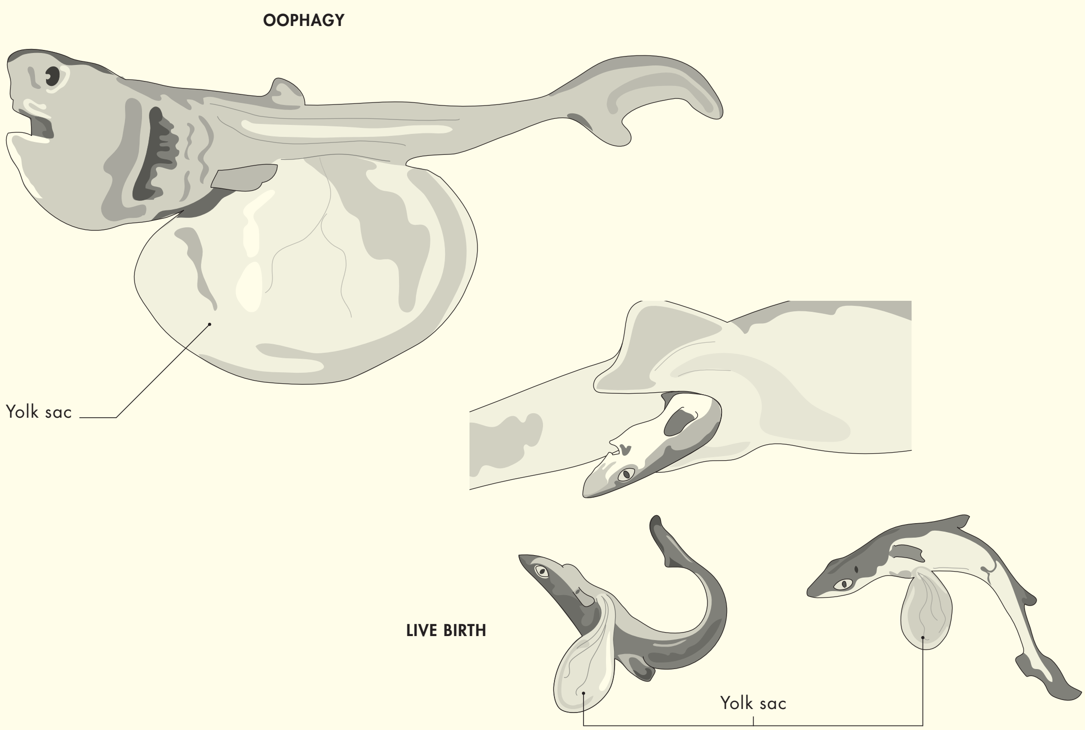


A few modes of embryonic development in sharks

From left to right: Oviparity, or egg-laying—an egg case from a cat shark with embryo inside; yolk-sac viviparity in a dogfish; oophagy, or egg-eating, in a mackerel shark embryo, with its enlarged yolk stomach; live birth of a dogfish. Embryos are shown with yolk sacs which will be fully absorbed prior to birth.

sharks, dogfish sharks, and other relatives retain the fertilized eggs internally, often with multiple eggs wrapped in a single envelope. In these species, most or all of the energy needed by the developing embryos comes from the yolk sac, with little to no nourishment provided by the mother. In mackerel sharks, including the White Shark, the mother ovulates huge numbers of unfertilized eggs to feed her developing offspring (called oophagy, or egg-eating). After the yolk sac is depleted, the embryos gorge themselves on these eggs until their stomachs become extremely distended. This represents a significant energetic investment from the mother. One species, the Sand Tiger (*Carcharias taurus*; page 236), takes this a step further, with the embryos not only eating the ovulated eggs, but the largest one eating all of its siblings in utero (talk about sibling rivalry!).

In the requiem sharks, hammerheads, and many of the houndsharks, the maternal investment goes a step further. Following depletion of the yolk sac reserves, the embryos' yolk stalks attach to the wall of the mother's uterus, forming a pseudo-placental connection analogous to the mode of nourishment used by placental mammals. Through this umbilicus, the female provides the bulk of the developing embryos' nourishment by shunting uterine milk (called histotroph) directly into their digestive tract.



FECUNDITY FIGURES

The number of offspring produced by female sharks can vary from as few as one to as many as 300, and even varies among reproductive modes. Egg-laying Small-spotted Catsharks (*Scyliorhinus canicula*) may produce 60 or more eggs in a season, while the Port Jackson Shark produces about 10–16 corkscrew-shaped eggs each year. The known record for shark fecundity is more than 300 in the Whale Shark (*Rhincodon typus*; page 144), a species that essentially holds encased eggs internally. Among the live-bearing yolk-sac species, the Bluntnose Sixgill (*Hexanchus griseus*; page 38) and Prickly Shark (*Echinorhinus cookei*) may produce more than 100 offspring, yet at least one species of gulper shark has only one pup after a gestation period of at least two years. In egg-eating and embryo-eating sharks, fecundity is quite low owing to the extreme level of maternal investment, and can range from just two per cycle in Sand Tigers and thresher sharks to perhaps 14 in White Sharks (*Carcharodon carcharias*; page 106). Fecundity in placental shark species also varies considerably, with Whitetip Reef Sharks (*Triaenodon obesus*; page 114) usually producing only 2–3 offspring, although Blue Sharks and Great Hammerheads (*Sphyrna mokarran*; page 44) may produce 40 or more pups.

↑ A cluster of cat shark egg cases. Note the tendrils—curly, wiry threads—that entangle with each other and the bottom, making removal of the egg cases very difficult.

→ An egg from a Port Jackson Shark on a beach in New South Wales, Australia. The eggs are often lodged between rocks, where they are protected and do not typically get washed onto the beach. Females have been observed carrying their eggs in their mouths and positioning them among the rocks.

Shark personality and individual recognition

The study of shark behavior has widened considerably in recent years. Early studies of sharks understandably focused on behaviors associated with shark bites and attacks, and this remains a popular subject of inquiry.

PREDATORY AND DEFENSIVE BEHAVIOR

One of the earliest notable observations was made in the 1970s by shark researcher Don Nelson. Divers in submersibles moving aggressively toward Grey Reef Sharks (*Carcharhinus amblyrhynchos*) in the wild repeatedly and predictably induced the sharks to move into a stylized series of postures. The more aggressive the divers and the fewer the escape options available to the sharks, the more pronounced the sharks' defensive and warning display, which often resulted in strikes on the submersible. Nelson's research was the first to correlate shark attacks on humans with a threat perceived by the shark, and not predatory behavior. Bull Sharks (*Carcharhinus leucas*; page 196) exhibit similar behaviors, and have been known to attack boats that move too close.

Understandably, studies of White Shark feeding behavior have captured the interest of the public, the media, and researchers. One particularly memorable behavior involves White Sharks ambushing juvenile Cape Fur Seals (*Arctocephalus pusillus*) in South Africa from beneath with an aerial attack in which the shark grasps the unsuspecting prey while launching its entire body out of the water. Overall success rates varied with time of day, but averaged slightly less than 50 percent.

In addition to trying to understand predatory behavior in sharks, recent studies have focused on their social lives, cognitive abilities, navigation, and predator avoidance. For example, researchers have found that juvenile Lemon Sharks (*Negaprion brevirostris*; page 230) in shallow mangrove-lined lagoons form groups at high tide, when predators—usually larger Lemon Sharks—are present. The smaller Lemon Sharks selected similar-sized individuals to hang out with, and even showed a preference for those they were familiar with from previous encounters. Individual recognition has also been shown in other shark species. Sharks of the same species may look alike to you, but not to one another!

(continued...)

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