CHAPTER 1

The Science of Ichthyology



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Summary

Fishes account for more than half of all living vertebrates and exhibit remarkable evolution and diversity. There are over 35,000 living species of fishes (approaching 36,000 as we prepare this edition), of which over 100 are jawless (hagfishes, lampreys), approximately 1100 are cartilaginous (sharks, skates, rays), and the remaining are bony fishes.

A fish can be defined as an aquatic vertebrate with gills and with limbs in the shape of fins. There are, however, exceptions to such general rules, including hagfishes (nonvertebrate craniates) and some fishes that have lost their paired fins over evolutionary time (e.g. moray eels). Included in this definition is a tremendous diversity of sizes (from 8 mm gobies and minnows to the 12 + m Whale Shark), shapes, ecological functions, life history scenarios, anatomical specializations, and evolutionary histories.

Our current understanding of the relationships among the major extant lineages of fishes and other vertebrates shows that fishes include members of four different classes of vertebrates. The hagfishes (class Myxini) are craniates but not vertebrates. The major groups of living vertebrates include the lampreys (class Petromyzontida), sharks and other cartilaginous fishes (class Chondrichthyes), and the bony fishes and their descendants (class Osteichthyes). The Osteichthyes include the subclass Sarcopterygii (the lobe-finned fishes and their tetrapod descendants) and the subclass Actinopterygii (the ray-finned fishes).

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The Diversity of Fishes: Biology, Evolution and Ecology, Third Edition. Douglas E. Facey, Brian W. Bowen, Bruce B. Collette, and Gene S. Helfman.
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Most (about 60%) living fishes are primarily marine, and the remainder live in freshwater; about 1% move between salt and freshwater as a normal part of their life cycle. The greatest diversity of fishes is found in the tropics, particularly the Indo-West Pacific region for marine fishes and tropical South America, Africa, and Southeast Asia for freshwater species.

Unusual adaptations among fishes include African lungfishes that can survive buried in dry mud for up to 4 years, Antarctic fishes that produce their own antifreeze compounds, deep-sea fishes that can swallow prey larger than themselves (some deep-sea fishes exist as small males that are entirely parasitic on larger females), species that live less than a year and other species that may live hundreds of years, fishes that change sex from female to male or vice versa, sharks that provide nutrition for developing young via a complex placenta, fishes that create an electric field around themselves and detect biologically significant disturbances of the field, light-emitting fishes, warm-blooded fishes, and at least one group, the coelacanths, that was thought to have gone extinct with the dinosaurs.

Historically important contributions to ichthyology were made by Linnaeus, Peter Artedi, Georges Cuvier, Achille Valenciennes, Albert Günther, David Starr Jordan, B. W. Evermann, C. Tate Regan, and Leo S. Berg, among many others.

Genetics and molecular techniques have become integral and essential components to understanding fish biology, evolution, and ecology. In many cases, similarities in DNA probably more accurately reflect evolutionary relationships among groups than do morphological similarities.

The literature on fishes is voluminous, including college-level textbooks, popular and technical books, and websites that contain information on particular geographic regions, taxonomic groups, or species sought by anglers or best suited for aquarium keeping or aquaculture. Scientific journals with a local, national, or international focus are produced in many countries. Another valuable source of knowledge is public aquaria. Observing fishes by snorkel or scuba diving will provide anyone interested in fishes with indispensable, first-hand knowledge and appreciation.

We encourage anyone interested in fishes to observe them closely and carefully, both in captivity and in their natural habitats. They are truly fascinating animals.

Introduction

We recognize the formal common names of fish species as proper names, and therefore they will be capitalized throughout this book. Hence, a green sunfish could be any sunfish (family Centrarchidae) that has a somewhat green color, whereas Green Sunfish refers only to *Lepomis cyanellus*. However, bluefin tuna is not capitalized because it could refer to any of the following three species: the Atlantic Bluefin Tuna (*Thunnus thynnus*), the Pacific Bluefin Tuna (*Thunnus orientalis*), and the Southern Bluefin Tuna (*Thunnus maccoyii*).

Fishes make up more than half of the over 60,000 species of living vertebrates. Along with this remarkable taxonomic diversity comes an equally impressive habitat diversity. Fishes are the cradle of vertebrate biodiversity, dating back more than 500 million years, giving rise to the amphibians, dinosaurs, modern reptiles, birds, and mammals, including you. Millions of years before humans emerged from Africa to spread across the planet, fish species had already attained global distributions in the planet's oceans, lakes, and rivers. Diminutive killifish flourish in the highest lakes of the Andes (Lake Titicaca at 3812 m elevation), and ghostly snailfish forage in utter darkness of the deepest ocean abyss (Mariana Trench at 8000 m depth), very near the physiological limit for life under pressure. In a good year, anchovies of the genus *Engraulis* will vastly outnumber humans, foraging for plankton in schools that can span 50 km. The largest fish, the Whale Shark (*Rhincodon typus*), can exceed 12 meters in length, whereas the minnow *Paedocypris progenetica* in the swamps of Sumatra measures less than 1 cm. From ice-covered polar oceans to oxygen-depleted swamps, from the deepest ocean to desert ponds that dry up for years, and through all the more benign environments in between, fishes have been the ecologically dominant vertebrates in aquatic habitats through much of the history of complex life. To colonize and thrive in such a variety of environments, fishes have evolved striking anatomical, physiological, behavioral, and ecological adaptations.

With an excellent fossil record, fishes are showcases of the evolutionary process, exemplifying the intimate relationship between form and function, between habitat and adaptation. These themes are the foundations for our journey through the diversity of fishes. However, a shadow darkens this narrative: some killifish species in Lake Titicaca are extinct due to introduced trout, anchovies are harvested in the millions of tons to supply fish oil, and the whale shark is no match for human impacts on the global environment. We hope that an appreciation for the diversity of fishes brings a mandate to protect this diversity, so that future generations of fishes can continue to generate remarkable adaptations, and future generations of students can appreciate this majesty.

What Is a Fish?

It may be unrealistic to define a "fish," given the diversity of adaptations that characterizes the multiple classes and thousands of species alive today, each with a unique evolutionary history going back over half a billion years. By recognizing this diversity, one can define a fish as an aquatic chordate with gills and often with paired limbs in the shape of fins. The term "fish" is not a formal taxonomic category but a convenient term for a variety of aquatic organisms as diverse as jawless hagfishes and lampreys; cartilaginous sharks and rays; primitive bony fishes such as lungfishes, sturgeons, and gars; and advanced ray-finned fishes.

Definitions are hazardous in science because exceptions may be viewed as falsifications of the definition (see Berra 2001). Exceptions to the preceding definitions do not negate them, but instead, reveal adaptations arising through powerful selection pressures. Hence the loss of scales and fins in eel-shaped fishes tell us that these structures are not beneficial to fishes

with an elongate body. Similarly, although most fishes are ectothermic (the same temperature as the surrounding water), heterothermy (partial warm-blooded physiology) in tunas, lamnid sharks, and opahs indicates the metabolic benefits of elevated body temperature to continuously moving predators in open sea environments. Lungs or other air-breathing structures in lungfishes, gars, African catfishes, and gouramis demonstrate adaptations to environmental conditions where gills are insufficient for transferring adequate oxygen to the blood. Deviations from the definition of "fish" are not invalidations of the definition but are lessons about evolutionary innovations.

Vertebrate Classes

When we (the authors) were first learning our fishes, many textbooks listed five classes of vertebrates: Pisces (all fishes) and four classes of tetrapods – the amphibians, reptiles, birds, and mammals. But Nelson (1969) demonstrated that this five-class system was biased by a human perspective that overemphasized differences among tetrapods while neglecting many of the profound differences among the different evolutionary lineages of fishes. This approach minimized the large morphological and evolutionary gap between the jawless fishes (lampreys and hagfishes) and other groups of fishes and exaggerated the more recently evolutionary divergences between bony fishes and tetrapods. Thus "Pisces" was not a monophyletic group with a single evolutionary history but rather a term used for convenience to describe all non-tetrapod vertebrates, which included several groups that are not closely related to one another (see Chapter 11). More recently, however, modern phylogenetics with an emphasis on utilizing DNA-based molecular appraisals of evolutionary lineages has yielded a more accurate view of the relationships among the major groups of vertebrates (Fig. 1.1).

The great diversity of fishes includes several major branches, and there is some difference of opinion among experts regarding the major taxonomic groupings. Nelson et al. (2016) and our previous edition recognized five classes that included fishes. Nelson et al. (2016) recognize four classes, whereas Eschmeyer and Fong (2017) recognize eight. There is general agreement that the jawless hagfishes and lampreys each belong in their own class, with hagfishes not quite qualifying as vertebrates (hence the term "craniate"). Nelson et al. (2016) put all cartilaginous fishes with jaws in one class (Chondrichthyes), whereas Eschmeyer and Fong consider the Holocephalans (ratfishes, chimaeras) as a class apart from the sharks, skates, and rays (Euselachii). Nelson et al. 2016 consider all jawed, bony fishes (and their descendants, including tetrapods) as members of the class Osteichthyes, with the Sarcopterygii (lobe-fins) and Actinopterygii (ray-fins) as separate subclasses. (These each had separate class status in Nelson 2006.) Eschmeyer and Fong separate the lobe-finned fishes (and their descendants) into three classes and consider all ray-finned fishes as members of a single class. The differences are due to somewhat different interpretations of the level of differences among groups – but should not cause undue concern or confusion to

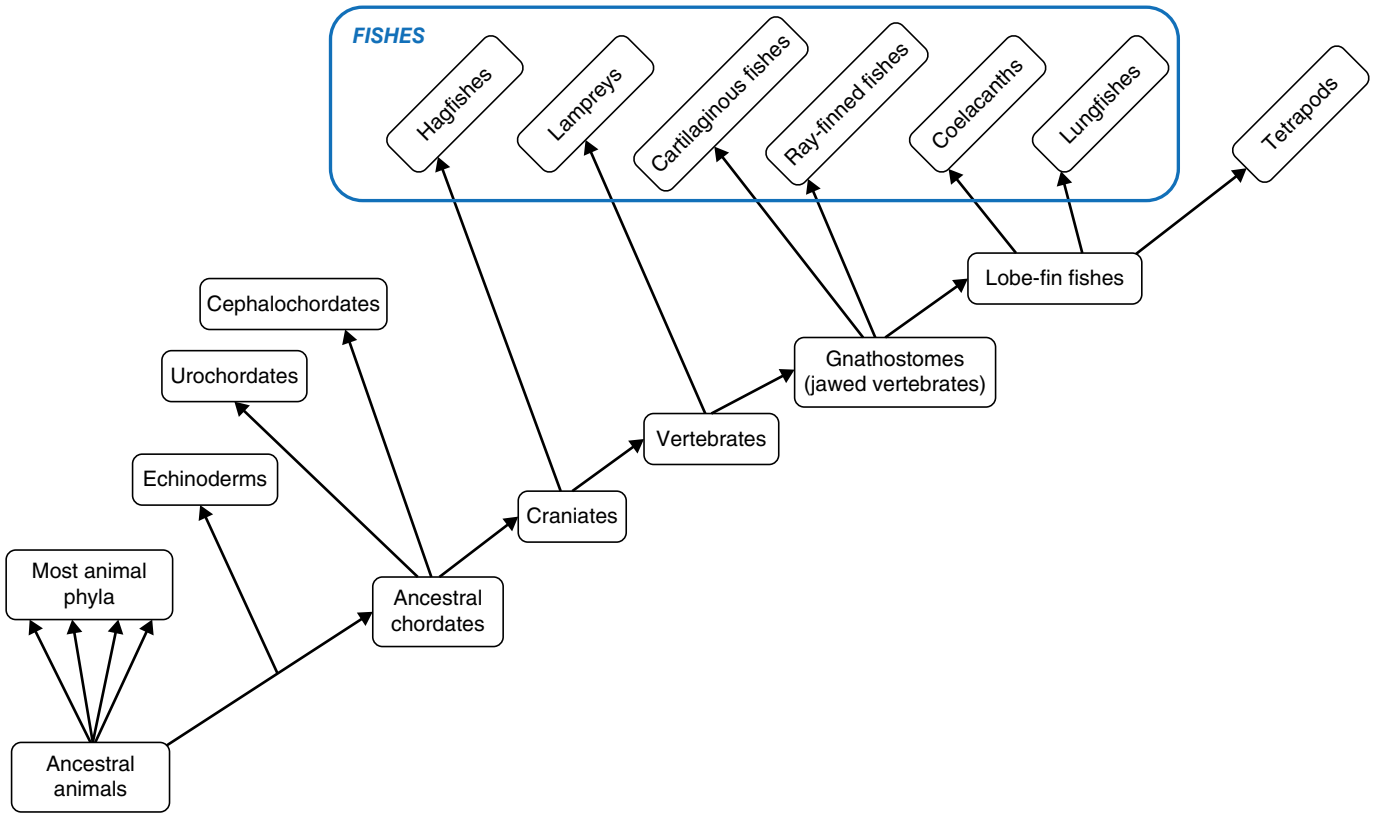


FIGURE 1.1 A cladogram showing the relationships of the major groups of chordates. Note that the fishes represent several major groups, and that the tetrapods are derived from a branch of the lobe-finned fishes.

TABLE 1.1 **The diversity of living fishes. Below is a brief listing of higher taxonomic categories of the Phylum Chordata, including living fishes, in phylogenetic order. This list is meant as an introduction to major groups of living fishes as they will be discussed in the initial two sections of this book. Many intermediate taxonomic levels, such as infraclasses, subdivisions, and series, are not presented here; they will be detailed when the actual groups are discussed in Part III. Only a few representatives of interesting or diverse groups are listed. Taxa mainly according to Nelson et al. 2016.**

PHYLUM CHORDATA
Subphylum Cephalochordata – lancelets
Subphylum Craniata
Infraphylum Myxinomorphi
Class Myxini – hagfishes
Infraphylum Vertebrata
Superclass Petromyzontomorphi
Class Petromyzontida – lampreys
Superclass Gnathostomata – jawed vertebrates
Class Chondrichthyes – cartilaginous fishes
Subclass Holocephali – chimaeras
Subclass Euselachii – sharklike fishes
Infraclass Elasmobranchii –extant sharks and rays
Grade Teleostomi
Class Osteichthyes - bony fishes and tetrapod descendants
Subclass Sarcopterygii – lobe-finned fishes and relatives (includes Infraclass Tetrapoda), but only fishes listed here
Infraclass Actinistia (Coelacanthimorpha) – coelacanths
Infraclass Dipnomorpha – lungfishes
Subclass Actinopterygii – ray-finned fishes
Infraclass Cladistia – bichirs
Infraclass Chondrostei – paddlefishes, sturgeons
Neopterygii – unranked clade including Holosteans and Teleosts
Infraclass Holostei
Division Ginglymodi – includes gars
Division Halecomorphi – includes Bowfin
Infraclass Teleosteomorpha
Division Teleostei
Cohort Elopomorpha – tarpons, bonefishes, eels
Cohort Osteoglossomorpha – bonytongues
Cohort Otocephala
Superorder Clupeomorpha – herrings
Superorder Ostariophysi – minnows, suckers, characins, loaches, catfishes
Cohort Euteleostei – further derived bony fishes
Superorder Protacanthopterygii – salmons, smelts, pikes, stomiiforms (bristlemouths, marine hatchetfishes, dragonfishes
Superorder Ateleopodomorpha - jellynose fishes
Superorder Cyclosquamata - greeneyes, lizardfishes
Superorder Scopelomorpha - lanternfishes
Superorder Lampriomorpha - opahs, oarfishes
Superorder Paracanthopterygii - troutperches, cods, toadfishes, anglerfishes
Superorder Acanthopterygii - spiny rayed fishes: mullets, silversides, killifishes, squirrelfishes, sticklebacks, scorpionfishes, basses, perches, tunas, flatfishes, pufferfishes, and many others

students of ichthyology. Our understanding of fishes continues to evolve, as do the fishes themselves. In this text, we follow Nelson et al. (2016) and recognize four classes: Myxini, Petromyzontida, Chondrichthyes, and Osteichthyes (which includes the subclasses Sarcopterygii and Actinopterygii, Table 1.1).

Regardless of differences in higher taxonomic rankings, it is worth noting that in all interpretations of the phylogeny of major groups of vertebrates, the tetrapods (amphibians, reptiles, birds, and mammals, including humans) are a subgroup of the lobe-fins. This means that lungfishes and coelacanths are more closely related to you than they are to an Atlantic Bluefin Tuna or a Largemouth Bass. And all of the bony fishes are more closely related to you than they are to sharks, which are in a completely different class representing jawed vertebrates that have a skeleton of calcified cartilage instead of bone.

The Diversity of Fishes

There are well over 35,000 living species of fishes (Eschmeyer & Fong 2017), with the number approaching 36,000 as we complete this update of our text. (Among ichthyologists, the word "**fish**" is used to refer to a single individual or multiple individuals of a single species, whereas "**fishes**" is plural for more than one species, see Fig. 1.2). The great majority of these species are bony fishes with jaws, but there are also many jawless fishes (hagfishes and lampreys) and cartilaginous fishes with jaws (sharks, skates, rays, and chimaeras). Increased study of remote habitats, combined with modern genetic techniques, helps to continuously add new species to our lists – 7841 new species of fishes were described between 1998 and 2017 (Eschmeyer & Fong 2017). Consult the online *Catalog of Fishes* for updated information, including lists by major taxa.

One reason for the enormous diversity of fishes is the diversity of habitats in which fishes are successful. Water covers about 71% of the earth's surface, and in many places is very deep so the total volume of potential habitats is enormous. Fishes occupy nearly all aquatic habitats that have liquid water throughout the year, including thermal and alkaline springs, hypersaline lakes, sunless caves, anoxic swamps, temporary ponds, torrential rivers, wave-swept coasts, high-altitude and high-latitude environments, open expanses of large lakes

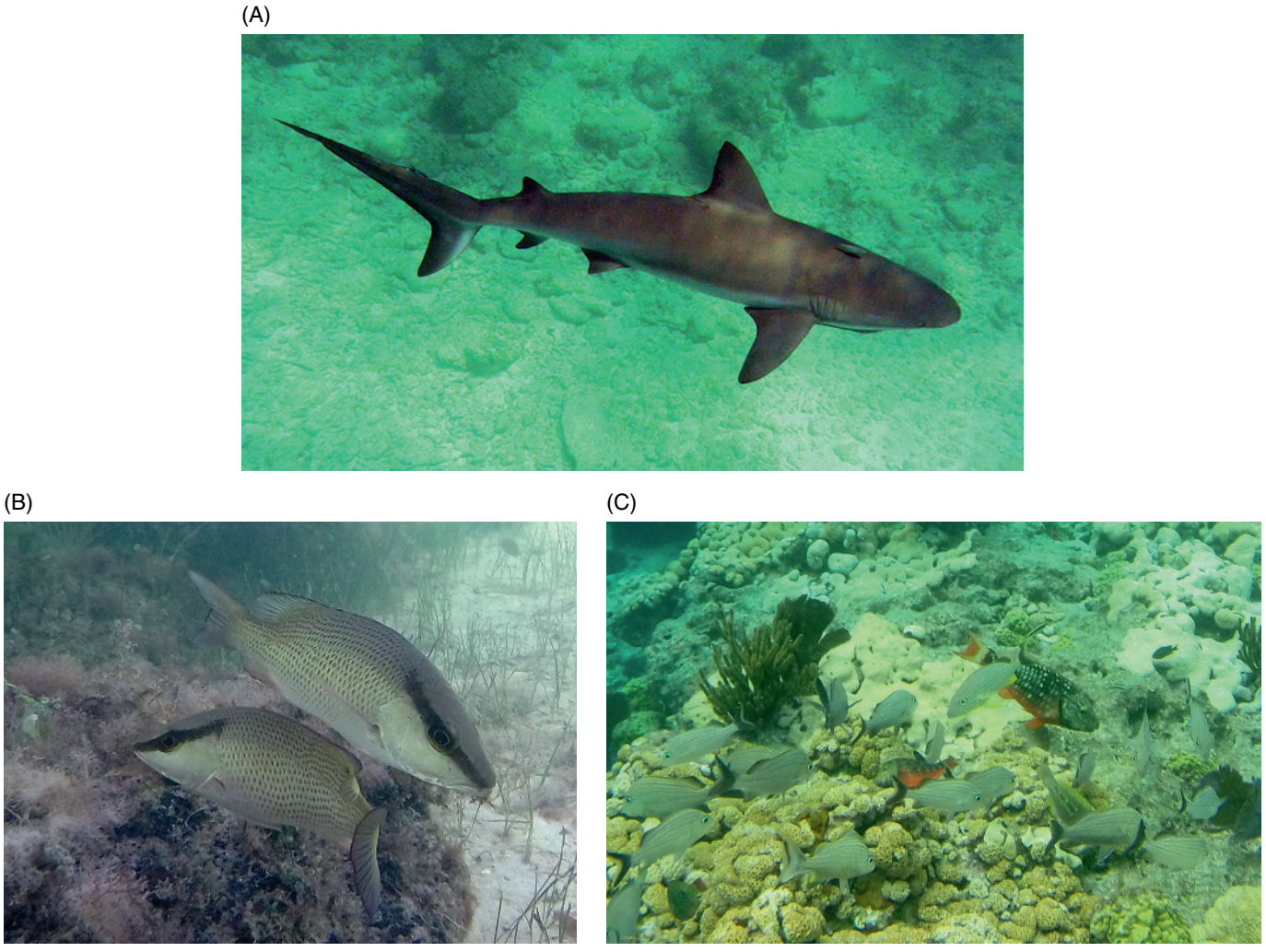


FIGURE 1.2 Fish versus fishes. By convention, "fish" refers to one or more individuals of a single species. "Fishes" is used when discussing more than one species, regardless of the number of individuals involved. (A) One fish, (B) two fish, (C) multiple fishes. (A) G. Helfman (Author); (B, C) D. Facey (Author).

and oceans, and deep ocean areas with no sunlight, low temperatures, and intense pressure. The altitudinal record is set by some nemacheiline river loaches that inhabit Tibetan hot springs at elevations of 5200 m; the record for unheated waters is Lake Titicaca in northern South America, where killifishes and pupfishes live at an altitude of 3812 m. The deepest living fishes are snailfishes and cusk-eels, which occur 8000 m down in the deep sea. When broken down by major habitats, a bit under 60% of fish species live in seawater, about 1% move between freshwater and the sea during their life cycles, and the rest live in freshwater. The highest diversities are found in the tropics. The Indo-West Pacific region known as the Coral Triangle (between Philippines, Indonesia, and New Guinea) has the highest marine diversity with an estimated 4000 species (Allen & Erdmann 2012), whereas South America, Africa, and Southeast Asia, in that order, contain the most species of freshwater fishes (Berra 2001; Lévêque et al. 2008).

Some fishes have adapted to life in water with little oxygen and can breathe air (see Chapter 3). There are even some species that make occasional excursions onto land (see Chapter 7). And we must not forget that over 530 million years of evolutionary adaptations have permitted some descendants of early lobe-finned fishes to become permanently terrestrial – but we call them tetrapods, reserving the term "fish" for those still mainly restricted to aquatic habitats.

Fishes show great variation in body length, ranging more than 1000-fold. The world's smallest fishes – and vertebrates – mature at around 7–8 mm and include the previously mentioned Indonesian minnow, *P. progenetica*, and two gobioids, *Trimmatom nanus* from the Indian Ocean and *Schindleria brevipinguis* from Australia's Great Barrier Reef. Parasitic males of a deep-sea anglerfish *Photocorynus spiniceps* mature at 6.2 mm, although females are 10 times that length. The world's longest cartilaginous fish is the Whale Shark *R. typus*, which can exceed 12 m, whereas the longest bony fish is the 8 m long (or longer) Oarfish *Regalecus glesne*. Body masses top out at 34,000 kg for whale sharks and 2300 kg for the Ocean Sunfish *Mola mola* (Fig. 1.3). Diversity in form includes relatively fishlike shapes such as minnows, trouts, perches, basses, and tunas, but also such unexpected shapes as boxlike trunkfishes, elongate eels

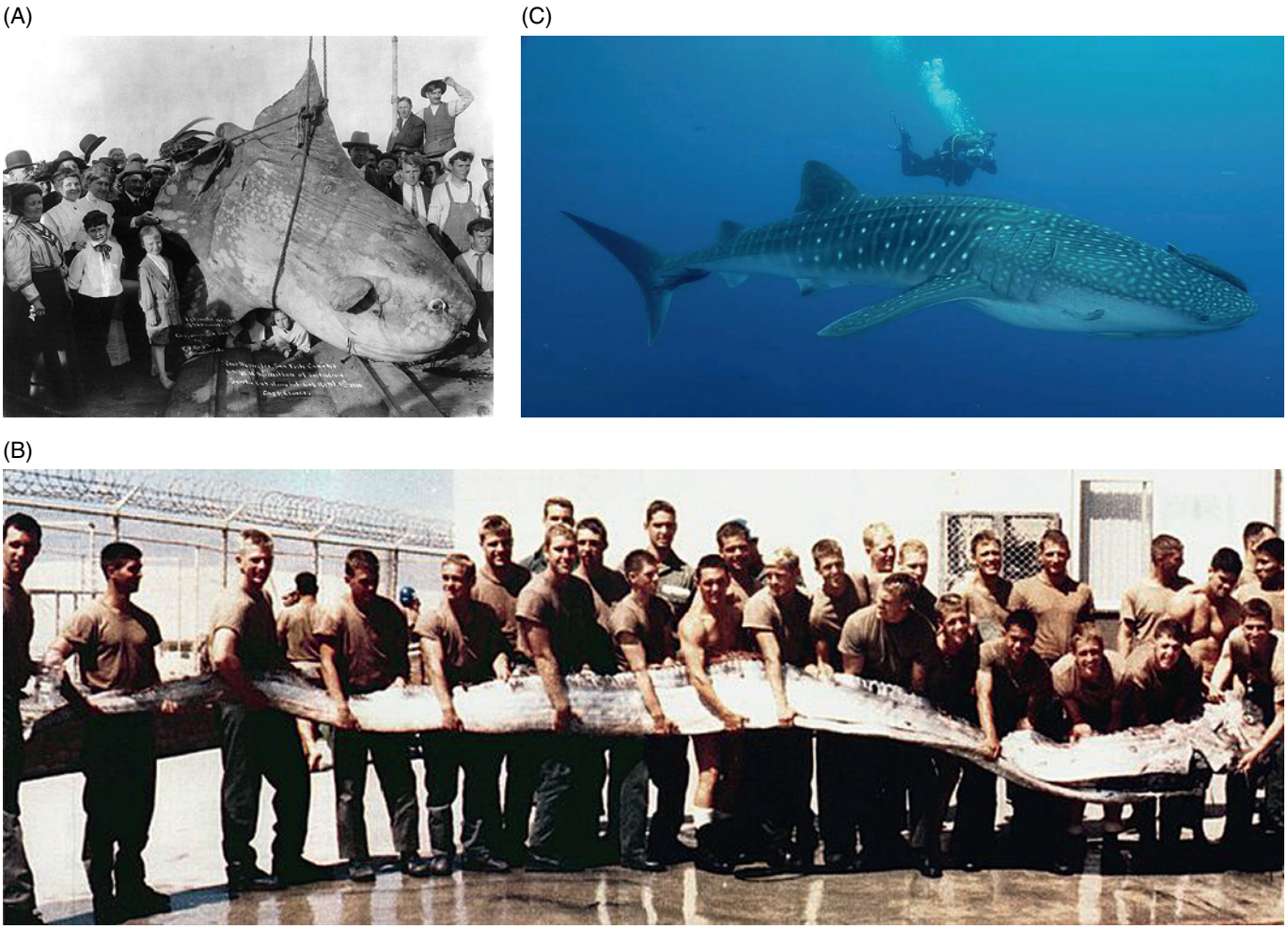


FIGURE 1.3 Some very large fishes. (A) The Ocean Sunfish (*Mola mola*) is estimated to be the heaviest of the bony fishes, with some estimated to weigh up to over 2000 kg . The Library of Congress / Public Domain. (B) The Oarfish (*Regalecus glesne*) is probably the longest bony fish in the world (can exceed 10 m) and is responsible for many reports of sea monsters . Photo by Wm. Leo Smith / Wikimedia Commons / Public Domain. (C) The Whale Shark (*Rhincodon typus*), a filter-feeding cartilaginous fish that can exceed 12 m and 21 tons, is the largest of the living fishes on the planet. Crystaldive / Wikimedia Commons / CC BY-SA 4.0.

and catfishes, globose lumpsuckers and frogfishes, rectangular ocean sunfishes, question-mark-shaped seahorses, and flattened and circular flatfishes and batfishes, in addition to the exceptionally bizarre fishes of the deep sea.

Superlative Fishes

A large part of ichthyology's fascination is the spectacular diversity of fishes. As a few examples:

- Coelacanths, an offshoot of the lineage that gave rise to the amphibians (and subsequently to all tetrapods), were thought to have died out with the dinosaurs at the end of the Cretaceous Period, about 65 million years ago. However, in 1938, fishers in South Africa trawled up a live Coelacanth. This fortuitous capture of a "living fossil" not only rekindled debates about the evolution of vertebrates but underscored the international and political nature of conservation efforts (see Chapter 13).
- Lungfishes can live in a state of dry "suspended animation" for up to 4 years, burying themselves in the mud and becoming dormant when their ponds dry up and reviving quickly when immersed in water (see Chapters 3, 13).
- Some Antarctic fishes don't freeze because their blood contains antifreeze proteins that prevent ice crystal growth. Some Antarctic fishes have no hemoglobin, and thus have clear blood (see Chapter 10).
- Deep-sea fishes include many forms that can swallow prey larger than themselves. Some deep-sea anglerfishes are characterized by females that are 10 times larger than males, the males existing as small parasites permanently fused to the side of the female, living off her bloodstream (see Chapter 10).
- Fishes grow throughout their lives, changing their ecological role several times. In some fishes, differences between larvae and adults are so pronounced that many larvae were originally thought to be entirely different species (see Chapter 9).
- Fishes have maximum life spans of as little as 10 weeks (African killifishes and Great Barrier Reef pygmy gobies) and as long as 400 years (Greenland shark; Neilsen et al. 2016). Several teleost fishes can live past 100 years (Randall & Delbeek 2009). Some short-lived species are annuals, surviving drought as eggs that hatch with the advent of rains. Longer-lived species may not begin reproducing until they are 20 or more years old (see Chapter 8).
- Gender in many fishes is flexible. Some species are simultaneously male and female, whereas others change from male to female or from female to male (see Chapter 8). Fishes, therefore, are the original genderfluid vertebrates and demonstrate that nature includes a broad range of gender identities.
- Fishes engage in parental care that ranges from simple nest guarding to mouth brooding to the production of external or internal body substances upon which young feed. Many sharks have a placental structure as complex as any found in mammals. Egg-laying fishes may construct nests by themselves, whereas some species deposit eggs in the siphon of living clams, on the undersides of leaves of terrestrial plants, or in the nests of other fishes (see Chapter 17).
- Many fishes can detect biologically meaningful, minute quantities of electricity, which they use to navigate and sense prey, competitors, or predators. Some groups can produce an electrical field and detect disturbances to the field, whereas others produce large high-voltage pulses to deter predators or stun prey (see Chapters 4, 16).
- Some fishes can produce light; this ability has evolved independently in different lineages and can be produced either by the fish itself or by symbiotic bacteria (see Chapter 10).
- Although the blood of most fishes is the same temperature as the water surrounding them, some pelagic fishes maintain body temperatures warmer than their surroundings and have circulatory systems that use countercurrent flow to conserve metabolic heat (see Chapter 7).
- Predatory tactics include attracting prey with lures made of modified body parts or by feigning death. Fishes include specialists that feed on ectoparasites, feces, blood, fins, scales, young, and eyes of other fishes (see Chapter 16).
- Fishes can erect spines or inflate themselves with water to deter predators. In turn, the ligamentous and levering arrangement of mouth bones allows some fishes to increase mouth volume by as much as 40-fold (see Chapters 3, 16).
- Some of the most dramatic demonstrations of evolution result from studies of fishes. Both natural and sexual selection have been experimentally manipulated in Guppy, swordtails, and sticklebacks, among others. These investigations show how competition, predation, and mate choice lead to adaptive alterations in body shape and armor, body color, vision, and feeding habits and locales (see Chapters 16, 20). Fishing has also proven to be a powerful evolutionary force, affecting the ages and sizes at which fish reproduce, body shape, and behavior (see Chapter 22).

Fishes have become increasingly important as model organisms for vertebrate research. Because of small size, ease of care, rapid growth and short generation times, and larval anatomical features, such species as Medaka, *Oryzias latipes*, and Zebrafish, *Danio rerio*, are used in studies of toxicology, pharmacology, neurobiology, developmental biology, cancer and other medical research, aging, genomics, and recombinant DNA methodology (e.g. Shima & Mitani 2004; Collins et al. 2010; Chang et al. 2013).

A Brief History of Ichthyology

Fishes would be just as diverse and successful without ichthyologists studying them, but what we know about their diversity is the product of the efforts of workers worldwide over several centuries. Science is a human endeavor and knowing something about historical ichthyologists and their contributions should help give a sense of the dynamics and continuity of this long-established science. Knowing the past can inform future directions.

Although natural historians, as well as many others, have studied fishes for millennia, the earliest treatment of fish behavior, reproduction, and classification in Western culture is Aristotle's *Historia Animalium*. Published about 2300 years ago, this wide-ranging text recognized cartilaginous and bony fishes and was hugely influential in zoology for two millennia. Modern science generally places the roots of ichthyology in the works of Carl Linne (Linnaeus), who produced the first organized system of classification. Zoologists have agreed to use the 10th edition of his *Systema Naturae* (1758) as the starting point for formal nomenclature. The genius of Linnaeus' system is what we refer to as **binomial nomenclature**, naming every organism with a two-part name based on **genus** (plural **genera**) and **species** (singular and plural, abbreviated **sp.** or **spp.**, respectively). Linnaeus did not care much for fishes, so his ichthyological classification, which put the diversity of fishes at less than 500 species, is based largely on the efforts of Peter Artedi (1705–1735), the acknowledged "father of ichthyology." Artedi fell into a canal in Amsterdam one night and drowned under suspicious circumstances (Pietsch 2010). Certainly not the last fish biologist to perish in the aquatic medium, he was buried in an unmarked pauper's grave, and it was left to his friend Linnaeus to publish the masterpiece *Ichthyologia* in 1738.

In the mid-1800s, the great French anatomist Georges Cuvier joined forces with Achille Valenciennes to produce the first complete list of the fishes of the world. During those times, French explorers were active throughout much of the world, and many of their expeditions included naturalists. Thus, the *Histoire naturelle de poissons* (1829–1849) includes descriptions of many species of fishes in its 24 volumes. This major reference is still of great importance to systematic ichthyologists, as are the specimens upon which it is based, many housed in the Museum National d'Histoire Naturelle in Paris.

A few years later, Albert Günther produced a multivolume *Catalogue of fishes in the British Museum* (1859–1870). Although initially designed to simply list all the specimens in the British collections, Günther included all the species of which he was aware, making this catalog the second attempt at listing the known fishes of the world.

The efforts of Linnaeus, Artedi, Cuvier and Valenciennes, and Günther all placed species in genera, and genera in taxonomic families, based on overall resemblance. A modern philosophical background to classification was first developed by Charles Darwin with his *On the Origin of Species* in 1859. His theory of evolution meant that species placed together in a genus were assumed to have had a common origin, a concept that underlies subsequent classifications of fishes and other organisms. In the same decade as Darwin's monumental publication, Woodward (1851) and Dana (1853) divided the waters of the world into biogeographic provinces based on species distributions, another fundamental contribution to understanding the origins of biodiversity (see Chapter 19).

A major force in American ichthyology was David Starr Jordan (1851–1931). Jordan moved from Cornell University to the University of Indiana and then served as founding president of Stanford University. He and his students and colleagues described the fishes collected during global expeditions in the late 1800s and early 1900s. In addition to a long list of papers, Jordan and his coworkers, including B. W. Evermann, produced several publications that form the basis of our present knowledge of North American fishes. This includes the four-volume *The Fishes of North and Middle America* (1896–1900), which described all the freshwater and marine fishes known from the Americas north of the Isthmus of Panama. Jordan (1923) published a list of all the genera of fishes that had ever been described, which served as the standard reference until it was updated and replaced by Eschmeyer et al. (1998).

Overlapping with Jordan was the distinguished British ichthyologist, C. Tate Regan (1878–1943), based at the British Museum of Natural History. Regan revised many groups, and his work formed the basis of most recent classifications. Unfortunately, this classification was never published in one place, and the best summary of it is in the individual sections on fishes in the 14th edition of the *Encyclopedia Britannica* (1929).

A Russian ichthyologist, Leo S. Berg, first integrated paleoichthyology into the study of living fishes in his 1947 monograph *Classification of Fishes, both Recent and Fossil*, published originally in Russian and English. He was also the first ichthyologist to apply the **-iformes** uniform endings to orders of fishes, replacing the classic and often confusing group names.

In 1966, three young ichthyologists, P. Humphry Greenwood at the British Museum, Donn Eric Rosen at the American Museum of Natural History, and Stanley H. Weitzman at the US National Museum of Natural History, joined with an old-school ichthyologist, George S. Myers of Stanford University, to produce the first modern classification of the majority of present-day fishes, the Teleostei. This classification was updated in Greenwood's 3rd edition of J. R. Norman's classic *A History of Fishes* (Norman & Greenwood 1975), and is the framework, with modifications based on more recent findings, of the classification used by Joseph Nelson (*Fishes of the World*, now in a 5th edition) and followed in this book. Over the past 65 years, John E. Randall, based at the Bishop Museum in Honolulu, has formally described over 800 species of fishes, more than any ichthyologist including Linnaeus.

Details of the early history of ichthyology are available in D. S. Jordan's classic *A Guide to the Study of Fishes*, Vol. I (1905). For a more thorough treatment of the history of North American ichthyology, we recommend Myers (1964) and Hubbs (1964). An excellent historical synopsis of European and North

American ichthyologists can also be found in the introduction of Pietsch and Grobecker (1987); a compilation focusing on the contributions of women ichthyologists appears in Balon et al. (1994). Some more recent and important discoveries are reviewed in Lundberg et al. (2000).

Introduction to Fish Genetics

All fields of biology, from the conservation of rare species to human medicine, have benefitted tremendously in recent decades from advances in genetics, and ichthyology is no exception. Modern genetics has added significantly to our understanding of evolution, ecology, and conservation of fishes. These areas will be discussed throughout this text where appropriate, but for those readers who could benefit from some updating or reminding, we offer the following general background.

DNA is the blueprint of life, and evolution is the architect. Across the 530 million-year history of fishes, natural selection has continually modified the blueprint to accommodate challenges and new opportunities. The result today is over 35,000 species with unique genetic features, and within each species are thousands or millions of genetically unique individuals. Scientists have learned to read the DNA blueprint in recent decades and have begun to resolve the history written there. Genetic studies can resolve relationships from family pedigrees to the most ancient vertebrate lineages. Between these extremes, genetic surveys are useful for discovering new species and resolving biogeographic patterns (see Chapter 19) and management units in conservation (see Chapters 20, 22).

Genetics contains many specialties. For example, cytogenetics is the study of chromosomes, ecological genetics can reveal breeding behavior, population genetics is used to define management units (or stocks) for fisheries, evolutionary genetics demonstrates the basis of novel organismal traits, and molecular phylogenetics is the application of DNA data to resolve branches in the tree of life. Accordingly, sections on genetics will appear in many chapters of this text – but here, we introduce some of the basic principles and terminology.

The Jargon Barrier

To some students of fish biology, the topic of genetics may seem dry, jargon-laden, and lab-based. It is true that some fish geneticists wear lab coats instead of scuba gear and discuss base pairs instead of bait. However, genetics is also a diverse and exciting field that has much to offer ichthyologists, especially with respect to the focal point of this book, the diversity of fishes. Like many disciplines, the field of genetics has a vocabulary that can be challenging to those unfamiliar with the concepts and terminology. Therefore, Appendix 1 contains concepts and terms needed to understand the parts of the text that focus on genetics and molecular techniques.

Fish Genomics

Genomics is the study of the entire DNA sequence of an organism, which in fishes includes the small mitochondrial genome and the enormous nuclear genome that can contain over a billion **base pairs** (**bp**). The earliest explorations of fish genomics were **chromosome** counts and **karyotypes**, but genomics now refers primarily to the intensive efforts to record the entire nuclear genome of a species. In the late 1990s, the technology applied to the Human Genome Project was redirected toward fishes and other vertebrates, and a cottage industry of fish genome projects is emerging. The first fish genomes to be completely described come from Zebrafish (*D. rerio*), Medaka (*Oryzias* sp.), and two pufferfishes. More recently, **next generation sequencing (NGS)** has revolutionized the field, providing millions of bp from individual specimens. Whole genomes have been generated for many fishes (e.g. blacktail butterflyfish; DiBattista et al. 2016b), and the list extends to at least 20 bony fishes (including the coelacanth *Latimeria chalumnae*; Amemiya et al. 2013) and two cartilaginous fishes (including the Whale Shark *R. typus*; Read et al. 2017). To provide the maximum accessibility for studies of evolution, development, and genetic function, a genome must be annotated. **Genome annotation** is the process of identifying where each gene is located and what it does. In most cases, researchers don't need whole annotated genomes, and they only need to find variable sites to resolve relationships from close relatives (kinship) to deep evolutionary lineages (phylogenetics). These studies rely on thousands of **single nucleotide polymorphisms (SNPs)** scattered throughout the genome (Puritz et al. 2014).

Genome Size

Fish genomes include 21 to 100+ chromosomes in the nuclear genome (nDNA) with two copies of every gene in most (diploid) species. Some 58% of examined teleosts (334 out of 580 species) have 48 or 50 chromosomes (Naruse et al. 2004), and 48 is believed to be the ancestral state for ray-finned fishes. Despite this conservation of chromosome number, overall genome sizes can differ by more than two orders of magnitude, with the lungfish having the largest fish genome (81.6 pg of DNA in a set of chromosomes; 1 pg = 10^{-12} g), the bichir having the largest actinopterygian (ray-finned fish) genome (5.85 pg), and the tetraodontiforms (such as pufferfish) having the smallest genomes (0.35 pg, Table 1.2), compared to 3.4 pg in the human genome. The number of chromosomes and genome size can vary even within a single genus (see the *Oncorhynchus* examples in Table 1.2). Three trends in genome size are apparent:

1. There is a progressive reduction in DNA content from the earliest to the most derived bony fishes.
2. Apart from lungfishes, elasmobranchs have the largest fish genomes, with 3–34 pg of DNA (Stingo & Rocco 2001). In contrast, the holocephalans (the other major group

of cartilaginous fishes) have among the most compact genomes (1.2–1.9 pg; Venkatesh et al. 2005).

3. In general, freshwater fishes have larger genomes than marine fishes (Yi & Streelman 2005). This is attributed to smaller population sizes in freshwater fishes, which can reduce the power of natural selection to produce a compact genome.

It is notable that fishes with the most radically derived morphology (tetraodontiforms) have the smallest nuclear genome. The pufferfish (genus *Fugu*) provided an ideal candidate for the first fish genome study, having much the same set of genes observed in mammals but in a package eight times smaller than the human genome. The insights from the first round of fish genome studies are many, and highlights include:

- Genomes are dynamic with many rearrangements between species and sometimes within species. Segments of the genome that are similar between fishes and mammals are rarely longer than four consecutive genes.
- Previous estimates of the vertebrate genome ranged from 60,000 to 150,000 genes, but that number now appears to be 30,000–40,000 genes.
- Regions of the genome of unknown function are highly conserved (very similar) between fishes and mammals. High similarity between fishes and mammals indicates that these gene regions have important functions that are retained by strong natural selection.

Polyploidization and Evolution

Polyploidization is the wholesale duplication of the nuclear genome, and most authorities agree that such an event lies near the base of the ray-finned fish (Actinopterygian) evolutionary tree. Such events are rare but important in the evolution of fishes. Ohno (1970) proposed that gene duplication is essential for major evolutionary innovations in vertebrates, as opposed to the single nucleotide mutations that can distinguish populations and species. In this view, the duplicated genes are under relaxed selection pressure, because there are now four copies (instead of two) available to get the job done. When polyploidy occurs, the original function of the gene can be maintained, freeing the extra copies to develop new functions (neofunctionalization), or they can double the capacity of a crucial metabolic pathway. Over tens of millions of years, some of the duplicated genes will prove to be redundant and lose their function in a process known as diploidization (returning to the diploid state).

Dramatic support for Ohno's model of evolution came from the Zebrafish (*D. rerio*) genome, and the discovery of seven **HOX** genes, which are important regulators of morphological development during embryonic growth. In mammals there are four HOX genes on four chromosomes, whereas the Zebrafish lineage had eight HOX genes on eight chromosomes, followed by the loss of one copy (Amores et al. 1998). The pufferfish genomes provide additional evidence of gene duplication and neofunctionalization.

When did this early genome duplication occur? The duplication does not appear in sturgeon or gar but is shared by all surveyed teleosts (Hoegg et al. 2004). Hence this event must have occurred in the basal teleost lineage, on the order of 300–400 million years before present (mybp). This genome duplication may have provided a powerful toolkit for diversification of the teleosts, by providing twice as many genes as existed in ancestral fishes (Roest Crollius & Weissenbach 2005).

The ancient polyploidization in teleosts is not the only genome duplication in bony fishes. Additional whole-genome duplications have occurred in the ancestors of modern salmon 25–100 million years ago (mya) (Allendorf & Thorgaard 1984), in catostomids (suckers) about 50 mya (Uyeno & Smith 1972), and in carp about 12 mya (David et al. 2003). Partial duplications of the genome are probably more common, either as unequal exchanges during genetic recombination or the unequal sorting of chromosomes during meiosis. This phenomenon can occur when two species hybridize, as observed in poecilliiform fishes (guppies and mollies), occasionally giving rise to parthenogenic (unisexual) species (Vrijenhoek 1984; see Chapter 8).

Mitochondrial Genome

Mitochondria are the energy factories in living cells of all eukaryotes, and they have their own compact genome (**mtDNA**). In fishes and most other vertebrates, the mtDNA genome is about 16,500 bp, coding for 13 proteins, 22 tRNAs, 2 rRNAs, and has a distinct segment for the origin of gene replication known as the control region. In the first decades of molecular genetic studies, the mitochondrial genome was much more accessible than the nuclear genome because it has more copies per cell, a small size, and is constructed like a single chromosome. Hence the study of mitochondrial genomics has proceeded much more rapidly than nuclear genomics, with over 2900 complete fish mtDNA genomes resolved at this time (Miya et al. 2003; see MitoFish database at University of Tokyo: **http://mitofish.aori.u-tokyo.ac.jp/**). In contrast to the nuclear genome, the mtDNA has retained the same genes in the same locations, and genome size is very similar across the vertebrates (Table 1.2).

Transgenic Fishes

There has been considerable interest in genetically modified fishes to produce pharmaceutical products, novel aquarium pets, and faster-growing strains for human consumption. This was originally attempted by "shotgunning," injecting many copies of the desired gene into the nucleus of the eggs, a process with a very low success rate. Subsequent methods have grown more sophisticated, using viruses that can insert desired genes into a chromosome (Dunham 2004). With the advent of advanced CRISPR technology (Hsu et al. 2014), researchers

TABLE 1.2 **Chromosome number, nuclear genome size, and mitochondrial genome size in select fishes. C-values indicate the amount of DNA in a haploid complement (a single copy of the chromosomes), measured in picograms per cell. References for chromosome number and C-value are available from the Animal Genome Size database (http://www.genomesize.com). The nuclear genome sizes, in millions of base pairs (mb), are from Roest Crollius and Weissenbach (2005). References for mitochondrial genome sizes are given, and sizes are presented in thousands of base pairs (kb). In some cases, the chromosome number could not be obtained from the same species used to estimate genome size, so values are obtained from congeners (fish in the same genus) as follows: the chromosome number for *Anguilla japonica* is based on congeners *A. rostrata* and *A. anguilla*, for *Sardinops* it is based on *S. sajax*, for *Fugu* on *F. niphobles*, and for *Tetraodon* on *T. palembangensis*. The mtDNA genome size for dogfish is based on *Scyliorhinus canicula*.**

Species	Number of chromosomes	Nuclear genome size (C-value/mb)	Mitochondrial genome size (kb)
Sea lamprey *Petromyzon marinus*	168 (Vialli 1957)	2.44/n.a.	16.201 (Lee & Kocher 1995)
White Shark *Carcharodon carcharias*	82 (Schwartz & Maddock 1986)	6.45/n.a.	n.a.
Dogfish *Squalus acanthias*	60 (Pedersen 1971)	6.88/n.a.	16.696 (Delarbre et al. 1998)
Coelacanth *Latimeria* spp.	48 (Cimino & Bahr 1974)	3.61/n.a.	16.446 (Inoue et al. 2005)
Lungfish *Protopterus dolloi*	68 (Vervoort 1980)	81.6/n.a.	16.646 (Zardoya & Meyer 1996)
Bichir *Polypterus ornatipinnis*	36 (Bachmann 1972	5.85/n.a.w	16.624 (Noack et al. 1996)
Eel *Anguilla japonica*	38 (Hinegardner & Rosen 1972)	1.40/n.a.	16.685 (Inoue et al. 2001)
Sardine *Sardinops melanostictus*	48 (Ida et al. 1991)	1.35/n.a.	16.881 (Inoue et al. 2000)
Carp *Cyprinus carpio*	100 (Hinegardner & Rosen 1972)	1.70/n.a.	16.575 (Chang et al. 1994)
Zebrafish *Danio rerio*	48 (Hinegardner & Rosen 1972)	1.8/1700	16.596 (Broughton et al. 2001)
Stickleback *Gasterosteus* spp.	42 (Hinegardner & Rosen 1972)	0.70/675	
Chinook Salmon *Oncorhynchus tshawytscha*	56 (Ojima et al. 1963)	3.04/3100	16.644 (Wilhelm et al. 2003)
Rainbow Trout *Oncorhynchus mykiss*	60 (Rasch 1985)	2.60/2700	16.660 (Zardoya et al. 1995)
Medaka *Oryzias* sp.	48 (Uwa 1986)	0.95/800	
Pufferfish *Fugu rubripes*	44 (Ojima & Yamamoto 1990)	0.42/380	16.447 (Elmerot et al. 2002)
Green Pufferfish *Tetraodon nigroviridis*	42 (Hinegardner & Rosen 1972)	0.35/350	

can insert genes in the desired location with surgical precision, using nuclease (DNA cutting) enzymes and customized RNA segments. (CRISPR stands for "clusters of regularly interspaced short palindromic repeats.") The journal *Science* named CRISPR genome editing technology as the 2015 breakthrough of the year, because of the far-reaching implications for repairing defective genes, eliminating disease, and modifying the genomes of plants and animals. No doubt, these benefits will include revelations about fish biology and evolution.

The first genetically modified fish was announced in 1984, based on Rainbow Trout (*Oncorhynchus mykiss*) eggs injected with metallothionein (toxic metal resistance) gene (Maclean & Talwar 1984). Another early success was a transgenic Nile Tilapia (*Oreochromis niloticus*) modified with a gene for growth hormone. It attained three times the size of normal tilapia (Martínez et al. 1996). Rainbow Trout and Coho Salmon (*Oncorhynchus kisutch*) have also been modified with a salmon growth hormone gene that produced larger fish (Devlin et al. 2001). The first transgenic aquarium fish is the **glofish®**, a Zebrafish (*D. rerio*) with red, green, and orange fluorescent colors. Other species of glofish® have since been developed for the aquarium trade (see **http://www.glofish.com/**). This fluorescence gene may eventually be used to detect aquatic pollution by switching on a bright color in fishes that are exposed to environmental contaminants. There are now at least 50 transgenic fishes in research and aquaculture. In 2015, the US Food and Drug Administration approved the first transgenic fish for human consumption, the AquAdvantage salmon, an Atlantic salmon (*Salmo salar*) with a growth hormone gene from Chinook Salmon (*Oncorhynchus tshawytscha*) and a gene promoter from Ocean Pout (*Zoarces americanus*).

Many authorities regard transgenic fishes as a potential boon to aquaculture, allowing higher survival, faster growing fishes, and larger yields. Indeed, genetically modified fishes have the potential to alleviate hunger and promote human health in impoverished corners of the globe. However, other authorities warn of the hazards of transgenic fishes, especially escaping into the wild (Muir & Howard 1999, Bailey 2015). These hazards are similar to those of non-native fish introductions (see Chapter 22), with the additional threat that transgenic fishes could breed with native stocks. In a study of a transgenic Medaka (*O. latipes*), the modified males had greater mating success when introduced into a natural population, presumably because of their larger size, but their offspring had significantly lower survival (Muir & Howard 1999). In these circumstances, the accidental introduction of transgenic fishes might jeopardize future reproduction, possibly leading to extinction. Clearly, the benefits of this technology have to be balanced against significant risks.

Additional Sources of Information

This book is one view of ichthyology, with an emphasis on diversity and adaptation (please read the preface). It is by no means the final word nor the only perspective available. As undergraduates, we learned about fishes from other textbooks; all of these books are valuable. We have read or reread them during the production of this book to check on topics deserving coverage, and we frequently turn to them for alternative approaches and additional information. Among the most useful are Lagler et al. (1977), Bone et al. (1995), Hart & Reynolds (2002a, 2002b), Moyle & Cech (2004), and Barton (2006). For laboratory purposes, Cailliet et al. (1986) and Hastings et al. (2014) can be helpful. From a historical perspective, books by Jordan (1905, 1922), Nikolsky (1961), and Norman and Greenwood (1975) are informative and enjoyable.

Three references have proven indispensable during the production of this book, and their ready access is recommended to anyone desiring additional information and particularly for anyone contemplating a career in ichthyology or fisheries science. Most valuable is Nelson et al. *Fishes of the World* (5th edn, 2016). For North American workers, the current edition of Page et al. *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* (7th edn, 2013) is especially useful. Finally, of a specialized but no less valuable nature, is Eschmeyer et al.'s *Catalog of Fishes* (**https://www.calacademy.org/scientists/projects/catalog-of-fishes**). The first two books, although primarily taxonomic lists, are organized in such a way that they provide information on currently accepted phylogenies, characters, and nomenclature; Nelson et al. (2016) is remarkably helpful with anatomical, ecological, evolutionary, and zoogeographic information on most families. Eschmeyer's volumes are invaluable when reading older or international literature because they give other names that have been used for a fish (**synonymies**) and indicate the family to which a genus belongs.

Of a less technical but useful nature are fish encyclopedias, such as Wheeler's (1975) *Fishes of the World*, also published as *The World Encyclopedia of Fishes* (1985), *McClane's New Standard Fishing Encyclopedia* (McClane 1974), or Paxton & Eschmeyer's (1998) *Encyclopedia of Fishes* (the latter is fact-filled and lavishly illustrated). Helfman & Collette (2011) address many common, and some not-so-common, questions about fishes. Species guides exist for most states and provinces in North America, most countries in Europe (including current and former British Commonwealth nations), and some tropical nations and regions. These are too numerous and too variable in quality for listing here; a good source for titles is Berra (2001, 2007). Two of our favorite geographic treatments of fishes are as much anthropological as they are ichthyological, namely Johannes' (1981) *Words of the Lagoon* and Goulding's (1980) *The Fishes and the Forest*. A stroll through the shelves of any decent public or academic library is potentially fascinating, with their collections of ichthyology texts dating back a century, geographic and taxonomic guides to fishes, specialty texts and edited volumes, and works in or translated from many languages. Among the better known, established journals that specialize in or often focus on fish research are *Ichthyology and Herpetology* (formerly *Copeia*), *Transactions of the American Fisheries Society*, *Environmental Biology of Fishes*, *North American Journal of Fisheries Management*, *US Fishery Bulletin*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Canadian Journal of Zoology*,

Journal of Fish Biology, *Journal of Ichthyology* (the translation of the Russian journal *Voprosy Ikhtiologii*), *Australian and New Zealand Journals of Marine and Freshwater Research*, *Bulletin of Marine Science*, and *Japanese Journal of Ichthyology*.

The internet has developed into an indispensable source for technical information, spectacular photographs, and updated conservation information concerning fishes. Although websites come and go – and although web information often suffers from a lack of critical peer review – many sites have proven themselves to be both dependable and reliable. For general international taxonomic information, the Integrated Taxonomic Information System (ITIS, **www.itis.usda.gov/index.html**) and Global Biodiversity Information Facility (GBIF, **www.gbif.org**) are starting points. For user-friendliness and general information, FishBase (**www.FishBase.org**) is the unquestioned leader. Photographs and drawings are most easily accessed via Google Images (**http://images.google.com**). Wikipedia entries on individual species and groups are often written by experts in the field and corrected and updated frequently. For conservation status and background details, **www.redlist.org** is the accepted authority on international issues, and NatureServe (**www.natureserve.org**) is the most useful clearinghouse for North American taxa. Several museums maintain updated information on fishes; our favorites are the Australian Museum (**https://australianmuseum.net.au**), University of Michigan Museum of Zoology (**https://lsa.umich.edu/ummz**), Florida Museum of Natural History (**www.flmnh.ufl.edu/fish**, which is especially good for sharks), and the California Academy of Sciences (**www.calacademy.org/research/ichthyology**). For North American freshwater fishes, see the Texas Memorial Museum (**www.utexas.edu/tmm/tnhc/fish/na/naindex**) and the North American Native Fishes Association website (**http://nanfa.org/checklist.shtml**). The best sites provide links to many additional sites that offer more localized or specific information.

The internet also provides access to a seemingly endless and ever-changing array of videos that show what many of us find so fascinating about fishes – including their enormous diversity in form, function, and behavior. These videos range from segments of professionally produced programs to home-grown postings on YouTube ®. The nature of a printed text and the often changing nature of the web make it impractical to cite these website references in this book, as web postings often come and go.

Snorkeling and scuba diving are valuable methods for acquiring detailed information on fish biology. Time spent underwater observing fishes was formative and essential to each of us in developing our interest in and understanding of fishes. A full appreciation for the wonders of adaptation in fishes requires that they be viewed in their natural habitat, as they would be seen by their conspecifics, competitors, predators, and neighbors (it is fun to try to think like a fish). We strongly urge anyone seriously interested in fish biology to acquire basic diving skills, including the patience necessary to watch fishes going about their daily lives. **Public and commercial aquaria** are almost as valuable, particularly because they expose an interested person to a wide range of species, or to an intense selection of local fishes that are otherwise only seen dying in a bait bucket or at the end of a fishing line. Our complaint about such facilities is that, perhaps because of space constraints or an anticipated short attention span on the part of viewers, large aquaria seldom provide details about the fascinating lives of the animals they hold in captivity. Home aquaria are an additional source for inspiration and fascination, although we are ambivalent about their value because so many tropical fishes are killed or habitats destroyed in the process of providing animals for the commercial aquarium trade, particularly for marine tropical fishes. Advances in captive rearing are badly needed to alleviate the pressure on natural populations of marine ornamental fishes.

Supplementary Reading

Websites

Eschmeyer, WN and JD Fong. 2017. Species by family/subfamily in the Catalogue of Fishes. Catalogue of Fishes, California Academy of Sciences (**http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp**)
the Integrated Taxonomic Information System (ITIS, **www.itis.usda.gov/index.html**)
Global Biodiversity Information Facility (GBIF, **www.gbif.org**)
FishBase (**www.FishBase.org**)
www.redlist.org
NatureServe (**www.natureserve.org**)
Australian Museum (**https://australianmuseum.net.au**)
University of Michigan Museum of Zoology (**https://lsa.umich.edu/ummz**)
Florida Museum of Natural History (**www.flmnh.ufl.edu/fish**)
California Academy of Sciences (**www.calacademy.org/research/ichthyology**)
Texas Memorial Museum (**www.utexas.edu/tmm/tnhc/fish/na/naindex**)
the North American Native Fishes Association website (**http://nanfa.org/checklist.shtml**)