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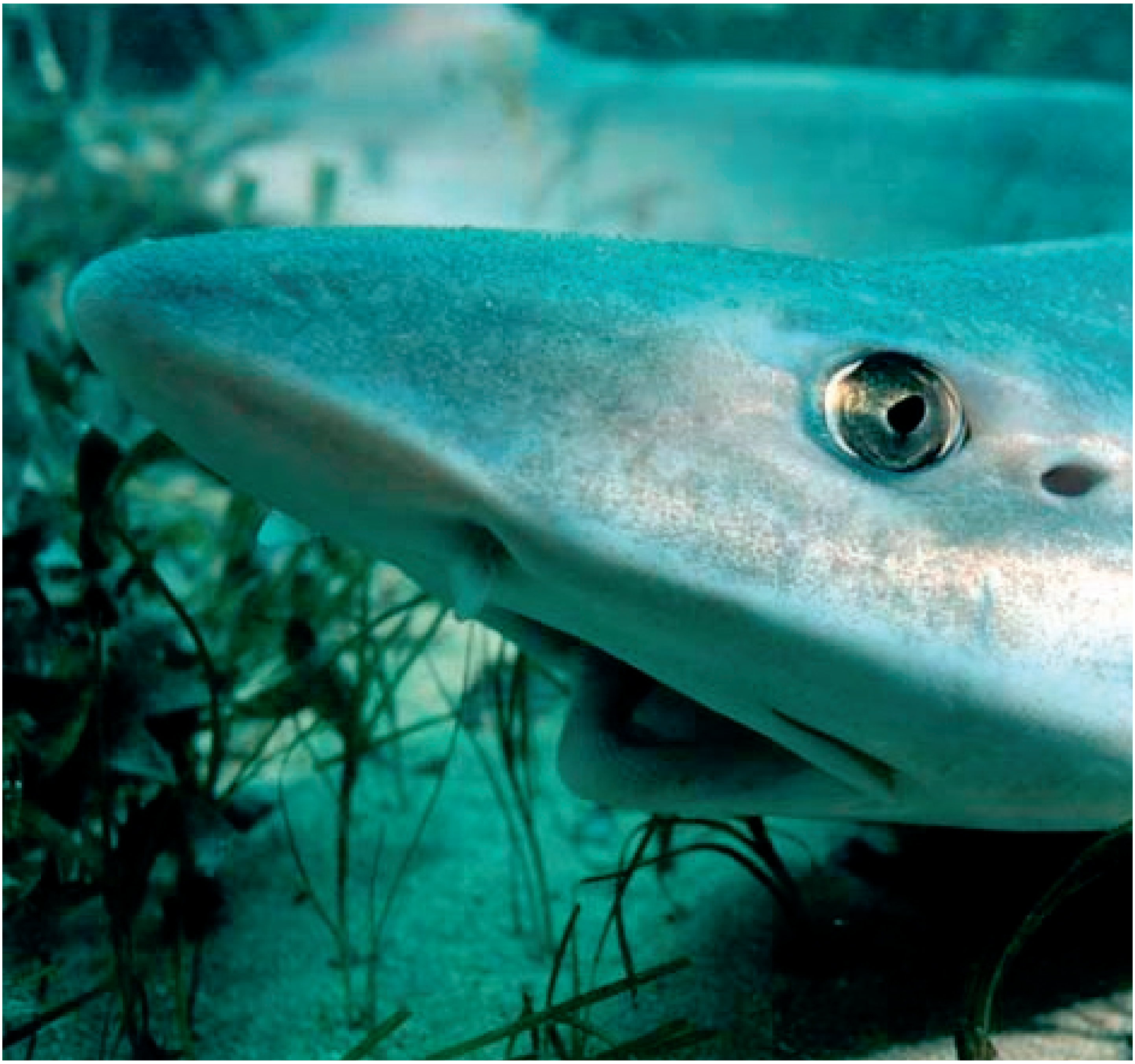

Gummy shark (*Mustelus antarcticus*) (© Ken Hoppen, oceannotions@primus.com.au)

GENERAL BIOLOGY OF CHONDRICHTHYAN FISHES

By Terence I. Walker

Marine and Freshwater Systems, Primary Industries Research Victoria, PO Box 114, Queenscliff, Victoria, 3225 Australia

Background

Sharks and rays belong to the group Elasmobranchii. Chimaeras, the nearest relatives, belong to the group Holocephali. The Elasmobranchii and Holocephali together comprise the Chondrichthyes.

Chondrichthyans form only a small proportion of all living fishes. They share many features with the other fish, known as the bony fishes, but they also have several features that separate them from all other animals.

The cartilaginous skeleton is a key feature of chondrichthyan fishes distinguishing them from the bony fishes and other higher vertebrates (amphibians, reptiles, birds and mammals), which all have harder more dense skeletons made of bone. However, they do share the feature of a cartilaginous skeleton with the more primitive vertebrates (cyclostomes and lancelets), but these latter animals do not have jaws.

Some of the cartilaginous skeletal structures of chondrichthyan fishes are strengthened and hardened by the process of mineralisation (also referred to as calcification), whereby various salts are deposited into growing cartilage. In contrast to the minerals deposited in the bone tissues of the higher vertebrates that can be resorbed and redeposited, minerals deposited in the cartilaginous structures of chondrichthyans remain inert and cannot be resorbed.

Basic design of chondrichthyan fishes

The basic design of chondrichthyan fishes includes a skull, jaws with teeth, a vertebral column (backbone), and fins; but, unlike the bony fishes, they lack ribs. Through more than 400 million years of evolution, adaptation of this structure has given rise to various shapes and sizes specialised for a range of ecological niches.

The upper jaw is only loosely attached to the underside of the skull by ligaments and connective tissue in living sharks and rays, but is fused to the underside of the skull in the holocephalans. It is this type of jaw suspension (‘holocephaly’) that gives the holocephalans their scientific name.

Chondrichthyan teeth vary in size and shape between the various groups of these animals. The upper and lower jaws of sharks and rays bear teeth that are embedded in the gums rather than attached to the jaws, and are continuously replaced. The teeth of chimaeras are non-replaceable and attached to grinding tooth plates in a beak-like arrangement. Many demersal sharks, such as the bullhead sharks, have small, sharp teeth for grasping their prey, and flattened back teeth for crushing hard shell. Other demersal sharks, such as the hound sharks and the rays, have all flattened teeth. Pelagic species have larger sharp teeth more suited to cutting their prey. The whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*), and manta ray (*Manta birostris*) lack teeth and have evolved gill rakers for straining out plankton from large volumes of water taken in through the gaping mouth and passed out over the gills as the animal breathes.

The vertebral column comprises a series of vertebrae held in place by connective tissue, and provides the animal with a flexible body. Concentric banding observed in vertebrae and other hard tissues of many species, formed by mineralisation of cartilage, is often used for estimating the ages of these animals.

Figure 1. Scientist capturing a shark
(© Ken Hoppen, oceannotions@primus.com.au).

Chondrichthyan animals have three types of unpaired fins (dorsal, anal and caudal) and two types of paired fins (pectoral and pelvic). However, through evolution, some groups (dogfish, sawsharks, angel sharks, and rays) have lost the anal fin, and the chimaeras and some rays (stingarees, stingrays, eagle rays) have modified caudal fins to form long whip-like or ribbon-like tails. In the sharks and chimaeras, the pectoral fins extend from the body below and behind the head whereas in the rays, the pectoral fins are attached at the back of the skull and part of the body stem and are greatly enlarged to form a body disc. Most ray species have small dorsal and caudal fins, and many species lack them completely.

Body shape and method of locomotion vary between the chondrichthyan groups. The body of most species of shark is shaped for hydrodynamic efficiency where swimming is achieved by side-to-side undulations of the tail (figure 1). In rays, the body is highly flattened from the top and bottom, the tail is reduced in size, and locomotion is achieved by undulation of the tips of the pectoral fins. Chimaeras move by rapid movement of the pectoral fins or by slow lateral movements of their tails.

Gills and spiracles

In common with the bony fishes and the lower vertebrates lacking jaws, chondrichthyans have gills to extract oxygen from the water in which they live. Most shark species possess five pairs of gill openings, with several shark species possessing six or seven pairs. Ray species have five or six pairs of gill openings. Chimaeras have four pairs of gill arches and, in common with the bony fishes, possess a gill cover called the operculum and have only a single opening to the gills. In sharks and most chimaera species, the gills are located behind the head and on the sides of the body, whereas in the rays they are located underneath the body.

The rays and many of the bottom-dwelling sharks possess well-developed spiracles (figure 2) behind the eyes. These are apertures that enable the animals to take in water for breathing while they rest on the seabed. Adult chimaeras lack spiracles, but they are present in embryos. Fast-swimming torpedo-shaped sharks also lack spiracles and depend on water entering the mouth and passing out through the gill openings. This ramjet mode of ventilation of the gills requires the animals to continue swimming to breathe. Chimaeras take in water for breathing through large nostrils rather than the mouth.

Figure 2. Gummy shark (*Mustelus antarcticus*). Note: spiracle behind the eye (© Ken Hoppen, oceannotions@primus.com.au).

Placoid scales

Another feature of chondrichthyan animals is that the outer skin comprises numerous placoid scales, known as denticles. Formed in the skin, they are usually less than a millimetre wide. The surface of the denticles consists of hard enamel that covers a dentine layer and pulp cavity. The enamel crowns have multiple sharp ridges that reduce drag during swimming and provide some protection from injury. Placoid scales are absent in adult chimaeras except for their presence on male copulatory appendages and for tiny denticles present in the skin on the upper surface of the body and head of hatchlings and juveniles.

Chondrichthyan animals variously possess several other hard structures, developed from placoid scales, associated with their body form. Placoid scales have been adapted to form teeth in all chondrichthyan groups and strong thorns in some rays. Sawsharks and the group of rays known as the sawfishes possess blade-like snouts (rostrum) with hard sharp lateral rostral teeth on each side that can be used offensively. Two groups of shark (dogfish and horn sharks) possess two dorsal spines; one is attached to the leading edge of each of the two dorsal fins. Chimaeras have only one spine and this is attached to the front of the first dorsal fin; the spine is large and often has a venom gland at the base. One or more stinging spines occur on top of the tail of many stingrays and stingarees and some eagle rays and butterfly rays. These are hard, flattened structures that taper to a sharp point; venom is produced in two narrow grooves on the underside of the sting.

Sensory systems

Among chondrichthyan species there are at least eight well-developed sensory systems, several of which are formed from highly sensory cells that can discharge an electrical impulse to a comparatively large brain. The paired eyes provide for an excellent field of vision and the retina has colour-distinguishing cone photo-receptor cells and low-light sensitive rod photo-receptor cells. Another adaptation to low-light conditions is the presence behind the retina of the tapetum lucidum consisting of mirror-like crystals. An acute sense of smell is provided by two olfactory sacs under the snout associated with the large front section of the brain (olfactory lobes). In each olfactory sac, water passes over sensory lamellae where dissolved molecules and suspended particles are detected by olfactory-receptor cells. Taste-receptor cells to determine the palatability of prey, occur on taste buds that cover small bumps in the mouth. Touch-receptor cells occurring near the skin surface respond to contact, and small capsules deeper in the skin respond to the bending of the body and fins through the stretching and contracting of muscles. Sawsharks have a pair of barbells attached to the rostrum to help locate prey, but these are absent in the sawfish. Senses of balance, orientation, and body movement depend on the vestibular system comprised of a complex of fine membranous organs inside the ear. As the animal moves, fluids inside three semi-circular canals at right angles to each other press against hair cells, connected to a conglomerate of hard calcium granules, and stimulate nerve impulses. Hearing is acute, even though chondrichthyans lack external ear structures. Sounds are channelled through cartilaginous tubules and are detected by tiny paired hair-cell organs (macula neglecta) located near the top of the skull above the semi-circular canals. Clusters of sensory hair cells (neuromasts) detect water movement or vibration. Those in the skin are called pit organs and can detect water movement relative to the body surface. To detect water acceleration, neuromasts also form an extensive network of small water-filled canals immediately below the surface of the skin in the lateral lines, which run across each side of the head and body.

Electrosense is present in all chondrichthyans, but uncommon among other groups in the animal kingdom. Chondrichthyan electosensory organs (ampullae of Lorenzini) are able to detect weak electric fields generated by the movement of prey, predators, and ambient water in the Earth's magnetic field. It is likely that these animals can navigate long distances by detecting slight variations in the Earth's magnetic field caused by variation of metal deposits in their environment. The electrosense is so acute that chondrichthyan animals can detect voltage gradients of less than 5 billionths of a volt across a distance of 1 cm. The ampullae are lined with hair cells attached to an insulated tube filled with a conductive jelly. A network of interconnected ampullae located in pores on the head, lower jaw, and trunk enables the animal to measure voltage gradients at different positions on its body. Torpedo rays have evolved paired kidney-shaped electric organs located on each side near the centre of the disc, capable of producing more than 200 volts. These are used for defence and stunning prey, and possibly also for electro-location of prey, predators, or mates, and for social communication.

Reproduction

Chondrichthyan fishes have separate sexes. Females have paired or single ovaries and paired urogenital tracts where each is differentiated into an oviduct, oviducal gland, and uterus, which open into a common urogenital sinus. Males have external paired calcified claspers, which are extensions of the pelvic fins, and internal organs that include the paired testes and genital ducts leading to the seminal vesicles.

Figure 3. School shark (*Galeorhinus galeus*) in utero (© Terence I. Walker).

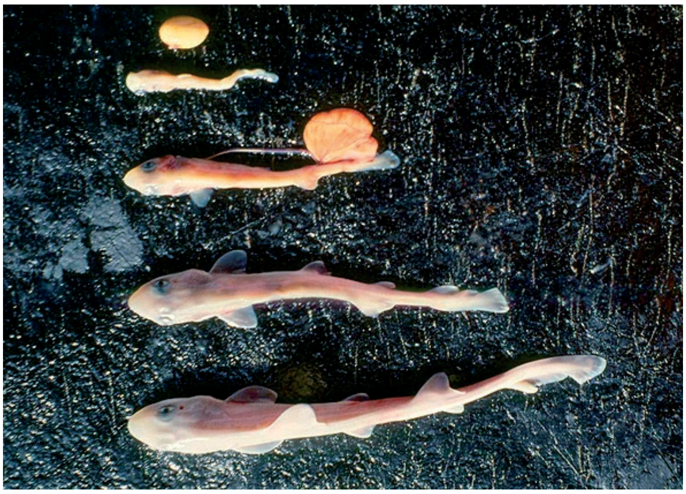

Figure 4. Developmental stages of the gummy shark (*Mustelus antarcticus*)–egg to juvenile (© Terence I. Walker).

Holocephalan males have evolved pre-pelvic claspers covered in numerous placoid scales, which are probably inserted into complementary pre-pelvic slits in the female to maintain a grasp during copulation. In addition, they possess a cranial tenaculum covered with well-developed placoid scales (teeth), which is probably also used for grasping the female during copulation. Holocephalan females possess a pouch posterior to the cloaca, which in mature animals usually contains a sperm plug after mating.

The ovaries and testes function to generate germ cells and to synthesise and secrete hormones. The germ cells in ovaries mature to accumulate yolk and are eventually ovulated as ova that enter the oviducts and pass through the oviducal gland where they are fertilised and encapsulated with egg jelly and a flexible egg-case membrane or a tough egg case. The germ cells in testes eventually develop into sperm. These are stored in the seminal vesicles until copulation, when seminal fluids carrying sperm are passed to female uteri via one or both claspers. Following insemination of a female, sperm are stored in the oviducal gland for subsequent fertilisation following ovulation.

Chondrichthyans are either egg laying or live bearing (figures 3 and 4), and there are four reproductive modes for live-bearing conditions based on the source of nutrition for the developing embryo. The first is where the embryos rely on a yolk sac formed from the ovum that persists throughout gestation. The second mode is where the yolk in the yolk sac is absorbed and the uterus wall then secretes uterine milk (histotroph) to nourish the developing embryos. The third mode is where the yolk sac is absorbed and the embryos feed on ovulated eggs or smaller sibling embryos (intrauterine cannibalism). The fourth mode is where the yolk sac depletes and differentiates into a functional placenta and umbilical cord similar to that in placental mammals. The number of eggs layed or number of young born varies widely with species and size of maternal animal and the period of gestation can vary from several months to well over one year.

Further information

For terms in this text that may be unfamiliar to you please visit fishbase:
http://www.fishbase.org/search.cfm

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