

# Ichthyology: The Science

The study of fishes, broadly termed "ichthyology," encompasses many aspects. Some ichthyologists are most concerned with studies of the diversity, distribution, and interrelationships of fishes. Others concentrate on the physiology or functional morphology of fishes, seeking to determine how the various body parts of fishes interact to facilitate feeding, locomotion, respiration, or other vital functions. Studies of fish genetics have become numerous in recent years and offer much potential information to those studying both the diversity and relationships of fishes as well as insights for those attempting to manage fish population resources. Still other ichthyologists specialize in behavioral studies, gathering and analyzing both qualitative and quantitative data, based on observations of fishes in natural environments and aquaria, to learn more of their movement patterns and behavior associated with feeding, courtship and spawning, schooling, protection, and other aspects. Studies on fish biology, including basic life histories and fish ecology (how fish interact with their environments), are very important to a better understanding of these animals. Within the past couple of decades, a great deal of emphasis has been placed on the study of the early life history (larval development) of fishes. Other kinds of studies include those of fish population dynamics, management techniques for economically important species, propagation, fishing techniques, and fish diseases. Those who specialize in these latter, somewhat more applied, aspects are most often referred to as "fisheries biologists." Nearly all aspects of ichthyology or fishery biology are germane to the subject matter of this book at some level, but those of central interest are the systematics, taxonomy, and distribution of fishes, as well as basic biological information. The following sections are intended to acquaint the readers with these aspects in particular. Those wishing to find more extensive information on ichthyology or fishery biology should consult the works of Lagler (1956), Lagler et al. (1977), Bond (1979), Moyle and Cech (1988), Nielsen and Johnson (1983), and Schreck and Moyle (1990). Extensive bibliographic information on fishes can be found in Dean (1916–1923) and in the Pisces section of the *Zoological Record*.

## Systematics and Taxonomy of Fishes

Systematics is the theory or practice of discerning the orderliness of nature or other systems. Taxonomy is the theory and practice of classifying that orderliness in a worded system (Mayr, 1969). Systematists work with units, collectively called "taxa," which may consist of the smallest recognizable units (usually a population or group of populations), often referred to as species, subspecies, or races, or they may consist of groupings of species into more inclusive taxa such as genera, families, and orders. Information follows on nomenclature of these taxa, and additional information is given in the section "How to Use the Family and Species Accounts." Readers who want to obtain information beyond what follows on systematics and taxonomy, as well as on the evolution of different ideas and approaches to systematics, and the controversies surrounding them, should consult the works of Simpson (1961), Sokal and Sneath (1963), Hennig (1966), Blackwelder (1967), Mayr (1969), Eldredge and Cracraft (1980), Nelson and Platnick (1981), Wiley (1981), Lundberg and McDade (1990), and many papers published in the journals *Systematic Zoology* and *Cladistics*.

*Alpha Taxonomy and Zoological Nomenclature.* In taxonomy, the species is the most generally accepted basic unit, and studies that strive to discern these basic units are known as "alpha taxonomy." Readers should be aware that species concepts vary among taxonomists. Also, some choose not to name units below the level of species while others subscribe to subspecies concepts, which may also differ among workers. Perhaps one of the oldest and most widely adhered to concepts is that of the "biological species" which defines a species as a group of interbreeding or potentially interbreeding populations reproductively isolated from all others (Mayr, 1969). Such a concept is, of course, very difficult to test or perceive in nature for many groups of organisms, such as freshwater fishes isolated in different drainage basins. Subjective decisions must be made concerning whether some populations may be capable of inter-

breeding, or “intergrading,” with others, and subspecies designations are often invoked under this concept. A second concept is that of “evolutionary species” (Simpson, 1961) which views species as representing lineages maintaining identities from other such lineages and having their own evolutionary tendencies and historical fate. Polytypic (having subspecies) species are often recognized under this concept as well. A third concept is that species are populations or groups of populations of monophyletic (common ancestral) origin which have differentiated from others (sometimes referred to as the “phylogenetic” or “cladistic” concept) (Rosen, 1978, 1979; Cracraft, 1983; Lundberg and McDade, 1990). Differentiation is detected by the presence of presumed apomorphic (uniquely derived) traits. In practice, all of these concepts involve some degree of subjectivity; the species is thus an arbitrary unit of taxonomic convenience. No matter what the concept, in most cases what taxonomists really must do is identify populations of organisms and what they feel to be consistent variation (morphological or genetic) between these populations, arbitrarily specify acceptable limits to variation in a species, and make decisions based on these limits, perhaps lending credence to Regan’s (1926) statement that a species “is what a competent taxonomist says it is.” This, of course, has been a simplified explanation of species concepts; there are numerous, much more involved, philosophical treatments of such matters (e.g., Rosen, 1978; Wiley, 1978; Cracraft, 1983, 1987; Loevtrup, 1987; Chandler and Gromko, 1989; de-Queiroz and Donoghue, 1988, 1990; several works in Ott and Endler, 1989; and Wheeler and Nixon, 1990).

A taxonomist who believes he or she has identified a species new to science gives it “official” status (according to the International Rules of Zoological Nomenclature) by publishing a formal description in the scientific literature and giving it a unique name, the *species epithet*. In that publication, a museum specimen, called a *holotype*, is designated to forever serve as the standard of reference for the new species. Under older practices, multiple types (syntypes or type series) were designated which, in some cases, later proved to comprise more than one actual species, and the practice was discontinued. Other specimens used in the description may be designated as *paratypes*. When the type of a species is lost, or syntypes are polytypic, and clarification is needed, a revising taxonomist may designate a new one, a *neotype* in the former case or a *lectotype* in the latter, to serve the same function as the holotype. Another term, *topotype*, is often seen in taxonomic literature and simply refers to specimens collected from

the same locality as the holotype, either concurrently or at other times; topotypes have no formal taxonomic status but are occasionally employed in resolving nomenclatural problems in the absence of type material.

In the system of binomial nomenclature formalized by the Swedish biologist Carolus Linnaeus in the 1700s, the name of a species (always italicized or underlined) consists of the name (capitalized) of the genus it is placed in, plus the species epithet (lowercase) (e.g., *Etheostoma blennioides*). Subspecies names (trinomials) follow the species epithet (e.g., *Etheostoma blennioides blennioides*). When subspecies of a species are recognized and published by a taxonomist, the subspecies encompassing the population from which the species was originally described must retain that species’s name, as in the above example, and is known as the *nominate subspecies*, while other populations may be given other names (e.g., *Etheostoma blennioides guselli*). Only names published since 1758, beginning with Linnaeus’s *Systema Naturae*, are considered valid under the international rules of nomenclature (ICZN, 1985), which govern taxonomic practices. When a taxonomist judges two previously published species to be the same, the first (older) published name has priority and the newer (more recent) name may be placed in *synonymy* in a subsequent revision.

*Classification.* Systematists attempt to reflect evolutionary relationships in hierarchical classification systems. In the most basic classification system, modified from that first erected by Linnaeus in the 1700s, species hypothesized to be closely related are grouped within genera, related genera within families, families into orders, and orders into classes. Beyond the basic classificatory levels of the Linnaean hierarchy, the systematist may choose to recognize intermediate-level categories (e.g., subgenera, tribes, subfamilies, superfamilies, suborders, or superorders). With respect to nomenclature, each genus has a *type species* to serve as the standard for that grouping and with which the generic name must always remain, regardless of what other species might be assigned to it. A large percentage of the fish genera ever described are listed in Jordan (1917–1920), Golvan (1962), and Eschmeyer (1990). If subgenera are to be recognized, a nomenclatural convention similar to that of subspecies applies. The subgeneric grouping containing the type species retains the name of that genus, as for example, *Etheostoma (Etheostoma) blennioides*, while other subgeneric groupings may receive other names, as in *Etheostoma (Nothonotus) rufilineatum*; species names are most often written as binomials, but

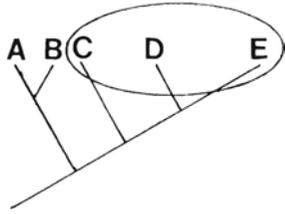
if the subgeneric allocation is to be indicated, it is placed in parentheses as above. In the literature, when a genus and its nominate subgenus are being interchangeably discussed, they may be distinguished by referring to the genus in its entirety as “sensu latu” (in the broad sense) (e.g., *Etheostoma* s.l.) and the subgenus in the restricted sense, “sensu strictu” (*Etheostoma* s.s.). At higher levels, each family has a type genus. Family names (all ending in “idae”) are extensions of the type genus name (e.g., *Perca*—Percidae); names of orders stem from one of the component families and end in “iformes” (e.g., Perciformes). Like species, genus and subgenus names and names of higher rank may be synonymized or resurrected as deemed necessary by taxonomists publishing revisionary studies.

There are three basic approaches or schools of thought on how to arrive at classifications: *evolutionary*, *phenetic*, and *phylogenetic*. The relative merits of these have been hotly contested among systematists in recent years. Evolutionary systematists take a varied (sometimes referred to as “synthetic”, e.g., Nelson, 1984) approach to classification, placing taxa into groups both according to relative similarity within and between groups, interpreted as the degree of change between common ancestors and descendant groups, and, to the extent that these are based on a phylogenetic framework, on probable “derived” characters (see below). In some cases, these classifications may also be influenced by opinions as to where taxa are most likely to fall into hypothetical lineages perceived in the fossil record or according to processes believed to be acting on these lineages, such as geological history. Pheneticists construct groups purely on overall similarity within and between groups with no regard to either historical information or the advanced or primitive natures of those individual features which contribute to similarity. This method has been most commonly applied at lower taxonomic levels (species relationships, etc.). On the other hand, phylogenetic systematists, or *cladists*, strive to construct groups defined strictly on what are believed to be shared evolutionary novelties, or “shared derived” characters (synapomorphies), characters passed down through common lines of descent, which denote the genealogy of the group. In this way they hope to attain “natural” classifications based solely on *monophyletic* groups, that is, groups descended from common ancestors.

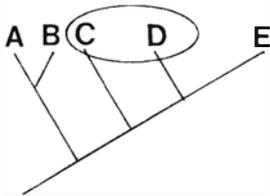
In cladistic analyses, conditions, such as a particular type of bony structure or color pattern, shared between organisms under study which are candidates for inclusion in a group (ingroup) at a particular level of classifi-

cation, are deemed primitive or derived by comparison to an “outgroup,” consisting of species presumed to be more distantly related than the organisms under study are to one another. Conditions also found among the outgroup are considered to be primitive (i.e., attributable to a distant common ancestor) while those that are not present in that group might be considered derived evolutionary novelties indicative of more recent common ancestry and, hence, closer relationship. Decisions must also be made, often aided by the sum of overall evidence in a *phylogeny* (branching scheme of relationships), as to whether similar attributes are *homologous* (of common genetic origin) or *homoplasous* (of separate genetic origin but similar because of evolutionary convergence or happenstance); only the former can be considered shared derived characters. Only derived characters are used in support of hypotheses of close relationships and the identification of closest relatives or “sister groups”; those deemed to be primitive, while they may contribute to the overall similarity of the organisms, are not considered important at the level of the ingroup. Though somewhat controversial (see Nelson, 1978, 1985; Mabee, 1989a,b), developmental (ontogenetic) information is also sometimes used in character analysis, with those features that develop later in the ontogeny of, for example, a larval fish, generally considered more derived. Whatever the method of character analysis, among the possible “phylogenetic trees” arrived at, the one with fewest branchings or steps (the “most parsimonious”) is usually accepted as the most tenable hypothesis of relationships. Cladistic methodology was introduced to the United States by Willi Hennig (1965, 1966) and is gaining acceptance in recent years among fish systematists as the preferred approach to determining phylogenies on which to base truly natural classifications.

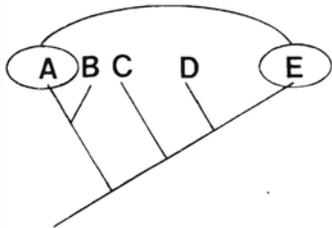
Systematists may make two kinds of “mistakes” in erecting classifications and naming groups. Rather than attaining the desired monophyletic groupings, some classifications may result in *polyphyletic* or *paraphyletic* groupings. Polyphyletic (error of inclusion) groups contain members which do not share most recent common ancestors, thus stemming from separate lines of descent and not being one another’s closest relatives. Paraphyletic (error of omission) groups do not contain all of the descendants of a given ancestor necessary to result in a “complete” monophyletic group because some actual descendants remain arbitrarily assigned to another group. Thus systematists must continually attempt to resolve relationships among organisms and update classifications to reflect these relationships in order to avoid



**monophyletic  
group**



**paraphyletic  
group**



**polyphyletic  
group**

Diagrams (i.e., cladograms) of actual evolutionary (phylogenetic) relationships among five taxa, A-E, showing different kinds of groupings a systematist may hypothesize: **monophyletic group**—a correct hypothesis that taxa C, D and E have a common most recent ancestor (i.e., a correct natural grouping); **paraphyletic group**—an incorrect hypothesis that taxon E does not share a most recent common ancestor with taxa C and D and thus E omitted from group; **polyphyletic group**—an incorrect hypothesis that taxa A and E have a most common recent ancestor when, in fact, three most recent common ancestors are not shared.

such groupings. Classifications are always provisional and constantly changing to reflect new hypotheses. Several groupings, especially higher groupings of fishes, are strictly provisional, erected for practical convenience, until such time as higher relationships are better understood.

Classifications of fishes have evolved for over three centuries, beginning even before the concepts published by Linnaeus (1758) in *Systema Naturae*, which were based primarily on those of Linnaeus's fellow Swede, Peter Artedi, and a few even earlier (mid-1600s) concepts of Englishman Francis Willoughby. In the late 1700s and early 1800s, European ichthyologists greatly expanded on the knowledge of Linnaeus's time and published several comprehensive faunal works reflecting their ideas of classification. From 1798–1803, the French ichthyologist B. G. E. Lacepede published his *Histoire Naturelle des Poissons*, and German ichthyologists Marcus E. Bloch and Johann G. Schneider published *Systema Ichthyologiae* in 1801. Later came one of the great classifiers of the animal kingdom, the Frenchman Georges Cuvier, who published *Le Regne Animal* (1816) and began the classic 22-volume work *Histoire Naturelle des Poissons* with Achille Valenciennes (1828–1849). In the 1830s, the Swiss zoologist Louis Agassiz (later of Harvard) published fish classifications with particular emphasis on fossil forms, and English ichthyologist William Swainson (1839) published a work devoted strictly to fish classification; he may have been the first to formalize the “idae” endings to family names within fishes. Classifications of higher groups of fishes were hypothesized by Mueller (1844) and Agassiz (1862). More comprehensive works reflecting then-current views of classification ensued in the following decades (Gill, 1872; Guenther, 1859–1870; Boulenger, 1904). Jordan (1923) and Berg (1940) published major classifications based in a large part on previous concepts of C. T. Regan (1909) of the British Museum. Jordan's classification included genera in addition to families, an effort repeated by Norman (1957). A new, considerably revised, provisional classification was attempted by Greenwood et al. (1966) with a particular focus on attempting to reflect the genealogy of groups. Most recently, classifications somewhat modified from those of Greenwood et al. were published by Nelson (1976, 1984). The order of the latter publication is largely followed in this book. The sequence of listing of groups within a higher classification of organisms, once relationships are hypothesized among the groups to determine proximity in the listing, is generally from what is deemed evolutionarily most primitive to most

derived (e.g., from the primitive sturgeons to the “higher” perciform fishes).

*Biogeography.* Studies attempting to discern the distributional history of lineages are termed “biogeography.” Geographical distributions of these lineages are considered in light of relationships hypothesized from systematics studies to infer the distributional history of ancestral forms and possible causal factors, such as geologic or climatic events, for their subsequent speciation. For instance, closely related fishes in adjacent drainages may have had a continuously distributed common ancestor occurring at a time when both drainages were interconnected; subsequent isolation of the drainages and division of the ancestral population resulted in speciation into two forms (*vicariant* event). Or the ancestor may have initially occupied only one drainage and subsequently entered the other through some temporary connection where it evolved into a second species (*dispersal* event). These scenarios are often debated among biogeographers and, in the cases of freshwater fishes, the distinction between them can sometimes be unclear. Problems with interpreting the distributional history of North America’s freshwater fishes are made abundantly clear in the several works published in Hocutt and Wiley (1986) and those of Tennessee in particular in Starnes and Etnier (1986).

To learn more about biogeography in general, and the evolution of the many perceptions and theories associated with this science, readers should consult the works of Darlington (1957), Simpson (1965), Udvardy (1969), Pielou (1979), Nelson and Platnik (1981), Nelson and Rosen (1981), and papers found in the journals *Systematic Zoology* and *Biogeography*.

*Methods for Fish Taxonomic Studies.* Ichthyologists use several approaches to study distinctions and relationships among fishes, including “traditional” morphological methods, biochemical methods, chromosomal studies, and, most recently, molecular approaches. In morphological studies, *meristic* data (counts that relate to body segments such as scales and fin rays) and other counts (e.g., gill rakers, sensory pores and other features) and *morphometric* (body measurements) data are extremely important (see Counts and Measurements section). The ichthyologist may gather such data on large comparative series of specimens and subject it to a variety of techniques, including univariate and multivariate statistics, in order to understand the variation within and among populations. Detailed analyses of shapes in fishes using body measurements, often using

computer-assisted multivariate analyses such as principal components or discriminant functions, are termed *morphometrics* and have been of some utility in distinguishing closely similar forms (see Bookstein et al., 1985; Strauss and Bond, 1990). Increasingly, video-camera images of fishes are fed directly into a computer and are then digitized in Cartesian coordinates to facilitate easy designation of landmarks for instantaneous distance and angle measurements (e.g., Ehlinger, 1991). In addition, more qualitative attributes, such as color patterns, fin configurations, skeletal and muscular features, and distributions of breeding tubercles may be utilized in the analysis of differences and similarities among fishes under study.

Skeletal (*osteological*) and muscular (*myological*) studies have been extremely important over the years, particularly in the study of higher (intergeneric, interfamilial etc.) relationships among fishes. Dried skeletons were used in early studies and are still used to a lesser extent for certain information, particularly from larger specimens. These are prepared by either boiling and picking flesh from the skeleton, a very time-consuming technique, or by allowing bacterial decomposition or carrion-eating organisms to clean the bones. Large specimens may be left out-of-doors, covered by hardware cloth or similar arrangement to prevent removal by larger scavengers, where insects will clean the skeleton over a period of several weeks. Institutions that prepare large numbers of skeletons maintain colonies of dermestid beetles whose larvae perform this function. Also, see Mayden and Wiley (1984) for an additional method of skeletal preparation. Nowadays, most ichthyologists study specimens that have been cleared and stained and stored in glycerin rather than dry skeletons. These specimens, which necessarily must be relatively small, are usually cleared with potassium hydroxide solution and have the flesh digested away with an enzyme, such as trypsin. The bones may be stained red with alizarin solution, and cartilage may be counterstained with alcian blue. Several papers are available on clearing and staining techniques, including Taylor (1969a), Dingerkus and Uhler (1977), and Taylor and Van Dyke (1985). Radiographs (X rays) are also used in osteological studies; these do not usually have sufficient resolution for detailed studies but can provide information on presence or absence of structures and facilitate vertebral counts on series of specimens without damaging them. In addition to figures herein (13,17) Lagler et al. (1977), Bond (1979), and Caillet et al. (1986) provided reasonably good illustrations of fish skeletons. Other guides are Gregory (1933) and Weitz-

man (1962), though it should be noted that the former has several errors.

Myological studies require careful dissection to ascertain and compare the origins and insertions of various muscles of fishes being studied. Winterbottom (1974) provided a valuable guide to muscle nomenclature among various groups of fishes.

The advent of powerful microscopes that can magnify thousands of times, such as light transmission and scanning electron scopes, has opened up a new area of investigation for fish systematists. Knowledge of the microstructure of features such as scales, teeth, gill rakers, and many others, promises to add a great deal of new insight to studies of fishes.

In the past two decades, protein data has become very important to fish systematics. Analyses of variation in proteins within and among fish groups by electrophoretic techniques has become commonplace. Variation can be compared visually by the banding patterns that result when extracts from fish muscle, liver, eyes, or other tissues are subjected to electric current passed through a bed of starch gel or other medium treated with buffers and stained for specific proteins. Differences in banding patterns result from differences in electric charges associated with different protein molecules which determine mobility. Data from electrophoretic studies, aside from its utility in discrimination between different "electromorphs," and thus species-level taxonomy, can be, as with morphological data, subjected to both phenetic and cladistic methods to assess relationships among organisms. Much more information on electrophoretic techniques is available in Brewer (1970), Buth (1984), Richardson et al. (1986), Aebersold et al. (1987), Hillis and Moritz (1990), and Leary and Booke (1990).

More recently, DNA techniques have entered the realm of systematic studies. Analysis of maternally inherited genetic material (mitochondrial DNA) or nuclear DNA from cells of fishes or other animals is now possible through the use of restriction enzymes which recognize specific codon sequences and, with repeatable consistency, cut DNA into fragments at these sites. Fragment sizes may be compared through the use of electrophoresis to detect differences in sequences between organisms. It is also possible, by recombinant methods too detailed to discuss here, to clone and sequence the DNA fragments for further comparative studies. DNA "probes," prepared from bacteriophages or in a mechanical synthesizer, can be "hybridized" to fish DNA to allow detection of variation down to the level of individuals (see Wilson et al., 1985; Ferris and Berg, 1987; Gyllensten and Wilson, 1987; Moritz et

al., 1987; Hallerman and Beckman, 1988; Hillis and Moritz, 1990). Extremely refined data results from such studies, to the point that, based on mitochondrial DNA, maternal "pedigrees" can be reconstructed for animals studied. Such studies will offer a tremendous new source of data for studies of relationships among fishes as well as addressing questions pertaining to hybridization phenomena and population biology.

Finally, some ichthyologists have conducted systematics studies of fishes by comparing chromosome number and morphology. In a process called "karyotyping" (see Denton, 1973; Blaxhall, 1975; Kligerman and Bloom, 1977; and especially Thorgaard and Disney, 1990), spreads of metaphase (undergoing division) chromosomes from individual cells are prepared so that they may be counted and compared with respect to configuration. Some surprising information with regard to chromosome numbers among closely related fishes has emerged from these studies. For example, some may have evolved twice as many chromosomes as others through a process called tetraploidy. Further, unisexual species, such as those discussed herein under Poeciliidae, may be triploids. Karyotypy, which examines only the gross morphology of chromosomes, may have somewhat limited utility in elucidating relationships of fishes, but recently developed techniques to reveal banding patterns on chromosomes have some promise of revealing additional variation for analyses.

It should be pointed out that, no matter what the methods and data source utilized in systematics studies of fishes or other organisms, the interpretation of that data among different workers is always subject to controversy. The concept of what constitutes sufficient variation among populations for formal recognition as a species or other taxon varies among taxonomists. What constitute "significant characters" on which to base ideas about relationships are always in dispute. Moreover, relationships hypothesized on the same body of data treated by the different approaches to classification (phylogenetic or other) may result in very different outcomes. These same basic problems have arisen successively in morphological, chromosomal, and protein studies and are emerging in DNA studies as well.

### **Biological Studies of Fishes**

Ichthyologists who study the biology of fishes may be concerned with any of several aspects, including reproduction, early life history, age and growth characteristics, population dynamics, food and feeding habits, predation and parasitism, habitat parameters throughout

the year, and other ways in which fish interact with their environment and the community of organisms they live with (ecology). The results of such studies have provided much valuable information cited throughout this book's species accounts.

Studies of reproduction include determination of spawning season and habitat, *fecundity* (number of ova spawned by a female), courtship and actual spawning behavior, and post-spawning behavior, such as nest-guarding by males. Actual "reproductive success" is a function of how many progeny survive to an age to contribute to production of subsequent generations and is thus related to "recruitment" (see discussion of population characteristics, below). Much of what is known about reproduction in fishes was summarized in systematic fashion by Breder and Rosen (1966).

Spawning season can generally be determined by collecting individuals as the year progresses and observing the increasing fullness of the females as the ovaries become expanded with maturing eggs, a condition known as being *gravid*. Males of many species have secondary sexual characteristics, such as breeding colors or tubercles, which heighten in development. More precise estimates of spawning season can be obtained when females are so "ripe" that eggs flow freely from the vent with the application of a little pressure to the abdomen. Males, too, may flow milt at this time, but sometimes some flow can begin well before the females reach actual spawning condition. For fecundity estimates, it is generally necessary to dissect the ovaries of a series of females at the beginning of the season in order to obtain an average of mature ova; fecundity generally increases with the size and age of the female. These estimates are probably often confounded by the fact that, in species with extended spawning seasons, more ova may have matured in a given female as the season progressed. The general spawning habitat of fishes is relatively easy to ascertain as they will congregate in that area, in some cases after a long migration, during the height of the season. On the other hand, spawning microhabitats for more specialized spawners can be much more difficult to ascertain and may require lengthy observations and searches for egg deposition sites. These are still not known for many fishes that spawn in habitats with poor accessibility.

Observations of pre-spawning behavior, such as nest construction, courtship and spawning behavior, and post-spawning can be relatively easily obtained for a few species which are tolerant of life in aquaria, but this information must be gotten in the natural habitat of the majority of fishes, either by stream-side observation, snorkeling, or diving. It requires a tremendous

amount of time and luck to encounter sufficient behavior for detailed observations, and many fishes spawn in habitats that are of limited accessibility or visibility. Consequently, this information is nonexistent or fragmentary for many fishes.

Early life history studies of fishes entail a great deal of tedious work with fragile organisms. With some species it is possible to gather eggs from the natural spawns of known parents or to "strip" (extrude eggs by massaging the abdomen) from a ripe female and artificially fertilize them with milt extruded from a male; this method is also very often used for artificial propagation of fishes in hatcheries. Often, spawning is induced by administering gonadotropic hormones (e.g., pituitary extracts) to fishes nearing spawning condition. Eggs are then hatched in captivity and periodically observed microscopically to gather data on development times and the progressive morphology of the developing larvae. Rearing of larvae has proved very difficult in some groups of fishes, limiting collection of such data. In other groups it has been necessary to collect larvae periodically over a season with fine mesh plankton nets (either towed or situated in current) and then attempt to determine development from a preserved series by "backtracking," beginning with specimens large enough to definitely identify to species and associating them with progressively younger stages. Such associations facilitate larval taxonomy, and together with collection data, provide valuable information on habitats essential to the fishes' early life history. While there has been tremendous progress with such studies in the last two decades, detailed data are still only available for a small percentage of all fishes. For further information on methods see Snyder (1983) and several papers presented in Moser et al. (1984).

Biologists studying the age and growth characteristics of fishes use a variety of techniques ranging from simple to rather sophisticated. One of the simplest methods is to collect large series of individuals from a population over a short period of time and try to infer age classes from histograms of length data (*length frequency*); for example, a trimodal histogram would indicate three year classes. Because populations are usually heavily skewed towards younger individuals, and because growth increments are often small in older fishes, discerning older length (age) classes can be difficult with this method, especially in longer-lived species. Length-weight data is also sometimes utilized as an estimator of fish growth.

Other methods of determining growth in fishes usually involve relating growth rings in hard parts to fish lengths. Scales have been most commonly used for this

form of analysis with measurements made by placing slide-mounted scales in some type of projector and measuring the image from the focus of the scale to various annuli (see Anatomy and Function section, above). The age-length relationship, based on measurements from scales removed from a large series of fishes of known lengths, facilitates a "back-calculation" procedure so that lengths at certain ages can be predicted and fishes from that population can be aged approximately by simply noting their length. However, there are often problems with this procedure because growth rates may not be uniform (*isometric*) over time or between body parts (thus being *allometric*) and, in some populations, scale annuli, for various reasons, can be difficult to discern. Other structures that have been used for aging studies are cross-sectioned fin spines (particularly of catfishes), opercular bones, vertebrae, and otoliths (see Anatomy and Function, above). Otoliths, sectioned and projected on a scanning electron microscope, can provide extremely refined growth information, with even daily growth rings discernible. For more information on aging of fishes consult the works of Lagler (1956), Weatherly (1972), Bagenal (1974), Moyle and Cech (1982), Jearld (1983), and Summerfelt and Hall (1987).

Studies of population characteristics include estimates of density, total population, age structure, recruitment of young into the population, survival, and predator-prey density relationships, as well as studies of distribution and movements. Such studies require considerable sampling over several seasons and the analysis of much data. Sampling methods (see fish collection methods in following section) include intensive netting of an area with unbiased gear, trawl surveys, and ichthyocide applications to a given area, and investigation of anglers' catches. Such sampling facilitates the extrapolation of density estimates of varying validity, and age analysis of the fishes caught yields data on age structure, recruitment (and thus overall reproductive success), and survival. Fishery biologists have attempted to better understand and perhaps predict trends in fish population dynamics by modeling them with computer-assisted techniques. Tagging and marking (catch, tag, release, recapture) studies have been very important in gathering data on movements, as have radio telemetry studies in which a tiny transmitter is surgically implanted in a fish which is then released and tracked. There is still a great deal to be learned about the vagaries of fish populations, especially among those

species not in the mainstream of economic importance. Further information on fish population studies appears in Weatherly (1972), Weatherly and Gill (1987), and Cushing (1983); instructions on related techniques appear in several chapters of Nielsen and Johnson (1983).

Studies of food and feeding may involve direct observation of feeding behavior and food selection as well as detailed analysis of stomach contents. The differences in feeding behavior and specific feeding sites among fishes may be subtle; to ascertain them can require many hours of observation in the natural habitat, and of course, some habitats do not lend themselves to this kind of observation at all. Stomach contents, coupled with detailed knowledge of the distribution of food organisms, such as immature aquatic insects, in the habitat can offer tremendous insight, not only to food preferences but to specific feeding habitats. Periodic coincidental sampling of both fishes and potential food organisms in the habitat through the seasons, and moreover, periodic sampling of fishes over the course of a day, can provide detailed data on seasonal and chronological trends in consumption and diet preferences. Fishes and samples of potential food organisms are generally preserved in the field and returned to the lab until such time as the fishes can be dissected for stomach contents and these contents, as well as the samples from the environment, sorted and identified. Of course, an ability to sort and identify potential and actual food items—such as aquatic insects, mollusks, small fishes, or others—is critical. Potential food organisms should be carefully sampled both qualitatively and quantitatively to ascertain specific sites of occurrence (to reveal where fishes are eating) and estimates of density, which can be compared with occurrence in stomachs to give indications about food selection. Stomach contents of predatory species also, of course, are a key source of information on predator-prey relationships. A good introduction to these methods is found in Bowen (1983) and further information is given in Ivlev (1961).

While the biology and ecology of economically important species have been studied for many years, and there has been some emphasis on lesser-known species in recent years, a tremendous amount is yet to be learned. Even some of the well-studied species continue to surprise us with unexplainable fluctuations in population levels, reminding us how little we presently know about their interactions with the environment; of course, we have barely scratched the surface for many, more obscure, fishes.