

Chapter 11

Methods for Assessing Fish Populations

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11.1 INTRODUCTION

Fisheries managers are likely to assess fish populations at some point during the fisheries management process. Managers that follow the fisheries management process (see Chapter 5) might find their knowledge base insufficient during the steps of problem identification or management action and must assess a population before appropriate actions can be taken. Managers will implement some type of assessment during the evaluation step as a means of measuring progress relative to objectives. Choosing how to assess a population is an important decision because managers strive to maximize their knowledge of a population while minimizing the time and money expended to gain that knowledge.

A fish population is defined as a group of individuals of the same species or subspecies that are spatially, genetically, or demographically separated from other groups (Wells and Richmond 1995). A population will have a unique set of dynamics (e.g., recruitment, growth, and mortality) that influence its current and future status. The terms population assessment and stock assessment are used interchangeably by some fisheries managers. In general terms, a fish stock is a portion of a population, or a subpopulation. Stock assessment often refers to that portion of the fish population that is exploitable by a fishery, but we use the more inclusive population assessment throughout this chapter. Distinction is also made between a fish population and a sample of that population. Biologists almost never examine all the fish in a population, but rather base inferences on a sample of individuals from a population. How, where, and when those samples are drawn has a tremendous influence on the quality of data and validity of inferences.

In this chapter, methods for assessing inland fish populations to support management decisions are presented. It is important to consider bias (the unequal probability of sampling members of a population), precision (the degree of reproducibility of results), and the benefits of standardized sampling methods. A variety of population parameters and indices currently used to evaluate fish populations are reviewed, as are their respective strengths and limitations. This chapter will help students understand that proper design, analysis, and interpretation of assessment data are the foundation for appropriate management decisions.

11.2 NEED FOR ASSESSMENT

The best management decisions are based on knowledge that is sufficient to infer cause-and-effect relationships between management actions (e.g., harvest regulations) and a fish

population (Radomski and Goeman 1996). Complete knowledge is rare or impossible to obtain, so managers attempt to acquire as much information about a fish population as resources allow. Frequent assessments may be necessary because population size, structure, and distribution fluctuate in response to environmental variation (Lett and Doubleday 1976; McRae and Diana 2005). Natural disturbances, such as floods, droughts, or fires, and anthropogenic changes, such as new fishing technologies, regulation changes, or nonnative fish introductions, can alter fish populations. Thus, status and trends in abundance, size or age structure, maturity schedules, or fecundity of fish in a population are central to informed decision making (Ault and Olson 1996; Post et al. 2003).

Although fisheries managers still spend time attempting to understand the ecology and population dynamics of sport fish species (Francis et al. 2007), the trend toward ecosystem management (Cowx and Gerdeaux 2004) has caused managers to devote more attention to nongame species (Angermeier et al. 1991). Assessments of sport and nongame fish populations are similar but driven by different motivations. For instance, population assessments of sport fish are often influenced by a desire to provide recreation or harvest for anglers, whereas population assessments of nongame fish typically aim at maintaining or enhancing the distribution and abundance of these species. Fisheries professionals must integrate population assessments of both types of fishes to implement ecosystem management properly.

Finally, the tendency of the public to become increasingly involved in resource management decisions (Caddy 1999; Bettoli et al. 2007) has increased the need to understand fish populations. General information about fish populations is widely available (e.g., Froese and Pauly 2008; NatureServe 2008) and sophisticated user groups can gain access to technical data, conduct analyses, and draw independent conclusions about particular fish populations (Beierle 2002). Managers can successfully interact with such groups by providing the results of population assessments with comprehensive analyses and interpretations based on sound scientific practices, including comparison with other findings published in peer-reviewed journals.

11.3 SAMPLING CONSIDERATIONS

11.3.1 Bias and Precision

Choosing how to sample and how to characterize a population are generally accorded the most emphasis in assessment programs. Determining sampling bias and precision are also important because bias or low precision make it difficult to identify the status of a population. For example, using electrofishing and the removal method to estimate the number of trout in a stream reach almost always results in an underestimate of fish abundance because the susceptibility of fish to capture by electrofishing declines as the number of capture attempts conducted over relatively short intervals (e.g., less than 1 h) increases (Riley and Fausch 1992). Moreover, the probability of capture of fish by electrofishing is also related to fish length, habitat complexity, stream size, water depth, water conductivity, species being sampled, and fish density. Adherence to consistent sampling protocols does not correct for bias, but if effort and catchability of fish remain constant among sampling events, the size and direction of the bias tend to remain constant and may permit meaningful population inferences. Still, testing for this constancy is important (Box 11.1). Alternatively, a lack of precision can indicate that

sampling efficiency is not constant or that too small a sample has been obtained. More intensive sampling may increase precision and reduce bias (White et al. 1982), but identifying and accounting for the ecological, demographic, or habitat-related factors that affect sampling efficiency will produce the most reliable estimates of fish population parameters.

Understanding bias and precision becomes particularly important when determining whether to estimate population parameters directly or to estimate population parameters indirectly by means of indices. An index is defined as a number or property that is presumably related to a parameter of a fish population. Indices often require less effort or fewer resources than do estimates of population parameters but still provide useful information. For example, obtaining a census of bluegill in a lake is difficult, but counts of fish obtained from nets set overnight are relatively easy to obtain and generally reflect fish abundance. Despite their popularity, indices should be used with caution. Often the form of the relationship between an index and the population parameter of interest may be poorly understood, temporally or spatially variable, or based on untested assumptions (Anderson 2003). Nevertheless, if these relations can be well defined, indices can be a powerful tool for understanding population status and trends (McKelvey and Pearson 2001; Hopkins and Kennedy 2004).

11.3.2 Standardized Sampling

If the bias and precision of sampling gears, especially in variable environments, are unknown, standardized sampling may provide a means to assess trends (Bonar et al. 2009). Standardized sampling is defined as sampling with identical gear during the same season (or set of environmental conditions) in the same manner over time or among fish populations. Doing so does not eliminate bias but theoretically holds the bias constant so that differences in indices computed from samples among years or fish populations can be attributed to relative changes in a population or relative differences among populations. Other benefits of standardized sampling include improved communications among fisheries professionals and production of large-scale data sets beneficial for current and future assessments (Bonar and Hubert 2002).

Failure to adopt standardized sampling approaches can prevent managers from detecting population trends or assessing population status. For example, electrofishing catch rates of smallmouth bass are generally greater at night than during the day (Paragamian 1989). If electrofishing samples are collected during the day in some years and at night in others and the difference in vulnerability to capture is not addressed, a monitoring program may erroneously conclude that the smallmouth bass population is unstable.

Standardized sampling protocols cannot substitute for an understanding of fish biology, population dynamics, and gear selectivity. For instance, fyke nets of a certain mesh size and overall dimensions are regularly used in reservoirs to sample age-0 black crappie during the fall as an index of recruitment, but smaller fish are less likely to be captured than are larger fish (McInerney and Cross 2006). In years with early spawning by adult black crappie, many large age-0 fish may be captured during fall sampling and give the appearance that spawning and early survival were ample. In contrast, delayed spawning might result in fewer fall captures because age-0 black crappie would be smaller, giving the appearance that spawning and early survival were inadequate. A rigorous education in fisheries science that includes sampling theory and fish ecology is a prerequisite for implementing standard fish sampling protocols and analyzing the associated data.

Box 11.1. Removal Model Abundance Estimates: Wrong but Useful?

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All models are wrong, but some models are useful—a truism to live by for fisheries managers. Consider the removal model, which uses standard depletion methods to generate an estimate of fish abundance. A primary assumption of the model is that sampling efficiency, or the proportion of fish removed from a site per capture event, is the same for all depletion capture events. However, fish that remain after the first depletion event are often more difficult to capture during subsequent events because they seek cover that is difficult to sample or continue to evade netters due to their relatively small size. When sampling efficiency declines from depletion event to depletion event, the removal model yields biased results: an underestimation of population size and an overestimation of sampling efficiency (e.g., Riley and Fausch 1992; Peterson et al. 2004).

This was the case for rainbow trout in small, headwater streams in the Boise River basin in Idaho (Rosenberger and Dunham 2005). Rainbow trout were marked and left in 31 sites (approximately 100 m in length) between two block nets to form “known” population sizes (following Peterson et al. 2004). After overnight recovery from initial capture and marking, marked trout were sampled by means of standard backpack electrofishing depletion procedures. The removal model generated rainbow trout abundances from depletion data that nearly always underestimated the number of marked fish actually present, averaging only 75% of marked fish.

The model yielded biased results. But could it still be useful? Managers faced with this kind of bias may assert that, although the estimates are incorrect, removal estimates can still be used as a relative index of fish abundance over space and through time. Methods need only be standardized and consistent, creating a highly precise, though wrong, answer. Further, estimates could be calibrated to known values with a simple correction factor to reflect actual fish numbers. This practice assumes that bias, though present, is consistent and based primarily on the methods used. It should not be influenced by variables that will change through space and time.

A study in Idaho unfortunately refutes the assumption of constant sampling efficiency (Rosenberger and Dunham 2005). Not only were the removal estimates of rainbow trout abundance biased, but bias was inconsistent and influenced by stream habitat. Larger streams and streams with more instream structure in the form of dead wood yielded more biased estimates than did smaller streams with less instream cover. These stream features negatively affected electrofishing sampling efficiency, implying that what decreases sampling efficiency can increase the bias of removal estimates (also see Peterson et al. 2004). Common differences among sites over space and through time, including size of habitat, presence of structure, size of fish, water temperature, and the density of fish, can affect the sampling efficiency of electrofishing (e.g., Bayley and Dowling 1993; Dolan and Miranda 2003; Peterson et al. 2004). The Idaho study indicates that thorough validation of the removal model for generating absolute or comparable estimates of fish abundance is needed before use. Therefore, a new motto is suggested: all models are wrong; validate and proceed cautiously.

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11.3.3 Probabilistic Sampling

Statisticians frequently separate sampling designs according to whether probability or nonprobability sampling procedures are used (Levy and Lemeshow 1991). Probability sampling occurs when all possible samples are included in the selection process, the probability of selection is known, and the selection process is random (or an approximation thereof). The most basic probability sampling procedure used in fish population sampling is simple random sampling, in which a predetermined number of sampling sites is selected from all possible sampling sites such that every potential site has an equal chance of being selected (Hansen et al. 2007). Estimates of population parameters from probability sampling can enable inferences about the entire population. Furthermore, precision (e.g., standard errors) of estimates can be determined from probability sampling (Wilde and Fisher 1996).

Probability sampling may be impractical in many cases. Examples include small-scale assessments that occur in ponds or specialized habitats of rare organisms or situations in which information needed to design a probability sampling procedure is lacking. Nonprobability sampling may be used to provide information on trends in indices of population parameters (e.g., catch rate or size structure) of interest to managers (Wilde and Fisher 1996). Nonprobability sampling generally involves the nonrandom selection of sample sites, frequently based on judgment or convenience, and limits the scope of inference about fish populations. For example, samples collected from subjectively selected fixed sites, a nonprobability sampling procedure commonly used in fish surveys (King et al. 1981), are applicable only to those individuals or locations actually sampled (Wilde and Fisher 1996)—that is, findings should not be extrapolated to the whole population.

11.3.4 Geographic Boundaries of Fish Populations

Assessing a fish population requires the manager to delineate the extent of the population. In simple aquatic systems (e.g., isolated lakes or headwater streams with movement barriers), the boundaries are obvious. There are few barriers to interbreeding in simple aquatic systems and the population parameters are common to all individuals in a given species. Large, complex aquatic systems, however, make geographic delineation of a population challenging. For example, fish in floodplain lakes may have the opportunity to mate with fish from other floodplain lakes during annual spring floods. Similarly, fish in different tributaries to a large river may not be different populations because of movement of individuals among locations. Alternatively, large lakes or complex riverine networks may host demographically-distinct populations of some species that overlap during some seasons or life history phases (Dunham et al. 2002).

11.4 CHARACTERISTICS, STATISTICS, PARAMETERS, AND INDICES

Assessment is often based on characteristics of individual fish in a population. Typical data include their length and weight (Anderson and Neumann 1996) and sometimes their sex, maturity, gonad weight, or liver weight (Strange 1996). Likewise, hard structures (scales, fin

rays, or bone) can be used to age individual fish (DeVries and Frie 1996). The amount and type of food in the stomach can be described (Bowen 1996). Numbers of lesions, parasites, or deformities can be recorded, and blood or tissue samples can be collected for genetic or chemical analyses (Strange 1996).

Data from individual fish are summarized with statistics to estimate parameters of the population from which the sample was taken. Such statistics include the prevalence of fish of different sizes and ages. These statistics can be combined to provide estimates of growth rates (Isely and Grabowski 2007). In addition, length and weight data can be combined to gauge the condition or “plumpness” of fish in a population (Pope and Kruse 2007). Use of data from a single sample to estimate population parameters may be inferior to data from multiple collections, but the practice of generating such data from a single sample is common in fisheries management.

An assessment is also likely to include statistics for a population that are not based on summaries of characteristics from individual fish. For example, recruitment and mortality rates are not averages of individual characteristics of fish in a population. Rather, these rates are generally estimated from trends in abundance across years or age-groups.

Assessment of a fish population may involve comparisons of estimates of population parameters from a current sampling effort to estimates of parameters from other populations or to management objectives. Analysis and interpretation are also likely to include modeling exercises that combine relevant estimates into a yield model (Power 2007). Several computer-based yield (or harvest) models (e.g., GIFSIM [Taylor 1981] and FAST [Slipke and Maceina 2001]) simplify the process for fisheries managers. These models allow the prediction of changes in a population or harvest resulting from management actions to limit fishing mortality (see Chapters 2 and 7). Managers must be aware of and acknowledge the uncertainty inherent in model predictions and in the population parameter estimates because assumptions, bias, and uncertainty are compounded when they are incorporated into yield models.

This chapter contains a presentation (expanded from Gibbons and Munkittrick 1994) of some of the common parameters and indices used by inland fisheries managers (Table 11.1). Each parameter or index has advantages and disadvantages because of inherent assumptions associated with its use, limitations of particular data sets, and preferences of investigators. Thus, it is prudent to use multiple tools in assessments of fish populations (see Box 11.2).

11.4.1 Population Dynamics

Population dynamics are the processes responsible for changes in abundance or biomass of a population through time and are a subset of possible population parameters. Estimates of population dynamics can provide greater insight into fish populations than can indices, which are a static portrayal of the population. Estimates of population dynamics can indicate how a population arrived at its current state and how it might change in the future.

A population assessment might focus on determining whether the size of a population is relatively constant, increasing, or decreasing, for which one would need population abundance data and age data to calculate birth and death rates. Other data, including individual weights, are necessary if population biomass is of interest. For many inland fisheries, such as those in natural lakes and small impoundments, birth and death rates tend to be regarded

Table 11.1. Categorized population characteristics that are frequently assessed or monitored by fisheries scientists and a brief description of the type of data required for quantifying the specific characteristic. Information presented is an expansion of categorizations of population parameters originally outlined by Gibbons and Munkittrick (1994).

Category and parameter or index	Type of data
Population dynamics	
Larval or juvenile abundance	Relative abundance and age
Recruitment	Relative abundance and age
Growth	Age and weight or length data
Mortality	Relative abundance and age
Exploitation	Absolute abundance and harvest (from creel data) or tag-reward data
Genetics	
Genetic composition	Tissue and blood samples
Abundance, density, and distribution	
Absolute abundance	Area subsample, mark–recapture, or depletion
Relative abundance	Catch per unit effort
Density	Population estimate and system size
Distribution	Presence–absence data
Population structure	
Mean length	Length
Proportional size distribution	Length
Mean age	Age
Year classes per sample	Age
Length at age	Age and length
Juvenile : adult ratio	Maturity status
Sex ratio	Sex
Age at maturity	Age, sex, and maturity status
Weight at maturity	Weight, sex, and maturity status
Energy acquisition, storage, and use	
Percent feeding	Stomach status and relative abundance
Relative weight	Length and weight
Hepatosomatic index	Weight and liver weight
Tissue lipid levels	Tissue sample
Gonadosomatic index	Weight and gonad weight
Length- or weight-specific fecundity	Length or weight and fecundity
Contaminants and diseases	
Proportion of population with anomalies	Lesion inspection
Proportion of population with parasites	Parasite inspection
Presence of toxicant, pollutant, or heavy metals	Tissue and blood samples
Viral and bacterial status or load	Tissue and blood samples

as more important than immigration and emigration rates, whereas the influence of movement rates is more widely recognized in migratory fishes. Considerably more effort must be expended to determine immigration and emigration rates, and the task is difficult in systems without barriers to fish movement.

Box 11.2. Pitfalls of Relying Solely on Size Structure Indices and Catch per Unit Effort for Management Decisions

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Size structure indices and catch per unit effort (C/f) are commonly used by fisheries managers to draw inferences about fish population dynamics. Proportional size distribution (PSD) and C/f are numerical descriptors of length frequency and relative abundance, respectively. However, fisheries managers should use caution if basing decisions solely on calculations of one or both of these indices. These indices are best used in conjunction with a suite of diagnostic information, including fish growth, condition (relative weight; W_r), and recruitment, as well as angler creel data. An example illustrating this principle is derived from data collected on largemouth bass in a reservoir in western Texas.

O. H. Ivie Reservoir is a 7,770-ha impoundment on the Colorado and Concho rivers. The reservoir is operated to store and supply municipal water to two cities and numerous smaller communities. Because of its arid location the reservoir is subject to prolonged periods of low water followed by years of partial recovery following occasional floods. Largemouth bass harvest was managed with a 457-mm minimum length limit and five-fish-daily bag limit for the first 11 years that recreational fishing was allowed on the reservoir. Largemouth bass, sunfish, and gizzard shad populations were evaluated in autumn by means of a boat-mounted electrofisher and according to standardized procedures. Surveys were conducted, in total, seven times from 1991 through 2000. However, for the sake of illustrative brevity, this box example focuses on sample years 1999 and 2000. In addition, supplemental sampling in the form of angling was used in 1999 to increase sample size and length distribution of largemouth bass used for age and growth analysis.

During 1999 and 2000, sampling of the largemouth bass population showed, respectively, mean catch rates of 94 and 72 bass per hour of electrofishing (see figure below), PSD (quality length) values of 69 and 64, and PSD-P (preferred length) values of 32 and 30 (see table below). The PSD and PSD-P values fell in the range recommended by Gabelhouse (1984) for “balanced” and “big bass” management strategies (see Chapter 16), and the C/f of largemouth bass indicated their relative abundance was adequate in relation to other area reservoirs. Relying solely on these two indices, fishery managers might infer the largemouth bass population was in desirable condition.

(Box continues)

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Recruitment, growth, and mortality rates are the primary population dynamics (often termed rate functions) influencing the harvestable segment of a fish population (Brown and Guy 2007). Assessing population dynamics of fish is best achieved using long-term data collected with standardized methods because biotic and abiotic influences on population dynamics typically vary from year to year. Unfortunately, such data sets are rare because they are expensive to obtain. In lieu of long-term data, methods have been developed to estimate population dynamics.

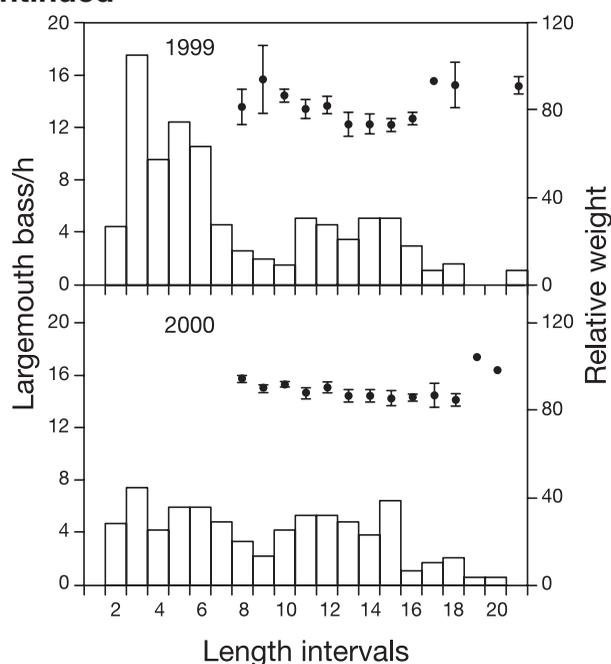
Box 11. 2. Continued

Figure A. Number of largemouth bass caught per hour (C/f) and mean relative weights \pm SE (W_r ; circles) for fall electrofishing surveys, O. H. Ivie Reservoir, Texas, 1999 and 2000. Length-group definitions are in 25.3-mm intervals (e.g., 2 = 50.8–76.1 mm and 3 = 76.2–101.5 mm). In 1999, total $C/f = 94.5$ (16; 189) (the relative standard error [RSE = $SE/\bar{x} \times 100$; $N = 24$ stations] and total number of fish caught are given in parentheses). In 2000, total $C/f = 72.5$ (19; 139).

Table. Proportional size distribution of quality-length (PSD) and preferred-length (PSD-P) largemouth bass collected by electrofishing from O. H. Ivie Reservoir, Texas, 1999 and 2000. Standard errors and sample sizes (number of stock-length largemouth bass) are given in parentheses.

Year	PSD (SE, N)	PSD-P (SE, N)
1999	69 (5, 71)	32 (7, 71)
2000	64 (7, 77)	30 (6, 77)

(Box continues)

Annual recruitment is typically the most variable factor affecting the dynamics of fish populations but can provide substantial insight into why fish populations may vary in size and structure (Gulland 1982; Allen and Pine 2000; Maceina and Pereira 2007). Larval or juvenile abundance can be an early indication of year-class strength and future recruitment to a fishery (Sammons and Bettoli 1998). Conversely, year-class size may be more closely related to abiotic factors than to larval abundance (Kernehan et al. 1981). Variability in recruitment of fish

Box 11.2. Continued

The relative abundance and size distribution of gizzard shad (see figure below) indicated adequate forage availability, which typically equates to better body condition and growth rates. Gizzard shad electrofishing C/f in 1999 and 2000, respectively, was 242 and 292 per hour, and the index of vulnerability (IOV; DiCenzo et al. 1996) indicated that 75% and 85% of the gizzard shad population were available to most predators those years. The IOV is the percentage of all gizzard shad that are 200 mm or shorter in length and is an index of the proportion of the gizzard shad population that is susceptible to predation by most predators.

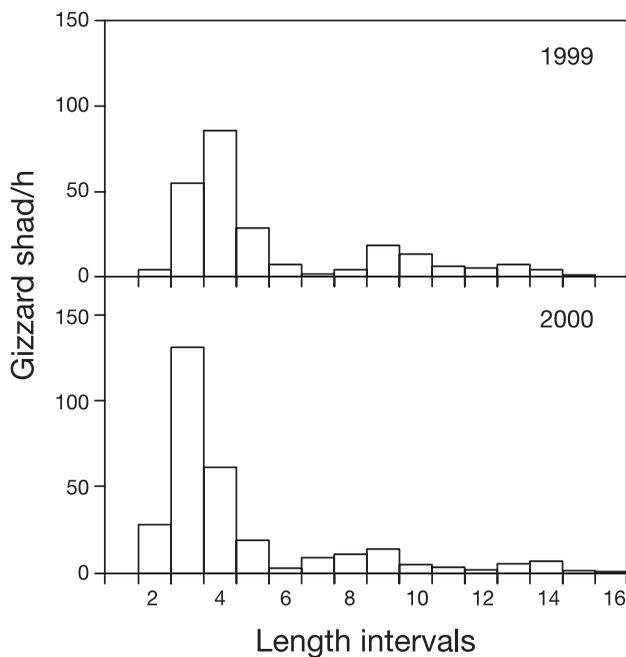


Figure B. Number of gizzard shad caught per hour (C/f) for fall electrofishing surveys, O. H. Ivie Reservoir, Texas, 1999 and 2000. Length-group definitions are in 25.3-mm intervals (e.g., 2 = 50.8–76.1 mm and 3 = 76.2–101.5 mm). In 1999, total $C/f = 242.0$ (34; 484) (values in parenthesis are as described above). The 1999 index of vulnerability (IOV) = 75.21 (SE = 8.7; $N = 484$). In 2000 total $C/f = 292.2$ (24; 560), and IOV = 84.82 (4.6; 560).

(Box continues)

into the harvestable population can be estimated with the recruitment variability index (Guy and Willis 1995), or with the coefficient of determination (r^2) resulting from simple linear regression of $\log_e(\text{catch at age})$ on age (Isermann et al. 2002).

Growth rates of fish in a population are intricately linked with mortality and recruitment rates. Growth rate influences survival and age at sexual maturity. Growth of fish is commonly indexed with various coefficients of the von Bertalanffy growth model (see Chapter

Box 11.2. Continued

Examination of additional data, however, revealed a different story. Both the growth rates and conditions of largemouth bass were undesirable. Poor largemouth bass conditions were manifested by mean W_r values less than 90 for many of the sampled groups, especially for fish in length-groups 13–18 (Figure A). In addition, age and growth data indicated a stockpiling of largemouth bass in length-groups 14, 15, 16, and 17, representing bass from 356 to 457 mm in total length, where five to seven different age-groups were represented (see figure below). In an effort to alleviate stockpiling and increase fish growth rates, fishery managers responded by changing the regulation and allowing the harvest of two largemouth bass less than 457 mm per day in 2001. Fishery managers would not have had the insight to modify the harvest regulation in 2001 by relying only on C/f and PSD data as these indices remained consistent concomitant to significant changes in the largemouth bass population.

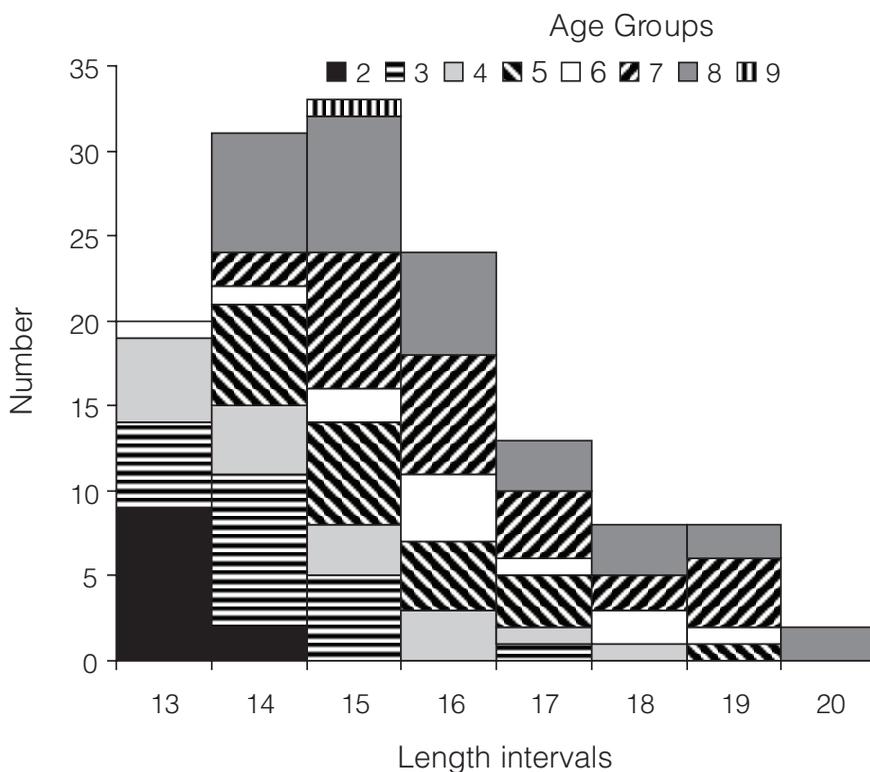


Figure C. Age composition for largemouth bass measuring 330.2–530.8 mm collected from O. H. Ivie Reservoir, Texas, 1999. Length-group definitions are in 25.3-mm intervals (e.g., 13 = 330.2–355.5 mm and 14 = 355.6–380.9 mm).

2), which is widely used to describe the lifetime pattern of somatic growth of organisms, such as fish, with indeterminate growth (Ricker 1975). Other growth models (e.g., Gompertz 1825; Richards 1959) may be more appropriate than the von Bertalanffy model for some situations. In addition, specific growth rate (the change of the logarithm of weight or length per unit time), relative growth rate (the relative change of the weight or length per unit time), and length at age (e.g., mean length at age 3), either measured at time of capture or back-calculated from hard structures such as otoliths, are also used to index growth. Quist et al. (2003) developed a relative growth index (RGI) by which the length at age from a population sample is compared with the age-specific standard length predicted by a von Bertalanffy growth model derived from pooled data for a species throughout its geographic distribution. The RGI is expressed as a percentage of the age-specific standard length achieved by the sampled population, and values greater than 100 indicate that growth is above average. Regardless of how growth is expressed, it is one of the most important rates estimated during a population assessment. Further, it is common for males and females in a population to mature on different schedules (Brown et al. 2006; Coelho and Erzini 2006) or to have different growth rates. Understanding differences in growth rates between sexes can allow managers to design more appropriate management strategies.

A population assessment might include an estimate of total annual mortality (i.e., the proportion of the population that dies in one year). Total annual mortality is related to total instantaneous mortality. Total instantaneous mortality can be estimated using a catch curve. The slope of the regression of \log_e (frequency) over age-groups equals the negative instantaneous mortality rate (Ricker 1975; Miranda and Bettoli 2007). Fisheries managers frequently partition total annual mortality of sport or commercial species into two components: (1) natural mortality, attributable to natural processes (e.g., old age, predation, competition, starvation, or disease) or those altered by human activities (e.g., habitat degradation or loss or population isolation), and (2) fishing mortality attributable to harvest or handling by recreational or commercial fishers (see Chapter 2). Agencies attempt to regulate fishing mortality by controlling harvest with gear restrictions, seasons, and length and bag limits (Radomski 2003) and monitor the results by means of creel surveys (Colvin 1991) or tag-reward studies (Reed and Davies 1991).

Exploitation is the portion of the fishing mortality attributed to fishers who harvest what they catch. Exploitation is often considered synonymous with fishing mortality because estimation of other forms of fishing mortality, such as bycatch or postrelease mortality, is difficult. Exploitation can be calculated from an estimate of absolute abundance and a harvest estimate based on creel surveys (Malvestuto 1996). The product of harvest per unit effort multiplied by annual effort provides an estimate of annual harvest. Annual exploitation can be determined by a tag-reward study, by which the ratio of the number of fish tagged and caught in a year divided by the total number of fish tagged the same year is exploitation (Miranda and Bettoli 2007). Exploitation is an important part of an assessment of a fished population because of the influence fishing pressure can have on many other population parameters.

11.4.2 Genetics

The most obvious forms of assessing fish populations involve counting or measuring individual fish, but another suite of characteristics can be very informative—their genes. Genetic assessment can be used to identify cryptic species, determine whether individuals have moved among populations recently or in the distant past, suggest the typical size of a population, and forecast a population's evolutionary future. Assessing these and other properties relies on

identifying sets of genetic markers—the proteins expressed by different genes, different-sized fragments of DNA, or variation in the sequence of individual base pairs (White et al. 2005; DeHaan et al. 2006). Markers that are unique to a particular species or population are referred to as diagnostic, and their presence or absence is used to differentiate between groups. Even when no diagnostic markers are present, the relative abundance of shared markers can indicate similarity between populations. The relative abundance of shared markers can also be used to assign individual fish to a particular source population.

For fish species of conservation concern, such as those listed under the U.S. Endangered Species Act, Canada's Species at Risk Act, or the United Mexican States' Norma Oficial Mexicana de Ecología, the genetic characteristics of populations and sometimes of the entire species are relevant to their management. This is in part because the retention of genetic variation is crucial to the short-term avoidance of problems such as inbreeding depression (i.e., expression of deleterious alleles resulting from mating of related individuals; Allendorf and Ryman 2002) and to the long-term potential for continued evolution in changing environments (e.g., climate change). Genetic variation can be expressed in a number of ways. Commonly used parameters include heterozygosity, sometimes measured as the proportion of gene loci for which a population contains more than one allele, and allelic diversity, which is the number of alleles observed in the sample of individuals from a population. A related concept is effective population size, which is the size of an idealized population that would show the same rate of loss of genetic variation as the population in question (Frankham et al. 2002). The retention of genetic variation is directly related to effective population size, which is generally much lower than the number of adult fish present. In addition to diversity, other genetic characteristics of interest may include population genetic structure (Nielsen and Sage 2002), the geographic distribution of genetic variation among and within populations (Wenburger and Bentzen 2001), or historical and current gene flow (Neville et al. 2006a; Box 11.3).

Genetic markers can be used to determine whether exposure of native species to closely related, but typically nonnative, species has led to hybridization between them. This is common between native cutthroat trout subspecies and introduced rainbow trout in the Rocky Mountain region and Guadalupe bass and smallmouth bass in the Edwards Plateau region of Texas. Genetic analyses can determine whether offspring of such crosses are viable and leading to introgression of nonnative genes into the native species' gene pool. Conversely, genetic analyses can determine whether the hybrid crosses are limited to the first generation of offspring. Such information is important because it may inform managers of whether hybrid progeny have low survival rates or are infertile, such as hybrids between bull trout and brook trout (Allendorf et al. 2001). Assessing the prevalence of hybridized populations is sometimes the basis for conservation action (Allendorf et al. 2005).

Until recently, the genetic analysis of fish was often prohibitively expensive and difficult to conduct in a timely fashion, but technological advancements are alleviating these problems. For example, Chinook salmon in the Yukon River may be of U.S. or Canadian origin, and maintaining harvestable stocks in both countries is regulated by treaty (Pacific Salmon Treaty). Genetic monitoring is now used to identify the source of fish as they enter the river, which enables managers to regulate the harvest of the two stocks to ensure that sufficient fish reach their natal streams (Smith et al. 2005). Genetic analyses will play a prominent role in future assessment and monitoring of fishes with commercial or conservation value because genetic analyses provide information not obtainable by other methods and the efficiency and power of such analyses continue to increase (Schwartz et al. 2007).

Box 11.3. Use of Genetic Data to Understand the Biology and Conservation Status of Trout and Salmon Populations

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In the face of unprecedented environmental change, understanding the ecology, evolution, and conservation status of fish populations is becoming increasingly important. Yet collecting the data needed to assess fish population characteristics—metrics such as effective population size, reproductive success, or dispersal rates—by means of traditional demographic methods (e.g., censuses, mark–recapture, or telemetry) is often logistically difficult and sometimes impossible to achieve. Molecular genetic data offer promising tools for measuring various characteristics of populations and for monitoring changes in them over time. Among other questions in fisheries management, genetic data have been used to monitor the influences of fish from hatcheries or aquaculture on native stocks (e.g., Hansen 2002; Coughlan et al. 2006), assess hybridization between native and nonnative species (e.g., Hitt et al. 2003; Rubidge and Taylor 2005), evaluate the success of captive breeding and translocation or reintroduction efforts (e.g., Dowling et al. 2005; Yamamoto et al. 2006), follow population trends over time (e.g., Nielsen et al. 1999; Hansen et al. 2006), understand the impact of harvest on particular stocks (e.g., Beacham et al. 2004), and contribute to forensic investigations (e.g., Withler et al. 2004). They will also likely be invaluable in monitoring the effects of climate change on fish in the future (Schwartz et al. 2007). Benefits of genetic data include that they are cost-effective to collect, allow evaluation across broad spatial scales (tens to thousands of kilometers) at both ecological (current) and evolutionary (historical) time frames, and require low-impact sampling given the ability to amplify tiny amounts of DNA. Collection of DNA can be achieved with little impact by use of scales or small fin clips from live animals or even from postspawn carcasses and museum specimens.

For example, Neville et al. (2006b) used genetic data to learn about the ecology and conservation needs of Lahontan cutthroat trout (LCT). Historically this subspecies of cutthroat trout had access to many connected headwater and main-stem habitats in the Humboldt River system in northern Nevada, and these large, complex habitats likely sustained resident and migratory life histories of the subspecies. Among inland cutthroat trout, resident fish can complete their entire life cycle in a small headwater reach (tens to hundreds of meters), whereas migratory fish may move long distances (tens to hundreds of kilometers) between headwater spawning areas and main-stem rivers or lakes. However, LCT (and other cutthroat trout subspecies) currently persist mostly as isolated resident populations in small, fragmented headwater streams, and there are few connected watersheds remaining that could potentially allow them to migrate between spawning areas in headwater tributaries and larger habitats in main-stem rivers.

In the study by Neville et al. (2006b), the authors collected small fin clips from over 1,100 individuals and used variability at DNA microsatellite markers to assess population connectivity, size, and stability, and the potential for migratory life history diversity in one

(Box continues)

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Box 11.3. Continued

of these connected watersheds. They observed that several headwater populations were genetically differentiated from samples collected just a couple of kilometers downstream in the same tributary, even where there were no barriers preventing movement between sites. This suggested that fish in these reaches were behaviorally isolated and likely to exhibit resident life histories. Effective sizes in headwater populations were extremely small (N_e varied from 2 to 36), and many populations (particularly those in poor-quality habitats or those isolated by barriers) had undergone genetic bottlenecks, indicating that these LCT populations fluctuate and undergo occasional extreme reductions or even local extinctions. Fish caught in the river main stem, however, were genetically mixed, and their genes “assigned” them as having originated from populations throughout the watershed. This pattern is consistent with the idea that fish from different populations use the main stem as migratory habitat. Overall, genetic data were an efficient and effective way to gain insight about life history diversity and gave important information about LCT conservation needs. The main management implications were that poor habitat quality has negative demographic and genetic impacts on these fish and that habitat connectivity and movement among populations were probably important for the long-term persistence of LCT living in hydrologically variable streams.

In another study, Neville et al. (2006a) used DNA collected from postspawn carcasses to learn about the homing behavior of Chinook salmon. It has long been known that these and other salmon return to the river where they were born after spending several years feeding and growing in the ocean, but how accurately they are able to do this is still not very well understood. From a genetic perspective, if individuals do home to a specific natal site (the site where they were born), they should be surrounded by other individuals born in that area who are their relatives. By looking at patterns of relatedness among individual genotypes throughout the Middle Fork Salmon River in Idaho, it was found that individuals showed patterns of relatedness that indicated accurate homing at scales as small as 2 km. Interestingly, this genetic clustering was found only in females; males showed no patterns of relatedness at any spatial scale within the river basin. Such sex-biased movement makes sense in light of the species’ ecology: females, which choose where to deposit eggs, might be under strong selection to return to a known environment (i.e., that where they were born), whereas males, which compete for mates, should benefit more from searching widely for and mating with as many females as they can within their natal river, regardless of exactly where in the river they were born.

11.4.3 Abundance, Density, and Distribution

The absolute abundance of fish in a population is often of fundamental interest to fish managers. However, determining absolute abundance requires extensive data collection, such as a precise estimate of density at sampling sites and a probability-based array of those sites (Hayes et al. 2007; Schwartz et al. 2007). Estimating absolute abundance is costly and time

consuming, but may be warranted for highly valued populations (e.g., economically valuable species or species of conservation concern). For many populations, indices of relative abundance are sufficient for assessment. Catch per unit effort (C/f) is a relative abundance index, which is often directly related, though not always in a linear fashion, to absolute abundance (Rose and Kulka 1999; Hubert and Fabrizio 2007). Estimates of C/f are considerably easier to obtain than are estimates of absolute abundance. Like absolute abundance, relative abundance will vary among species and systems. For example, 200 stock-length fish (e.g., largemouth bass ≥ 200 mm or bluegill ≥ 80 mm.; Anderson and Neumann [1996]) per hour of electrofishing in reservoirs is a high catch rate for largemouth bass and only a modest catch rate for bluegill (Brouder et al. 2009). Similarly, 300 stock-length bluegill per hour of electrofishing is a high catch rate for small (<200 ha) reservoirs in the Great Plains ecological region of North America and only a modest catch rate for small reservoirs in the eastern temperate forests ecological region (Brouder et al. 2009). Estimates of fish density (the number or biomass per unit area or volume) are related to C/f , but effort is standardized by the length, area, or volume of water sampled. Precise relative abundance estimates are often collected from one or a few areas thought to be representative of an entire system, but the absence of randomly distributed samples that could account for spatial variation in fish abundance limits the value of this approach (Williams et al. 2004). Nonetheless, this sampling strategy does provide information on trends in indices of population parameters (see nonprobability sampling in section 11.3.3).

The distribution of some species may need to be understood before undertaking relative abundance estimation, particularly for species that are rare or poorly sampled. Assessing the distribution of a population or a species relies only on its presence or absence at particular sites. This relaxes some of the requirements associated with relative abundance estimation but reemphasizes the need for biologists to understand the vulnerability of different fishes to capture. An additional problem is determining where to sample to define a species' distribution. Randomly-distributed samples may lead to robust inferences about fish distributions, but sampling can be made more efficient by focusing on areas that provide potentially suitable habitat (Peterson and Dunham 2003).

11.4.4 Population Structure

Indices of size and age structure rely on estimates of length, weight, and age from a random sample of individual fish (Anderson and Neumann 1996; DeVries and Frie 1996). These indices tend to paint a static picture of a population, although it is possible to draw inferences about population dynamics from a population structure. For example, suppose mean length of fish in standardized samples from a population is used as an index of population structure; shifts to smaller mean lengths of sampled fish may indicate increasing exploitation. One index of population structure that is particularly appropriate for exploited populations is proportional size distribution (Guy et al. 2007), formerly known as proportional stock density (Anderson 1978) and relative stock density (Wege and Anderson 1978). Individual fish are assigned to length categories (many individuals fit in multiple categories), and the index is calculated as the proportion of fish in the stock-length category that also fall into the length category of interest. For example, proportional size distribution of quality-length (PSD) largemouth bass and proportional size distribution of preferred-length (PSD-P) largemouth bass are calculated as the proportions of stock-length largemouth bass (≥ 200 mm in total length [TL]) that are,

respectively, also quality-length largemouth bass (≥ 300 mm TL) and preferred-length largemouth bass (≥ 380 mm TL). A value greater than 70 for PSD might result if growth is rapid, if exploitation is low, or if both are true. A value less than 30 for PSD might result if high recruitment leads to “stunting,” if size-specific exploitation systematically removes older, larger fish, or if habitat quality is poor. The effectiveness of length-limit regulations are often evaluated relative to changes in proportional size distribution. A PSD-P value that is too low because of size-specific exploitation might be increased by implementation of a minimum length limit (see Chapter 7). The objective of the minimum length limit might be a specified increase in PSD-P over a specified time interval. When anglers are restricted from harvesting older, larger fish, the proportion of those fish in the population should increase, consequently increasing PSD-P. This example further illustrates the challenge of interpreting and using an index for making management decisions. If a PSD-P value is low because of stunting, implementing a minimum length limit would likely reinforce the mechanism(s) that caused the stunting. Care must be used because indices generally do not identify the underlying mechanisms that regulate them.

Estimation of fish population dynamics are often based on age structures (Everhart and Youngs 1981; Isely and Grabowski 2007). To obtain an accurate estimate of age structure, biologists must obtain a random sample of a population. Aging techniques for many important sport fish in North America have been validated (DeVries and Frie 1996), and it is important to use the standard techniques (Beamish and McFarlane 1983). If fish are aged correctly, then estimates of population dynamics will be correct (Marzolf 1955) and should lead to wise management and resource allocation decisions (Isely and Grabowski 2007). Determining age of fish takes considerably more effort than measuring and weighing fish but is usually warranted during population assessments.

The mean age of fish and the number of year-classes in a sample from a population are useful indices because many populations of fish exhibit variable recruitment (i.e., weak year-classes interspersed with strong year-classes). For example, a population of a long-lived species with only young age-groups present in random samples could be experiencing high exploitation or environmental stress. Similarly, another population with several missing age-groups in a random sample could be experiencing poor or failed recruitment (Guy and Willis 1995).

Several indices combine age data with other types of data. Population assessments occasionally rely on a length-at-age index as a proxy for growth rates of fish (Purchase et al. 2005). Aging a subsample of fish within length groups that encompass the possible lengths of fish of a specified age can allow managers to estimate the mean length of fish in that age-group. A large value for a length-at-age index indicates fast growth, whereas a small value for a length-at-age index suggests slow growth. For example, a brook trout that is 160 mm at age 3 is slow growing in a stream, whereas a brook trout in a similar system that is 260 mm at age 3 is fast growing (Brouder et al. 2009). The advantage to this index is that only a few length groups need to be aged. It is important to treat the data as a stratified sample, not a random sample, when size at age is calculated from a subsample of aged fish from several length groups. Calculating the mean length and variance of an age-group from subsampled data can introduce bias unless the subsample is extrapolated to the sample and the statistics are calculated on the entire sample (Bettoli and Miranda 2001).

Maturity status and sex identification allow the calculation of several useful indices. The juvenile-to-adult ratio can indicate important aspects of the dynamics of a fish population

(Reynolds and Babb 1978). A large ratio of juveniles to adults can be an indication of substantial exploitation, optimal spawning conditions in a particular year, or consistently successful recruitment. A population with recruitment difficulties will be characterized by fewer juveniles relative to adults. The ratio of males to females in a population can be important because sex ratio may be altered by size-selective harvest in sexually dimorphic populations. Sex ratio may also provide an indication of anthropogenic influences on the population. Estrogen from municipal sewage and androgens from biotransformation of pulp and paper mill effluents can skew the 1:1 sex ratio common in most healthy fish populations (Larsson et al. 2000). Determining sex and maturity status is relatively easy in fish that are sexually dimorphic but may only be possible during the spawning season in some fish species.

Age at maturity can be determined during a population assessment. Selection pressure (e.g., harvest aimed at larger, older individuals) at the population level could lead to maturity at a younger average age. An abundance of food resources can also lead to maturity at a younger age. Age at maturity is an index that requires age, sex, and sexual maturity data for a year class over several years (i.e., until the year class is fully matured). It can also be indexed with a single assessment, assuming a constant maturity schedule among year classes (Purchase et al. 2005). It is common for males and females of a species to mature on different schedules (Diana 1983), so age at maturity is often calculated separately for the sexes. Changes in weight at maturity can also indicate changes in the population. A decrease in age at maturity typically correlates with a decrease in weight at maturity because a strong relation exists between age and weight. Lifetime reproductive output can be altered when individuals mature at a younger age or smaller size (Quince et al. 2008) because of the strong relation between size and fecundity (Wydoski 2001). Collection of size, age, sex, and maturity information on individual fish can be challenging, but indices give considerable insight into the reproductive pressures acting on a population.

11.4.5 Energy Acquisition, Storage, and Use

Several fish population indices describe the processes of energy acquisition and storage. One simple index is the percentage of fish without food in their stomachs. A high percentage of empty stomachs indicates that acquisition of prey may be problematic for a population, that gut evacuation was rapid since last feeding, or that the sampling method caused regurgitation. Alternatively, a low percentage of empty stomachs indicates a recent availability of prey. Percentage of empty stomachs could also be influenced by time of sampling, especially for non-continuous-feeding fish. If prey availability is not a limiting factor, then growth should be adequate. Determining whether a fish has food in the stomach is fairly simple, and in many instances can be accomplished without sacrificing fish (Kamler and Pope 2001).

A common energy acquisition and storage index is relative weight. Relative weight is the length-specific weight of fish in a sample from a study population relative to a standard for the species. This index is relatively easy to compute. Length and weight data for some fish species have been collected from samples of a large number of populations throughout each species' range and have been used to determine length-specific standards for these species (Blackwell et al. 2000; see Chapter 2 for a description of length-weight equations). If average relative weight for a population or subpopulation exceeds 100, then most individuals in that population or subpopulation are heavier than the standard for the species. This is taken as a

positive sign and interpreted as an indication that individuals in a population or subpopulation are doing well. A population or subpopulation with an average relative weight less than 80 is likely prey limited. Care is required when assessing these types of indices because they are highly influenced by season (Pope and Willis 1996).

Another index of energy storage is the hepatosomatic index, which is the liver weight relative to total body weight expressed as a percentage. When fish acquire more energy than necessary to meet basic metabolic and growth requirements, some excess energy is stored in the liver as glycogen. The size of the liver relative to the body is large when a considerable amount of energy is stored in the liver, so a large hepatosomatic index is indicative of a fish that is well fed (Plante et al. 2005). This index is easy to compute but requires sacrificing fish.

Fish also store excess energy as lipids. Lipids are twice as energy dense as proteins or carbohydrates, thus the level of lipid in muscle tissue can be used as an index of energy storage (Kaufman et al. 2007). Large amounts of lipid are likely to be stored in muscle tissue only if a fish is acquiring more energy than is necessary for metabolism and growth. Determining lipid levels in fish tissue is time consuming and requires specialized laboratory equipment.

A different class of population indices expresses or reflects how energy is being allocated by fish populations. Perhaps the simplest index describing energy allocation is the gonadosomatic index (GSI). The GSI is the gonad weight relative to total body weight, usually expressed as a percentage. If the fish population is not nutrition limited, then a large amount of energy will be directed toward gonad development. In this case, GSI values will be relatively large. Large average GSI values usually indicate a favorable status for the fish population.

An important index that indicates energy utilization is length-specific or weight-specific fecundity. On a population level, there is a strong relation between fish size and fecundity. However, there is also variability in fecundity among similar-sized individuals in a population (Taube 1976). Before a fish matures, most energy not required for basic metabolism is used for growth. After a fish matures, excess energy is divided between growth and reproduction. Populations with a variable size-specific fecundity may be manipulating reproductive output to influence growth (Leaman 1991) or responding to specific environmental conditions (Scopettone et al. 2000). Populations with a low size-specific fecundity may be experiencing stress from lack of adequate prey or from other environmental pressures. This is a moderately complex index to calculate because it requires an estimation of eggs in the ovaries of a large number of individuals.

11.4.6 Contaminants, Diseases, and Parasites

Fish populations are sometimes characterized according to their health status. Inspection of individual fish in a random sample can provide data on the proportion of a population with lesions, parasites, or other anomalies (Wilson et al. 1996). Determining the proportion of a sample with health anomalies can be done rapidly, often with only a visual inspection. A sample with a high proportion of individuals with lesions or parasites is indicative of a population that is likely under stress from either disease or environmental conditions. Stressed individuals may consume less food (Hoffnagle et al. 2006), grow more slowly (Szalai and Dick 1991; Koehle and Adelman 2007), reproduce less successfully (Carter et al. 2005), and suffer a higher mortality rate (Szalai and Dick 1991).

Several other methods of characterizing the overall health of fish in a population are available to managers. Tissue or blood from sampled fish can be screened for toxicants or heavy

metals. Techniques for assessing the presence of pollutants are straightforward. Most states or provinces have departments of environmental quality that regularly monitor fish and the environment for contaminants. Such tests are relatively expensive, and particular care must be taken during collection of samples to avoid contamination. Toxicant screening is usually conducted only when a suspicion of pollutant effects on a fish population exists. Fish populations can also be screened for viral or bacterial infections. Mortality, growth, and recruitment rates can be negatively affected by high viral or bacterial loads. Equipment and standard methods for detecting and diagnosing infections are available through fish pathology laboratories. These laboratories often require live specimens for a complete health assessment. If this type of health check is going to be part of a fish population assessment, specific protocols should be acquired from the pathology laboratory prior to fish collection (American Fisheries Society 2007).

11.5 DISTINCTION BETWEEN ASSESSMENT AND MONITORING

Typically, population assessments are one-time evaluations of the status of a fish population. Assessment requires comparisons of population attributes with reference values based on the probable relationships between environmental characteristics and population responses. Examples include comparisons of population density or age structure with regional averages or literature values.

Adaptive resource management (Holling 1978; Walters 1986) requires population monitoring to determine the necessity for changes in management actions based on the outcomes of the original management actions. Managers with a vision for the future of a fish population are more likely to engage in efforts to monitor progress toward management goals. In contrast to population assessment, population monitoring is the continuous or repeated observation, measurement, and evaluation of fish population parameters or indices, ideally using standardized methods for data collection. Comparisons of population parameters to regional averages or literature values are de-emphasized in favor of detecting population trends. Monitoring usually involves the collection of fewer types of data than does an assessment. Often, monitoring allows estimates of population dynamics and their variability. For example, changes in the relative abundance of a year-class over time reflect annual mortality rates, and recruitment variability may be monitored when an index of recruitment is estimated over several years (Quist 2007). It is common for thresholds to be incorporated into a population-monitoring program such that when values of key attributes fall above or below thresholds, a more comprehensive assessment might be undertaken.

11.6 CONCLUSIONS

A variety of parameters, indices, and models are available for assessing and monitoring fish populations. Each provides some insight about a fish population, and the decision of which to include in an assessment should be based on available resources, objectives of the assessment, and management goals. Assessing and monitoring fish populations can be costly and time consuming, but these are not reasons to avoid population assessments. Rather, these costs represent the reality that science-based fisheries management requires a significant investment of resources. It is incumbent on managers to gather the best information possible

and base management decisions on sound science. Hence, population assessments will be an important component of fisheries management, and the wise use of appropriate indices will be an important component of fish population assessments.

11.7 REFERENCES

- Allen, M. S., and W. E. Pine III. 2000. Detecting fish population responses to a minimum length limit: effects of variable recruitment and duration of evaluation. *North American Journal of Fisheries Management* 20:672–682.
- Allendorf, F. W., R. F. Leary, N. P. Hitt, K. L. Knudsen, M. C. Boyer, and P. Spruell. 2005. Cutthroat trout hybridization and the U.S. Endangered Species Act: one species, two policies. *Conservation Biology* 19:1326–1328.
- Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* 16:613–620.
- Allendorf, F. W., and N. Ryman. 2002. The role of genetics in population viability analysis. Pages 50–85 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago.
- American Fisheries Society. 2007. Suggested procedures for the detection and identification of certain finfish and shellfish pathogens (blue book edition 2007). American Fisheries Society, Fish Health Section, Bethesda, Maryland.
- Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Society Bulletin* 31:288–291.
- Anderson, R. O. 1978. New approaches to recreational fishery management. Pages 73–78 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Angermeier, P. L., R. J. Neves, and L. A. Nielsen. 1991. Assessing stream values: perspectives of aquatic resource professionals. *North American Journal of Fisheries Management* 11:1–10.
- Ault, J. S., and D. B. Olson. 1996. A multicohort stock production model. *Transactions of the American Fisheries Society* 125:343–363.
- Bayley, P. B., and D. C. Dowling. 1993. The effects of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. *Polskie Archiwum Hydrobiologii* 40:5–14.
- Beacham, T. D., M. Lapointe, J. R. Candy, K. M. Miller, and R. E. Withler. 2004. DNA in action: rapid application of DNA variation to sockeye salmon fisheries management. *Conservation Genetics* 5:411–416.
- Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirements for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112:735–743.
- Beierle, T. C. 2002. The quality of stakeholder-based decisions. *Risk Analysis* 22:739–749.
- Bettoli, P. W., and L. E. Miranda. 2001. Cautionary note about estimating mean length at age with subsampled data. *North American Journal of Fisheries Management* 21:425–428.
- Bettoli, P. W., G. D. Scholten, and W. C. Reeves. 2007. Protecting paddlefish from overfishing: a case history of the research and regulatory process. *Fisheries* 32(8):390–397.
- Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. *Reviews in Fisheries Science* 8:1–44.
- Bonar, S. A., and W. A. Hubert. 2002. Standard sampling of inland fish: benefits, challenges, and a call for action. *Fisheries* 27(3):10–16.

- Bonar, S. A., W. A. Hubert, and D. W. Willis, editors. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.
- Bowen, S. H. 1996. Quantitative description of diet. Pages 513–532 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Brouder, M. J., A. C. Iles, and S. A. Bonar. 2009. Length frequency, condition, growth, and catch per effort indices for common North American fishes. Pages 231–282 in S. A. Bonar, W. A. Hubert, and D. W. Willis, editors. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.
- Brown, M. L., and C. S. Guy. 2007. Science and statistics in fisheries research. Pages 1–29 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Brown, P., K. P. Sivakumaran, D. Stoessel, and A. Giles. 2006. Population biology of carp (*Cyprinus carpio* L.) in the mid-Murray River and Barmah Forest Wetlands, Australia. *Marine and Freshwater Research* 56:1151–1164.
- Caddy, J. F. 1999. Fisheries management in the twenty-first century: will new paradigms apply? *Reviews in Fish Biology and Fisheries* 9:1–43.
- Carter, V., R. Pierce, S. Dufour, C. Arme, and D. Hoole. 2005. The tapeworm *Ligula intestinalis* (Cestoda: Pseudophyllidae) inhibits LH-expression and puberty in its teleost host, *Rutilus rutilus*. *Reproduction* 130:939–945.
- Coelho, R., and K. Erzini. 2006. Reproductive aspects of the undulate ray, *Raja undulata*, from the south coast of Portugal. *Fisheries Research* 81:80–85.
- Colvin, M. A. 1991. Population characteristics and angler harvest of white crappies in four large Missouri reservoirs. *North American Journal of Fisheries Management* 11:572–584.
- Coughlan, J., P. McGinnity, B. O'Farrell, E. Dillane, O. Diserud, E. de Eyto, K. Farrell, K. Whelan, R. J. M. Stet, and T. F. Cross. 2006. Temporal variation in an immune response gene (MHC I) in anadromous *Salmo trutta* in an Irish river before and during aquaculture activities. *ICES Journal of Marine Science* 63:1248–1255.
- Cowx, I. G., and D. Gerdeaux. 2004. The effects of fisheries management practices on freshwater ecosystems. *Fisheries Management and Ecology* 11:145–151.
- DeHaan, P. W., S. V. Libants, R. F. Elliott, and K. T. Scribner. 2006. Genetic population structure of remnant lake sturgeon populations in the upper Great Lakes basin. *Transactions of the American Fisheries Society* 135:1478–1492.
- DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Diana, J. S. 1983. Growth, maturation, and production of northern pike in three Michigan Lakes. *Transactions of the American Fisheries Society* 112:38–46.
- DiCenzo, V. J., M. J. Maceina, and M. R. Stimpert. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. *North American Journal of Fisheries Management* 16:888–895.
- Dolan, C. R., and L. E. Miranda. 2003. Immobilization thresholds of electrofishing relative to fish size. *Transactions of the American Fisheries Society* 132:969–976.
- Dowling, T. E., P. C. Marsh, A. T. Kelsen, and C. A. Tibbets. 2005. Genetic monitoring of wild and repatriated populations of endangered razorback sucker (*Xyrauchen texanus*, Catostomidae, Teleostei) in Lake Mohave, Arizona–Nevada. *Molecular Ecology* 14:123–135.
- Dunham, J. B., B. E. Rieman, and J. T. Peterson. 2002. Patch-based models to predict species occurrence: lessons from salmonid fishes in streams. Pages 327–334 in J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Hauffer, and B. Wall, editors. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California.

- Everhart, W. H., and W. D. Youngs. 1981. Principles of fishery science, 2nd edition. Cornell University Press, Ithaca, New York.
- Francis, R. C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston. 2007. Ten commandments for ecosystem-based fisheries scientists. *Fisheries* 32(5):219–233.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, UK.
- Froese, R., and D. Pauly, editors. 2008. FishBase. Available:www.fishbase.org. (April 2008).
- Gabelhouse, D. W., Jr. 1984. A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* 4:273–285.
- Gibbons, W. N., and K. R. Munkittrick. 1994. A sentinel monitoring framework for identifying fish population responses to industrial discharges. *Journal of Aquatic Ecology and Health* 3:227–237.
- Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London* 115:513–585.
- Gulland, J. A. 1982. Why do fish numbers vary? *Journal of Theoretical Biology* 97:69–75.
- Guy, C. S., R. M. Neumann, D. W. Willis, and R. O. Anderson. 2007. Proportional size distribution (PSD): a further refinement of population size structure index terminology. *Fisheries* 32(7):348.
- Guy, C. S., and D. W. Willis. 1995. Population characteristics of black crappies in South Dakota waters: a case for ecosystem-specific management. *North American Journal of Fisheries Management* 15:754–765.
- Hansen, M. J., T. D. Beard Jr., and D. B. Hayes. 2007. Sampling and experimental design. Pages 51–120 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Hansen, M. M. 2002. Estimating the long-term effects of stocking domesticated trout into wild brown trout (*Salmo trutta*) populations: an approach using microsatellite DNA analysis of historical and contemporary samples. *Molecular Ecology* 11:1003–1015.
- Hansen, M. M., E. E. Nielsen, and K. L. Mensberg. 2006. Underwater but not out of sight: genetic monitoring of effective population size in the endangered North Sea houting (*Coregonus oxyrhynchus*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:780–787.
- Hayes, D. B., J. R. Bence, T. J. Kwak, and B. E. Thompson. 2007. Abundance, biomass, and production. Pages 327–374 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Hitt, N. P., A. Frissell, C. C. Muhlfeld, and F. W. Allendorf. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1440–1451.
- Hoffnagle, T. L., A. Choudhury, and R. A. Cole. 2006. Parasitism and body condition in humpback chub from the Colorado and Little Colorado rivers, Grand Canyon, Arizona. *Journal of Aquatic Animal Health* 18:184–193.
- Holling, C. S. 1978. Adaptive environmental assessment and management. John Wiley and Sons, New York.
- Hopkins, H. L., and M. L. Kennedy. 2004. An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. *Wildlife Society Bulletin* 32:1289–1296.
- Hubert, W. A., and M. C. Fabrizio. 2007. Relative abundance and catch per unit effort. Pages 279–325 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.
- Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

- Isermann, D. A., W. L. McKibbin, and D. W. Willis. 2002. An analysis of methods for quantifying crappie recruitment variability. *North American Journal of Fisheries Management* 22:1124–1135.
- Kamler, J. F., and K. L. Pope. 2001. Nonlethal methods of examining fish stomach contents. *Reviews in Fisheries Science* 9:1–11.
- Kaufman, S. D., T. A. Johnston, W. C. Leggett, M. D. Moles, J. M. Casselman, and A. I. Schulte-Hostedde. 2007. Relationships between body condition indices and proximate composition in adult walleyes. *Transactions of the American Fisheries Society* 136:1566–1576.
- Kernehhan, R. J., M. R. Headrick, and R. E. Smith. 1981. Early life history of striped bass in the Chesapeake and Delaware Canal vicinity. *Transactions of the American Fisheries Society* 110:137–150.
- King, T. A., C. J. Williams, W. D. Davies, and W. J. Shelton. 1981. Fixed versus random sampling of fishes in a large reservoir. *Transactions of the American Fisheries Society* 110:563–568.
- Koehle, J. J., and I. R. Adelman. 2007. The effect of temperature, dissolved oxygen, and Asian tapeworm infection on growth and survival of the Topeka shiner. *Transactions of the American Fisheries Society* 136:1607–1613.
- Larsson, D. G., H. Hällman, and L. Förlin. 2000. More male fish embryos near a pulp mill. *Environmental Toxicology and Chemistry* 19:2911–2917.
- Leaman, B. M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environmental Biology of Fishes* 30:253–271.
- Lett, P. F., and W. G. Doubleday. 1976. The influence of fluctuations in recruitment on fisheries management strategy. *International Commission for the Northwest Atlantic Fisheries Selected Papers* 1:171–193.
- Levy, P. S., and S. Lemeshow. 1991. *Sampling of populations: methods and applications*. Wiley, New York.
- Maceina, M. J., and D. L. Pereira. 2007. Recruitment. Pages 121–185 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Malvestuto, S. P. 1996. Sampling the recreational creel. Pages 591–623 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Marzolf, R. C. 1955. Use of pectoral spines and vertebrae for determining age and rate of growth of the channel catfish. *Journal of Wildlife Management* 19:243–249.
- McInerney, M. C., and T. K. Cross. 2006. Factors affecting trap-net catchability of black crappies in natural Minnesota lakes. *North American Journal of Fisheries Management* 26:652–664.
- McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of indices versus estimators revisited. *Canadian Journal of Zoology* 79:1754–1765.
- McRae, B. J., and J. S. Diana. 2005. Factors influencing density of age-0 brown trout and brook trout in the Au Sable River, Michigan. *Transactions of the American Fisheries Society* 134:132–140.
- Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229–277 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- NatureServe. 2008. NatureServe explorer: an online encyclopedia of life, version 7.0. NatureServe, Arlington, Virginia. Available: www.natureserve.org/explorer. (April 16, 2008).
- Neville, H. M., J. B. Dunham, and M. M. Peacock. 2006b. Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* 21:901–916.
- Neville, H. M., D. J. Isaak, J. B. Dunham, R. F. Thurow, and B. E. Rieman. 2006a. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. *Molecular Ecology* 15:4589–4602.
- Nielsen, E. E., M. M. Hansen, and V. Loeschcke. 1999. Genetic variation in time and space: microsatellite analysis of extinct and extant populations of Atlantic salmon. *Evolution* 53:261–268.

- Nielsen, J. L., and G. K. Sage. 2002. Population genetic structure in Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 131:376–388.
- Paragamian, V. L. 1989. A comparison of day and night electrofishing: size structure and catch per unit effort for smallmouth bass. *North American Journal of Fisheries Management* 9:500–503.
- Peterson, J. T., and J. Dunham. 2003. Combining inferences from models of capture efficiency, detectability, and suitable habitat to classify landscapes for conservation of threatened bull trout. *Conservation Biology* 17:1070–1077.
- Peterson, J. T., R. F. Thurrow, and J. W. Guzevich. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. *Transactions of the American Fisheries Society* 133:462–475.
- Plante, S., C. Audet, Y. Lambert, J. de la Noue. 2005. Alternative methods for measuring energy content in winter flounder. *North American Journal of Fisheries Management* 25:1–6.
- Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423–471 in M. L. Brown and C. S. Guy, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Pope, K. L., and D. W. Willis. 1996. Seasonal influences on freshwater fisheries sampling data. *Reviews in Fisheries Science* 4:57–73.
- Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* 23:22–34.
- Power, M. 2007. Fish population bioassessment. Pages 561–624 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Purchase, C. F., N. C. Collins, G. E. Morgan, and B. J. Shuter. 2005. Predicting life history traits of yellow perch from environmental characteristics of lakes. *Transactions of the American Fisheries Society* 134:1369–1381.
- Quince, C., P. A. Abrams, B. J. Shuter, and N. P. Lester. 2008. Biphasic growth in fish II: empirical assessment. *Journal of Theoretical Biology* 254:207–214.
- Quist, M. C. 2007. An evaluation of techniques used to index recruitment variation and year-class strength. *North American Journal of Fisheries Management* 27:30–42.
- Quist, M. C., C. S. Guy, R. D. Schultz, and J. L. Stephen. 2003. Latitudinal comparisons of walleye growth in North America and factors influencing growth of walleyes in Kansas reservoirs. *North American Journal of Fisheries Management* 23:677–692.
- Radomski, P. 2003. Initial attempts to actively manage recreational fishery harvest in Minnesota. *North American Journal of Fisheries Management* 23:1329–1342.
- Radomski, P. J., and T. J. Goeman. 1996. Decision making and modeling in freshwater sport-fisheries management. *Fisheries* 21(12):14–21.
- Reed, J. R., and W. D. Davies. 1991. Population dynamics of black crappies and white crappies in Weiss Reservoir, Alabama: implications for the implementation of harvest restrictions. *North American Journal of Fisheries Management* 11:598–603.
- Reynolds, J. B., and L. R. Babb. 1978. Structure and dynamics of largemouth bass populations. Pages 50–61 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.
- Richards, F. J. 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10:290–300.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. *North American Journal of Fisheries Management* 12:768–776.

- Rose, G. A., and D. W. Kulka. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences* (Supplement 1):118–127.
- Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management* 25:1395–1410.
- Rubidge, E. M., and E. B. Taylor. 2005. An analysis of spatial and environmental factors influencing hybridization between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and introduced rainbow trout (*O. mykiss*) in the upper Kootenay River drainage, British Columbia. *Conservation Genetics* 6:369–384.
- Sammons, S. E., and P. W. Bettoli. 1998. Larval sampling as a fisheries management tool: early detection of year-class strength. *North American Journal of Fisheries Management* 18:137–143.
- Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22:25–33.
- Scopetone, G. G., P. H. Rissler, and M. E. Buettner. 2000. Reproductive longevity and fecundity associated with nonannual spawning in cui-ui. *Transactions of the American Fisheries Society* 129:658–669.
- Slipke, J. W., and M. J. Maceina. 2001. Fisheries analysis and simulation tools (FAST). Auburn University, Auburn, Alabama.
- Smith, C. T., W. D. Templin, J. E. Seeb, and L. W. Seeb. 2005. Single nucleotide polymorphisms provide rapid and accurate estimates of the proportions of U.S. and Canadian Chinook salmon caught in Yukon River fisheries. *North American Journal of Fisheries Management* 25:944–953.
- Strange, R. J. 1996. Field examination of fishes. Pages 433–446 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Szalai, A. J., and T. A. Dick. 1991. Role of predation and parasitism in growth and mortality of yellow perch in Dauphin Lake, Manitoba. *Transactions of the American Fisheries Society* 120:739–751.
- Taube, C. M. 1976. Sexual maturity and fecundity in brown trout of the Platte River, Michigan. *Transactions of the American Fisheries Society* 105:529–533.
- Taylor, C. J. 1981. A generalized inland fishery simulator for management biologists. *North American Journal of Fisheries Management* 1:60–72.
- Walters, C. J. 1986. *Adaptive management of renewable resources*. McGraw Hill, New York.
- Wege, G. J., and R. O. Anderson. 1978. Relative weight (Wr): a new index of condition for largemouth bass. Pages 79–91 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.
- Wells, J. V., and M. E. Richmond. 1995. Populations, metapopulations, and species populations: what are they and who should care? *Wildlife Society Bulletin* 23:458–462.
- Wenburg, J. K., and P. Bentzen. 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. *Transactions of the American Fisheries Society* 130:1049–1069.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico.
- White, M. M., T. W. Kessler, D. P. Philipp, and S. A. Schell. 2005. A genetic assessment of Ohio River walleyes. *Transactions of the American Fisheries Society* 134:661–675.
- Wilde, G. R., and W. L. Fisher. 1996. Reservoir fisheries sampling and experimental design. Pages 397–409 in L. E. Miranda and D. R. DeVries, editors. *Multidimensional approaches to reservoir fisheries management*. American Fisheries Society, Symposium 16, Bethesda, Maryland.

- Williams, L. R., M. L. Warren Jr., S. B. Adams, J. L. Arvai, and C. M. Taylor. 2004. Basin visual estimation technique (BVET) and representative reach approaches to wadeable stream surveys: methodological limitations and future directions. *Fisheries* 29(8):12–22.
- Wilson, D. S., P. M. Muzzall, and T. J. Ehlinger. 1996. Parasites, morphology and habitat use in a blue-gill sunfish (*Lepomis macrochirus*) population. *Copeia* 1996:348–354.
- Withler, R. E., J. R. Candy, T. D. Beacham, and K. M. Miller. 2004. Forensic DNA analysis of Pacific salmonid samples for species and stock identification. *Environmental Biology of Fishes* 69:275–285.
- Wydoski, R. S. 2001. Life history and fecundity of mountain whitefish from Utah streams. *Transactions of the American Fisheries Society* 130:692–698.
- Yamamoto, S., K. Maekawa, T. Tamate, I. Koizumi, K. Hasegawa, and H. Kubota. 2006. Genetic evaluation of translocation in artificially isolated populations of white-spotted char (*Salvelinus leucomaenis*). *Fisheries Research* 78:352–358.

