

Chapter 2

Fish Population Dynamics: Mortality, Growth, and Recruitment

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Fisheries management is a rewarding career because it is challenging and fun and, most importantly, has a real impact on the quality of people's lives. Decisions made by fisheries managers about a commercial fishery directly affect the income of fishers. Decisions about a recreational fishery can influence angler satisfaction and the level of participation, which has direct economic effects on tackle shops, motel and restaurant owners, and fishing guides. Because these decisions can have an impact on a community or region, it is critical to have the best available information about fisheries resources, including habitat quality and species interactions, as well as the needs of human users of a resource. Methods to evaluate many of these factors are described in other chapters of this text.

The focus of this chapter is the use of quantitative methods to evaluate how management actions regarding harvest may influence fish abundance, the size of fish in a population, angler catch, and total yield (i.e., biomass of fish removed from a population). Assessment of these basic population characteristics enables a fisheries manager to detect changes occurring in a population in response to fishing. Diagnosing the condition of overfishing is an important step in fisheries management, and identifying management actions that can improve fish abundance and angler catches is obviously required for sustaining and improving fisheries. Thus, fish population dynamics and assessment are literally where "the rubber meets the road" in fisheries management.

Assessment of fish populations usually contains much uncertainty. John Shepherd's adage that "fish are like trees, except they are invisible and they move," provides a first look at the difficulties in evaluating fish populations. Fish are not typically visible, and thus our "view" of a fish population usually comes from a variety of sources, including anglers, commercial fisheries, and different sampling gears. All sampling gears have inherent sampling biases, and fisheries managers almost always work with incomplete information about fish stocks.

The literature contains a wide range of complex methods to analyze fish populations from sampling data, and reading through the latest journal articles can be discouraging to students trying to gain a basic understanding of fish population dynamics. Although some facets of fisheries assessment require highly quantitative methods and sophisticated software programs, we contend that most fish population assessments can be relatively straightforward and require only simple mathematics and practice with spreadsheet software. Canned software packages are useful, but they are not as helpful in learning how methods work and are often inflexible

in their analysis options. In contrast, the spreadsheet methods presented here can be used to tailor population models to specific needs of investigators. The objective of this chapter is to summarize the basics of fish population dynamics and the skills needed to evaluate fisheries management scenarios. Spreadsheet examples are provided so the reader can learn by doing the analyses and apply them (see <http://fishweb.ifas.ufl.edu/allenlab/courses.html> for spreadsheets).

2.2 OVERVIEW OF DYNAMICS IN INLAND FISH POPULATIONS

The abundance of fish (or any animal) is limited by available resources. Fish populations in new reservoirs and farm ponds previously devoid of fish will exhibit a brief period of unlimited exponential population growth. This occurs because resources are initially unlimited, but as the fish population expands, food and space resources become limiting and fish abundance is then regulated by density-dependent growth and (or) survival. A common representation of this process is the logistic growth model:

$$B_{t+1} = B_t + rB_t\left(1 - \frac{B_t}{K}\right), \quad (2.1)$$

where B is the biomass at time t , r is the maximum population growth rate, and K represents the carrying capacity, the maximum equilibrium biomass that can be supported by the resources available in the system. Notice from equation (2.1) that if B_t is low, the population will grow rapidly because resources are not limited (i.e., $1 - B_t / K$ is close to 1). This period of unlimited population growth is considered the exponential growth phase (Figure 2.1), and the rate of increase is determined by the parameter r . As B_t approaches K , population growth is slowed by density dependent processes until the population reaches K (Figure 2.1).

However, the biomass of fish populations does not remain static but fluctuates around an average abundance due to changes in environmental conditions, habitat quality and quantity, fishing mortality, and interactions with other species such as predators or competitors (Figure 2.1). Fishing can hold average fish biomass well below the carrying capacity for the system, but in these cases random fluctuations in biomass still occur due to variation in fish recruitment. Most fisheries managers attempt to manage fish stocks that are varying around some average abundance, which may or may not be close to K .

The specific factors that influence fish abundance and biomass are typically described by three dynamic rate functions: mortality, growth, and recruitment. Mortality is usually divided into two categories: death due to fishing and death due to natural causes. Fishing mortality is often the focus of fisheries managers because it can be controlled with management actions. Natural mortality is almost always unobserved and is often outside managers' control. Growth is the increase in size of individual fish and can be measured in terms of length or weight. Growth affects a fish's vulnerability to predation and fishing, as well as the food resources available to each individual fish. Recruitment refers to young fish entering the population, and from a management perspective it usually means recruitment to the fishable stock. If new recruits are not replacing losses due to mortality, then the population will eventually decline to zero. Recruitment and growth both increase the biomass of a cohort (year-class), whereas mortality causes both the number of fish and total biomass of a cohort to decline.

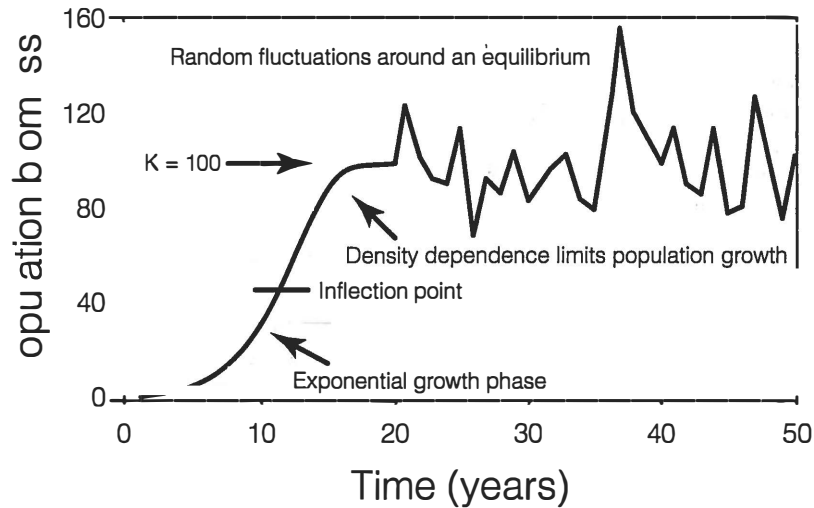


Figure 2.1. Example of a logistic population growth model with maximum growth rate, r , equal to 0.5 and carrying capacity, K , equal to 100. The inflection point indicates the change from exponential to decreasing incremental population growth. Random fluctuations after 20 years demonstrate a fish population whose abundance fluctuates around an equilibrium biomass value.

A good understanding of fish population dynamics (i.e., how mortality, growth, and recruitment interact to affect abundance) is required for informed fisheries management. An example of how important these factors can be is illustrated by the case of the endangered Kootenai River white sturgeon (Paragamian et al. 2005). Surveys have shown that this population has had essentially no recruitment since the early 1970s. Harvest was prohibited in 1984 to help protect the remaining adult stock. The fishery closure substantially reduced annual mortality, but the population still declined by about 9% each year. Field studies have been conducted to learn where and when spawning occurs and what habitat changes may be causing the lack of recruitment. Population models have been developed to predict future abundance of the population and to understand how releases of small fish produced in hatcheries contribute to the overall population. The hope is to use all these sources of information to bring about the population's recovery.

Studies of population dynamics usually involve the development of models. Some fisheries managers are skeptical about the use of models to inform management decisions; however, an experienced manager generally has an idea of how the population or fishery operates. Constructing a model with numbers and equations forces the investigator to be explicit about the hypothesized processes that influence fish population size. Thus, population models should be viewed as hypotheses for management and future research needs. For example, rather than speculating that low recruitment is limiting the abundance of fish in a population, constructing a model can highlight the need to estimate recruitment trends to evaluate the impacts. The model can help identify data gaps and can guide future research toward the areas of greatest uncertainty. When managers do have a good understanding of a stock's dynamics or how a fishery operates, the model serves as a repository for knowledge and experience that may have been gained over many years (Hilborn et al. 1984). Many fish population models are fairly simple because managers rarely have enough data to justify elaborate population models. In many cases, relatively simple population models perform better for management than

do complex models because of the high uncertainty associated with numerous parameters required by complex models (Walters and Martell 2004).

Population models are usually developed for exploited species. One reason for this pattern is that it is easier to justify the cost of conducting surveys and catch sampling programs for a species that supports an important fishery. Modeled scenarios can be used to examine potential effects of fishing and to predict how harvest regulations may increase population size or fishery yield (i.e., biomass of fish harvested). Often the purpose of a population model is to determine whether overfishing is occurring. Overfishing is generally defined as a fishing mortality rate above some target level; for example, the rate that is estimated to result in the maximum long-term (sustainable) yield. Overfishing may occur in two ways—growth overfishing or recruitment overfishing. Growth overfishing results in reduced yield because fishing mortality is too high on young or small fish. If the rate of fishing is reduced or the size at first harvest is increased, fish would have additional time to grow before being harvested and long-term average yields would increase. Recruitment overfishing means that fishing has reduced the spawning stock (large adult fish) to a level at which recruitment is limiting population abundance. If recruitment overfishing continues, the population will decline to very low levels, eventually causing the collapse of the fishery. If the rate of fishing can be reduced, the spawning stock will increase, resulting in higher recruitment and sustainable long-term yield.

Population models also play an important role in the study of rare or threatened species. As in the case of exploited populations, when managing for threatened fishes the need is to understand which factors regulate abundance. The difference is that the information is used not to regulate harvest but to aid in rebuilding the population to a viable level. There is no fishery in the case of rare species, so biological data generally come from research or management surveys rather than commercial or recreational harvest.

2.3 METHODS OF ESTIMATING POPULATION PARAMETERS

2.3.1 Expressions of Mortality

Estimates of mortality are an essential part of assessing fish populations. Fish populations typically exhibit very high mortality during larval and juvenile life stages (often exceeding 99%), followed by lower mortality rates during adult life. Most fisheries investigations are concerned with fish mortality during adulthood, and thus managers emphasize adult fish mortality rates. Estimates of mortality are required to understand how fishing influences fish abundance, angler harvest (numbers of fish), and yield (weight of fish). We begin with some expressions of mortality rates that are commonly used in fisheries investigations, describe how estimates of mortality rates are obtained, and then discuss the advantages and disadvantages of various methods. Definitions of all symbols are found in Table 2.1.

Mortality is typically separated into two components: fishing mortality and natural mortality. Fishing mortality can be controlled via length and creel limits, closed seasons, closed areas, or restrictions on fishing effort (see Chapter 7). Thus, managing fishing mortality is one of the most common practices of fisheries managers. Natural mortality occurs due to predation, disease, parasitism, and any other natural cause. Natural mortality of adult fish is not typically controlled by fisheries management actions, but the level of natural mortality is very

Table 2.1. Population parameters, their definitions, and common methods for estimation of each parameter.

Parameter symbol	Definition	Estimation methods
Z	Instantaneous total mortality	Catch curve, tagging study, $F + M$
M	Instantaneous natural mortality	Tagging study, surrogate methods, subtraction ($M = Z - F$)
F	Instantaneous fishing mortality	Tagging study (angler reported or telemetry), catch or population size estimates, catch-at-age methods
A	Annual total mortality	As above for Z , $A = u + v$
S	Annual total survival	e^{-Z} , $1 - A$, $S = N_{t+1} / N_t$
S_0	Annual natural survival	e^{-M}
u	Annual exploitation rate	As above for F
v	Annual natural mortality rate	As above for M
cf	Conditional fishing mortality	As above for F
cm	Conditional natural mortality	As above for M
L_∞	Asymptotic length	Age-growth, tagging study
k	Growth rate	Age-growth, tagging study
t_0	Age at zero length	Age-growth, tagging study

important for establishing harvest criteria. We provide some basic mortality expressions here, and detailed analysis methods are described by Miranda and Bettoli (2007).

First, we describe finite and instantaneous mortality rates. Finite mortality rates are the fraction of the fish stock that dies in a finite time period (e.g., a year). Instantaneous mortality rates can be calculated from finite rates and are useful for estimating the number of fish at any continuous time interval (e.g., fractions of a year). For a cohort (year-class) of fish, the decline in numbers over time usually follows an exponential pattern (Figure 2.2).

The change in cohort size (N) per unit time (t) depends on the total instantaneous mortality rate (Z) and population size (more deaths per unit time when N is large):

$$\frac{dN}{dt} = -ZN, \quad (2.2)$$

After integration, we obtain an exponential decline in N per unit time as:

$$N_t = N_0 e^{-Zt}, \quad (2.3)$$

where N_t = number alive at time t , N_0 = number alive initially (at t_0), Z = instantaneous total mortality rate, and t = time units since t_0 .

Fisheries managers frequently work in time step units of a year. Given a finite time step of 1 year, the annual total survival rate is: $S = N_{t+1} / N_t$. The value of Z can be determined by $S = e^{-Z}$ and thus $Z = -\log_e(S)$. Box 2.1 shows an example of how to work between finite and instantaneous rates.

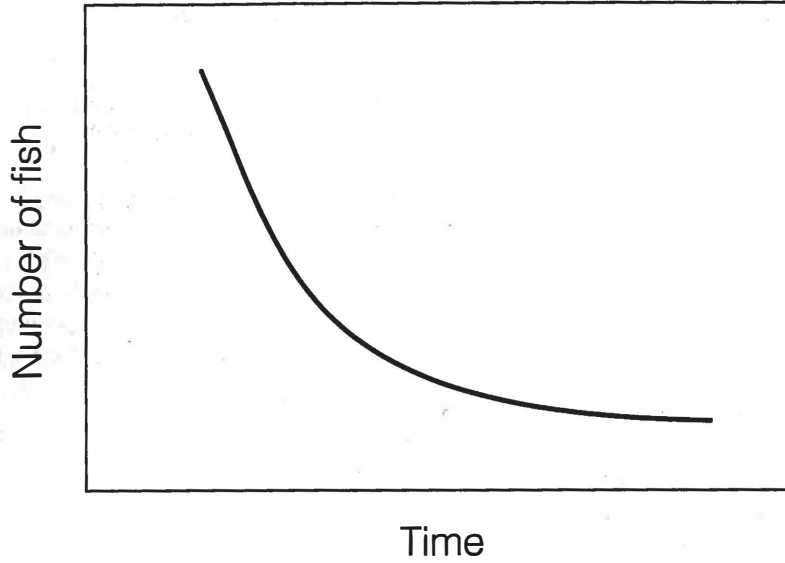


Figure 2.2. Depiction of an exponential decline in numbers of fish with time. The finite mortality rate is a constant proportion of the population at each incremental time step.

Discrete (type I) fisheries.—A discrete fishery is one in which fishing mortality and natural mortality occur separately within the year. Examples would be highly-seasonal fisheries in which most fishing mortality occurs in a short time period, and natural mortality can be assumed to be separated in time. The mortality expressions for discrete fisheries are

$$u = cf = 1 - e^{-F}, \quad (2.4)$$

$$v = cm = 1 - e^{-M}, \quad (2.5)$$

where u is the annual exploitation rate (the fraction of the fish stock harvested within a year), cf is the conditional fishing mortality rate, F is the instantaneous fishing mortality rate, v is the annual natural mortality rate (the fraction of a fish stock that dies due to natural mortality within a year), cm is the conditional natural mortality rate, and M is the instantaneous natural mortality rate (Table 2.1). Instantaneous total mortality (Z) is defined as $Z = F + M$. In discrete fisheries, because M and F are assumed to operate separately, the conditional rates (cf and cm) are the annual fishing (u) and natural mortality (v) rates.

Although it may seem that truly discrete fisheries are relatively rare, many fisheries have highly seasonal rates of fishing mortality with most of the harvest occurring during relatively short periods of the year. In practice, many fisheries models use $S_0 = e^{-M} = (1 - v)$ to approximate the survival rate from natural mortality (S_0), and u to represent annual exploitation even if the fishery is continuous. The F in this case of discrete fisheries can be found by $F = -\log_e(1 - u)$ (as per equation 2.4 above). Box 2.2 shows mortality expressions used for discrete fisheries and in other applications. Recent fish stock assessment textbooks have utilized the discrete mortality equations for fisheries where F and M occur together because the approximation is

Box 2.1. Finite and Instantaneous Mortality Rates

Suppose you start with 1,000 fish at time zero 0 and lose 9% per year due to total mortality. The number of fish in each yearly step is simply the number the year before times 0.91.

Year	0	1	2	3	4	5
Number of fish	1,000	910	828	753	686	624

Let's define the following:

A = annual total mortality rate,
 S = annual total survival rate, and
 Z = instantaneous total mortality.

In this example, $A = 0.09$, and

$$S = 1 - A = 0.91, \text{ given that}$$

$$S = e^{-Z},$$

$$Z = -\log_e(S).$$

Therefore

$$Z = -\log_e(0.91) = 0.0943.$$

Now use the instantaneous rate, $N_t = N_0 e^{-Zt}$, to predict the number of fish at age 5 (N_5).

$$N_5 = 1,000 e^{-0.0943(5)} = 624.$$

Thus, any mortality rate can be described either as a finite or instantaneous rate, and this example shows the ease of transferring between the rate types.

typically satisfactory even when fishing and natural mortality occur simultaneously throughout the year (Walters and Martell 2004).

Continuous (type II) fisheries.—A continuous fishery is one in which fishing mortality and natural mortality operate concurrently, so use of instantaneous rates F and M is required to model this relationship. Annual survival is indicated by $S = e^{-Z} = e^{-(F+M)}$. The relationships

Box 2.2. Discrete Fishery Mortality

Suppose a fish stock is determined to have the following mortality rates:

$$u = 0.3, \text{ and}$$

$$M = 0.2.$$

Here we transform this instantaneous mortality rate to a natural survival rate as

$$S_0 = e^{-0.2} = 0.82.$$

Using this format and starting with 1,000 age-2 fish, we calculate the number of fish surviving from age 2 to age 3:

$$N_3 = 1,000 \times (0.82) \times (1 - 0.3) = 574.$$

Natural deaths are: $1,000 \times 0.18 = 180$, and the total catch would be $1,000 \times 0.82 \times 0.3 = 246$, because we have assumed that fishing took place after natural mortality occurred. So, the total deaths are 426 fish (i.e., 180 from natural causes and 246 from fishing). Notice that the total deaths (426) plus survivors (574) is the original value of 1,000 fish. This is because we assumed that fishing and natural mortality operate separately within the year.

between instantaneous and finite rates are proportional, such that the exploitation rate can be obtained as the fraction of total annual mortality (A) that is due to F :

$$u = \frac{F}{Z} \times A, \quad (2.6)$$

In continuous fisheries, the total annual mortality rate A is found by

$$A = cf + cm - (cf \times cm), \quad (2.7)$$

where the quantity $cf \times cm$ signifies that some fish that die due to fishing mortality would have died due to natural mortality, and vice versa. This is a key difference between the discrete fishery model and the continuous fishery model because the equations accounting for a discrete fishery do not impart any interaction between fishing mortality and natural mortality: they are assumed to occur separately in time. The equations accounting for a continuous fishery explicitly model the fact that fish dying from one cause of mortality (e.g., fishing) are no longer available to die from the other cause of mortality (e.g., natural mortality) and vice versa.

2.3.2 Estimation of mortality rates

Total mortality.—Fisheries managers seek to estimate mortality to understand how fishing mortality and natural mortality rates are influencing fish populations. The most basic approach is to estimate total annual mortality, which is frequently evaluated as the change in fish abundance with age. Catch curves are a regression of the natural log of the number of fish at age on fish age, and the slope of the relationship is an estimate of Z (see Box 2.3). The assumptions of a catch curve are that (1) mortality rate is constant across ages, (2) recruitment is constant, and (3) the age sample is a random sample of fish abundance with age. Although these assumptions are not strictly met in most applications, catch curves usually provide general estimates of Z . Assumption 1 is usually addressed by including only fish that are expected to have similar mortality rates. Assumption 2 is often not a major problem provided that recruitment has not exhibited an increasing or decreasing trend through time. Random recruitment variation tends to make a catch curve bumpy but does not bias the slope (Ricker 1975). Selectivity of the sample gear must be considered relative to assumption 3 and the youngest fish not fully vulnerable to the gear are typically excluded from catch curves (see Box 2.3).

Passive tagging estimates of fishing mortality.—Estimates of fishing mortality may be obtained using passive tagging or active tagging methods. Passive tagging involves tagging fish with external tags and obtaining anglers' reports of harvesting tagged fish. The estimate of annual exploitation rate is obtained by:

$$u = \frac{C}{T} , \quad (2.8)$$

where u is the exploitation rate, C is the corrected number of tagged fish caught, and T is the corrected number of tagged fish in the population. Values of C must be corrected for nonreporting of tags, and values of T should be corrected for short term tag loss and tagging-associated mortality. If long term tag loss is substantial, T can also be adjusted downwards to account for chronic tag loss. Angler reporting rates are the most difficult issue with this approach. The most common method of estimating reporting rates is to use some high-reward tags for which it can be assumed that reporting rate is 100%, then adjust the number of standard tags returned based on the assumption that capture rate of fish by anglers is not influenced by reward value (Pollock et al. 2002):

$$\hat{\lambda} = \frac{\left(\frac{C_S}{T_S} \right)}{\left(\frac{C_H}{T_H} \right)} , \quad (2.9)$$

where $\hat{\lambda}$ is the estimated reporting rate for standard tags, C_S is the number of standard-tag fish reported by anglers, T_S is the number of fish tagged with standard tags, C_H is the number of high-value-tag fish reported by anglers, and T_H is the number of fish tagged with high-value-reward tags. Once an estimate of $\hat{\lambda}$ is obtained, it can be used to correct C in equation (2.8) for the standard-tag fish.

Correcting estimates of C and T for tag loss and tagging mortality is typically required. Tag loss is frequently evaluated through double tagging a subset of fish to estimate the tag loss

Box 2.3. Catch Curve Analysis

Age structure was determined by means of an age-length key. Ten fish per centimeter-group were aged and the aged fish applied back to the total length sample (see DeVries and Frie 1996). The age structure data are shown below.

Table. Age structure data for largemouth bass from the Apalachicola River, Florida.

Age	N	$(\log_e N)$
0	155	5.04
1	283	5.65
2	128	4.85
3	285	5.65
4	73	4.29
5	31	3.43
6	22	3.09
7	4	1.39
8	2	0.69
9	5	1.61
10	0	
11	2	0.69

If abundance at time t is defined as $N_t = N_0 e^{-Zt}$, then the log-transformed equation is linear ($\log_e N_t = \log_e N_0 + -Zt$, with intercept $\log_e N_0$ and slope $-Z$). Results of the regression show that $Z = 0.64$. Annual total survival and total mortality can be obtained as: $S = e^{-Z} = 0.53$, and $A = 1 - S = 0.47$. So, total annual mortality in this population is around 47%. Notice that we did not use ages 0, 1, 10, or 11 in the regression. Ages 0 and 1 were excluded because they were apparently not fully vulnerable to the gear. Ages 10 and 11 were excluded because of low sample size. Older ages with less than five fish are often removed from a catch curve to reduce their influence on the overall estimate of Z . Although ages 10 and 11 were removed, techniques are available that allow their inclusion in the catch curve analysis (i.e., weighted catch curves; Miranda and Bettoli 2007). Note that the catch curve exhibits some bumpiness, likely due to both variation in recruit-

(Box continues)

Box 2.3. Continued.

ment and sampling variability. Age-3 fish appeared to be from a relatively strong year-class, whereas fish ages 7 and 8 were from relatively weak year-classes. See Maceina (1997) for more discussion of how residuals around a catch curve can provide an index of past recruitment.

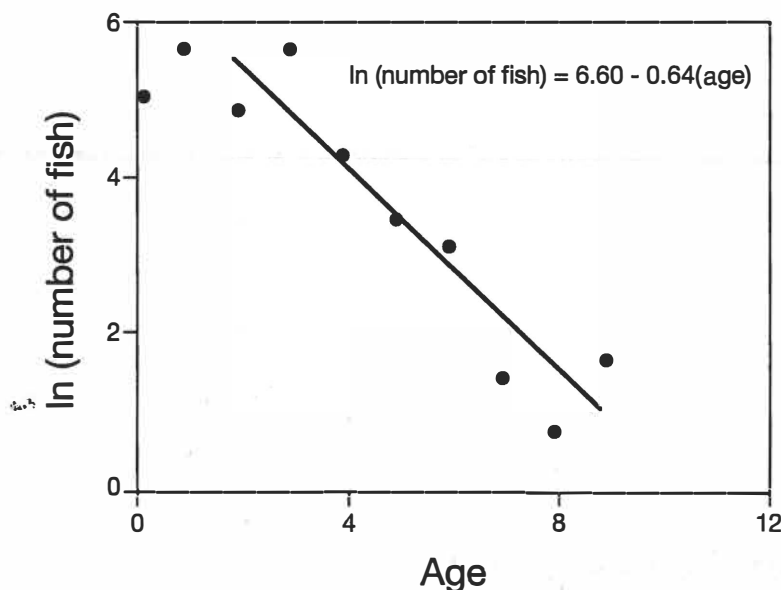


Figure. Example of a catch curve for largemouth bass from the Apalachicola River, Florida. Fish were collected with electrofishing by Florida Fish and Wildlife Conservation Commission biologist Rich Cailteux.

rate for single-tagged fish. Tagging mortality is usually conducted with cage experiments to evaluate short-term mortality from the tagging process (Box 2.4). Pine et al. (2003) provided a detailed discussion of the assumptions and methods of estimating angler reporting rates, tag loss, and tagging mortality (see Box 2.4). A detailed example of how to deal with these biases through time during a tagging study is shown by Smith et al. (2009).

If a multiyear tagging program is established, both fishing and natural mortality can be estimated (Hoenig et al. 1998; Jiang et al. 2007). As in the above short-term approach, addressing practical issues such as tagging mortality, tag loss, and nonreporting of tags is critical. An auxiliary estimate of the reporting rate (e.g., through the use of high-reward tags) is generally necessary to separate total mortality into F and M .

Active tagging methods for estimating F and M .—Active tagging involves the use of telemetry techniques to estimate fishing mortality and natural mortality (Hightower et al. 2001). By means of this method, fish tagged with sonic or radio transmitters are located at regular intervals. The status of each fish is based on movement (or lack of movement) between searches. Fish that move between successive locations are obviously still alive, whereas fish that stop moving are classified as natural mortalities. Live fish are sometimes found in the same location on consecutive searches,

Box 2.4. Estimate of Fishing Mortality from a Passive-Tagging Study

Here we describe the steps for estimating fishing mortality for redear sunfish from Lake Panasoffkee, Florida. Data were obtained from Crawford and Allen (2006). Estimates of fishing mortality were obtained in 1998 and 1999, but in this example we focus on the 1999 estimates. In January 1999, 753 redear sunfish greater than 15 cm in total length (TL) were collected by means of electrofishing, tagged with passive dart tags, and released into Lake Panasoffkee.

To estimate tag loss, 163 of the fish were double tagged. The estimate of annual tag loss from reported fish was 25% (in 1999, two of the eight double-tagged fish that were returned had only a single tag). Anglers were contacted to verify that harvested fish contained only one tag at time of capture.

Short-term tagging mortality was estimated with a cage experiment in both 1998 ($N = 2$ cage treatments for 3 d) and 1999 ($N = 1$ cage treatment for 6 d). Fish mortality through 3 d was 0 for all replicates, indicating that short-term tagging associated mortality was nil.

Nonreporting was estimated directly via a creel survey in both years. The creel clerk recorded tagged fish numbers in angler creels, and the reporting rate (λ) was estimated directly in this case as the proportion of tagged fish observed in angler creels that were reported. In 1999, the reporting rate was 83%. See Crawford and Allen (2006) for discussion of a second method for estimating reporting rates in this study by use of a variable reward system.

Anglers returned a total of 55 tagged redear sunfish. Therefore, the approximate estimate of the number of fish available for capture by anglers (T) was

$$T = 753 \times 0.75 \times 1 = 564,$$

where 753 is the number tagged, 0.75 is the tag retention rate (1 minus tag loss) and 1 is the tag survival because short-term tagging mortality was estimated as 0. The estimate of the number of fish caught by anglers (C) was

$$C = 55 / 0.83 = 66,$$

where 0.83 is the reporting rate.

The estimate of annual exploitation (u ; equation 2.8) was

$$u = 66 / 564 = 0.12.$$

Therefore the annual fishing mortality for fish greater than 15 cm at Lake Panasoffkee was 12%.

so classifying a fish as a natural mortality should be done only after several searches indicate no movements. Fish that are harvested disappear from the system, so those fish provide an indirect estimate of fishing mortality. However, not every fish with a transmitter is located on each search occasion, so the probability that a fish was harvested depends on how many consecutive searches it has not been found. The study area should be closed to emigration to avoid the risk of confusing emigration and fishing mortality. If emigration can occur (e.g., in a section of river), then an array of receivers should be set up to detect emigrating fish. Those fish are then censored from the tagged population so that they are not incorrectly classified as fishing mortalities.

Advantages of this approach are that it does not rely on angler-reported tags, natural mortality is directly estimated, and the study can be carried out over a shorter interval than can the multiyear tagging approach described above. Mortality estimates can be made over a fine time scale (e.g., monthly or quarterly), and estimates of fishing mortality can be highly seasonal (Hightower et al. 2001; Waters et al. 2005; Thompson et al. 2007). Another benefit of this approach is that periodic searches provide valuable information about fish movements and habitat use, in addition to estimates of fishing mortality and natural mortality.

2.3.3 Growth

One of the first steps in developing a management plan for a fishery is to characterize growth. The growth rate of a fish determines various aspects of its ecology (e.g., vulnerability to predation and sexual maturation) as well as its recruitment into a fishery. For recreational fisheries, the growth rate determines when fish reach a size that would be considered desirable, either for harvest or as trophy fish.

Harvest regulations for recreational fisheries are usually defined in terms of fish length. For example, a minimum length of 356 mm (14 in) might be established for a largemouth bass fishery to protect age-3 and younger fish from harvest and thereby increase the number of adults. Growth rates strongly influence the potential for a minimum length limit to improve the abundance of large fish in a population. Enacting minimum length regulations on fish populations with slow growth could exacerbate management problems (see Chapter 7).

Although growth is usually discussed in terms of length, fish growth in weight is used in some analyses. For example, weight can be used as a surrogate for fecundity or the contribution of females to the spawning population. Harvest regulations in some fisheries are set to allow the average weight of fish to increase, with the expectation that protecting large, highly fecund females will improve recruitment.

Information about growth also indicates the “health” of a population relative to its food resources and the quality of the aquatic environment. Fast growth suggests that fish density is in balance with food resources and that habitat quality is adequate. If fish are growing slowly (e.g., small mean length at a given age), it could indicate that the density is too high (relative to the food supply) or that habitat is not suitable to support an adequate prey base.

One way to summarize growth is to fit a model relating age to length or weight. For example, age in years and total length in centimeters could be determined for a random sample of fish. A model can be fitted to the data to describe the relationship. The model is typically a curve because the rate of growth usually decreases with age (e.g., Figure 2.3). A growth curve is convenient for modeling because the pattern developed from many data points can be described using a single curve with only two or three parameters.

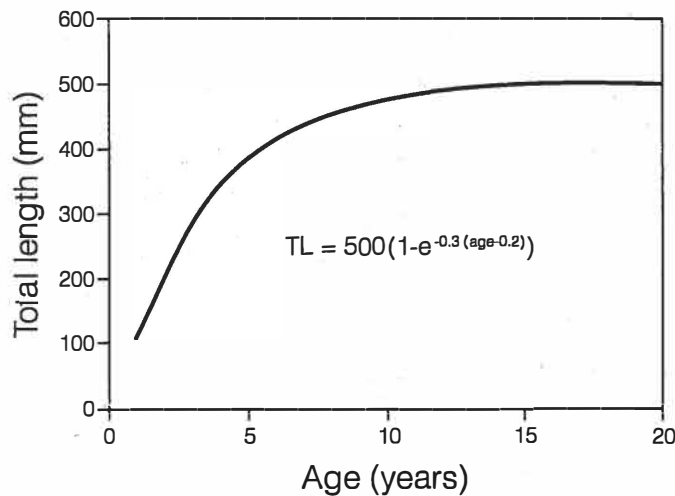


Figure 2.3. Example of a von Bertalanffy growth curve relating total length (TL) to age. Notice that incremental growth between ages declines with age.

A single model is typically appropriate for only one life stage (e.g., adult fish) because fish growth usually varies with age. Rapid growth occurs at the larval and juvenile stages, and then growth slows for adult fish as energy is diverted from somatic growth to gonadal development. The adult life stage is generally of greatest interest to fisheries managers because it is the life stage of harvestable fish.

Another way of estimating growth is through tagging (e.g., Smith and McFarlane 1990; Smith and Botsford 1998; Quinn and Deriso 1999). Ideally, fish of a range of lengths are tagged and released. When tagged fish are encountered either through surveys or by anglers, length is again determined. The time at large and the change in length between tagging and recapture are used to estimate growth rate and maximum length. For instance, the change in length might be considerable for a small fish that is growing rapidly or for a fish that is at large for many months. A fish that is close to its maximum length when tagged will not grow substantially regardless of the time at large. An advantage of this approach is that it is not necessary to estimate fish ages. This means that the method can be used on fish for which aging is not possible or can be used as an independent check on a growth curve derived from age data. It is important that the length at recapture be measured accurately, so lengths reported by fishers must be used with caution. Detailed analyses of growth data are shown in Isely and Grabowski (2007) and Quist et al. (in press).

Weight-length relationships.—In many fisheries management applications, it is useful to predict fish weight from length or vice versa. The relationship between fish weight and length is typically exponential and can be described by

$$W = aL^b, \quad (2.10)$$

where W is fish weight, a is the intercept of the weight-length relationship, L is fish length, and b is the exponent that describes the steepness of the change in weight as fish grow in length. Most fish exhibit b near 3, which is commonly called isometric growth. Allometric

growth occurs when b is lower or higher than 3, which means that the fish changes shape (in terms of weight) with an incremental change in length. Equation (2.10) has historically been estimated with \log_{10} transformations of both length and weight data followed by computation by linear regression, but the ease of computer optimization routines in spreadsheets means that least-squares fits of the nonlinear equation (2.10) are simple and obtain nearly identical parameter estimates (see “Model fitting” below).

Models for length and weight at age.—The model most commonly used for length-at-age data is the von Bertalanffy growth curve:

$$L_t = L_{\infty} \left(1 - e^{-k(t-t_0)} \right), \quad (2.11)$$

where L_t is length at age t (usually in years), L_{∞} is the asymptotic length, k is the growth rate, and t_0 is the theoretical age at which the fish would have a length of 0 (Table 2.1). The von Bertalanffy growth curve describes growth that slows with age, as fish approach their maximum length (Figure 2.3)—a relationship that frequently occurs with adult fish. Note that individual fish may be larger than L_{∞} , because L_{∞} simply represents the expected average maximum length. The growth rate k , sometimes referred to as the growth completion rate, is the rate at which fish approach L_{∞} . The parameter t_0 will generally be close to 0 if the growth data include young fish. If the growth data are from fish of harvestable length (so that t_0 represents a considerable extrapolation), the estimate of t_0 may be far from 0 and have no real biological meaning. Other growth curves have been put forward (e.g., Schnute 1981), but the von Bertalanffy curve continues to be widely used because it fits observed data for a variety of organisms (Cushing 1981), the parameters have a biological interpretation, and many published parameter estimates are available for comparison across populations of a given species.

Inspection of a von Bertalanffy curve (Figure 2.3) shows that the growth rate (tangent to the curve) is continuously decreasing towards a growth rate of 0 at $L_t = L_{\infty}$, such that the incremental growth (e.g., growth per year) declines with age. This assumption appears to work well to model the adult (i.e., age 1 and older) phase for most fish species when the growth measure of interest is change in length with age.

When growth is described in terms of increasing weight, the growth rate typically increases at younger ages, reaches a maximum at some intermediate ages, and then decreases at older ages. For this situation, a curve with an inflection point is needed. The Gompertz curve can be used to model growth in size (Quinn and Deriso 1999):

$$Y_t = Y_{\infty} e^{\left(\frac{1}{k} e^{-k(t-t_0)} \right)}, \quad (2.12)$$

where Y is length, weight, or some other measure of size, and the other parameters are as defined for equation (2.11).

Model fitting.—Growth curves can be fitted using least-squares methods where the squared differences between the observations and the fitted curve are minimized. In linear regression there are exact formulas for calculating the slope and intercept. In fitting a nonlinear model, parameter estimates are obtained iteratively (over a series of steps) by making small changes in the parameter estimates until no further improvement in the error sum of squares can be

made. The calculations are readily done in a spreadsheet (see Box 2.5). Starting values must be chosen for each parameter. For a von Bertalanffy growth equation, the maximum observed length in the data is usually a good starting value for L_{∞} . A value of 0.2 or 0.5 tends to work well for k , and a starting value of 0 should be sufficient for t_0 . The same final estimates should be obtained from any reasonable starting values if the model fits well and the data cover a reasonable range of ages and sizes.

Several factors affect the reliability of the fitted growth model. The most important factor is having a range of lengths, including older fish with lengths approaching L_{∞} . It is common to overestimate L_{∞} if the growth data include only young, fast-growing fish. Small sample sizes at older ages can be a source of bias, depending on whether the curve is fitted using means by age or individual observations. It is generally more convenient to fit the curve using means, but the disadvantage is that each mean is given the same weight regardless of the number of observations. Means at older ages are often quite variable because of the small sample sizes. There are techniques for weighting each observation based on its sample size or inverse of the variance at each age, but a simpler approach is just to fit the curve to the individual observations. Aging error can introduce bias depending on whether the errors are random and unbiased or systematic (e.g., consistent underaging). In most instances where aging bias is a problem, the age of older fish is often underestimated, which results in an overestimate of k (Leaman and Beamish 1984).

2.3.4 Recruitment

Fish recruitment is typically defined as the number of fish that survive to a specific age or size in a given year. Although recruitment can be defined in a number of ways, it is most commonly specified as either the number of fish that reach age 1 each year or the number of fish that survive to the first age at which they may be captured in a fishery. Thus, the term recruitment can be used to denote the number of fish at various life stages (age 0, age 1, or an older age), and it is important to specify the life stage at which fish are considered recruits. In most cases, fish are considered recruited to the population after they reach a size or age at which the very high larval mortality rates (see section 2.3.1) have already occurred and the fish can be considered part of the adult population.

Measures of fish recruitment are vital to assessing fish stocks. Recruitment can vary from year to year by orders of magnitude. This high variation in recruitment influences population abundance, age structure, and number of large fish, and it can influence fish growth rates when large year-classes cause density-dependent interactions. Thus, variation in recruitment strongly influences adult fish abundance as strong or weak year-classes move through a fishery, and understanding recruitment variation among years is an important consideration when evaluating harvest policies.

Fish recruitment is influenced by a variety of density-dependent and density-independent effects. Traditional fisheries management has used stock–recruitment relationships to predict recruits from spawning stock abundance (Ricker 1975). Stock abundance undoubtedly contributes to variation in recruitment, although it has been widely noted that recruitment tends to remain about the same (with high variation around an average value) across a distribution of stock abundances (Walters and Martell 2004). This infers that recruitment exhibits density dependence because recruits produced per spawner increase with declines in spawner abundance for nearly all fish stocks (see Myers et al. 1999). However, in many freshwater fisheries applications, the threat of recruitment overfishing via recreational fisheries is not as large as con-

Box 2.5. Fitting a von Bertalanffy Growth Curve in Excel

Fitting a least-squares estimate of growth parameters is easy in Microsoft® Office Excel 2007. In the table below are mean total-length-at-age estimates for black crappie *Pomoxis nigromaculatus* from Lake Dora, Florida. Data were obtained from the Florida Fish and Wildlife Conservation Commission and represent angler-caught black crappie at the lake in 2006. Ten fish per centimeter-group were selected for aging, and a larger sample of fish was measured for total length. Mean total-length-at-age estimates were obtained by means of the fixed-length subsampling methods of DeVries and Frie (1996). Copies of this and the other spreadsheets can be found at: <http://fishweb.ifas.ufl.edu/allenlab/courses.html>.

Table. Excel spreadsheet of mean total-length-at-age (TL, mm) estimates for black crappie from Lake Dora, Florida, used to fit a von Bertalanffy growth curve. See Table 2.1 for explanation of symbols; SSE is the sum of squared residuals.

A	B	C	D	E	F	G
2	L_{∞}	350				
3	k	0.41				
4	t_0	-0.49				
5					Predicted	
6			Age	TL	TL	Residuals ²
7			2	226	224	5
8			3	262	267	18
9			4	295	295	0
10			5	311	313	4
11			6	329	326	11
12			7	345	334	132
13			8	328	339	119
14						
15						SSE = 289

The following steps describe how a spreadsheet is used to fit a von Bertalanffy growth model. First input reasonable starting values, then create a column of predicted values based on those hypothesized growth parameters. Create a column that calculates the observed minus predicted values squared (i.e., the squared residuals). Now sum the squared residuals in cell labeled SSE. To obtain the least-squares parameter estimates, click "Data," then "Analysis," then "Solver." Choose the SSE cell G15 as the target cell, choose the option to minimize this cell, and then in the box "By Changing Cells," select cells C2 to C4. Now click "Solve" and notice that the parameter estimates change as Solver's optimization routine finds the least-squares parameter estimates. Solver tends to perform better when using the following options: "Automatic Scaling," "Quadratic Estimates," and "Central Derivatives." It is also useful to run Solver from more than one set of initial values to make sure the optimization routine converges on the same parameter values. The solved solution is shown below along with a graph of the observed and predicted values.

(Box continues)

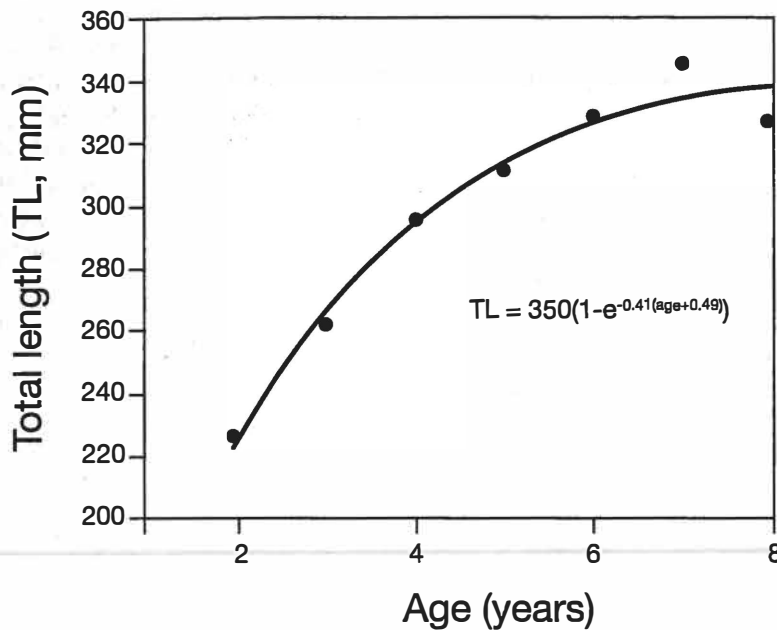
Box 2.5. Continued.

Figure. Fit of von Bertalanffy growth model to data.

cerns about growth overfishing. It may not even be feasible to estimate the stock–recruitment relationship because of the lack of information about recruitment at very low stock abundances at which recruitment would presumably be limited by stock size. Thus, in many freshwater applications, understanding stock–recruitment relationships is not as important as understanding the magnitude of recruitment variation and the factors that cause strong or weak year-classes for a particular water body. Fish recruitment in freshwater systems is often influenced by flow changes in rivers (Bain et al. 1988), water levels in reservoirs (Aggus and Elliot 1975; Ploskey 1986), aquatic plant abundance and species composition (Bettoli et al. 1993), and water temperatures (Cargnelli and Gross 1996). Here we present some common methods for measuring fish recruitment and show how these estimates can be used as part of freshwater fisheries stock assessments. For a detailed analysis of stock–recruit relationships and fitting methods, we refer the reader to Walters and Martell (2004) and Maceina and Pereira (2007).

Measures of fish recruitment and variability.—Most fisheries managers measure recruitment through catch per unit effort (C/f , also known as CPUE) indices. Electrofishing, trawls, trap nets, and hoop nets have been used to measure C/f of small fish. The “recruit” C/f is usually designated by the lengths of fish (e.g., first mode of a length-frequency distribution) or through aging fish to verify catches as recruits (e.g., age-1 fish). Use of C/f indices to measure fish abundance makes the implicit assumption that the relationship between catch rate and population abundance is

$$CPUE = \frac{C}{f} = q \times N, \quad (2.13)$$

where C = is catch, f = is fishing effort (e.g., trawl time or net night), q = is the catchability coefficient (the fraction of population caught per unit of effort), and N = is fish abundance (Ricker 1975). This equation infers a linear relationship between C/f and abundance, with a constant slope q . However, studies that evaluate relationships between C/f and N show substantial variation due to environmental conditions, changes in fish distribution and behavior, fish size, and gear selectivity (Hilborn and Walters 1992; Bayley and Austen 2002; Rogers et al. 2003). Thus, use of C/f data as an index of abundance should be accompanied by other methods that validate whether changes in C/f reflect changes in N . Alternately, managers could verify whether trends in C/f correspond to changes in recruitment using annual age structure estimates to verify strong and weak year classes moving through the population, or catch-at-age models (see below).

As an example, bottom trawl C/f data have been used to assess recruitment of black crappie at Lake Okeechobee, Florida (Figure 2.4). Substantial recruitment variability was indicated with mean annual age-1 catch per minute varying from near zero to nearly eight fish per minute over the period of record. Very strong year-classes were produced in 1981, 1987, and 1998 (caught in trawls a year later at age 1), whereas very weak year-classes were evident in other years. Weak year-classes in 2004 and 2005 were associated with hurricane events that caused lakewide changes in aquatic plant abundance (Rogers and Allen 2008). This time series shows a typical scenario of highly variable recruitment. Obviously, the quality of the black crappie fishery would be expected to vary with the large variation in recruitment, and it did! Angler catch per hour showed a lag effect where high angler catch rates occurred 1–2 years after high age-1 catches in the bottom trawl (Figure 2.4). This example shows how monitoring recruitment trends can allow fisheries managers to anticipate the quality of the fishery in the future.

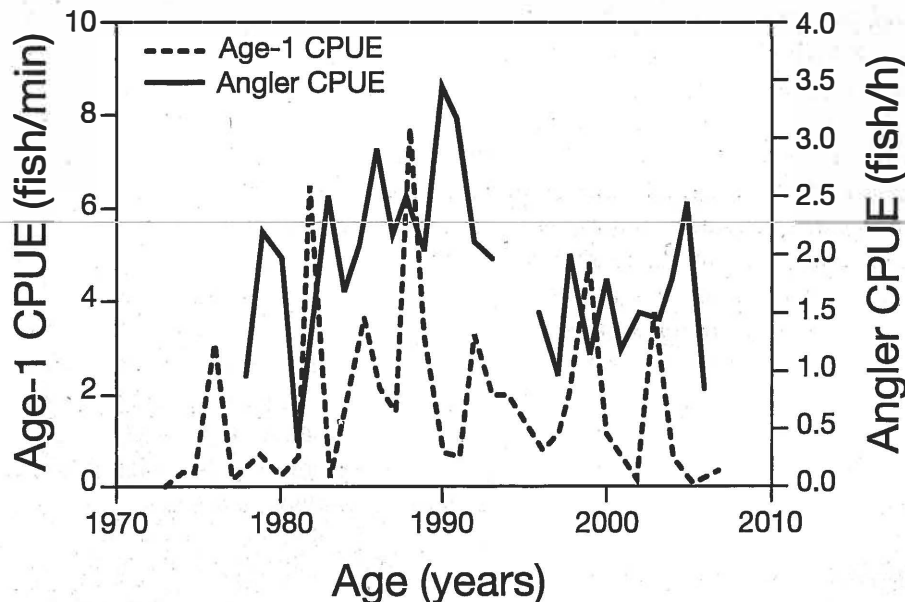


Figure 2.4. Age-1 black crappie catch per minute with a bottom trawl (CPUE, dashed line) and angler catch per hour (fish harvested/angler-hour, solid line) plotted on year for samples from Lake Okeechobee, Florida. Data were collected by Don Fox, Florida Fish and Wildlife Conservation Commission.

Estimating the magnitude of recruitment variation is important for fisheries management. Several authors have proposed indices to measure variation in recruitment through time. Maceina (1997) showed that residuals around a catch curve (see example Box 2.3) can serve as an index of recruitment variability. Isermann et al. (2002) and Quist (2007) compared a number of published methods for measuring recruitment variability. We have not reiterated all those methods, but the most straightforward method is to evaluate the coefficient of variation (CV) in recruit-size fish C/f across years. The CV is a standard measure of variability:

$$CV = \frac{s}{\bar{x}} \times 100\%, \quad (2.14)$$

where CV is the coefficient of variation, s is the standard deviation of the sample, and \bar{x} is the mean. Knowledge of the across-year CV in recruits is useful for population modeling exercises, because it allows the investigator to explore how variable adult fish abundance and angler catches are likely to be due to variation in recruitment. Allen and Pine (2000) found that recruitment variability could influence the ability of managers to detect fish population responses to changes in minimum length limits. Thus, understanding recruitment variability is a key component in managing recreational fisheries (Maceina and Pereira 2007).

2.4 USE OF BASIC FISHERIES MODELS

Fisheries managers can use population models to predict how estimates of growth, mortality, and recruitment will interact to determine fish yield, fish population size, and angler catch rates. Fish population models provide a conceptualization of how a fish population changes in abundance and age structure in response to harvest. Many fisheries textbooks provide complex model formulations that are mathematically challenging. There are cases in which such models are essential, but a key objective of this chapter is to show that building simple fish population models can be both easy and effective for exploring harvest policy options.

Several key points should be considered before beginning a modeling exercise. First, all models are a simplified version of reality, and no model considers all factors that influence a fish population. Models should not attempt to capture all dynamics influencing fisheries, but they should consider the major factors that influence abundance, such as fishing mortality and recruitment. Population models should not be used to make specific predictions but to compare the relative responses to a range of management actions (Hilborn et al. 1984; Johnson 1995). A good way to think about a modeling exercise is that the model is a hypothesis about how a fish population may respond to management actions. Models typically compile much of the existing data into one framework, which allows investigators to identify data gaps clearly. Thus, a modeling exercise may have as much value in guiding future sampling efforts to reduce uncertainty as in evaluating the relative response to a variety of management actions. In this section, we show how a simple age-structured yield-per-recruit model and a catch-at-age approach can be used to assess freshwater fish populations.

2.4.1 Yield-per-Recruit Models

Yield-per-recruit models are typically used to evaluate the potential for growth overfishing (i.e., fishing at a level that reduces the maximum yield per recruit). A number of formulations have

been proposed for these models. Here, we used a simple formulation by Botsford and Wickham (1979) and Botsford (1981a, b) that was summarized by Walters and Martell (2004). The approach uses Botsford incidence functions, which estimate the abundance and biomass per recruit for a fish population. Consider a fish population with only instantaneous natural mortality (M) of 0.2. The S_0 (annual survival from natural mortality) for this population is $e^{-M} = 0.82$. The number of fish alive at each age starting with 1,000 recruits to age-1 would therefore be found as follows.

Age	Number alive	Survival per recruit (lx_a)
1	1,000	1
2	820	0.820
3	670	0.670
4	549	0.549
5	449	0.449
6	368	0.368

Simply, the survivors to any age $a + 1$ is equal to the survivors to age a times 0.82. This example describes the survivorship schedule, lx_a , on a per recruit basis, which is useful for the calculations below. Now let us consider the same population with an annual exploitation rate (u) of 0.2. We assume that fish become vulnerable to fishing at age 3. The Botsford incidence functions can be used to predict survivors to each age. Survivorship at age 1, the youngest age in our simulated population, is

$$lx_1 = 1.$$

Survivorship at any older age a can be depicted as:

$$lx_a = lx_{a-1} \times S_0 \times (1 - u \times V_{a-1}), \quad (2.15)$$

where lx_{a-1} is the survivorship from the previous age, S_0 is survival from natural mortality, u is the annual exploitation rate, and V is a vulnerability parameter that determines whether fish are vulnerable ($V = 1$) to exploitation or not ($V = 0$). In this case, V is 0 for ages 1 and 2, and V is 1 for all older ages. Thus, the survivorship to age 2 would be: $1 \times 0.82 \times (1 - 0.2 \times 0) = 0.82$, because this age group is not yet vulnerable to fishing. Following through with our example, the number of fish at any age can simply be determined by $R \times lx_a$, where R is the number of simulated recruits at age 1.

We now have estimates of the number of survivors per recruit and can compute the vulnerable biomass per recruit as:

$$\phi_{VB} = w_1 V_1 + lx_2 w_2 V_2 + lx_3 w_3 V_3, \dots, \quad (2.16)$$

where ϕ_{VB} is the vulnerable biomass per recruit, l_a is the age-specific survivorship as defined above, w is the average weight of fish at each age, and V is the vulnerability schedule. Total vulnerable population biomass (B) is then simply:


$$B = R \times \phi_{VB}, \quad (2.17)$$

where R is the number of recruits at age 1. This per-recruit formulation of the population model makes then next step easy. The equilibrium yield is estimated as:

$$Y = u \times R \times \phi_{VB}, \quad (2.18)$$

where Y is yield in biomass expressed in the same units as fish weight (w). Botsford incidence functions (such as ϕ_{VB}) are easy to set up in a spreadsheet and they allow relatively complex population models to be expressed in simple terms. Box 2.6 shows a demonstration of the Botsford incidence functions and a yield-per-recruit model for black crappie at Lake Dora, Florida.

In some fisheries total yield (or weight of fish harvested) is not the variable of interest because anglers place little value on harvesting fish but high value on catching large numbers of fish, large-sized fish, or both. For instance many black bass *Micropterus* spp. anglers release their catch even if the fish is legal to harvest, and managers of black bass fisheries seldom consider yield as an important aspect of the fishery. The same could be said for some trout fisheries where the catch of large fish is a more important management objective than is total yield. In these cases, total catch or the total catch of large fish may be a more useful model output. As illustrated in Box 2.6, a change in one spreadsheet formula is all that is required to reflect numbers, rather than biomass, of fish caught under each management alternative. Additional relationships, such as discard mortality of fish caught and released and voluntary release of fish by anglers, can also be incorporated. Thus, spreadsheet models can be built to address the specific needs of the investigator, and their flexibility to handle a wide range of modeling approaches is an advantage to learning this approach.

Software.—There are a number of software packages that can be used for yield-per-recruit and other age-structured population models as well as simple model fitting, such as for growth curves and mortality estimation. Perhaps the most popular is the program FAST (Fisheries Analysis and Simulation Tools; Slipke and Maceina 2001), which is a user-friendly software package that can perform all these analyses in a straightforward Windows platform. The FAST model has been used by many state management agencies, and the user can fit growth curves and catch curves and conduct analyses of yield-per-recruit and more complex age-structured models. 

2.4.2 Catch-at-Age Methods

Management of a fish population is greatly enhanced if population size can be estimated. An estimate of absolute abundance can be compared with the catch to evaluate the impact of fishing on the population. Spawning stock abundance can be estimated to determine whether the stock abundance is low enough to limit recruitment. Population levels for prey and predator species can be used to estimate food resources for predators or the impact of predation on prey species. In combination, analyses that predict population abundance provide a wealth of information about mortality, recruitment, and growth that cannot be obtained from relative abundance (i.e., CPUE) data.

Box 2.6. Yield-per-Recruit Model

This yield-per-recruit (YPR) model for black crappie at Lake Dora, Florida, was based on data collected by Florida Fish and Wildlife Conservation Commission and University of Florida personnel. The purpose of the model was to evaluate whether growth overfishing was occurring in this fishery. Copies of the spreadsheet can be found at <http://fishweb.ifas.ufl.edu/allenlab/courses.html>.

Annual exploitation (M) was estimated with a variable-reward passive-tagging study during 2006; u was estimated at 0.42 (Dotson 2007). The first three cells contain parameters for a von Bertalanffy growth equation (see Box 2.5) used to predict mean total length at age (TL):

$$TL = 350[1 - e^{-0.41(\text{age} + 0.49)}].$$

Natural mortality ($M = 0.40$) was obtained from a literature review for black crappie, and thus $S_0 = e^{-M} = 0.67$. "Recruits" was used to designate the total number of recruits for this population and was set arbitrarily as 1,000. The next cell, "Reg," designated the fish length at entry to the fishery. These parameters were placed into the left column of the spreadsheet and were named as indicated below (see spreadsheet for how to name cells).

Table 1. Parameters for Excel spreadsheet for yield-per-recruit model for black crappie at Lake Dora, Florida. Symbols defined here and in Table 2.1.

L_{∞}	350
k	0.412
t_0	-0.49
M	0.40
S_0	0.67
u	0.42
a	6.310E-06 ^a
b	3.32
Recruits	1000
Reg	250
$^a 6.31 \times 10^{-6}$	

(Box continues)

Box 2.6. Continued.

Next we construct the length, weight, and mortality structure of the population.

Table 2. Values of each variable for eight ages of black crappie. Explanation of variables follow table.

Age	1	2	3	4	5	6	7	8
TL	161	225	267	295	314	326	334	339
wt	0.13	0.40	0.72	1.00	1.22	1.39	1.51	1.59
V	0	0	1	1	1	1	1	1
lx_{fished}	1.000	0.670	0.449	0.175	0.068	0.026	0.010	0.004

Total length in millimeters was estimated with the von Bertalanffy growth model, and weight (wt) in kilograms was estimated by the standard weight-length relationship for black crappie as $W = a \times TL^b$ (Anderson and Neumann 1996). The V (vulnerability) schedule was used to set the length and age at which fish become vulnerable to the fishery. In this case, we used an IF statement to set V equal to 0 if the mean length at that age was less than Reg and 1 if the mean length was equal to or larger than Reg. The row for " lx_{fished} " is the survivorship per recruit in the fished condition, found by $lx_a = lx_{a-1} \times S_0 \times (1 - u \times V_{a-1})$, where lx_{a-1} was the survivorship from the previous age, S_0 is annual survival from natural mortality, u was the annual exploitation rate, and V is a vulnerability parameter that determines whether fish are vulnerable to u or not, per equation (2.15).

The Botsford incidence function of vulnerable biomass per recruit (ϕ_{VB}) was calculated as SUMPRODUCT(wt, V, lx_{fished}). Yield per recruit was then found by $Y = u \times R \times \phi_{VB}$, where R was the number of recruits. A second incidence function was set up as vulnerable number of fish per recruit, ϕ_n , by SUMPRODUCT(V, lx_{fished}). Thus, total angler catch in numbers of fish was estimated as $C = u \times R \times \phi_n$.

Table 3. Summary of Botsford incidence function values.

Vulnerable biomass per recruit (ϕ_{VB})	0.64
Yield per recruit (YPR)	268.11
Vulnerable number per recruit (ϕ_n)	0.73
Catch per recruit (CPR)	307.69

To finish the analysis we simulated a range of exploitation rates and potential sizes of harvest (i.e., minimum length at harvest). We used the "Table" function in Excel to iterate the spreadsheet across a wide range of both values and show how equilibrium yield was predicted to change. See spreadsheet for instructions. The yield isopleth curve is shown below.

(Box continues)

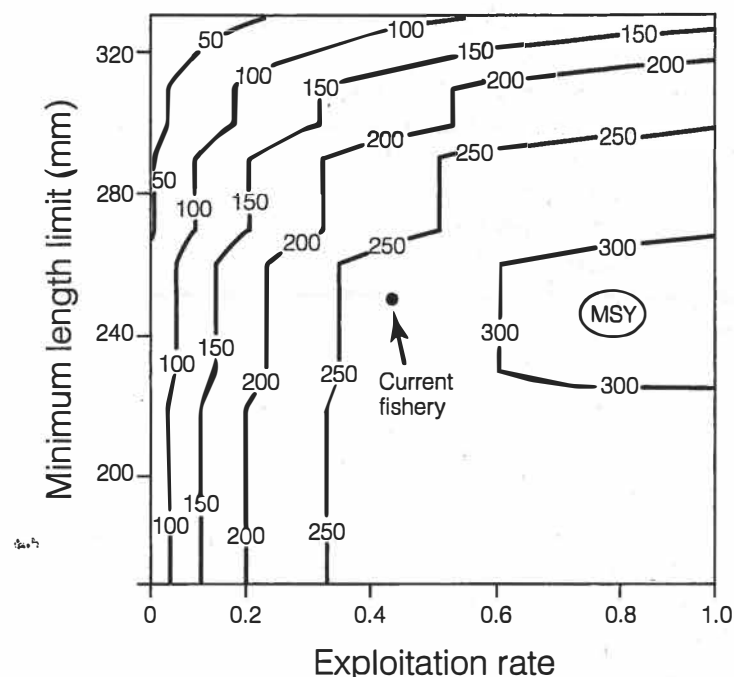
Box 2.6. Continued.

Figure. Yield isopleths (i.e., numbers in the plot represent yield in kilograms) for minimum length limit (y-axis) and exploitation rate (u , x-axis) combinations (MSY = maximum sustainable yield).

These yield isopleths (i.e., numbers within the plot represent yield in kilograms) show that the maximum sustainable yield (MSY) occurred at a minimum length limit of about 240–250 mm with annual exploitation rates of about 0.8. Growth overfishing was predicted to occur at u over about 0.6 if the minimum length at harvest was below 240 mm (notice the decline in yield if u was high [>0.80] and the minimum length limit dropped from 250 mm to 200 mm). This resulted because fish would be harvested before they reached the size that would maximize the yield. In this case the exploitation rate at Lake Dora was 0.42 (gray circle on plot). If the management objective was to maximize yield, increasing the exploitation rate would be recommended with about the same minimum length limit (250 mm TL). Establishing a minimum length limit above about 270 mm TL would cause declines in yield because many fish would die from natural mortality before reaching harvestable size. This example provides a way to construct YPR models to evaluate harvest policies in common recreational fisheries scenarios.

There are a variety of ways to estimate population abundance. For example, if a trawl is assumed to catch 100% of the fish in its path, the area swept by the trawl provides a measure of catch per unit area that can be used to estimate total abundance. Hydroacoustic sampling can provide estimates of total population abundance for certain species, depending on their vertical distribution (Brandt 1996). Capture–recapture methods can be effective in small systems such as streams or small lakes but are harder to apply in large lakes and rivers because of the difficulty in tagging and recapturing a sufficient fraction of the population. Overviews of capture–recapture methods can be found in Pine et al. (2003) and Hayes et al. (2007). One related approach that can be effective on larger systems is to use tagging in combination with a creel survey. Total harvest from the creel survey divided by the exploitation rate from the tagging program provides an estimate of absolute abundance.

An approach commonly used in large systems (e.g., large lakes) is to estimate the total harvest by age and then reconstruct the population from the catch-at-age matrix. This matrix of catches by age and year provides a record of removals from each cohort or year-class. The total catch from a cohort over its lifetime in the fishery is a minimum estimate of the initial size of that cohort. Correcting for natural deaths provides a better estimate of initial cohort size. Methods that attempt to recreate the stock abundance using historical catches are usually termed virtual population analysis (VPA).

An exceptional example of a catch-at-age dataset exists for the walleye *Sander vitreus* fishery at Lake Escanaba, Wisconsin, for the years 1956 to 1997 (Box 2.7). The entire catch-at-age matrix includes a few fish that were age 0 and older than age 12, but those have been omitted for this example. This lake is unique because anglers are required to report their entire catch when leaving the lake. Mandatory reporting has resulted in a high-quality dataset compared with the typical situation in which total harvest is estimated from a small subsample of catches. Walleye ages were determined from jaw tags and by examining scales. Catch sampling began in 1956, so age-1 fish caught in that year would be from the 1955 cohort (age 0 in 1955). Age-2 fish in 1956 are from the 1954 cohort. The earliest cohort in that year is the 1946 cohort at age 10. The most recent cohort that has completed its lifetime in the fishery is the 1985 cohort, which is age 12 in 1997. These completed cohorts are the simplest to analyze because it can be assumed that no fish from those cohorts remain (Hilborn and Walters 1992).

Estimates of age-1 abundance for the completed cohorts showed that recruitment has varied widely over time, from about 2,000 to 18,000 fish per year (Box 2.7). Strong and weak year-classes were apparent and can be tracked across years (e.g., the weak 1960 year-class is evident through at least age 6 in 1966). The ability to track strong and weak year-classes across years is a sign that the age data are reliable. The occasional strong year-classes (e.g., 1955, 1973, and 1981) can have a big impact on the population and result in several years of high catches. Slight modifications of the method shown here provide estimates for incomplete cohorts (Hilborn and Walters 1992), so that the catch-at-age matrix can be transformed into estimates of population size for every age and year. There are also statistically-based catch-at-age analyses that use the same information and produce similar results but provide estimates of the uncertainty in estimating population abundance and fishing mortality (Hilborn and Walters 1992; Quinn and Deriso 1999). These methods are beyond the scope of this chapter but are recommended for carrying out catch-at-age analyses.

Catch-at-age methods are dependent on an assumed value of natural mortality. Changing M produces a new set of population estimates that will be consistently higher or lower, depending on whether M is decreased or increased. Although absolute abundance will differ,

Box 2.7. Virtual Population Analysis

Table 1. Data based on catches of walleye by age (1–12) and year (1956–1997) from Escanaba Lake, Wisconsin (unpublished data, M. Hansen, University of Wisconsin–Stevens Point).

Year	1	2	3	4	5	Age 6	7	8	9	10	11	12
1956	702	2,247	448	309	492	97	129	23	11	1	0	0
1957	9	1,330	1,543	186	147	293	79	45	11	2	0	0
1958	1	26	452	462	49	36	108	29	13	5	0	0
1959	210	35	17	366	284	43	24	14	4	7	0	0
1960	736	553	58	28	581	336	38	7	14	1	1	7
1961	6	2,750	233	33	15	265	229	16	3	2	0	0
1962	27	34	1,869	111	20	61	134	225	8	0	0	0
1963	475	169	3	368	34	7	4	69	117	2	0	0
1964	428	963	122	6	112	11	23	25	28	34	1	0
1965	164	497	695	55	3	50	8	21	6	20	0	0
1966	73	1,739	389	328	35	5	61	96	7	5	0	27
1967	0	35	2,130	247	137	65	26	36	25	10	6	33
1968	2	175	220	371	141	37	26	14	12	12	0	0
1969	27	201	352	180	221	34	15	9	3	3	2	0
1970	164	682	430	454	181	198	33	9	6	2	2	7
1971	85	579	872	325	301	129	164	26	9	3	3	3
1972	41	131	171	223	157	25	16	16	12	5	1	2
1973	67	271	381	278	99	54	30	24	7	3	3	0
1974	112	121	239	193	213	71	61	38	13	12	3	3
1975	4	2,846	278	382	370	277	177	88	37	8	3	0
1976	38	789	1,801	345	133	171	116	60	32	16	7	2
1977	97	387	1,519	866	65	34	21	8	3	0	0	0
1978	120	625	749	1,178	468	93	38	24	9	3	0	0
1979	6	716	766	393	418	213	81	55	33	31	9	5

(Box continues)

Box 2.7. Continued.**Table 1. Continued.**

Year	1	2	3	4	5	Age 6	7	8	9	10	11	12
1980	9	140	2,040	335	129	183	116	47	38	26	9	4
1981	77	496	144	539	80	22	24	13	2	5	0	0
1982	124	442	971	139	251	54	24	17	7	5	0	0
1983	8	1,495	283	450	101	241	37	18	15	6	1	1
1984	6	107	2,172	129	126	19	103	29	20	4	3	1
1985	17	101	348	1,960	54	31	21	43	12	6	3	2
1986	4	336	374	109	370	17	14	3	14	2	3	0
1987	64	567	1,734	370	61	90	16	9	0	1	0	0
1988	148	1,788	1,469	754	117	15	30	4	3	0	3	1
1989	37	622	2,804	577	165	27	10	12	3	0	0	0
1990	5	354	811	1,188	220	48	10	3	4	1	0	0
1991	8	52	415	300	208	23	10	2	2	1	0	2
1992	21	1,068	107	245	136	87	29	7	1	2	4	0
1993	8	137	998	138	174	97	68	14	10	8	1	2
1994	5	171	315	498	51	71	31	47	7	9	2	1
1995	40	135	525	277	216	31	28	28	17	1	1	0
1996	0	0	362	220	102	55	13	8	6	2	1	1
1997	0	0	1,952	298	111	50	30	4	5	6	6	1

Box 2.7. Continued.

Each cohort can be reconstructed by summing the catches and adjusting upward for natural mortality. Because natural deaths are not observed, the instantaneous rate of natural mortality (M) is often an assumed value based on the life history characteristics of that species. Here, a value of 0.4 is assumed.

The abundance estimate for each cohort begins at the oldest age and works backward. This is very convenient for cohorts that have completed their life in the fishery because it can be assumed that no fish from that cohort remain in the population. Abundance at the start of age 11 is the population abundance at age 12 (assumed to be the catch), adjusted upward for a year of natural mortality (simply divided by $S_0 [e^{-M}]$), plus the catch of age-11 fish that year. For the 1955 cohort, the expression would be

$$N_{11, 1966} = N_{12, 1967} / S_0 + C_{11, 1966}.$$

The equation for the number at age 10 is

$$N_{10, 1965} = N_{11, 1966} / S_0 + C_{10, 1965}.$$

A similar calculation is made for each age, working backwards up the diagonal to age 1.

(Box continues)

Box 2.7. Continued.**Table 2.** Abundance estimates for each cohort of walleye from Escanaba Lake, Wisconsin.

Year	Age											
	1	2	3	4	5	6	7	8	9	10	11	12
1956	16,462											
1957	1,817	10,564										
1958	1,579	1,212	6,190									
1959	5,570	1,058	795	3,846								
1960	13,166	3,593	686	521	2,333							
1961	1,125	8,332	2,038	421	331	1,174						
1962	2,133	750	3,742	1,210	260	212	609					
1963	6,625	1,412	480	1,255	737	161	101	319				
1964	5,164	4,122	833	320	595	471	103	65	167			
1965	14,297	3,175	2,118	477	210	324	308	54	27	93		
1966	4,627	9,473	1,795	954	283	139	183	201	22	14	49	
1967	6,676	3,053	5,185	942	419	166	90	82	71	10	6	33
1968	6,826	4,475	2,023	2,047	466	189	68	43	31	31	0	0
1969	8,679	4,574	2,883	1,208	1,124	218	102	28	19	13	12	0
1970	8,690	5,799	2,932	1,696	689	605	123	58	13	11	6	7
1971	7,253	5,715	3,430	1,677	833	341	273	61	33	4	6	3
1972	5,675	4,805	3,443	1,715	906	356	142	73	23	16	1	2
1973	5,055	3,777	3,133	2,193	1,000	502	222	84	38	7	7	0
1974	17,344	3,343	2,350	1,845	1,284	604	300	129	41	21	3	3
1975	13,118	11,551	2,160	1,415	1,107	718	357	161	61	18	6	0
1976	5,823	8,790	5,835	1,262	693	494	295	121	49	16	7	2
1977	5,975	3,878	5,363	2,704	614	375	217	120	41	11	0	0
1978	12,928	3,940	2,340	2,577	1,232	368	229	131	75	25	7	0
1979	1,918	8,586	2,222	1,066	938	512	185	128	72	44	15	5
1980	5,796	1,282	5,275	976	451	348	201	69	49	26	9	4

(Box continues)

Box 2.7. Continued.**Table 2. Continued.**

Year	1	2	3	4	Age 5	6	7	8	9	10	11	12
1981	2,540	3,879	765	2,169	430	216	111	57	15	7	0	0
1982	17,237	1,651	2,268	417	1,092	235	130	58	29	9	1	0
1983	2,135	11,471	810	869	186	564	121	71	28	15	2	1
1984	3,566	1,426	6,687	354	281	57	216	56	36	8	6	1
1985	8,989	2,386	884	3,027	150	104	25	76	18	10	3	2
1986	8,189	6,014	1,532	359	715	65	49	3	22	4	3	0
1987		5,486	3,806	776	168	231	32	23	0	5	1	0
1988			3,298	1,389	272	72	95	11	10	0	3	1
1989				1,226	426	104	38	43	4	4	0	0
1990					435	175	52	19	21	1	3	0
1991						144	85	28	11	11	0	2
1992							81	50	17	6	7	0
1993								35	29	11	2	2
1994									14	13	2	1
1995										5	2	0
1996											2	1
1997												1

The exploitation rate (u) can be estimated as the ratio of catch to population abundance (e.g., 702 / 16,462 for age-1 walleye in 1956). The instantaneous fishing mortality rate (F) is $-\log_e(1 - u)$, resulting in the following matrix of F estimates.

(Box continues)

Box 2.7. Continued.**Table 3.** Instantaneous fishing mortality rate estimates for walleye from Escanaba Lake, Wisconsin.

Year	1	2	3	4	5	Age		8	9	10	11
						6	7				
1956	0.04										
1957	0.00	0.13									
1958	0.00	0.02	0.08								
1959	0.04	0.03	0.02	0.10							
1960	0.06	0.17	0.09	0.06	0.29						
1961	0.01	0.40	0.12	0.08	0.05	0.26					
1962	0.01	0.05	0.69	0.10	0.08	0.34	0.25				
1963	0.07	0.13	0.01	0.35	0.05	0.04	0.04	0.24			
1964	0.09	0.27	0.16	0.02	0.21	0.02	0.25	0.49	0.18		
1965	0.01	0.17	0.40	0.12	0.01	0.17	0.03	0.50	0.25	0.24	
1966	0.02	0.20	0.24	0.42	0.13	0.04	0.40	0.65	0.38	0.44	0.00
1967	0.00	0.01	0.53	0.30	0.40	0.50	0.34	0.58	0.44		
1968	0.00	0.04	0.12	0.20	0.36	0.22	0.48	0.40	0.49	0.50	
1969	0.00	0.04	0.13	0.16	0.22	0.17	0.16	0.39	0.17	0.27	0.18
1970	0.02	0.13	0.16	0.31	0.30	0.40	0.31	0.17	0.64	0.20	0.37
1971	0.01	0.11	0.29	0.22	0.45	0.48	0.92	0.56	0.32	1.10	0.70
1972	0.01	0.03	0.05	0.14	0.19	0.07	0.12	0.25	0.73	0.37	
1973	0.01	0.07	0.13	0.14	0.10	0.11	0.15	0.33	0.20	0.51	0.51
1974	0.01	0.04	0.11	0.11	0.18	0.13	0.23	0.35	0.39	0.85	
1975	0.00	0.28	0.14	0.31	0.41	0.49	0.68	0.79	0.94	0.57	0.70
1976	0.01	0.09	0.37	0.32	0.21	0.42	0.50	0.69	1.07		
1977	0.02	0.11	0.33	0.39	0.11	0.10	0.10	0.07	0.08	0.00	
1978	0.01	0.17	0.39	0.61	0.48	0.29	0.18	0.20	0.13	0.13	0.00
1979	0.00	0.09	0.42	0.46	0.59	0.54	0.58	0.56	0.62	1.20	0.92
1980	0.00	0.12	0.49	0.42	0.34	0.74	0.86	1.13	1.51		

(Box continues)

Box 2.7. Continued.**Table 3. Continued.**

Year	1	2	3	4	5	Age 6	7	8	9	10	11
1981	0.03	0.14	0.21	0.29	0.21	0.11	0.24	0.26	0.14	1.18	
1982	0.01	0.31	0.56	0.41	0.26	0.26	0.20	0.35	0.27	0.85	0.00
1983	0.00	0.14	0.43	0.73	0.78	0.56	0.36	0.29	0.78	0.51	0.51
1984	0.00	0.08	0.39	0.45	0.59	0.41	0.65	0.72	0.82	0.64	0.70
1985	0.00	0.04	0.50	1.04	0.44	0.35	1.74	0.83	1.07	0.85	
1986	0.00	0.06	0.28	0.36	0.73	0.30	0.34		1.00	0.64	
1987		0.11	0.61	0.65	0.45	0.49	0.69	0.49		0.20	0.00
1988			0.59	0.78	0.56	0.24	0.38	0.47	0.37		
1989				0.64	0.49	0.30	0.31	0.32	1.10	0.00	
1990					0.71	0.32	0.22	0.17	0.21		0.00
1991						0.17	0.13	0.07	0.21	0.09	
1992							0.44	0.15	0.06	0.43	0.85
1993								0.51	0.42	1.30	0.51
1994									0.69	1.23	
1995										0.24	0.51
1996											0.51

It is not possible to estimate F for the last nonzero catch for a cohort. Notice that values of F increase across ages 1–4 for each year as fish grow and become more vulnerable to angling. The fishing mortality rates can be viewed across years, as desired for management (see figure below). This analysis suggested that fishing mortality varied widely from 1965 to 1986 but also showed a general increase through time.

(Box continues)

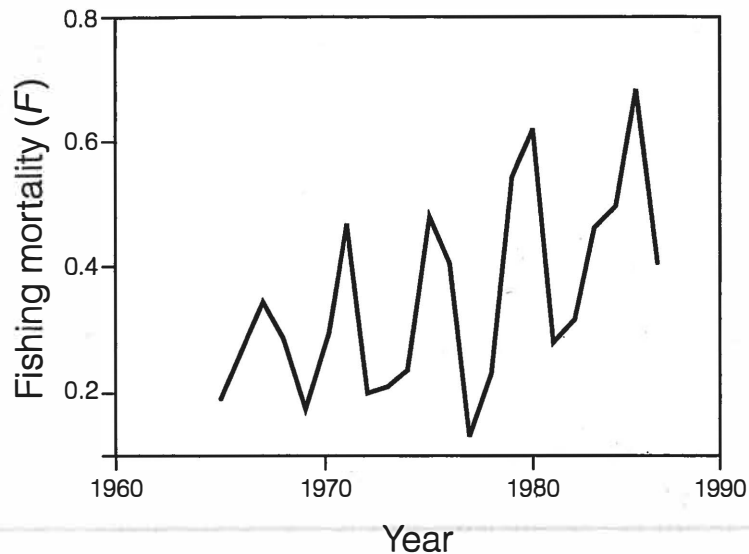
Box 2.7. Continued.

Figure A. Fishing mortality of walleye from 1965 to 1986 in Escanaba Lake, Wisconsin.

Other useful results from a virtual population analysis (VPA) include population abundance (totaled across all ages) and annual recruitment to age-1 (shown below). Notice how the strong and weak year-classes are evident simply by reconstructing the cohorts in the VPA.

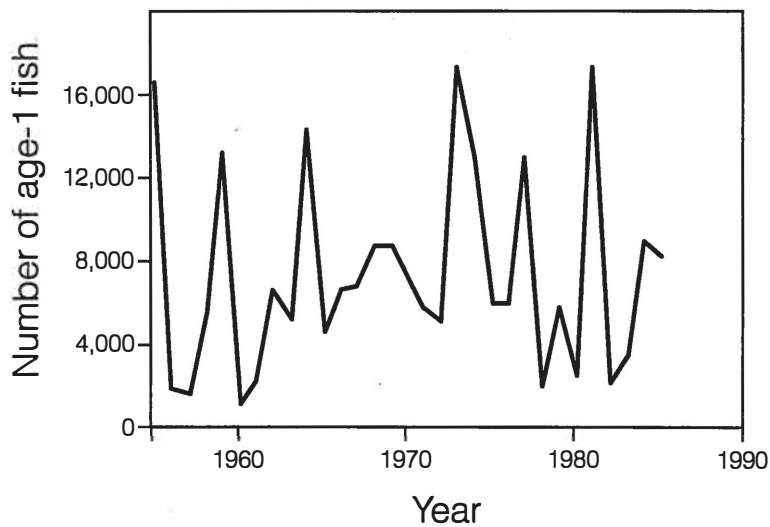


Figure B. Annual recruitment of age-1 walleye at Escanaba Lake, Wisconsin.

Population biomass can also be calculated by multiplying each abundance estimate by the associated average weight-at-age value.

the trend and year-to-year variability in year-class strength will be similar for different assumed values of M . Field studies to estimate M (e.g., a tagging study) can be used to reduce this source of uncertainty.

Catch-at-age models are routinely used in marine fisheries, but they have not been commonly used in freshwater systems other than the Great Lakes. They require more effort than do relative abundance surveys, but they can be derived from creel survey data if accompanied by estimates of age composition of the angler catch. The abundance estimates provide a strong foundation for single-species or multispecies models and are superior to relative abundance data for selecting an appropriate harvest rate.

2.5 CONCLUSIONS

Fisheries management requires making choices about harvest regulations, fish stocking programs, and habitat restoration. Those choices influence fisheries resources and the human users who benefit from those resources. Estimating fish population parameters including mortality, growth, and recruitment and integrating those estimates into simple population models improves understanding of the factors influencing fish abundance and angler harvest. The methods outlined in this chapter serve as a first step towards proficiency in assessment of fish populations. Quantitative analysis of fish populations will always be a critical element for effective management, and the purpose of this chapter has been to show that most analyses are not difficult to draw basic fishery conclusions needed in most instances. When combined with effective use of harvest restrictions and other management strategies related to fish habitat and species composition, quantitative fisheries assessment methods will inform management decisions and improve fisheries in the future.

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