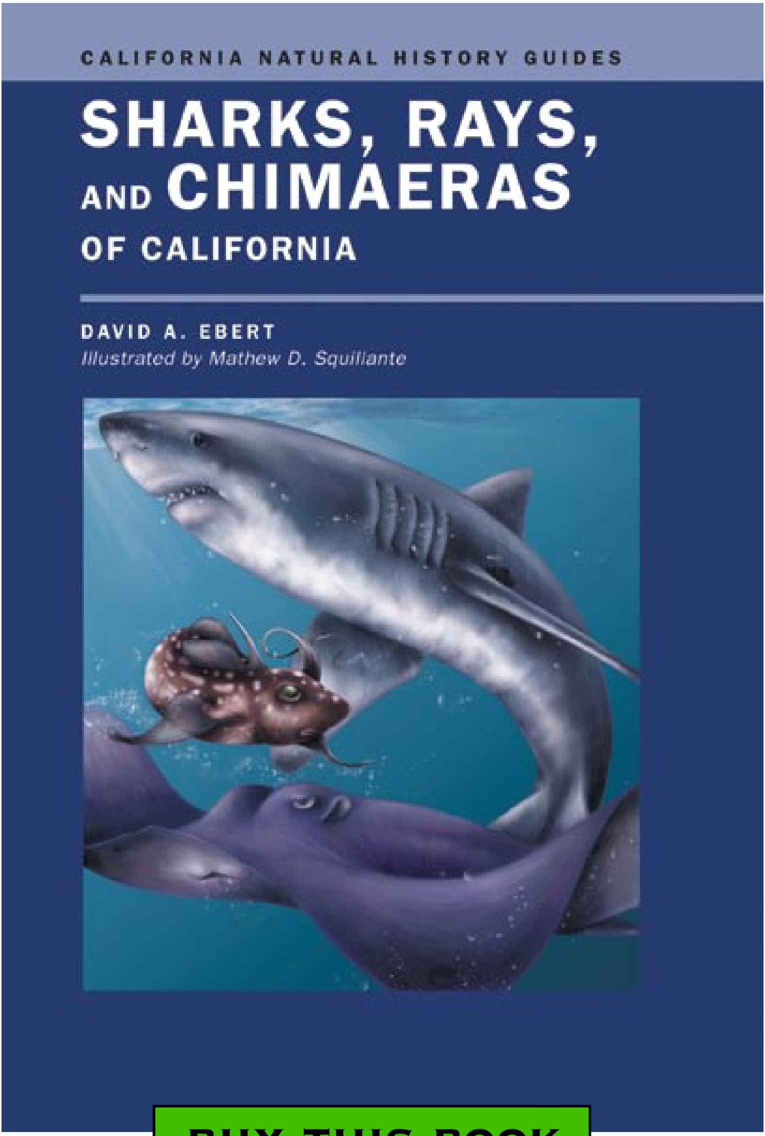

CALIFORNIA NATURAL HISTORY GUIDES
SHARKS, RAYS, AND CHIMAERAS OF CALIFORNIA
DAVID A. EBERT
Illustrated by Mathew D. Squillante

INTRODUCTION

don't realize how colorful many of these species are. Geographically the guide reaches from the innermost shallow bays and estuaries to 500 miles offshore.

The introductory sections on chondrichthyan biology, ecology, and diversity are intended only as a brief overview, as other contemporary authors have treated these subjects in more detail. The guide is primarily intended to be useful in the field, where users can simply match the illustration to the specimen or work through the identification keys to each species. Once a tentative identification has been made, the reader can turn to the species description and natural history notes.

California's Marine Environment

The California coastline (map 1), which extends over 1,100 miles in a north–south direction from the Mexican border (32 degrees N latitude) to the Oregon border (42 degrees N latitude), is composed of three major geographic regions: northern California (the Oregon border to San Francisco), central California (San Francisco to Point Conception), and southern California (Point Conception to the Mexican border). The general flora and fauna shift from warm-temperate water species in the south to cold-temperate water species in the north, whereas the transition of the elasmobranch fauna seems to occur in the central California region, where warm-temperate water species give way to cool-temperate nearshore species. Species such as the Pacific Sleeper Shark, some skates, and the White-spotted Ratfish, which occur in deep water in southern California, occur in relatively shallower water in the northern part of the state.

The temperature of the water along the California coast is influenced by the California Current, a major surface current that flows north to south, from the Gulf of Alaska, down the coastline to Point Conception, where it veers offshore. The area south of Point Conception where the coastline bends eastward is known as the Southern California Bight and is less affected by the California Current than the waters to the north. The less dominant Davidson Current brings warmer water from the south along the coastline to the north influencing the Southern California Bight and the Channel Islands. A seasonal fluctuation in the movement

Map 1. The California coast.

of these currents combined with strong seasonal winds causes an upwelling of cold, nutrient-rich water along the coast, an effect most prominent in central and northern California during the spring and summer.

Water temperature is an important factor influencing the distribution of California's cartilaginous fish fauna. The gradient of surface water temperatures ranges from approximately 68 degrees F in the south during summer to about 48 degrees F in the north during winter and spring, with Point Conception being the major area of demarcation. South of Point Conception the water temperature is usually 4 to 11 degrees F warmer than to the north. Temperature changes created by surface winds also occur throughout the water column, forming stratified layers of warm and cold water known as a thermocline.

The seasonal movement of warm or cool water masses influences the movements of many species of cartilaginous fish. In summer warm water from the Davidson Current pushes northward increasing the water temperature, bringing warmer water species into California waters. Conversely, in winter and spring cooler water masses lower the water temperature, bringing cold-temperate species into our waters. Occasionally rapid changes occur in these warm- or cold-water masses, causing a localized mortality in temperature-sensitive populations. Young dead or dying cold-water salmon sharks occasionally wash ashore along the beaches of central and southern California following a rapid increase in water temperature. Warm-water species may also be affected by a rapid cooling of the water.

California is subject to an unusual phenomenon that at times can dramatically alter weather patterns with an associated increase in water temperature. El Niño (Spanish meaning The Child, in reference to the Christ Child), which occurs every two to seven years for unknown reasons, can range from mild to quite severe, as occurred from 1982 to 1983, when the state experienced intense winter storms. During or immediately preceding an El Niño event at least 16 species of California's known cartilaginous fish fauna were first reported in our waters, including the Pelagic Thresher Shark and Manta Rays (seen around the Channel Islands). Both species are typically found much farther south off Baja and in the Sea of Cortez. As opposed to El Niño, La Niña brings cooler water to our area and thus a more cold-temperate water fauna.

Oceanographic conditions, especially water temperature, have exhibited major cyclic fluctuations over the past several thousand years, with changes in the average water temperature occurring every few hundred years. Historical evidence indicates that as recently as the mid-1800s the coastal waters of central and southern California reflected an environment that was more warm-temperate to subtropical than is seen today. Conversely, 400 years ago, cold-temperate species now rarely seen south of central California inhabited the coast as far south as the tip of Baja. This may explain why several seemingly cool-temperate species such as the Sevengill Shark and Leopard Shark have apparently isolated populations in the northern Gulf of California.

Classification of Cartilaginous Fishes

All living organisms are grouped into a hierarchy of categories from broad down to the most specific. The basic groups, in descending order, are kingdom, phylum, class, order, family, genus, and species (table 1). Each higher level group contains one or more members of the group below it, so a class would contain one or more orders, an order one or more families, and so on down to the species level. A single scientific name is assigned to the members of each group, except at the species level, at which members are given a binomial name (*bi* meaning two and *nomial* meaning name). The scientific name is made up of a given genus and species name, both of which are usually *italicized* or underlined.

Scientific names are often followed by the name of the person who originally described the family, genus, or species, and the year in which it was first described. If the species was subsequently placed into a different genus, the person's name is put in parentheses. The Sevengill Shark, for example, was originally described by François Peron in 1807 as *Squalus cepedianus,* but was later placed into a new genus, *Notorynchus,* by William Ayres (1855). Thus, the proper citation is *Notorynchus cepedianus* (Peron, 1807).

The person's name and date of description allow researchers to trace the taxonomic history of a specific species to determine

TABLE 1. Classification for the Sevengill Shark*

Kingdom	Animalia	All Animals
Phylum	Chordata	Animals with Backbones
Class	Chondrichthyes	Cartilaginous Fishes
Order	Hexanchiformes	Cow and Frilled Sharks
Family	Hexanchidae Gray, 1851	Cowsharks
Genus	*Notorynchus* Ayres, 1855	Sevengill Shark
Species	*Notorynchus cepedianus* (Peron, 1807)	Sevengill Shark

*The classification is used to demonstrate the basic hierarchical structure of scientific names. Common names are given in the right-hand column.

whether it was previously described or is undescribed. If two species are found to be the same, the oldest description has precedence over the newer name, which then becomes invalid (commonly referred to as a junior synonym). The species names for many of the cartilaginous fishes from California waters were originally classified under different names in earlier publications.

In each species account in this guide, the full scientific name appears at the beginning of the nomenclature subsection.

What Are Cartilaginous Fishes?

Among the five vertebrate groups, the fishes are the largest and most diverse with over 25,000 species described. By comparison, the other four vertebrate groups—amphibians, reptiles, birds, and mammals—collectively have less than 20,000 known species. The fishes can be subdivided into two distinct groups: those with a bony skeleton, known as the bony fishes or teleosts, and those with a cartilaginous skeleton, referred to as cartilaginous fishes.

All living sharks, rays, and chimaeras belong to the class Chondrichthyes (Greek, *chondro* meaning cartilage and *ichthos* meaning fish), a group of aquatic, gill-breathing, finned vertebrates. In contrast to the bony fishes or class Osteichthyes (Greek, *osteos* meaning bone and *ichthos* meaning fish), these fishes have a simplified internal cartilaginous skeleton and lack true bone. Other distinguishing characteristics of the chondrichthyans include fins without bony rays, a true upper and lower jaw, and nostrils on the underside of the head. Their teeth are typically inconspicuous transverse rows or fused tooth plates, and they are continuously being replaced from inside the mouth. Cartilaginous fishes have no bony plates on the head; their scales appear in the form of small, toothlike dermal denticles known as placoid scales; and they have internal fertilization.

The class Chondrichthyes can be subdivided into two major groups, the large subclass Elasmobranchii (*elasmo* meaning plates and *branchii* meaning gills), which includes several groups of fossil sharks and all of the modern living sharks and rays, and the small subclass Holocephali (*holo* meaning entire and *cephali* meaning head), which includes all of the chimaeras. The ordinal classification used here follows Compagno (2001) but recognizes that there is still some disagreement among modern systematists (scientists who study the classification of organisms) regarding the definition of these higher groups. There are currently ten recognized orders of "sharks," a term which in the broad sense includes the rays and chimaeras. Eight of these orders comprise the "typical" sharklike fishes while the rays and chimaeras are each in their own order (table 2). For simplicity, the term "shark" will be used when referring to "typical" sharks, the term "ray" when referring to the

TABLE 2. Approximate Numbers of Families, Genera, and Species as of 31 October 2001*

Orders	Number of Families	Number of Genera	Number of Species
Hexanchiformes	2	4	5
Squaliformes	7	23	101
Pristiophoriformes	1	2	5
Squatiniformes	1	1	15
Heterodontiformes	1	1	8
Orectolobiformes	7	14	35
Lamniformes	7	10	16
Carcharhiniformes	8	49	225
Rajiformes	22	71	543
Chimaeriformes	3	6	35

*The numbers are based on the author's own database.

raylike sharks (order Rajiformes) and the term “chimaera” when referring to the chimaeras (order Chimaeriformes).

The elasmobranchs are the dominant chondrichthyan group with approximately 56 families representing 96 percent of the species; the remaining 4 percent, which includes three families, are the chimaeras. In higher taxonomic groups (genera and above) the sharks are more diverse than the rays, but among all elasmobranch species there are more rays (57 percent) than sharks (43 percent). Worldwide approximately 988 species of cartilaginous fishes have been described, with another 150 or more awaiting formal description by researchers.

What Is a Shark?

Sharks are cartilaginous fishes with a cylindrical or flattened body, five to seven paired gill openings on each side of the head, a large caudal fin, and one or two dorsal fins, with or without erect,

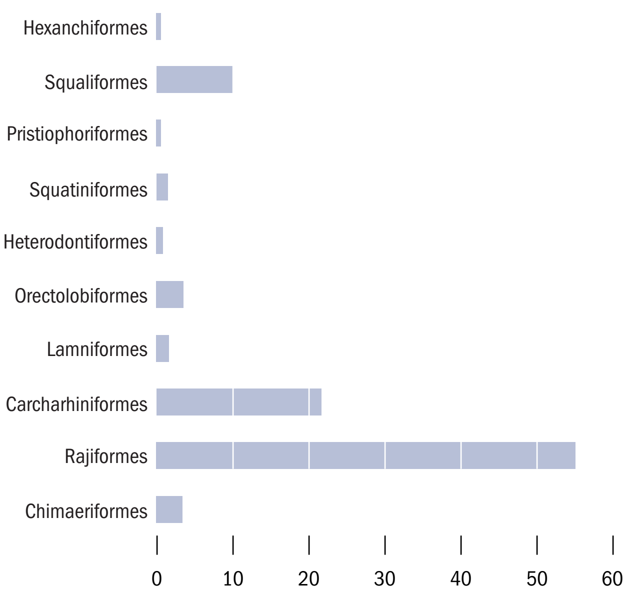


Figure 1. Relative percentage of shark orders by total number of species.

immovable spines. The moderate-sized pectoral fins are not attached to the head above the gill openings. An anal fin may be present. Lacking a swim bladder, sharks have a liver that helps them achieve neutral buoyancy.

What we think of as "typical" sharks are divided into eight major orders, each of which is easily distinguished by specific external characteristics. Of these, the largest group is the ground sharks (order Carcharhiniformes), representing about 24 percent of the shark families and about 55 percent of all shark species (fig. 1). In fact, approximately 24 percent of all elasmobranchs are members of the Carcharhiniformes. Of elasmobranchs only the rays are larger in total number of species with 543. Eight orders of shark contain 34 families and over 100 genera, and cumulatively contain at least 410 or more described species, with another 60 or so awaiting formal description. The California shark fauna is extensive, with representatives from 20 families, 30 to 31 genera, and 40 to 43 species.

What Is a Ray?

The rays, also known as batoids, are flattened or "winged" sharks whose pectoral fins expand forward and are fused to the sides of the head over the gill openings, which are on the underside of the head. Rays have a short, flat body; five or six paired gill openings; and a tail that varies from large, thick, and sharklike to slender and whiplike. One or two dorsal fins may be present but always lack a fin spine. Some species, particularly the stingrays, have tail spines, whereas most of the skates have enlarged thorns on the back and tail. Rays lack an anal fin. The pectoral fins, the main propulsive organ in rays, are greatly modified in some of the more specialized species, such as the stingrays, which have a slender whiplike tail, and the skates, which may have a small caudal fin.

The rays are the largest elasmobranch order with 22 families, 71 genera, and over 540 described species. Of ray species, the skates comprise over 44 percent (a number likely to increase as new species are described), the whiptail rays over 34 percent, the guitarfishes 11 percent, the electric rays nine percent, and the sawfishes and sharkfin guitarfishes less than one percent. The California ray fauna is represented by 10 families, 14 genera, and at least 22 species.

What Is a Chimaera?

The chimaeras are compressed, often silvery cartilaginous fishes differing from the elasmobranchs in having four pairs of gill openings, all protected by a soft gill cover with a single pair of external gill openings. Chimaeras lack the dermal denticles found in sharks and rays. Their teeth are fused into three pairs of ever growing tooth plates similar in appearance to rodent incisors, hence the common names ratfish or rabbitfish for some species. The first dorsal fin always has a spine, which can be erect or depressed. Male chimaeras have claspers on the pelvic fins, a pair of claspers (prepelvic tenacula) in front of the pelvic fins, and a single clasper (frontal tenaculum) on the forehead. Each clasper has hooklike denticles that help the male hold the female during copulation. Chimaeras propel themselves by large, fan-shaped pectoral fins.

Chimaeras have one order, three families, six genera, and over 35 described species, with as many as 15 or more species awaiting formal description. The fossil record indicates that in the past the chimaeras were far more abundant than they are today. The California chimaera fauna is represented by two families, two genera, and two described species. There is one and perhaps two undescribed species found in very deep water.

Distribution

There are two main faunal components of California's cartilaginous fishes: a cold-temperate fauna north of Point Conception and a warm-temperate fauna south of Point Conception, both heavily influenced by the prevailing surface water temperatures. The number of families, genera, and species increases as you move from northern to southern California (map 2). The southern California area appears to be a transitional zone between the warm- and cold-temperate regimes. The fauna south of Point Conception is remarkably similar to the Mexican fauna at the family level, with all but two shark and three batoid families found in both regions. Conversely the

Oregon, Washington, British Columbia, Gulf of Alaska			
	Families	Genera	Species
Sharks	11	16	16
Batoids	4–5	4–5	11–12
Chimaeras	1	1	1

California			
	Families	Genera	Species
Sharks	20	30–31	40–43
Batoids	10	13	22
Chimaeras	2	2	2

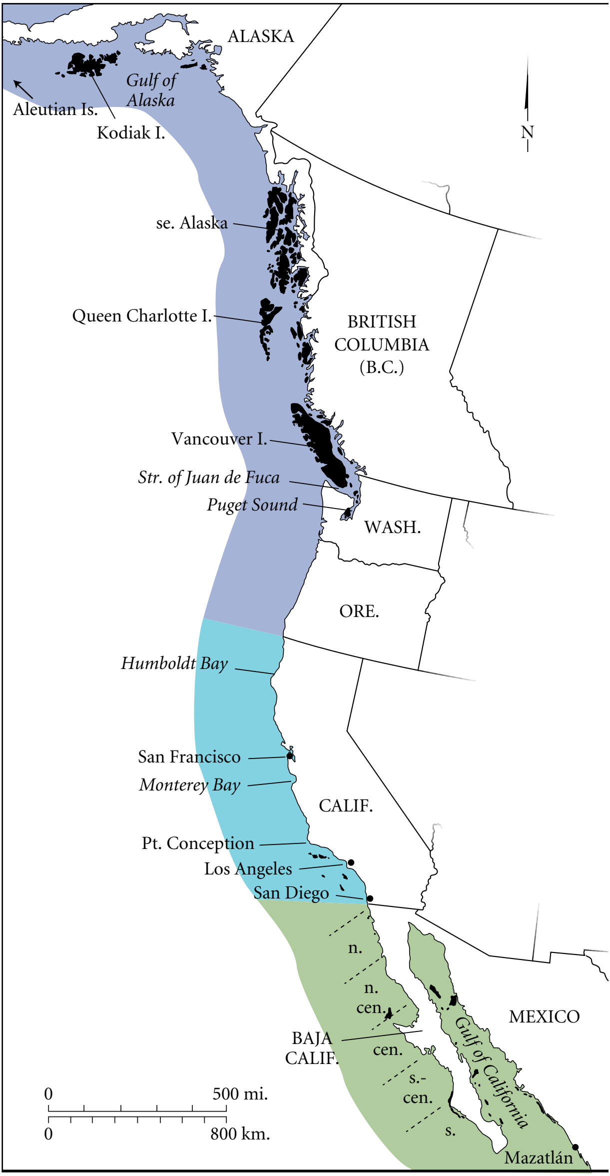
Mexico			
	Families	Genera	Species
Sharks	21	37	61–67
Batoids	11	19	42
Chimaeras	2	3	4

Worldwide			
	Families	Genera	Species
Sharks	34	104	410
Batoids	22	71	543
Chimaeras	3	6	35

Map 2. The approximate number of described chondrichthyan orders, families, genera, and species in the eastern North Pacific and worldwide. These numbers do not include those species awaiting formal description.

fauna north of Point Conception is similar to the Alaskan fauna, with most of the families also represented in the Gulf of Alaska. The most significant changes are in the species composition. The skates, in particular, become the prominent batoid group north of Point Conception with the whiptail rays becoming scarce.

The California shark fauna is composed of warm- to cool-temperate species. Most (71 percent) are fairly wide ranging, with 17 percent endemic to the eastern North Pacific; seven percent are antitropical, as they are also found in the temperate waters of Chile and Peru, and five percent are considered


ALASKA
Gulf of Alaska
Aleutian Is.
Kodiak I.
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se. Alaska
Queen Charlotte I.
BRITISH COLUMBIA (B.C.)
Vancouver I.
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Puget Sound
WASH.
ORE.
Humboldt Bay
San Francisco
Monterey Bay
CALIF.
Pt. Conception
Los Angeles
San Diego
n.
n. cen.
BAJA CALIF.
cen.
s.- cen.
s.
MEXICO
Gulf of California
Mazatlán
0
500 mi.
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800 km.

tropical. There are no shark species found only in California waters. By comparison, of the shark fauna 48 percent of Australian species and 30 percent of southern African species are endemic.

California's batoid fauna is composed of two distinct groups: a cold-temperate skate fauna that occurs in increasingly deeper water south of Point Conception and a warmer temperate component composed of nearshore species of the families Dasyatidae, Myliobatidae, Rhinobatidae, and Urolophidae, among others. In contrast to the sharks, 60 percent of the batoids are endemic to the eastern North Pacific. Only 20 percent of the species are considered wide ranging, with five percent being antitropical and 15 percent having a tropical influence. Of the rays, 73 percent of Australian fauna and 38 percent of southern African fauna are endemic.

The California chimaera fauna is composed of two families and two genera, with two species and a third as yet undescribed species found only in very deep water. Of the two described species, one is endemic to the eastern North Pacific and the other is fairly wide ranging. Slightly more than 50 percent of the chimaeras found in Australia and about 33 percent of those found in southern Africa are endemic.

General Biology

Reproduction

Elasmobranchs undergo an elaborate and complex courtship behavior, beginning when the male repeatedly bites the female, usually around the pectoral, pelvic, and anal fins, along the abdomen, and around the gill openings. This continues until the female is receptive. Unreceptive, females may bite or snap at the male to discourage him. The skin of most females has evolved to be slightly thicker than that of the males as protection from this behavior. Larger males usually grasp the female around the gill openings or on the pectoral fin and lie side by side from head to vent with the male's body curving around the female's body so that the male can insert the claspers. One or two claspers may be inserted depending on the species. In smaller sharks, particularly catsharks, the male wraps himself around the female without biting on the gill openings or pectoral fins. During copulation the pair either sinks slowly to the bottom, gently swims together, or lies on the bottom. What induces courtship behavior is unknown as there are very few instances of actual observations. However, as in other animal groups, pheromones may play an important role in determining whether a female will be receptive.

Cartilaginous fishes have a complex and involved life cycle (fig. 2). Fertilization is internal and the mode of reproduction varies from oviparous or egg laying to viviparous or live bearing, whereby the young are nurtured internally by an independent yolk supply (ovoviviparous or aplacental viviparity) or by the mother (viviparous or placental viviparity). Male cartilaginous fishes have paired claspers located on the pelvic fins, which are the intromitten organ for fertilization. During mating, one or both claspers may be inserted into the female's cloaca, secured with spurs, hooks, or sharpened terminal edges designed to splay open after insertion.

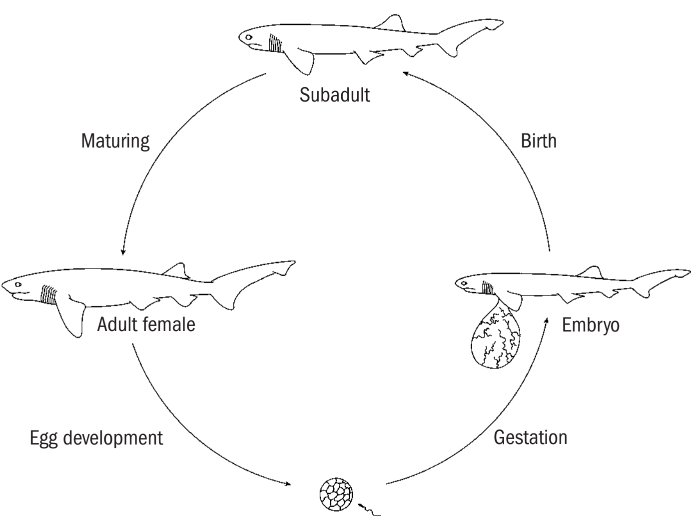

Figure 2. Generalized chondrichthyan life cycle as depicted by the Sevengill Shark.

Oviparous or egg-laying chondrichthyans usually deposit their egg cases on the bottom in mud, sand, or on rocky and coral reefs. The egg cases are usually purselike, have a conical or spindle-like shape, and have horns, tendrils, or spiral flanges to help wedge or otherwise anchor them to the bottom (fig. 3). Some species have nesting sites that are repeatedly used by several females. At least one group, the Horn Sharks, is known to pick up their egg cases with their mouths after laying them and carefully place them in an appropriate nesting site. Little information exists on incubation time for egg cases, although species reared in captivity seem to require a longer incubation period than those reared in the wild. Once born, the young immediately begin to feed on their own. There does not appear to be any maternal or paternal care for the eggs once they are laid and in fact some shark males feed on the egg cases of their own species. Besides sharks, some species of marine snails (gastropods) attack the egg cases by drilling holes in them and sucking out the yolk. Approximately 40 percent of sharks, 44 percent of rays, and all of the chimaeras lay eggs.

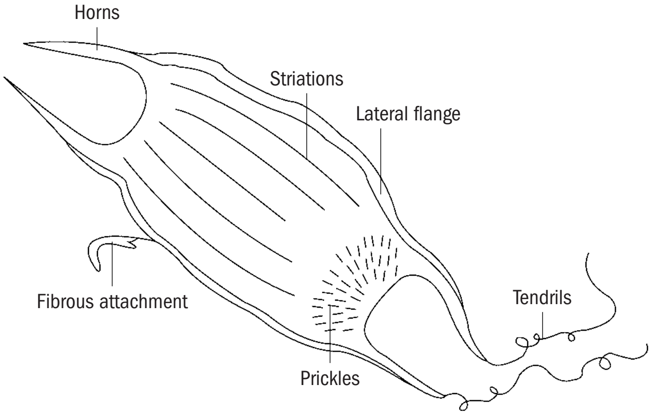

Figure 3. General illustration of chondrichthyan egg case terminology.

Viviparous (live-bearing) elasmobranchs nourish the developing embryo in one of two ways: either with or without placental attachment (fig. 4). In aplacental viviparity the developing embryo, not attached to the uterine wall, relies primarily on a large yolk sac for nourishment. Once the yolk sac has been exhausted the embryo is near full term and birth occurs shortly thereafter. In some of the more advanced rays, particularly the stingrays, the nourishment supply to the embryo is enhanced by secretion of a fluid milky nutrient through villilike extensions (trophonemata) of the uterine wall. This may in part explain why rays in general have a shorter gestation period and small litters with relatively large newborns. A rather bizarre twist to this reproductive mode, found mainly in mackerel sharks and false catsharks (family Pseudotriakidae), is that of oophagy (egg eating) and intrauterine cannibalism (embryo eating). Oophagous development is similar to that of other aplacental elasmobranchs except that when their yolk sac is used up the developing embryos begin to actively feed on ovulating eggs within the uterus. A more voracious form of intrauterine cannibalism (referred to as adelphophagy) occurs when the largest developing embryo actively attacks, kills, and eats all of the other smaller embryos within the uterus before feeding on the ovulating eggs. In sharks that exhibit intrauterine cannibalism no more than a single embryo per uterus usually survives unless its siblings are about the same size.

In viviparous or placental viviparous sharks (rays do not exhibit this mode of reproduction) the yolk supply is consumed early in the development of the embryo, at which time it becomes connected to the uterine wall of the mother, forming a yolk sac placenta. This is analogous to the mammalian placenta and serves to transfer nutrients from the mother directly to the embryos. Only 10 percent of all living sharks exhibit placental viviparity.

Figure 4. Viviparous elasmobranchs such as this Spiny Dogfish bear their young live, which enter the world as miniature versions of the adults.

Live-bearing elasmobranchs typically have a long gestation period, ranging from several months to over three years for at least one species. The litter size can range from one or two to at least 300 or more depending on the species. Most live-bearing elasmobranchs produce on average between two and 20 young per litter. Because the length at birth of some species may be 1 m or more, newborn sharks have very few predators other than larger sharks.

Migratory Patterns

Many cartilaginous fishes exhibit fairly complex migratory patterns associated with their life history cycle. For example, before "pupping," females of many species will move into specific nursery areas that are high in nutrients (food is available for the newborns) and that have a reduced potential of predation on the young. Although no cartilaginous fishes are known to provide parental care after birth, by placing their young in areas of high nutrients and low predation they ensure that a fairly high percentage of the young will survive. This is important, especially considering the low number of offspring they produce. Adolescent congeners are often excluded from the nursery grounds until they mature, perhaps to reduce competition between juvenile and adolescent animals or to remove a potential predator of the newborns, as adolescents of some species will prey on the juveniles of their own kind. These nursery areas are very specific for some species and the same individuals will return seasonally to these areas to give birth. Courtship and copulation also occur in these areas, although this is not always the case. Some species may move into bays, estuaries, or lagoons, others may move offshore, some deepwater forms may migrate up continental slopes and onto the continental shelf to give birth, and some bottom-dwelling species have their young migrate into the midwater zone.

Over the course of a year, changes in prey composition, water temperature, and salinity will variously affect the abundance and composition of the cartilaginous fish species residing in a particular habitat. Adults of some species may disappear for portions of the year, although their juveniles may remain within the confines of the nursery grounds until they reach adolescence. This is particularly evident in several California bays, which serve as important areas for mating and as nursery grounds. The seasonal return of some species to these bays follows a pattern known as "sequential migration." For example, the return of adult Sevengill Sharks to San Francisco and Humboldt Bays typically follows the arrival of adult female Bat Rays and Houndsharks, both of which subsequently give birth. Juvenile Bat Rays and houndsharks are important prey for young Sevengills and thus the appearance of these species in bays provides a significant food resource.

Age and Growth

Chondrichthyans, unlike bony fishes, have very few hard parts that can be used for estimating age. The age of a chondrichthyan is usually estimated by counting the number of calcified bands across the vertebral centra, in much the same way as the age of a tree is determined by counting the rings on its trunk. A band typically consists of one translucent (light) band and one opaque (dark) band (fig. 5). The deposition of opaque and translucent bands can sometimes be correlated with summer and winter seasons, respectively. In addition to vertebrae, the bands on the dorsal fin spines may also be an aid to estimating age. These bands are usually enhanced through various staining techniques, sectioning, or X-ray. However, the interval at which

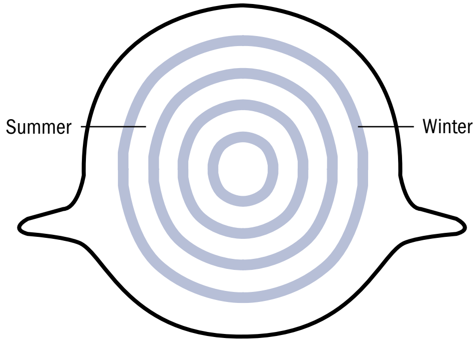

Figure 5. Cross-section of chondrichthyan vertebral centrum depicting light (summer) and dark (winter) bands.

these bands occur remains unknown for most species. Bands are generally assumed to be laid down once a year, but this has been validated for only a few species, such as the Leopard Shark and some of the smoothhound sharks. In the Basking Shark it appears that two bands are laid down every year. Furthermore, band deposition may not be correlated with age, as in the Pacific Angel Shark where it is associated with somatic growth. Pacific Angel Sharks are born with six or seven bands on their centra rather than the customary birth band observed in most species.

Size

Approximately 50 percent of all living sharks are less than 1 m in length—far smaller than the average size of a human—and 82 percent are less than 2 m long, with only about 18 percent of all shark species reaching a total length of more than 2 m. The average maximum length for living sharks is 1.5 m. Only 4 percent of all living shark species can be considered gigantic—sharks that regularly exceed 4 m and may grow up to 12 m or more in length. This includes the two largest living species, the Whale Shark and the Basking Shark, which may grow to lengths of 10 to 18 m. The Great White Shark, Sixgill Shark, Megamouth Shark, and Pacific Sleeper Sharks are other species known to exceed a maximum size in excess of 4.5 m. In contrast to these giants, some sharks are considered dwarfs or pygmies, reaching only 15 to 20 cm in length at maturity (e.g., the Pygmy Shark, which matures at a size of less than 20 cm). Most rays are less than 1 m in length at maturity, with fewer than 10 percent exceeding a length of 4 m or a width of 3 m. The largest rays include the Sawfishes, which can attain a length of 7 to 10 m, and the Mantas, which can have a disc width of 6 to 7 m. Chimaeras are small to moderately large, with most maturing at less than 1 m and only a few reaching over 1.5 m in length.

Food and Feeding Behavior

All living cartilaginous fishes are carnivorous predators consuming some type of animal protein for their diet. Although no known species are primarily herbivorous, some may inadvertently ingest algae while feeding. The size of prey items varies from minute crustaceans, ingested by some of the giant filter feeding sharks, to pinnipeds, cetaceans, and large oceanic fishes, consumed primarily by large sharks such as the Great White Shark or Tiger Shark. Some species are very selective feeders, focusing on bony fishes, crustaceans, or perhaps cephalopods, whereas others are extremely versatile and opportunistic predators. Most sharks have on occasion consumed some form of inorganic garbage, but by and large sharks tend to shy away from this type of food. The one exception is the Tiger Shark, which has a penchant for tasting unusual food items including leather, wood, coal, plastic bags, small barrels, cans, and other assorted junk related to human activity. Except for the Tiger Shark, which has often been called a garbage can with fins, the majority of sharks are not the blindly voracious predators of popular legend and generally feed on a very limited spectrum of mostly live prey. Cartilaginous fishes do not primarily scavenge, although some of the larger shark species will feed on carrion when available. Much of the misconception with regard to shark predation came from people watching them feed on refuse tossed over a ship or offal being discarded into the sea. As with any predator, sharks are unlikely to pass on an easy meal.

Sharks and rays, rather than being slow moving clumsy predators that feed more by chance, are actually extremely efficient hunters with a sophisticated predatory behavior pattern. The size and efficiency of the "hunter" relative to the size and behavior of its prey will greatly influence the way in which a shark or ray will attack. Depending on the species, variables such as size and shape, preferred habitat, life history stage, and season will be important factors in determining the size and type of prey it will consume. Studies on the foraging behavior of sharks and rays have shown that they possess a repertoire of strategies that they may employ when hunting specific prey items.

Perhaps the most interesting strategy by which sharks may feed, and one that greatly enhances the prey spectrum, is pack hunting (pl. 1). It was hypothesized over 30 years ago by Stewart Springer, a well-known shark biologist, that some of the tiny Lanternsharks (*Etmopterus* spp.) hunt in packs to subdue squids that were much larger in size than any one individual shark. Subsequent studies revealed that not only smaller sharks, but also larger species, including the Great White Shark, will hunt and feed cooperatively. These observations dispel the notion that all

Plate 1. Sevengill Sharks cooperatively hunting and feeding on a Harbor Seal (*Phoca vitulina*) in northern California.

sharks are lone marauders and indicate that many species are in fact quite social. Social hunting includes numerous advantages: sharks can (1) attack and subdue prey species that may be larger than any one individual predator, (2) forage over a wider area for food, (3) alert other sharks, through their behavior, to the presence of a food source, and (4) work cooperatively to herd numerous schooling prey species close together, thereby benefitting the whole group. Social facilitation in hunting prey items has been observed in Spiny Dogfish, Sevengill Sharks, Copper Sharks, Oceanic Whitetip Sharks, Blue Sharks, Hammerhead Sharks, and Bat Rays, among others. Likewise, rays will frequently forage in large groups searching for food, though less is known about their feeding behavior.

Other strategies that sharks and rays may incorporate in their hunting behavior include ambushing, burst speed, parasitizing, and filter feeding. Some sharks, and most rays, especially those that are not very mobile, catch their prey by ambushing it. They do this by lying in wait, like the Angel Shark, which lies partly buried in the sand or mud waiting for an unsuspecting prey item to swim by. Other sharks ambush their prey by stealth. With their neutrally buoyant livers sharks don't need to expend much energy to maintain their position in the water and thus are able to approach an unsuspecting prey item without creating any vibrations that the fish can detect. This is how apparently slow-swimming sharks are able to catch fast-swimming fishes such as tuna and salmon. Species such as the giant Pacific Sleeper Shark consume tunas in far greater quantities than it seems could have been scavenged. However, by approaching their prey in a very stealthy manner these sharks are able to get within striking distance before putting on a quick burst of speed. Several species, mainly oceanic forms, have tremendous speed and can catch their prey simply by running it down. The Mako and Salmon Sharks are excellent examples. Both are extremely active, fast-swimming species that commonly follow schools of tuna and salmon. The Great White Shark also is capable of catching fast-swimming species, as evidenced by a 5.5-m female shark caught off Anacapa Island that was found to have consumed two Blue Sharks, a Mako Shark, and two California Sea Lions.

Among these various feeding strategies are two forms of very specialized predation: parasitizing and filter feeding. The smallish Cookiecutter Shark (*Isistius* spp.) often attacks large Swordfishes, Elephant Seals, and whales by taking a gouging bite out of them (pl. 2). This probably causes its victim more irritation than anything else. The giant filter-feeding species have each developed a unique way in which to feed. The Whale Shark may swim passively with its mouth open, but more often than not it will come up through a school of small fish or crustaceans at the surface, raise its head out of the water, open its mouth, and by slowly sinking back into the water draw in its food. The Basking Shark uses even less energy to catch its food. It simply swims along at a pace of about 3 to 5 km/hr with its giant mouth open and allows water to pass over its gills, which, like the baleen in whales, catches the food. The Megamouth Shark uses a similar passive means of filter feeding, only this species migrates up and down the water column following its prey. The Manta gracefully glides through the water with its mouth open, passively ingesting its prey.

Cartilaginous fishes may migrate considerable distances to follow their major food sources. This is particularly true for many of the pelagic species such as the Thresher, Salmon, and Blue Sharks, which feed heavily on schooling pelagic fishes and squids. The movement of these sharks in pursuit of their primary prey species is in large part related to the behavior of the prey species.

Many cartilaginous fishes have special adaptations for catching their food. The long upper lobe of a Thresher Shark caudal fin may be used to stun or kill its prey before eating it. The long saw-like rostrum of the sawfishes (Pristidae) is used in a rapid side-to-side motion to stun or kill prey as well as for defense. The long abdomen of the Frilled Shark along with its highly distensible mouth allows it to engulf prey items more than one-half its own length. Other adaptations are less obvious, such as the long flattened snout of the Goblin Shark, which may act as a sensor for detecting prey in its deep-sea environment.

Other aspects of chondrichthyan predation that are less well known include prey behavior, foraging success, and prey-related injuries to the predator. The Swell Shark tends to hunt at night when many of its prey items are resting or asleep. By foraging at night this apparently lethargic shark is able to capture relatively active species that it probably could not capture during the day. Basking Sharks will congregate in areas of high productivity,

Plate 2. Cookiecutter Sharks ambushing a school of Dolphinfishes (*Coryphaena hippurus*).

usually from upwelling, where they will forage on certain planktonic species. The frequency of success of the predator is largely unknown, although scars on pinnipeds and cetaceans, which are more easily identified than scars left on a bony fish, may be one indication. Tooth scars left by sharks on Pacific Torpedo Rays would suggest that the electric voltage put out by these rays is sufficient to deter an attacker, yet this may be more the result of the size differential between the predator and its intended prey. A sufficiently larger predator would successfully subdue and consume the same Torpedo Ray. In addition to being used defensively, the electric organs of Torpedo Rays are used to hunt and subdue prey.

Another area of predatory behavior that is relatively unknown is prey-related injuries. The Torpedo Ray fending off a potential predator using its electric organs is one example. A swordfish bill was once found imbedded in a Mako Shark caught off Baja. The shark was alive when captured and the wound appeared to have healed. Spines from stingrays and various squaloid sharks are frequently found embedded in the head, mouth, and body cavity of sharks. It can be assumed that on occasion the predator may be killed by its intended prey during the attack.

Ecology

Cartilaginous fishes should be viewed as an integral and functioning part of any marine community, with each species occupying a distinct niche. The integral role these fishes play in the marine environment should not be underestimated, as in most instances they are among the apex predators. Yet despite their importance to the marine community, critical studies elucidating the precise role they play are seriously lacking. Much of the "research" conducted has not been beneficial, tending to focus either on the rare phenomenon of shark attack or on exploiting the public's imagination in the name of conservation or education. Historically cartilaginous fishes have often been lumped into a catchall category termed "sharks" or "rays" with little or no reference made to how many or what kinds of species are represented. This makes it difficult to study their ecological role.

Ecomorphology is the term used by ichthyologists to describe the study of the morphology and natural history of cartilaginous fishes in combination with their apparent life history.

Much can be inferred about a shark's life history by the design of its basic body form. The streamlined body form of fast-swimming oceanic sharks as exemplified by the Shortfin Mako and Blue Sharks is well designed for speed and agility. On the other hand the angel sharks, with their flattened, raylike body design, are well suited for a sandy bottom habitat. Many species of less active sharks, such as the Swell Shark, have a narrow, cylindrical body that is ideally suited for crawling over reefs and into cracks and crevices. The slightly compressed, flattened bodies of the batoids suit them well for cruising just off the bottom while searching for food. Although the general body form of most batoids is similar, they actually have a fairly complex suite of habitat requirements depending on the species and its preferred substrate type.

Ecosystems

Cartilaginous fishes may live on or near the ocean bottom, in what is called the benthic zone, or away from the bottom in the open sea, in what is known as the pelagic zone (fig. 6). Zone boundaries are crossed by numerous species of cartilaginous fishes and other marine animals, but because these zones are set up according to factors such as amount of light penetration,

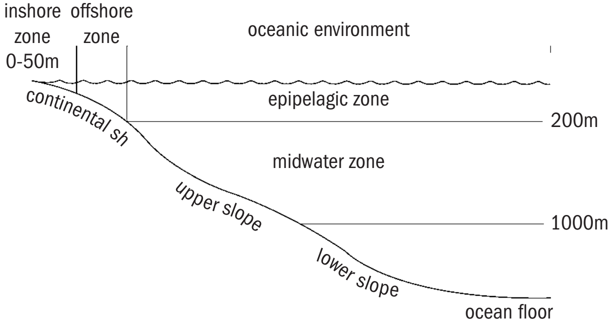

Figure 6. Generalized cross section of marine habitats along the California coast.

temperature, and the extent of the continental shelf and slope, they have considerable biological significance. Each of these two broadly classified zones, benthic and pelagic, is further subdivided into several distinct habitats, relative to the continental landmass, known as the continental shelf, continental slope, and oceanic habitats.

The continental shelf, which has a nearshore or coastal habitat that includes bays and estuaries, extends out to about 50 m in depth. Many of the cartilaginous fish species encountered in this zone are familiar to local anglers and others who spend time near the sea. Species that are common to the coastal environment and may be frequently encountered include the Sevengill Shark, Great White Shark, houndshark, Leopard Shark, Swell Shark, Horn Shark, Bat Ray, and Round Stingray. Beyond 50 m and out to a depth of approximately 200 m is the outer continental shelf. Species that are common to this outer shelf region include the Requiem Shark, Dogfish Shark, Thresher Shark, Hammerhead Shark, and Skate.

The cartilaginous fish fauna of a typical enclosed central or northern California bay environment can be differentiated both seasonally and spatially. Within a bay are a number of distinct habitats, from the deep central portion to its northern and southern reaches, where the bay fans out to form large expanses of mud fiats that become exposed during spring tides. These mud flats are often bisected by deeper channels, formed by runoff from small creeks and rivers. The bay ecosystem may consist of several elasmobranch species, each inhabiting one or more of these distinct areas. Typical members of this environment include the Brown Smoothhound, Leopard, and Sevengill Sharks as well as the Bat Ray. Leopard Sharks and Bat Rays tend to forage in the shallows of the mud flats, rooting out clams, burrowing worms, and mud shrimp, whereas the Brown Smoothhound, inept at mud rooting, swims just off the bottom in the deeper channels in search of crustaceans. Also hunting along these channels and occasionally venturing onto the mud flats are more active, powerful predators such as the Great White Shark and Sevengill Shark, both of which feed on, among other things, houndsharks, Bat Rays, and pinnipeds.

Open coastal areas also contain a variety of habitats, ranging from rocky reefs with kelp forests to sandy or mud bottoms with little vertical relief. Each habitat supports a different community of elasmobranchs. Nearshore rocky reef communities often consist of Bat Rays, Leopard Sharks, Horn Sharks, and Swell Sharks, whereas sandy beaches are ideal for the uniquely flattened Pacific Angel Shark, which lies quietly on the bottom and is often seen by divers, and for Torpedo Rays, Guitarfishes, and Thornback Rays, which patrol the bottom, each in search of its favorite prey. Farther offshore, but still on the continental shelf, are several species of benthic and pelagic elasmobranchs, such as the Thresher Shark, Requiem Shark, Catshark, Dogfish Shark, Stingray, and Skate.

Beyond the shelf is the continental slope, which can be divided into an upper (200 to 1,000 m) and lower (greater than 1000 m) slope. The continental slope is rich in species, with the dogfish sharks, catsharks, and skates representing the major groups of benthic cartilaginous fishes. Some species, such as the Sixgill Shark, move from the continental slope onto the shelf to pup during spring, and it is not uncommon to catch newborn and subadult Sixgills in relatively shallow water. The bizarre-looking but poorly known chimaeras are most abundant in this environment.

The California coast is bisected by numerous submarine canyons, with the grandest being the Monterey Submarine Canyon in Monterey Bay. These submarine canyons have their own unique set of habitats. Several deepwater species, such as the Prickly Shark, will congregate seasonally at the head of some submarine canyons in relatively shallow water for reasons that are still unclear. These submarine canyons are also unique in that they offer researchers the opportunity to study many deeper dwelling species without having to travel a great distance from land.

The oceanic environment is that region in which species move about in the water column with no reference points such as the bottom or pinnacles. This is the area in which many of the fast-swimming fishes, such as tunas, mackerels, and billfishes, are found. The oceanic elasmobranch fauna in California waters is mostly dominated by warm-temperate and tropical species, with only a few cold-temperate water species represented. Oceanic sharks include a variety of near-surface and deepwater species that range in size from the tiny Pygmy Shark to the giant Whale Shark. Oceanic sharks are generally wide ranging, with their distribution dependent mainly on the temperature of the water. Many species, particularly at the edge of their distribution, will migrate seasonally with the movement of water masses. Although some species occasionally visit the continental shelf, they are usually found far out to sea. In the case of the Oceanic Whitetip

Shark, considered one of the species most aggressive toward humans, this is probably good news for swimmers. Some sharks are known to give birth on the continental shelf, but the young as they mature migrate outward to the open ocean. Still other species, such as juvenile Spiny Dogfish, spend their first few years in an oceanic environment before settling into a more benthic lifestyle as adults. There are no known pelagic chimaeras.

The oceanic environment can be further subdivided vertically into an epipelagic zone and a midwater zone. The epipelagic zone is that area ranging from the surface down to a depth of approximately 200 m. This area is influenced by the degree of penetration of sunlight. Many of the shark species that occur in this habitat, like their bony fish counterparts, are fast-swimming species such as the Mako Shark, Silky Shark, and Blue Shark. In addition, there are some weaker swimming species such as the Oceanic Whitetip Shark or the Crocodile Shark. The Pelagic Stingray is usually found in the uppermost 100 m in this environment. Below the epipelagic zone is the midwater zone, an area that does not receive sunlight. Sharks in this zone are generally weaker swimmers such as the gigantic Megamouth Shark. Many of the shark species that occur in this zone migrate vertically into the shallower epipelagic zone at night to feed. One species, the Pygmy Shark, has been recorded to occur in water over 9,000 m deep, perhaps migrating this tremendous distance daily in search of food. The Cookiecutter Shark has been recorded from near the surface to a depth of over 3,500 m. It would not be surprising if larger species, such as the Megamouth Shark, also were found at considerable depths in the ocean.

Fisheries

The earliest fishery for cartilaginous fishes in California, started by indigenous people living along the coast, concentrated on common coastal species. In the mid-1800s Chinese immigrants to California fished for various coastal sharks and rays, particularly in and around San Francisco Bay. Interestingly, several species first described by ichthyologists were collected from fish markets in the Chinese communities along the central coast. Prior to 1936 the meat from sharks and rays was generally discarded, except in the Asian communities, where it was consumed.

The average price of shark and ray meat at this time was $0.10 to $0.20 per pound, although the fins, which are used as soup stock, sold for $2.50 per pound or more. During the 1900s, shark and ray commercial fisheries in California surged and regressed, experiencing two major cycles.

The first major cycle developed between 1936 and 1938 with the gradual realization that the livers of Soupfin and Spiny Dogfish Sharks, rich in vitamin A, could be sold on a competitive basis with cod liver oil. The outbreak of World War II in 1939 resulted in the curtailment of cod liver oil production and exportation from Europe. The west coast shark population therefore represented a tremendous source of raw material. The market for shark liver oil to replace the nonavailable cod liver oil improved rapidly and our expanding industry was soon supplying vitamin oils to Europe. However, by the mid-1940s the huge potential of the Pacific coast Soupfin and Spiny Dogfish Sharks supply had been tapped, synthetic vitamins were developed, and the fishery finally collapsed. The second major fishery cycle started in the mid- to late 1970s after the movie *Jaws* raised public awareness of sharks. This fishery mainly revolved around sharks as food for human consumption. The main species taken by commercial fisheries were the Blue, Shortfin Mako, Common Thresher, Angel, Soupfin, and Leopard Sharks and the Leopard Shark by recreational anglers, with other species such as the Sevengill, Sixgill, Great White, and Salmon Sharks, several of the skates, and the Bat Ray as minor catches.

Typically sharks and rays are initially caught in large numbers, but due to their low fecundity, slow growth, and late age at maturity, their populations quickly collapse. Unlike bony fishes, which are highly fecund, cartilaginous fishes have a very low fecundity rate. Sharks in particular tend to be inquisitive by nature and somewhat fearless, which makes them particularly vulnerable to overfishing. Rays, especially the skates, are taken in considerable numbers as a by-catch to other commercially important species in bottom trawl fisheries worldwide. Failure to record these catch data results in a gross underestimation of the numbers of rays actually caught.

It is unfortunate that it took the overexploitation of our local shark populations to finally prompt fishery agencies to adopt stringent regulations. However, to develop effective management plans fishery agencies need to know more about the life history of the commercially important shark species, need to realize the limitations the characteristics of the typical chondrichthyan life history impose, and need to understand the consequences of pressure from heavy fishing on shark and ray populations. Otherwise those regulatory agencies responsible for managing these fisheries will continue to fail.

In terms of abundance the White-spotted Ratfish is the only common chimaera species, but it has never been fished in California waters.

Injuries from Cartilaginous Fishes

Between 1950 and 1999 there were 106 shark attacks, including 11 fatalities, reported along the California coast (table 3). This represented an average of 2.1 attacks per year during this 50-yr period. The Great White Shark was identified as the culprit in 85 of these attacks. Other species implicated include the Blue Shark (three), Leopard Shark (two), Mako Shark (one), Hammerhead Shark (one), Sevengill Shark (one), and Tiger Shark (one). In 12 attacks, the species was unconfirmed. In addition, Sevengills have been implicated in about a dozen attacks on dogs in and around San Francisco Bay. A bather in at least one attack was playing with his dog in shallow water when a 1.5- to 1.8-m-long "spotted" shark attacked. Although the shark was unidentified, the attack occurred inside San Francisco Bay in an area in which Sevengills are fairly abundant.

The majority of shark attacks occurred while people were engaged in recreational water activities ($n = 98$) versus a commercial activity ($n = 8$). Of those people attacked along the California coast 73 percent were either surfing (24), skin diving (17), swimming (16), or scuba diving (15). Over the past 10 to 15 years kayaking and windsurfing have become popular activities and, not coincidently, there has been an increasing number of attacks on people engaged in these water sports.

Coastwide the majority of attacks have taken place north of Point Conception (74), with the Great White Shark being the primary culprit. Of these attacks 65 percent were in an area known as the red triangle, which stretches from Monterey Bay north to Bodega Bay and west to the Farallon Islands. Three locations, Tomales Point (seven), San Miguel Island (six), and the Farallon Islands (six), have the dubious honor of being the sites of most of the attacks (table 4).

TABLE 3. Number of Shark Attacks per Year along the California Coast between 1950 and 1999*

Year	Number of Attacks	Year	Number of Attacks	Year	Number of Attacks	Year	Number of Attacks	Year	Number of Attacks
1950	2	1960	2	1970	0	1980	1	1990	5
1951	0	1961	3	1971	1	1981	1	1991	4
1952	3	1962	2	1972	4	1982	4	1992	2
1953	0	1963	0	1973	0	1983	0	1993	5
1954	1	1964	1	1974	7	1984	3	1994	3
1955	4	1965	1	1975	5	1985	2	1995	4
1956	1	1966	1	1976	3	1986	1	1996	3
1957	2	1967	0	1977	1	1987	1	1997	1
1958	1	1968	1	1978	2	1988	2	1998	1
1959	7	1969	2	1979	1	1989	3	1999	2
Total	21		13		24		18		30

*Range: zero to seven attacks per year.

TABLE 4. Number of Shark Attacks by County and Location in California between 1950 and 1999

County	Total	Location	Total
Marin	12		
		Tomales Point	7
		Point Reyes	2
		Bird Rock	1
		Dillion Beach	1
		Stinson Beach	1
San Diego	12		
		La Jolla	5
		Imperial Beach	2
		Coronado	2
		Mission Beach	1
		Sunset Cliffs	1
		Oceanside	1
San Mateo	12		
		Pedro Beach	1
		Pigeon Point	3
		Point Purisima	1
		San Gregorio	1
		Ano Nuevo	2
		Tunitas	1
		Montara	1
		Linda Mar	1
		Franklin Point	1
Santa Barbara	11		
		San Miguel Island	6
		Santa Catalina Channel	1
		Point Conception	3
		Franklin Point	1
Monterey	9		
		Lover's Cove	1
		Pacific Grove	1
		Monterey	2
		Monastery Beach	2
		Point Lobos	1
		Point Sur	2

County	Total	Location	Total
Sonoma	8		
		Bodega Rock	2
		Salmon Creek Beach	2
		Sea Ranch	1
		Stillwater Cove	1
		Jenner	2
San Francisco	7		
		Baker's Beach	1
		Farallon Islands	6
Humboldt	7		
		Trinidad Bay	3
		Moonstone Beach	2
		Clam Beach	1
		Humboldt Bay	1
Los Angeles	7		
		Malibu	2
		Venice Beach	2
		San Pedro Channel	1
		Hermosa Beach	1
		Laguna Beach	1
Mendocino	6		
		Albion	1
		Bear Harbor	2
		Shelter Cove	2
		Westport	1
Santa Cruz	6		
		Santa Cruz	1
		Pajaro Dunes	1
		Davenport	3
		Waddell	1
San Luis Obispo	5		
		Pismo Beach	1
		Point Buchon	1
		Morro Bay	3
Ventura	2		
		Ventura	2
Del Norte	1		
		Klamath River Mouth	1
Orange	1		
		Seal Beach	1

The number of attacks is surprisingly small given the population of California (more than 30 million people and growing) and the fact that most people live near the ocean and/or participate in some form of marine activity. In the 1990s, with a rapidly growing ecotourism industry, the average number of attacks increased to 3.0 per year from an average of 1.8 per year in the 1980s. Along with California's growing human population, marine mammal populations are also on the rise, and although this has been good for the Great White Shark population, it may not be as good for beachgoers. Thus, increased interactions between humans and sharks are to be expected.

The number of attacks per year from 1950 to 1999 ranged from zero to seven with an average of 2.1 per year. Separating these 50 years into three categories based on number of attacks (zero to one, two to four, and five to seven) reveals that for 23 of these years there were zero or one attack for a total of 16 attacks. For the 22 years in which two to four attacks occurred there were a total of 61 attacks. Finally, looking at the five years in which the highest number of attacks took place there were 29 total attacks representing more than 25 percent of all attacks during this time. Why there are a higher number of attacks in some years compared with others is unknown, but this may be related in part to oceanographic conditions or human patterns of behavior.

Between 1950 and 1999 there were 26 years in which El Niño conditions persisted. During these years there were 54 attacks for an average of 2.1 attacks per year. Interestingly, although potentially dangerous warm-water species such as the Tiger Shark migrate into our area in El Niño years, there was no increase in shark attacks in these years as might have been expected. However, La Niña years did result in a slight increase, with an average of 2.5 attacks per year. The average number of attacks was 1.9 in years in which neither El Niño nor La Niña conditions prevailed.

Although oceanographic conditions are significant, patterns of human behavior and demographics may have a greater impact on the number of shark attacks. For example, it is well documented that young males tend to be attacked in higher proportions than other demographic groups. This being the case, it is interesting to note that during war years, with many young men away, the incidence of shark attacks decreased (1.25 attacks per year during the Korean War years of 1950 to 1953 and 0.9 per year between the Vietnam War years of 1963 and 1969. With the war in Vietnam over in 1973 the beaches were again filled with young men engaging in water sport activities, wet suits became increasing popular, and the number of shark attacks skyrocketed to 3.2 per year over the course of the remaining six years of the decade. The average number of attacks per year declined in the 1980s, most likely due to a combination of renewed interest in sharks as a commercial and recreational fishery, which caused the population of some sharks to decline, and severe El Niño and other oceanographic-related events in the early part of the decade. As the 1980s came to a close, recreational activities such as surfing, kayaking, and scuba diving became increasingly popular along with ecotourism. This trend continued throughout the 1990s, with 35 attacks, averaging about 3.0 per year, recorded between 1988 and 1999 (representing about one-third of all shark attacks that occurred between 1950 and 1999). Interestingly, in 1997 and 1998 (El Niño years), with the first of the "Baby Boomer" generation having turned 50, the number of attacks declined slightly, with only a slight increase in 1999 (a La Niña year!). It may be that as the population ages and the "Boomers" settle into a midlife lifestyle, the number of attacks will decline. Only time will tell!

Cartilaginous fish species other than sharks can inflict serious injuries on humans. Stingrays with their sharp, barbed, stinging spine can inflict a painful sting on people wading in the water. Seal Beach in southern California is notorious for having bathers stung by round stingrays, which use this popular beach area as a nursery ground (table 5). In 1963 over 500 people were stung by these rays in a 10-week period. In 2000, 385 people were stung on the northern end of Seal Beach, an area referred to as "Ray Bay." Because so many people have been stung by Round Stingrays in this area, local officials have started to clip the spines from hundreds of these rays to reduce the chances of bathers being stung. Removal of the spines does not injure the ray as they replace their spines annually. The spines of the Pelagic Stingray have been implicated in at least two fatalities. The dorsal fin spines of sharks and chimaeras can also inflict painful, although not fatal, wounds if mishandled. The Pacific Torpedo Ray can discharge 45 volts or more of electricity, enough to knock down a grown adult.

TABLE 5. Stingray Injuries at Seal Beach in Southern California between 1993 and 2001*

Year	Stingray Injuries
2001	299
2000	385
1999	290
1998	185
1997	132
1996	167
1995	209
1994	378
1993	31

*Injury statistics provided by Seal Beach lifeguards.

How to Use This Book

California's cartilaginous fish fauna should be no more difficult to identify than many of the bony fishes, birds, or marine mammals that occur along the coast. The common coastal species in particular are easily distinguishable from each other. Some of the less common to rare deepwater catsharks and skates, or those species that occasionally visit our area, may be a bit more difficult to identify. Most of the sharks in our area can be identified by focusing on particular characteristics, such as general body shape, number of gills, the presence or absence of fin spines, the position of the fins, body coloration, and tooth shape. Distinguishing batoid characteristics include the disc and tail shape, body color, the size and shape of the dermal denticles or enlarged thorns on the dorsal surface of the disc, and the presence or absence of tail spines. The chimaeras that occur off our coast can be distinguished from each other by their coloration, snout shape, and the presence or absence of an anal fin.

Experience is ultimately the best means by which you can quickly identify a species in the field. Keep in mind that a species not previously reported in our local waters may stray into our area. During extreme El Niño years a species commonly found in Mexican waters might migrate northward out of its usual range following the warmer water masses into our area. This is especially true for several of the requiem or hammerhead sharks, which can prove problematic even for the experienced ichthyologist. If you happen to collect or observe a particularly difficult-to-identify specimen, be sure to note where and when it was caught as it may be new to California. If the specimen is too large to keep be sure to take a good photograph of it in side view and save the teeth, jaws, and/or spines. Most local natural history museums, public aquariums, and universities have ichthyologists on staff who will gladly identify difficult specimens. A partial list of these institutions is provided at the end of this book.

Species Account

Under each species account is a color illustration of that particular species with a line illustration of the underside of the head and teeth. Following the illustrations is a description that can be used to identify the species, and pertinent information on its habitat and range, natural history, human interactions, nomenclature, and references. The species descriptions have been kept fairly simple, but it is advisable to consult the glossary and to examine the terminology illustrations (Figs. 7–9) to become familiar with the terminology used to identify cartilaginous fishes.

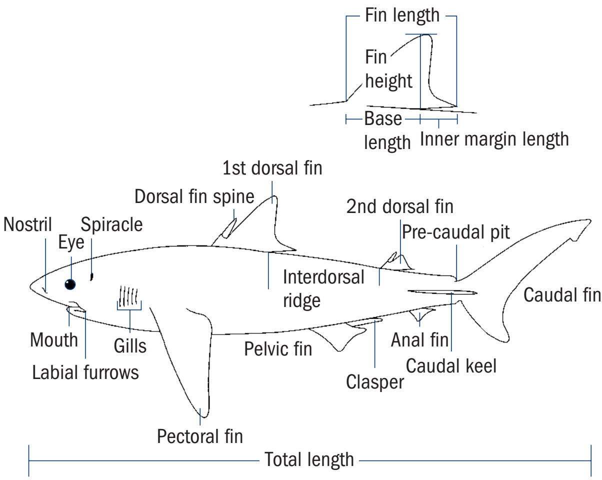

Figure 7. Shark terminology.

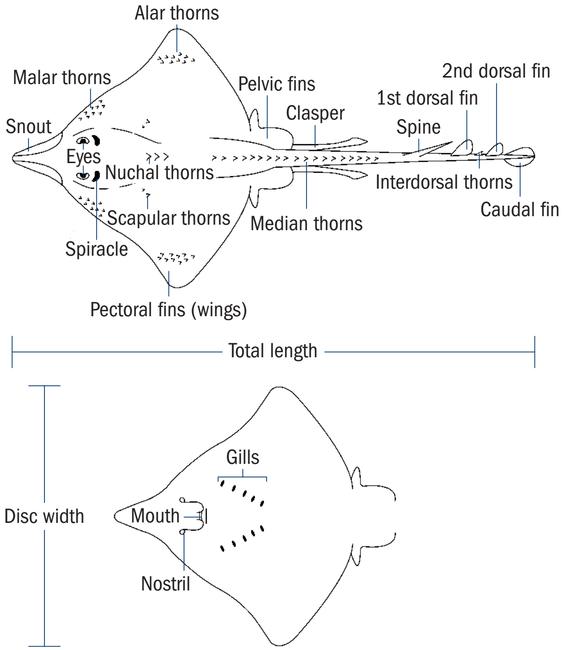

Figure 8. Ray terminology.

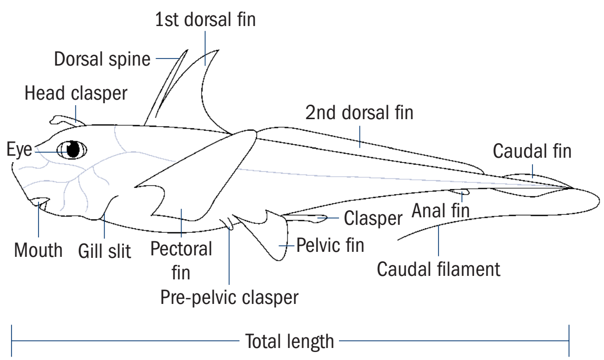

Figure 9. Chimaera terminology.

Illustrations

Color illustrations for all chondrichthyan species from off the California coast are based on the most "common" color scheme for each. In species whose color may vary regionally the most common local variant is illustrated. Juvenile coloration in newborns may vary considerably from that of the adult, although some species are very rare and have poorly described color features. This is particularly true for the skates and other rarely seen deepwater species. Every effort has been made to describe the color of living specimens where possible or to follow closely the description in the literature. In those instances in which color variants may differ dramatically these differences are described.

A line drawing of the underside of the snout and a representative upper and lower tooth is also included for most species. The teeth on many species may vary by position, and in some exhibit sexual dimorphism, but every attempt has been made to provide a drawing that should assist in identifying the species. Additional tooth descriptions have been provided under the species account.

Common and Scientific Names

The common names used here are taken from the American Fisheries Society (1991) publication, *Common and Scientific Names of Fishes from the United States and Canada,* or from the local vernacular used by fishermen, researchers, and others in referring to a particular species. Because the common name can change somewhat over the years, the most recent common name is used for each species. The scientific names used follow Compagno (1999) for the sharks and rays and Didier (1995) for the chimaeras.

Description

In this subsection a brief descriptive account of each species emphasizing key features such as body, snout, eye, mouth, fin, and tooth shape; number of gills; the presence or absence of dorsal and anal fins; the presence or absence of fin spines; and the relative position of fins to their approximate origin and/or insertion where appropriate is given. Ranges in the total number of (upper and lower) teeth, vertebra, and spiral valve counts are included, and although they may be of more use to ichthyologists, the amateur naturalist shouldn't be intimidated from using them to identify species. The counts used in this book come from several sources including my own research, unpublished data generously provided by colleagues, and literature accounts including, but not exclusively, those by Compagno (1988, 1990), Ebert (1990), Garrick (1982), Gilbert (1967), Nishida (1990), Notarbartolo-di-Sciara (1987), and Springer and Garrick (1964). Counts were taken for eastern North Pacific specimens except where little or no local information was available. An asterisk (*) is used to denote counts taken for specimens outside the eastern North Pacific region.

Habitat and Range

The geographic range in our waters is given as well as the range throughout the eastern North Pacific and general geographic distribution if applicable.

Natural History

The biological information for this subsection is based on original data I have collected over my many years of studying California's cartilaginous fish fauna, as well as data generously provided by colleagues, and from the many references cited in this book. Included in this subsection is information on species' mode of reproduction, size at maturity, size at birth, maximum size, migratory patterns, age at maturity, longevity, growth rate, diet, and foraging behavior as well as predators that feed on cartilaginous fishes.

Human Interactions

This subsection discusses the relationship between humans and cartilaginous fishes including commercial and recreational fisheries and injuries to humans caused by some of these fishes.

Nomenclature

The derivation of the Greek or Latin scientific name is included in this subsection as well as other common names that have been used in the literature. Common names from areas outside California waters are not included. Also in this subsection is a brief synonymy in instances in which taxonomic confusion has existed with regard to a particular species. The synonymy for each species is not complete, but includes those names frequently cited in earlier publications on the California fauna.

References

This subsection includes pertinent or significant literature based on studies from California or the eastern North Pacific. Additional references that were consulted for information on California's cartilaginous fish fauna, but that are not listed under each species account, include Castro (1983), Compagno (1984, 1988), Eschmeyer et al. (1983), Jordan and Evermann (1896), Roedel and Ripley (1950), Kato et al. (1967), Hart (1973), Miller and Lea (1972), Starks (1917, 1918), and Walford (1935).

Taxanomical Keys

A series of keys has been provided so that the reader can narrow down the list of options in identifying a particular species. At the end of this introduction is a key to the orders that will tell you whether the specimen is a shark, a ray, or a chimaera. By considering each pair of options and choosing the one that most accurately describes your specimen–regarding number of gill openings, presence or absence of fins, shape of the body, and so on–you will by a process of elimination arrive at the correct order.

Next, turn to the listing for that order (using the color coding in the table of contents) and you will mostly likely find a key to the families that comprise it. (There is no family key for the orders Squatiniformes, Heterodontiformes, and Orectolobiformes because they are monotypic, which means they are represented by only one family and one species in California waters.) As with the key to the orders, just work your way through the paired options to determine the family that your specimen is in.

From there, turn to the appropriate family–these are arranged phenotypically rather than alphabetically, so you may need to hunt through the order section a bit. In some cases, such as that of the frilled shark (Chylamydoselachidae), a single species is found; in others, such as the requiem sharks (Carcharhinidae), several genera are represented. Once you feel that you have keyed out the correct species, check to see if the description and illustration accurately describe your specimen. Remember that the color pattern shown is just one of several possible variants, and be sure to compare descriptions and illustrations of species in the same genus.