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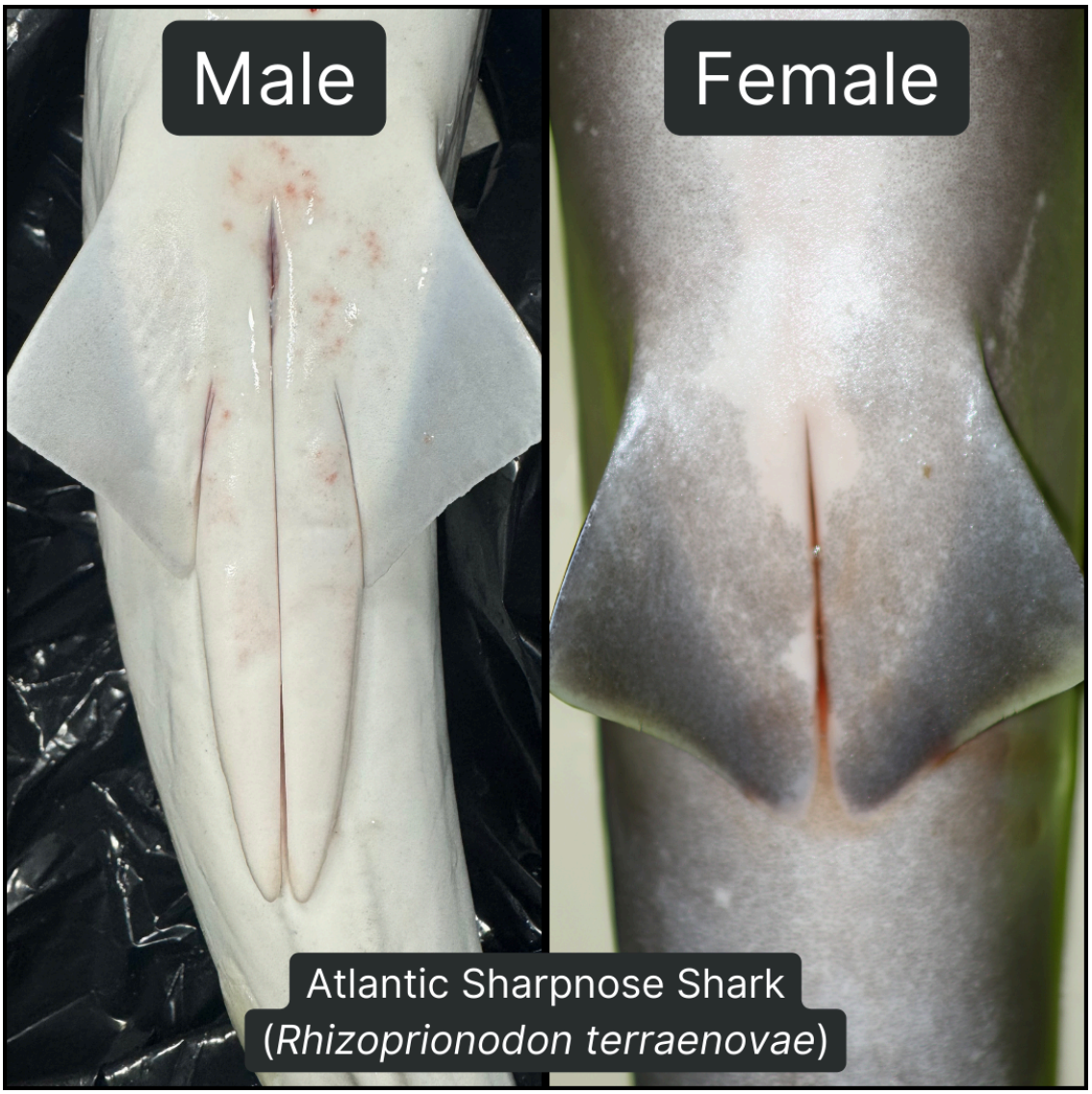
The Next Generation of Sharks: Reproductive Modes in Elasmobranchs

Eggs, Pups, and Claspers - Oh My!

Elasmobranchs (sharks, rays, and skates) are an incredibly diverse group of fishes, with over 1,000 documented species worldwide! Reproductive modes within elasmobranchs are equally diverse and range from egg-laying to placental-fed live birth. While bony fishes spawn by releasing sperm and eggs into the water column, which results in young developing apart from the parents, elasmobranchs reproduce through internal fertilization. Also, male and female elasmobranchs are externally distinguishable. Male sharks possess claspers, or external reproductive organs, whereas females do not. Interestingly, female elasmobranchs typically have one functional ovary and two paired uteri, which increases the capacity for pup production and development.



***Left:** A male Atlantic sharpnose shark's claspers. **Right:** A female Atlantic sharpnose shark, lacking claspers.*

The wide array of reproductive strategies and body sizes of elasmobranchs results in extraordinary variation of reproductive metrics, including the number of young per litter and gestation (i.e., pregnancy) period. Some sharks, such as the gulper shark (*Centrophorus granulosus*), may produce only one pup over the course of a 2-year pregnancy, while bonnetheads (*Sphyrna tiburo*) have short gestation periods that last around 5 months and a litter of 6-14 pups. Like gulper sharks, cownose rays (*Rhinoptera bonasus*) typically only have one pup per pregnancy, and on the other end of the spectrum, whale sharks (*Rhincodon typus*) can have around 300 pups per litter, which is the largest known brood size of any shark species. Interestingly, multiple males can sometimes father pups within the same litter, which is termed **multiple paternity**. This has been widely documented in many species, including nurse sharks (*Ginglymostoma cirratum*), shortfin makos (*Isurus oxyrinchus*), and scalloped hammerheads

(*Sphyrna lewini*).

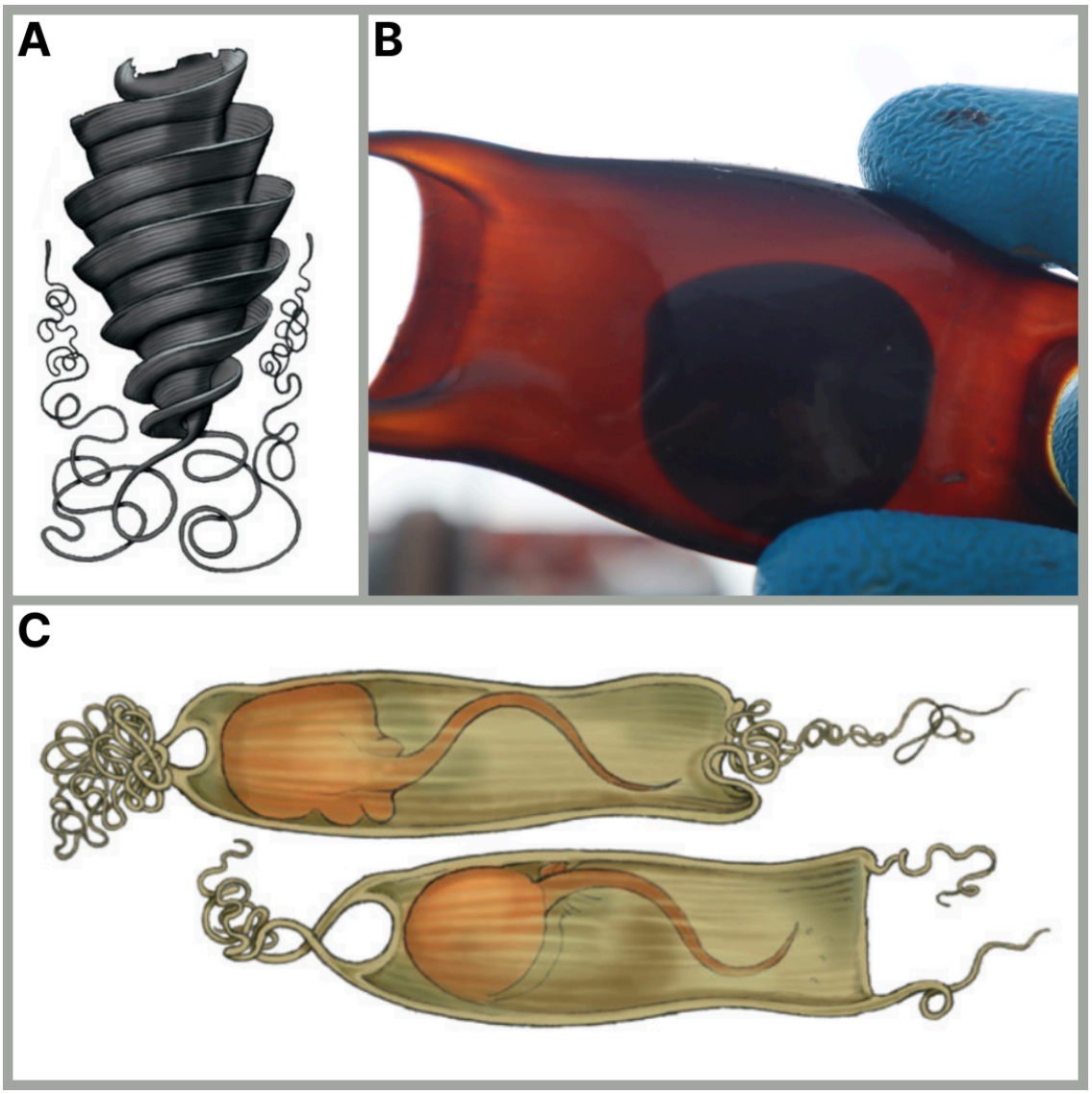
Scientists classify the plethora of elasmobranch reproductive strategies by dividing them into categories based on two criteria: 1) whether pups hatch from an egg or whether they are born free-swimming, and 2) the method of nutritional investment from the mother to the pups.

Let's dive deeper!

Which Came First: The Shark or the Egg?

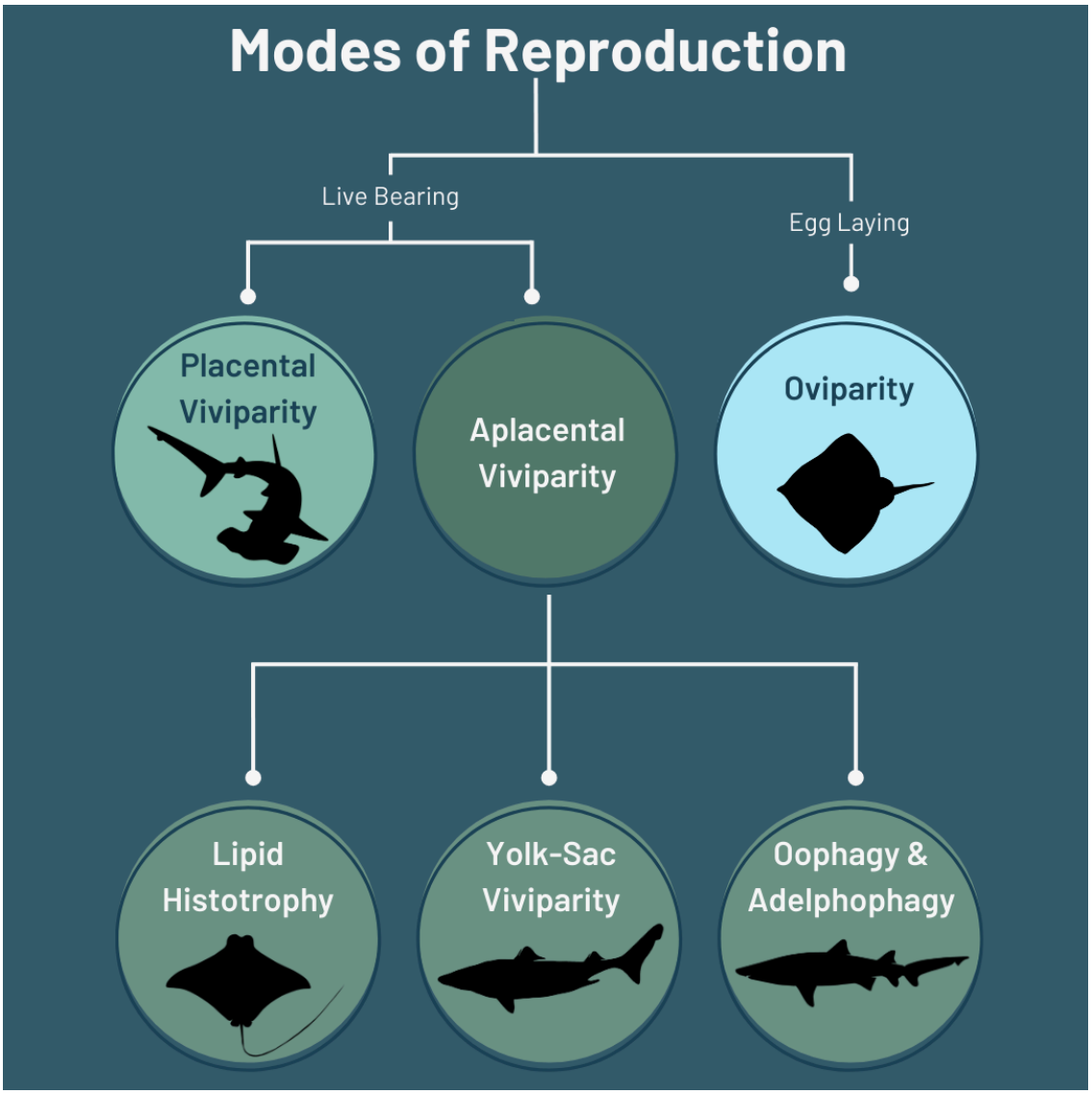
While all skates lay eggs (i.e., oviparity), only approximately 40% of shark species reproduce in this fashion. Elasmobranch eggs can take on a variety of sizes, shapes, and colors and often include tendrils or other appendages that get caught on rocks and other substrates. These appendages function to keep the egg secure rather than allowing the egg to drift with the currents. This reproductive strategy is generally characterized by some development of the pups outside of the mother; however, the extent varies across species. Egg-laying can be subdivided into **single oviparity** or **multiple oviparity** depending on the timing of the egg-laying event:

Single oviparity: This strategy is also called immediate oviparity; sharks and skates that use this strategy produce eggs one at a time in each uterus and repeatedly lay pairs of eggs. Single oviparity is advantageous for small species that do not have much space in their body cavities to support pup development; however, the eggs are left unprotected on the seafloor for extended periods of time while the pups develop. Species that use this strategy include horn sharks (*Heterodontus francisci*), epaulette sharks (*Hemiscyllium ocellatum*), and clearnose skates (*Rostroraja eglanteria*).



***A:** the egg case of a horn shark (Ebert et al. 2021). **B:** a skate egg case collected during a bottom longline survey in the northern Gulf of Mexico. **C:** the egg case of a cat shark (Ebert et al. 2021).*

Multiple oviparity: This strategy is also called retained oviparity and describes reproductive behavior in which a female shark gives their eggs a “head start” by keeping them in their uteri for up to a few months prior to laying them. In some cases, the female shark may lay their eggs only a few weeks before they hatch. Because eggs are retained in their uteri, there are often multiple eggs developing in each uterus at the same time, hence the term “multiple” oviparity. Zebra sharks (*Stegostoma tigrinum*) are one species that retain their eggs before laying them.



Reproductive modes in elasmobranchs include oviparity (e.g., clearnose skate, Rostroraja eglanteria*), placental viviparity (e.g., great hammerhead,* Sphyrna mokarran*), lipid histotrophy (e.g., cownose ray,* Rhinoptera bonasus*), yolk-sac viviparity (e.g., gulper shark,* Centrophorus granulosus*), and oophagy and adelphophagy (e.g., sand tiger shark,* Carcharias taurus*).*

Look Alive! These Pups Are Hot to Go

In contrast to egg-laying, all rays and approximately 60% of shark species give birth to free-swimming young (i.e., viviparity). The internal mechanisms resulting in live birth vary across families and can be divided based upon the mode of nutrient transfer to the young. In some elasmobranchs, pups are

nourished solely by a yolk without any additional input from the mother, while other mothers continue to supply nutrients to their pups after the initial yolk sac is depleted. Viviparous reproductive modes include **yolk-sac viviparity**, **lipid histotrophy**, **oophagy/adelphophagy**, and **placental viviparity**.

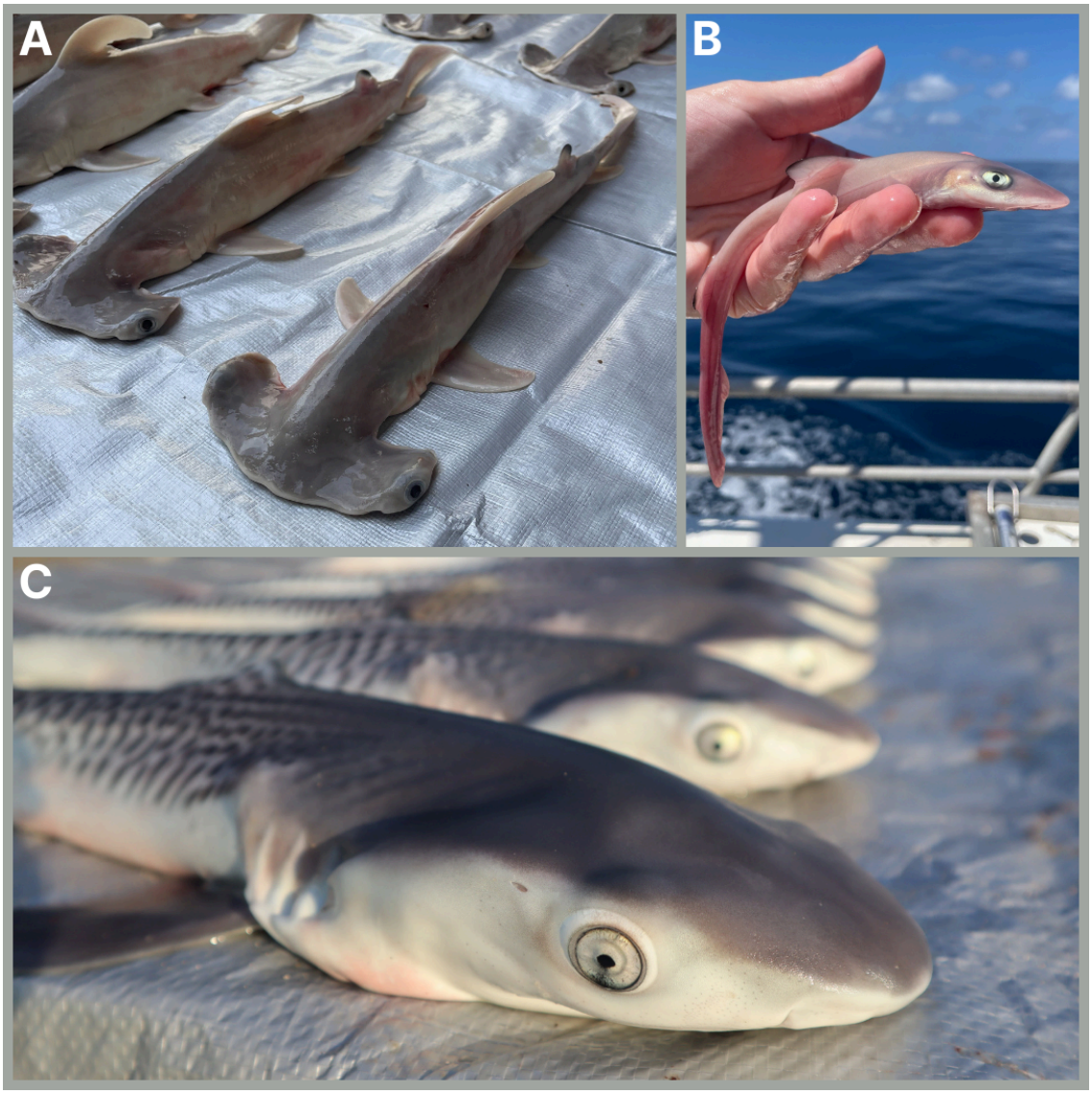
Yolk-sac viviparity: This reproductive mode, which is the simplest form of viviparity, is widespread across shark families and is used by about 40% of shark species. Pups are supplied with energy and nutrition through a yolk sac, without direct input from the mother; however, development still occurs within the uteri, and pups are born free-swimming. Because the pups' only nutrient supply is the yolk, pups are often born lighter than the weight of the initial yolk. Whale sharks (*Rhincodon typus*), gulper sharks (*Centrophorus granulosus*), Atlantic angel sharks (*Squatina dumeril*), and smalltooth sawfish (*Pristis pectinata*) use this reproductive strategy.

Lipid histotrophy: This strategy, primarily used by rays, involves developing pups feeding on a protein- and lipid-rich “uterine milk” through a special finger-like structure called the trophonemata. The transfer of nutrients from the mother to the pups is highly efficient and results in substantial growth before birth. Stingrays, including cownose rays (*Rhinoptera bonasus*) and southern stingrays (*Hypanus americanus*), exhibit this reproductive mode.

Oophagy/Adelphophagy: Oophagy (“egg-eating”) and adelphophagy (“brother-eating”) refer to live-birth strategies in which the developing pups gain nutrients by consuming unfertilized eggs or other developing embryos while in the uterus. Due to the energetic input required by the mother (in both strategies) and intrauterine cannibalism (in the case of adelphophagy), these reproductive modes typically only result in a few large offspring per litter. Oophagy is unique to just a few species of sharks, such as white sharks (*Carcharodon carcharias*), shortfin makos (*Isurus oxyrinchus*), and pelagic threshers (*Alopias pelagicus*), while adelphophagy is found only in sand tiger sharks (*Carcharias taurus*).

Placental viviparity: This reproductive mode is similar to mammalian reproduction. Young elasmobranchs receive initial nutrition from a yolk sac before transitioning to a placental connection attached to the uterine wall. For the remainder of the gestation period, developing embryos receive nourishment through the uterine-placental connection. This strategy typically results in the development of a few large, well-developed pups before they are born. Sharks

that use this strategy include bull sharks (*Carcharhinus leucas*), great hammerheads (*Sphyrna mokarran*), and blue sharks (*Prionace glauca*).



Shark pups encountered during the Mississippi State University Marine Fisheries Ecology Program's research sampling efforts. ***A:*** *great hammerhead* (Sphyrna mokarran). ***B:*** *Gulf smoothhound* (Mustelus sinusmexicanus). ***C:*** *tiger shark* (Galeocerdo cuvier).

Confused? You're Not Alone!

Given the diverse reproductive strategies used by elasmobranchs, it may not be surprising to hear that scientists are still learning about exceptions to these broad categories! For instance, tiger sharks (*Galeocerdo cuvier*) were recently recategorized into their own family based partly upon the discovery that they

are the only known shark species to engage in **embryotrophy**. Tiger shark pups get their nutrition from fluid-filled sacs, while their former relatives engage in placental viviparity. In 2016, scientists found that white sharks (*Carcharodon carcharias*) combine multiple strategies described above – prior to beginning oophagy, pups likely rely on lipid histotrophy for nutrition. The great lanternshark (*Etmopterus princeps*) is theorized to use a poorly understood form of histotrophy called **mucoid histotrophy**, wherein nutrients are provided to the pups through a mucus produced by the uterus. Finally, in 2020, a completely new form of oviparity was discovered in the sarawak swellshark (*Cephaloscyllium sarawakensis*)! Called **sustained single oviparity**, this strategy involves female sarawak swellsharks retaining eggs in their uteri while only having one set of eggs in the uteri (one egg per uterus, two total) at a time, in a blending of single oviparity and multiple oviparity.

To further muddy the waters of elasmobranch reproduction, some females can reproduce asexually in the absence of a male, as observed in aquarium settings – this is called virgin birth or **parthenogenesis**! Female elasmobranchs are able to store sperm for later use, sometimes for years, which can result in pregnancy without any recent male interaction; however, true parthenogenesis incorporates no input from a male. The recent viral story of Charlotte the stingray in a North Carolina aquarium sparked public attention around this remarkable adaptation. While Charlotte's pregnancy was later explained as an unfortunate misdiagnosis, parthenogenesis has been definitively documented using genetic techniques in egg-laying zebra sharks (*Stegostoma tigrinum*) and whitespotted bamboo sharks (*Chiloscyllium plagiosum*) and in live-bearing blacktip sharks (*Carcharhinus limbatus*), bonnetheads (*Sphyrna tiburo*), and spotted eagle rays (*Aetobatus narinari*).

While research on the reproductive strategies of sharks, rays, and skates continues to advance, many exciting questions remain to be answered. Who knows what we will learn in the coming years!

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