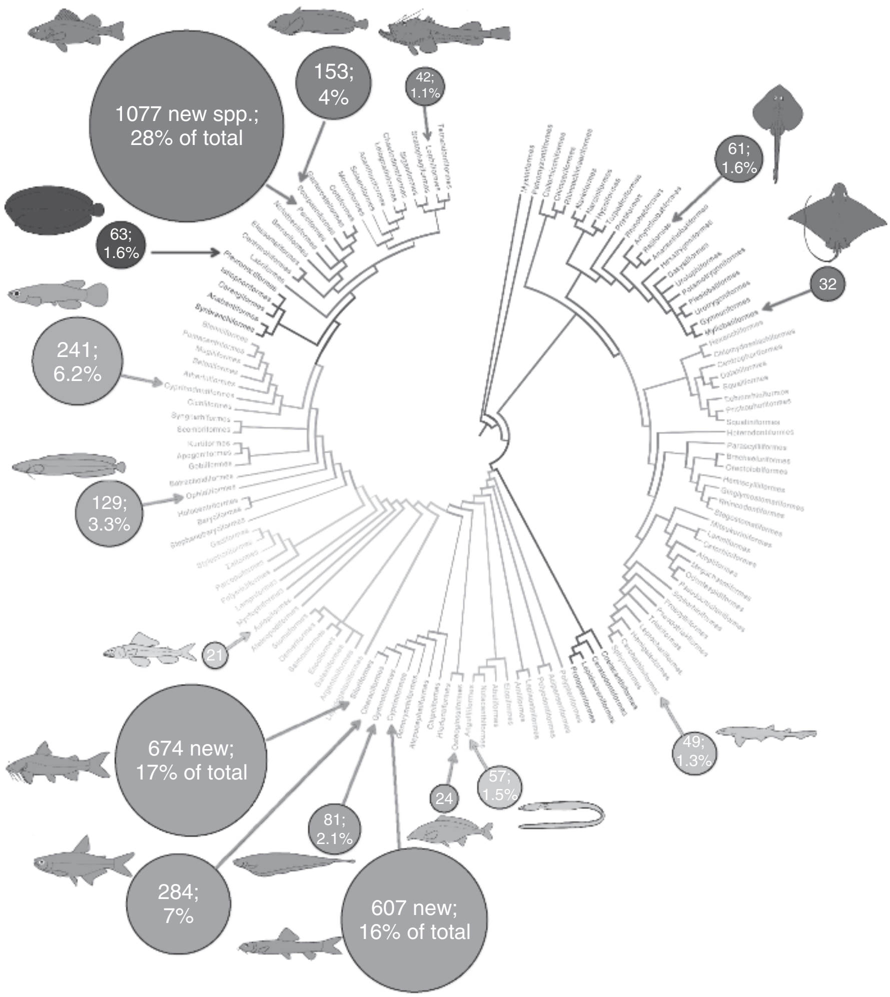
Introduction

Over one-half—32,000 species and counting—of the world's living vertebrates—more than 60,000 species—are fishes. They arose and began to radiate more than 500 million years ago and both now and in the past exhibit incomparable diversity in their morphology, in the habitats they occupy, in their physiology, and in their behavior. This diversity is, in part, what makes understanding their evolutionary history and establishing a classification so challenging and yet fascinating. From hagfishes and lampreys to sharks, lungfishes and flatfishes, fishes include a vast array of amazing adaptations to almost all aquatic environments on earth.

Since the last edition of *Fishes of the World* (2006), a great many (thousands) of important studies on fish diversity, biology, morphology, and phylogenetic relationships have been published. We now have a much better understanding of their evolutionary relationships than we had even a decade ago. Science is a continually forward-moving search for knowledge, and this book reflects scientific knowledge about fishes as it exists today. As is normal in science, future researchers will build upon and improve upon what we know now.

The body of information known about fishes is vast and includes all aspects of biology. Fishes are fascinating to researchers because of the wealth of information and diversity to be found, both in fossil and living (extant) taxa. Since the 2006 version of this book, exciting new discoveries about fish morphology and evolution have been published. These include studies about the evolution of jaws, teeth, paired fins, internal fertilization, mimicry, hearing, and the biomechanics of feeding and locomotion. There have also been revolutionary findings concerning phylogenetic relationships, such as the hypotheses that extinct placoderms may be paraphyletic, that the Holostei are again monophyletic, that elopomorphs rather than osteoglossomorphs are the basal lineage of crown teleosts, that *Lepidogalaxias* is the most basal living euteleost, and that paracanthopterygians are once again united, though with revised membership.

The toolbox of the fish systematist has expanded to include molecular sequence analysis, evolutionary (including molecular) developmental biology, and technological advances such as 3D imaging to visualize complex internal morphology of both fossil and extant species. The new tools are being applied to many of what were the most intractable problems in fish systematics, including the relationships of rays, catfishes and percomorphs. There has also been an explosion in the number and variety of web-based databases



Groups of fishes in which at least 20 new species were described in the decade 2005–2014. The area of each circle is approximately proportional to the number of new species in the group. The total number of new species described was about 3900, raising the total of known valid species to more than 32,000 (Eschmeyer and Fong, 2015).

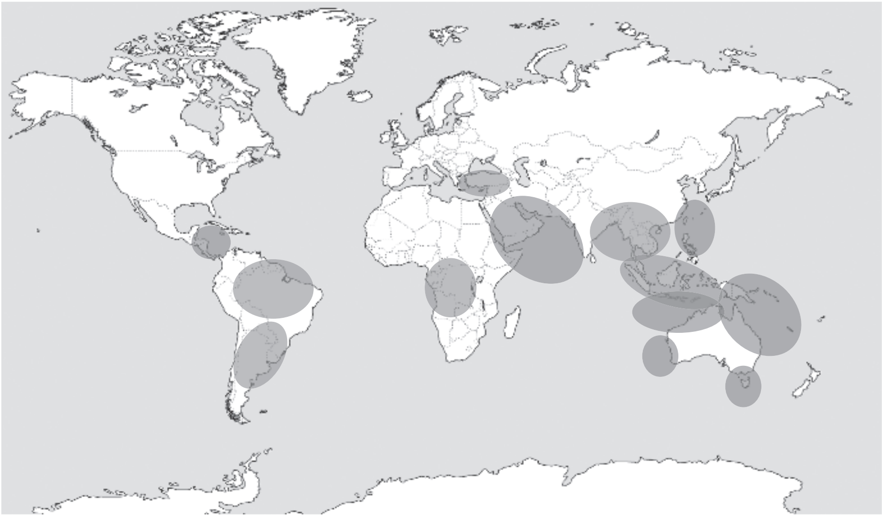
and interactive tools, including Encyclopedia of Life, Phenoscape, Fishbase, Catalog of Fishes, Index to Organism Names, World Registry of Marine Species (WORMS), online academic libraries, journal publishers' web sites, the Paleobiology Database, and Fossilworks, all of which are available to almost any researcher, and all of which have been consulted by us. We also compiled and consulted thousands of original journal articles to better understand the current state of ichthyological knowledge.

Taxonomic Diversity

Since the 2006 version, more than 3890 species have been named. The species numbers of fishes given in the text, as in previous editions, are intended to be conservative estimates of valid described species, not of all named species nor of what might be undescribed. They are based, as far as possible, on the latest taxonomic revisions of families and genera and the opinions of the specialists.

There are 85 orders and 536 families of fishes recognized in this edition. Interestingly, about two-thirds of all species in the largest families are freshwater fishes, whereas only about 43% of all fishes are predominantly freshwater species. Freshwater habitats comprise only a small proportion of the earth's surface water, but contain a disproportionately large number of the world's fish species. The known diversity of both freshwater and marine fishes continues to increase rapidly, and the regions of the world where the greatest number of new discoveries are being made are indicated in the following figure.

Hotspots for New Fish Species



Geographic regions of the world in which discoveries of new fish species have been most numerous. Newly discovered marine fishes have been found most often in the SW Caribbean, NW Indian Ocean, southern China Sea, and off the corners of Australia. Newly discovered freshwater fishes have been found most often in the Amazon Basin and the Parana Basin of South America, western Equatorial Africa, and southeastern Europe, especially near Turkey, as well as in Southeast Asia.

Importance to People

Fishes, like many other forms of life, are of immense value to humans. They have long been a staple item in the diet of many peoples, unfortunately leading to the downfall of many species (e.g., Atlantic Cod, *Gadus morhua*, fished to the brink of commercial extinction in the Western North Atlantic). Today fishes form an important element in the economy of many nations while giving incalculable recreational and psychological value to the naturalist, sports enthusiast, and home aquarist. They are also the subject of international and domestic agreements (Great Lakes Fishery Commission, a cross-border cooperation between the United States and Canada in the control of lamprey) and disagreements (suspension of albacore tuna fishing by Canadian fisherman in US waters in 2012). Many government institutions are devoted to the study of fish biology and propagation (e.g., propagation of *Esox lucius* and *E. masquinongy* for stocking by the Jake Wolfe Fish Hatchery, Illinois). Particular aspects of various species lend themselves to studies in behavior, ecology, evolution, genetics, and physiology. They are used as general indicators of pollution, partly to the direct benefit of humans and partly to protect what people consider a valuable and necessary part of their heritage and life.

Systematics and Classification

Systematics is the study of biological diversity, including reconstructing the phylogenetic (genealogical) relationships of organisms. Taxonomy is that part of systematics dealing with the theory and practice of describing diversity and erecting classifications. Classification is the practice of arranging items into groups or categories, and the resulting arrangement is called a classification. Taxa (singular taxon) are groups of organisms recognized in a classification and given biological names (e.g., Salmoniformes, Salmonidae, *Oncorhynchus*, *Oncorhynchus nerka*). A category is the level or rank at which the taxon is placed (e.g., order, family, genus, species). Generally, the objective in constructing a classification of a group of organisms is to reflect what are thought to be the evolutionary relationships of the various taxa in a hierarchical system of named groups.

We give examples of recognized generic names for each family; if the number is relatively small, we usually list them all. In choosing listed examples of generic names for large families, we have tried to choose: (1) genera with many species; (2) the type genus of the family, a subfamily, or a nominal family no longer recognized; (3) genera whose species exhibit some extreme biological diversity or unusual features, especially if mentioned in text; and (4) genera whose species are commonly encountered or are important in commercial fishery, sports fishery, or aquarium use. Generic synonyms are usually given only for genera recognized as valid in earlier editions of this book but that are now considered junior synonyms, or for cases when a family-group taxon is made synonymous because its type genus has been synonymized.

We consider fossils to be critical in understanding evolutionary relationships. Unfortunately, the fossil record in fishes is incomplete (more so in some than in other groups), and many decisions must be made with little or no evidence from fossils. However, we can answer many critical questions of interrelationships of higher taxa only with the assistance of the fossil record and not, conclusively at least, from extant material only. Many important fossil taxa are ranked along with extant taxa in the classification of this book, and many others are mentioned where appropriate.

A framework of formally named and ranked taxa is an important aid to understanding and communicating the implied relationships among groups of organisms. Completely unranked classifications are popular in some circles but are not used here because they communicate little information to those without specialized knowledge.

As in previous editions, we recognize a large number of named taxa in a formal hierarchy of taxonomic categories. The taxa are always intended to be monophyletic (i.e., clades), but in many cases future research may show that they are not, and the classification must be modified accordingly.

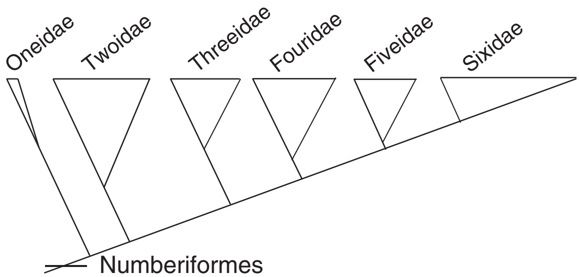
The categories used, and their endings in parentheses when consistent, are as follows: phylum, subphylum, superclass, grade, class, subclass, infraclass, division, subdivision, superorder (these 10 categories are centered in the text; the following categories are aligned left), series, subseries, infraseries, order (-iformes), suborder (-oidei), infraorder, superfamily (-oidea), family (-idae), subfamily (-inae), tribe (-ini), genus, subgenus, and species. Not all categories are employed within any one particular taxon. A dagger (†) denotes those taxa containing only fossil species.

Although there is a framework of named and ranked taxa, not all recognized (named) taxa are assigned a rank (i.e., placed in a named category). The following are examples of major taxa that are part of the classification but for which no formal rank is assigned: Vertebrata, Neoteleostei, and Acanthomorpha.

This edition, like earlier editions, adopts a simplified classification scheme, although even the simplified scheme can appear daunting. The number of categories and of named taxa are minimized by employing the "sequencing convention" for multiple named taxa at the same rank. For example, in a sequenced list of families within an order, the first family is the sister group of all others in the list, the second family is the sister of all except the first two, and so on. The last two families in the list are interchangeably each other's sisters. Consider this example classification of a hypothetical order with six families:

Order Numberiformes
Family Oneidae
Family Twoidae
Family Threeidae
Family Fouridae
Family Fiveidae
Family Sixidae

The sequence of the listed families tells us the phylogeny, using the sequencing convention. For example, Family Oneidae is the sister group of the clade of all five other families, and the Family Threeidae is the sister group of the clade of families Fouridae through Sixidae. The last two families could have been listed in either order, since they are each other's sisters. The tree that reflects these relationships is as follows:

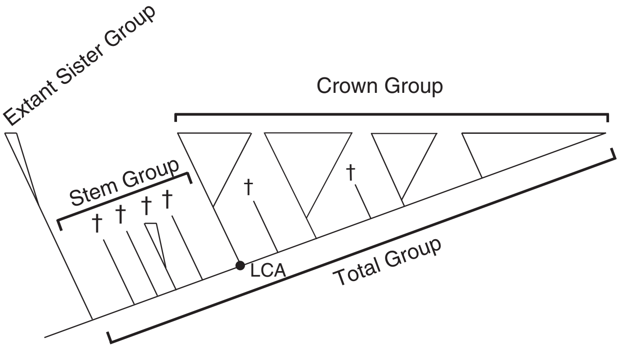


In some larger taxa, we use the term "basal" or "most basal" when referring to the lineage, usually of low diversity, that is sister to all others in the group. Some call these more basal lineages "early-branching lineages." Less often used but sometimes useful is the term "apical" or "more apical" to refer to a taxon that is high in the branching of the group's tree. A basal group is, of course, of equal age to its sister group and is not necessarily more primitive. In the tree shown above, the Family Oneidae would be considered basal while the families Fiveidae and Sixidae would be considered apical.

We report for many extant taxa the geologic age of the oldest reliably identified fossil members to give the reader an appreciation for the known fossil record. Such fossils give the minimum ages of lineages based on concrete data from the fossil record, even though in many cases the group in question must be considerably older than its first fossils because older fossils belonging to its sister-group are known. The difference between these two ages implies, for the lineage with the younger first fossil, a "ghost lineage": a period of time during which it is inferred to have existed but is not recorded by fossils found to date.

It has become popular in phylogenetic literature to include estimates of past divergence times of lineages based on rates and amounts of molecular evolution. We do not list them or use them here.

In discussing fossil relationships, we make use of the concept of stem and crown groups. For any given taxon with extant members, the crown group is all those species descended from the last common ancestor (LCA) of all the extant members (see figure). Note that certain fossil taxa can be members of the crown group.



Tree diagram illustrating stem-group and crown-group concepts.

The stem group or stem-group taxa are all those extinct taxa known by fossils that are more closely related to this particular crown group than they are to any other extant clade. The Total Group is the sum of the stem group and the crown group. Using a real example, the Teleosteomorpha are the Total Group for teleostean fishes. The Teleocephala are the Crown Group teleosts.

A friendly word on the terms “fishes” and “fish” and on capitalizing their common names: The term “fishes” is properly used when referring to individuals of more than one species. However, when referring to one or more individuals of one species, the term “fish” is appropriate. Hence, it is correct to refer to 100 Rainbow Trout as fish, but to two different trouts, such as one Brook Trout and one Brown Trout, as fishes (the plural form Rainbow Trouts is discouraged). The common names of the three species given in this example (which happen to be in three different genera) were capitalized. The principles of common names in fishes established in 1960 by a joint committee of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists, and explained in Nelson et al. (2004) are followed, except that the official common name of a species is treated as if it were a proper noun (see Nelson, Starnes, and Warren, 2002), as is common for some other groups of vertebrates (such as birds).

Anatomical Terminology

When given, the numbers of abdominal and caudal vertebrae are placed in parentheses after the total vertebral number—for example, 25 (10 + 15). When possible, the length is qualified by giving standard length (SL), fork length (FL), or total length (TL). Also included are estimated numbers of recognized (valid) genera and species (in some cases the number of species in each genus is also given). These figures are always for living forms, even if fossils are known for the taxon; selected fossil taxa are mentioned separately. The degree of agreement with these figures by specialists will vary from group to group (in part due to the subjective matter of lumping and splitting). For example, nearly everyone would agree that there are but two valid species of described percopsids, but one can easily find disagreement on the number of valid species of cichlids and gobiids that should be recognized.

Proposals to change the names of some bones from those used in previous editions to conform better with probable homologies have not been adopted unless otherwise indicated. For example, as noted in Janvier (1996) and Schultze (2008), what are commonly termed the frontals and parietals in actinopterygians, terms originally taken from human anatomy, are now known to be homologous with the parietals and postparietals, respectively, of early tetrapods.

Distribution and Biogeography

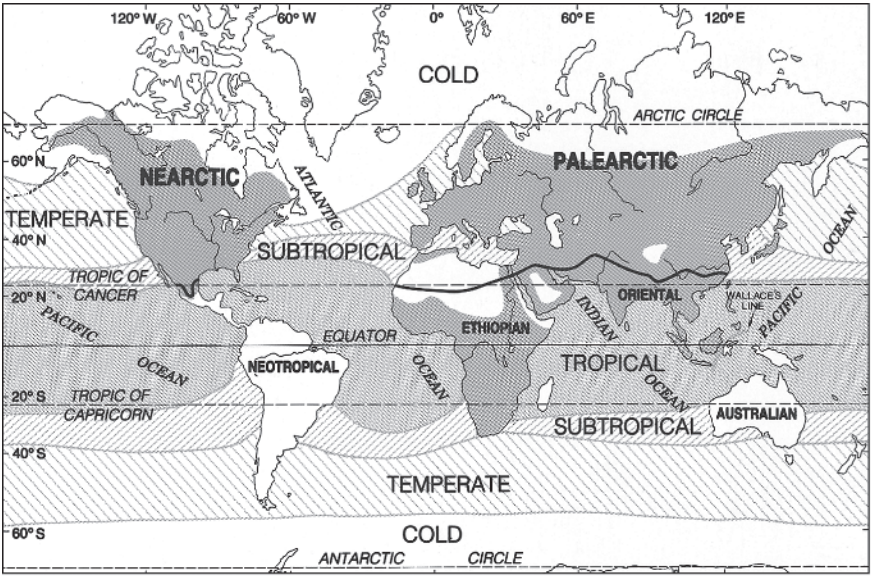
Fishes occur in lakes, streams, estuaries, and oceans throughout the world. In most species of fishes, all individuals live entirely either in fresh or in marine waters. Over 225 species are diadromous, regularly living part of their lives in lakes and rivers and part in the oceans. Among these, most are anadromous, spawning in fresh water but spending much of their time in the sea. A few are catadromous, spawning in the oceans but returning to fresh water. Classification of some species as marine, diadromous, estuarine, or freshwater is impossible, except as a generalization. Just as in an otherwise marine family there may be one species confined to fresh water, so in some species there are populations that occur in an environment opposite that of most others. Individuals of some otherwise marine species ascend rivers for short distances in part of their range, and those of some species that are usually freshwater are anadromous in some areas. Many freshwater and marine species are also common in brackish-water estuaries. About one-third of the 555 families have at least one species with individuals that spend at least part of their life in fresh water. Berra (2001) gives much information and distribution maps for the freshwater fish families.

Many environmental factors influence just where a certain species will predominate. Competition and other biological interactions may exert a strong influence along with physicochemical factors. In freshwater environments, species may show a preference for lakes or streams. Variations in preferences may exist over the range of a species. Among lakes they may show a preference for deep, cold, oligotrophic lakes or for shallower, warmer, and more productive mesotrophic and eutrophic lakes. In lake waters they may show a preference (horizontal and vertical) for the open-water limnetic zone, the benthic area, or shallow littoral areas. Fishes may even be restricted to certain types of bottom or do best under certain physicochemical conditions. Stream fishes may prefer riffle or quiet areas, and a zonation of species is usually found from the headwaters to the mouth. In the oceans, the vast majority of fishes are coastal or littoral. Most of those living beyond the 200-m-deep continental shelf (oceanic species) are deep-sea (mesopelagic, bathypelagic, abyssopelagic, or benthic at various depths); only a small minority regularly live close to the surface in the well-lighted upper 200-m zone (epipelagic), a region much larger in volume than the coastal waters. The epipelagic and mesopelagic fishes, which consist of both large predators and small plankton feeders, are varied, whereas most of the bathypelagic and abyssal fishes are relatively small.

Many species, both geologically young and old, have small ranges; the smallest is perhaps that of the Devils Hole Pupfish, *Cyprinodon diabolis*, found only in one spring in Ash Meadows, Nye County, Nevada. Many areas have a high degree of endemism. Marine fishes face the obvious land barriers (notably the New and Old World land masses) and mid-ocean barriers as well as many ecological and physiological barriers; freshwater species are limited by marine and land barriers. Some species have remarkably large ranges, and it would be interesting to know why some of their relatives have small ranges.

Over 130 marine species are known to extend around the world in tropical or subtropical waters. Many genera are represented in both the Pacific and Atlantic, but, almost always, different species are involved. Representatives of many marine genera and of some species occur in the temperate and polar faunas of both hemispheres. Individuals of some of these bipolar or antitropical taxa are surface-bound; others are deepwater. The vast majority of species, however, are tropical; most of the rest occur only in the Northern or only in the Southern Hemisphere. We know little of the abyssal depths and their species composition. Many abyssal species have been found at widely separated localities, which suggests that some may be virtually worldwide. No freshwater species is circumtropical, but two species, *Esox lucius* and *Lota lota*, are circumpolar and several others are almost so. No genus of freshwater fish has an antitropical distribution. Many freshwater fishes have shown a remarkable ability to disperse across newly exposed land areas following glaciation. In addition, they may occur in isolated waters in deserts as a result of a reduction of waters from times when drainage systems were connected.

In both fresh and marine waters, the largest number of species occurs in the tropics. There is a reduction toward the polar areas, although numbers of individuals in certain northern species are large. A great many species of freshwater fishes occur in tropical Africa, southeastern Asia, and the Amazon River—by far the world's largest river. For a tropical region, Central America has relatively few freshwater species because of the physiography and geological history of the area. Most oceanic islands lack indigenous fishes confined to fresh water, and continental areas recently exposed from the last ice age— for example, northern regions of North America, Europe (especially western Europe), and Asia—tend to have a relatively sparse fish fauna. In tropical areas, Africa exhibits the greatest diversity of nonostariophysan freshwater fishes; South America exhibits surprisingly little. In temperate areas, eastern North America shows the greatest diversity in nonostariophysan fishes. In marine waters, the Indo-West Pacific (Red Sea and Indian Ocean to northern Australia and Polynesia) is the richest, with the most species occurring in the New Guinea to Queensland area. In terms of diversity, southeastern Africa and Queensland appear to have the largest number of families of marine shorefishes. The West Indian or Caribbean fauna (southern Florida to northern Brazil) is also a rich one. The western African fauna, however, is relatively poor. Arctic and Antarctic faunas are depauperate. In all, the greatest number of fish species in the world inhabit the southeastern Asian region.



Broad surface thermal zones of the ocean, biogeographic regions of the continents, and native distribution of the family Cyprinidae, the most species-rich family of vertebrates. The biogeographical regions express degrees of endemism and are useful indicators of numbers and proportion of endemic organisms. We rarely use the continental regions in the text, and ichthyologists do not use them as much as in former times; the Nearctic and Palearctic are frequently combined into one region, the Holarctic. The thermal divisions of the sea denote tropical (or warm), subtropical, temperate, and cold (or polar) waters; warm temperate is sometimes used for all or part of the subtropical and warmer parts of the temperate (versus cool temperate) waters. Surface isotherms, used to define thermal regions, are subject to seasonal and annual changes. Major biogeographic regions recognized in the oceans include the Indo-West Pacific, tropical western Atlantic, tropical eastern Atlantic, North Pacific, North Atlantic, and Mediterranean-East Atlantic. Marine oceans share different similarities with one another; for example, for many families the tropical eastern Pacific shows a greater resemblance to the western Atlantic than to the Indo-West Pacific because of the mid-Pacific barrier and the relatively recent marine connection across the Isthmus of Panama. Information on the generalized thermal zones is based partly on Briggs (1974) and modified by numerous other sources. Distribution of the family Cyprinidae, shown by the shaded land area, is based on Berra (2001) and papers in Winfield and Nelson (1991).

Various methodological and philosophical approaches are used to explain the origin of distributional patterns of fishes, including areas of endemism. Both dispersal and vicariant events are important. Dispersal is regarded here as the movement, active or passive, of individuals to areas new to the existing population. Barriers of varying effectiveness may be involved as well as varying degrees of chance of reaching particular sites. It is of greatest biogeographic significance if the breeding range of the species is increased. Vicariance is the fragmentation of a former continuous distribution of the ancestral group into geographically separated units through the appearance of a barrier—for example, through plate tectonics. Both dispersal and vicariant approaches are used to explain disjunct distributions (the occurrence of a taxon in different areas with a marked geographical gap between them).

Examples of disjunct distributions include the following: occurrence of *Prosopium coulteri* in western North America and in Lake Superior; *Geotria australis* and *Galaxias maculatus* in Australia, New Zealand, and South America; cottids and agonids in cool temperate waters of the Northern and Southern Hemispheres; characiforms, aplocheiloids, and cichlids in Africa and South America. Plate tectonics had a profound effect on the distribution of many freshwater and marine fishes (e.g., it could well explain the occurrence of characiforms in South America and Africa), but not all disjunct distributions have a likely plate-tectonic explanation.

Human Impacts

We consider it desirable to maintain the fish diversity that systematists study, and systematists can play a leading role in protecting this diversity. We recognize the value of and our dependency upon fishes and other organisms, but our threats to the integrity of the environment also pose a serious threat to our fishes. As examples, according to the Great Barrier Reef Marine Park Authority, rising sea surface temperatures, ocean acidification, and rising sea level will negatively affect over 1600 species of fishes that live on the reef. Increased temperatures associated with lower dissolved oxygen levels in estuaries are affecting distribution patterns and abundance of Menhaden along the Atlantic and Gulf Coasts. The reduction of Menhaden, an important food source for larger fishes such as Bluefin (*Pomatomus saltatix*) and Bluefin Tuna (*Thunnus thynnus*), may likely have devastating effects on these fisheries.

Changing distribution patterns of many species and the extinction of native fishes has been directly linked to the human intervention. One recent and familiar example is the inadvertent introduction of the Round Goby (*Neogobius melanostomus*) native to central Eurasia, into the Great Lakes system via the ballast water of commercial tankers. In Lake Michigan, the Round Goby has outcompeted the native Mottled Sculpin (*Cottus bairdi*), causing its extirpation. The sheer mention of the famous Asian carp (actually the collective name for four species of carp that were imported in the 1970s to clean catfish ponds in the southern United States, but which then escaped and headed north) causes alarm. These carps are spreading widely in North American waterways, leading to habitat destruction and provoking sometimes unwise and expensive containment measures. Systematists have unique roles as experts on natural geographic distributions and as witnesses recording changes in biodiversity, whether natural or human-induced.