

$$w_t = w_0 e^{G(1-e^{-gt})}, \quad (6.49)$$

where  $w_t$  is weight at age  $t$ ,  $w_0$  is the weight of a fish at the beginning of the growth period,  $G$  is the instantaneous growth rate when  $t$  is 0 and  $w$  is  $w_0$ , and  $g$  is the instantaneous rate at which  $G$  decreases as  $t$  increases. Estimates of  $w_0$ ,  $G$ , and  $g$  can be made using observations of fish weight for a series of age-groups (Ricklefs 1967; Hilborn and Walters 1992).

The Gompertz model has been used less frequently than the von Bertalanffy model. Ricker (1975) suggested that this is not due to its inferiority but because the von Bertalanffy model became more well-known after it was adopted for use in yield models. However, the Gompertz model is gaining popularity for describing growth in length of larval fishes (Michaletz 1997), which often slows as the juvenile stage is approached. When used to describe growth in length, only the upper portion of the S-shape Gompertz curve (beyond the inflection point) is used. Consequently, the model appears as

$$l_t = L_\infty e^{-e^{-(G-gt)}}, \quad (6.50)$$

where  $L_\infty$  is the theoretical asymptotic upper length (as in the von Bertalanffy model), and  $G$  and  $g$  are as previously described (but for growth in length).

To fit this model to length-at-age data, equation (6.50) can be linearized as

$$\log_e \left( \log_e \frac{L_\infty}{l_t} \right) = G - gt, \quad (6.51)$$

and a regression of  $\log_e[\log_e(L_\infty / l_t)]$  versus age ( $t$ ) is used to estimate  $G$  from the intercept and  $g$  from the slope. An iterative procedure can then be used whereby values of  $L_\infty$  are selected until the best linear fit to the data is acquired. A Gompertz model for weight can also be linearized so that linear regression can be applied.

## 6.4 PREDICTION OF FISHERY TRENDS

A major activity of fisheries managers has been to predict the effects of different amounts of fishing effort on the numbers and sizes of fish obtained on a continuing basis from a stock. Models are developed within constraints imposed by data availability, types of predictions desired, and mathematical and computational complexity. Models are tools that should be as simple as possible while providing appropriate types of predictions—emphasis should be placed on making decisions regarding feasible management practices rather than impossible ones. Formulation of any mathematical representation of population dynamics will require certain assumptions, and the validity of the assumptions will affect the accuracy and meaning of predictions from a model. Evidence of failure of assumptions does not necessarily mean that the model

is useless; rather, the manager should recognize the limitations of the model and determine if such limitations will have a significant effect on decisions or recommendations that will be made (Gulland 1983; Johnson 1995). Models often can be used to explore the influences of different management options on a specific fishery even if the predicted values are known to be only approximately proportional to the actual values. Recent examples of the application of models for inland fisheries management include models of crappie populations in reservoirs (Colvin 1991), channel catfish in rivers (Gerhardt and Hubert 1991), and whitefish stocks in the Great Lakes (Walker et al. 1993) and models of the effects of harvest regulations on numerous species (Johnson et al. 1992; Luecke et al. 1994; Allen and Miranda 1995; Beamesderfer and North 1995).

Three general types of models have been used for fisheries predictions. Models of the first type, surplus production, consider trends in a population as a whole in relation to harvest. The influences of growth, mortality, and reproduction are combined into a model of overall population change (Shaefer 1968). The second type predicts the yield that would be obtained from a year-class of fish throughout its lifespan as a function of harvest practices. These are known as yield-per-recruit models because the predictions are usually expressed as the yield per fish that is newly recruited to the stock. Such models do not explicitly account for the effects of variable recruitment on yield. The most common of these models is known as the dynamic-pool yield model, which was first proposed by Beverton and Holt (1957). The third category of models treats each age-group of a population separately and sums yield predictions among ages and years to obtain an overall estimate of long-term yield. Such predictions are used as a reference, or index, in determining optimal management policies (Walters 1969). Age-structured models require estimates of age-specific rates of reproduction, growth, and mortality, meaning that data requirements are greater than those of surplus production or yield-per-recruit models, which rely primarily on data that are readily available from commercial fishery landings.

#### **6.4.1 Surplus Production Models**

Surplus production models can be used to predict yield for a fishery by using information on either stock abundance or fishing effort. Surplus production models do not explicitly consider the growth, reproduction, and mortality rates in a population; rather, they deal primarily with relationships among overall stock biomass, yield, and fishing effort. These models have been popular because their parameters can be estimated from commonly available statistics, such as annual records of commercial harvest and effort.

Biological assumptions of surplus production models are similar to those discussed for stock-recruitment relationships. Populations are assumed to be regulated by density-dependent processes that affect reproduction and control survival and growth early in life, prior to the size (or age) at which fish are harvestable. Survival after this time is assumed to be density independent and is not necessar-

ily compensatory. An unexploited population would be expected to occur at some equilibrium level of abundance at which the number of fish added each year equals the number dying. If the stock is subjected to a fixed level of fishing mortality annually, the population is expected to reach a new equilibrium abundance at which the number of recruits produced annually exceeds the number of adults required to produce them. This excess of new recruits, termed surplus production, is available for exploitation. It is reasonable to expect that the greatest harvestable surplus will occur at some level of stock abundance that is less than the primitive equilibrium because at this equilibrium density-dependent regulation limits the number of recruits, and, by definition, there is no surplus production when recruitment exactly equals the stock size required for replacement.

Graham (1935) proposed a surplus production model based on the assumption that the annual change in biomass of a stock is proportional to the actual stock biomass and also to the difference between present stock size and the maximum biomass the habitat can support:

$$\frac{dB}{dt} = kB \frac{B_{\infty} - B}{B_{\infty}}, \quad (6.52)$$

where  $B$  is stock biomass,  $B_{\infty}$  is maximum biomass,  $k$  is the instantaneous rate of increase of stock biomass, and  $t$  is time in years (Ricker 1975).

This equation describes how the stock biomass would increase ( $dB/dt$ ) following a reduction of biomass from  $B_{\infty}$  to  $B$ . If the reduction in biomass to  $B$  has been brought about by human harvest, and if the level of fishing mortality (or effort) operates in a manner that stock biomass remains at  $B$  from year to year, the stock is regarded as being at equilibrium, and the yield that could be obtained annually from the fishery is  $dB/dt$ . Hence, equation 6.52 can be rewritten as:

$$Y = kB \frac{B_{\infty} - B}{B}, \text{ or} \quad (6.53)$$

$$Y = kB - \frac{k}{B_{\infty}}(B^2), \quad (6.54)$$

where  $Y$  is the annual yield when the stock is at equilibrium biomass  $B$ .

The primary purpose of developing the model usually is to determine maximum sustainable yield, the level of fishing effort required to obtain maximum sustainable yield, and the stock size at which this would occur. Equation (6.54) is a parabolic relationship (Figure 6.7) with the greatest yield ( $Y_{\max}$ ) at a stock abundance ( $B$ ) equal to  $B_{\infty}/2$ . By substituting  $B = B_{\infty}/2$  into equation (6.54), the maximum sustainable yield is found to be

$$Y_{\max} = \frac{kB_{\infty}}{4}, \quad (6.55)$$

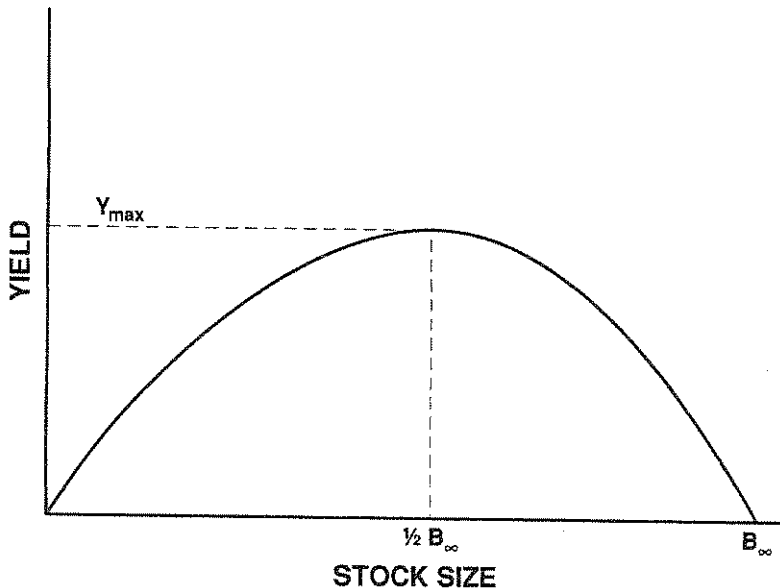
showing that estimates of  $k$  and  $B$  are needed to determine the maximum sustainable yield. Data on equilibrium yield obtained at two or more different levels of fishing effort are used to estimate these parameters (Ricker 1975). Shaefer (1954) outlined methods for estimating the parameters for nonequilibrium situations.

#### 6.4.2 Yield-per-Recruit Models

Dynamic-pool yield models are based on the premise that stock biomass varies with growth and mortality rates in the stock. Hence, yield is taken by humans from a changing, dynamic pool of available biomass that is increased by recruitment and diminished by mortality. Because biomass is the product of the average fish weight times the number of fish present, it is possible to predict yield ( $Y$ ) as

$$Y = \int_{t_c}^{t_p} FN_t W_t dt. \quad (6.56)$$

This indicates that total yield from a given cohort of fish in a stock is the integration of the force of fishing ( $F$ ) times the number of fish alive at age  $t$  ( $N_t$ ) and the average weight per fish at age  $t$  ( $W_t$ ) for the period of life during which the cohort is exploited. This period begins at the age when fish are first exploited ( $t_c$ ) and ends at the cohort's theoretical maximum age ( $t_p$ ). If a stock is at a stable equilibrium, the total yield each year would equal the total harvest of a cohort during its life, so equation (6.56) also estimates the annual equilibrium yield in such cases (Shaefer 1968).



**Figure 6.7** Relationship between yield and stock size for the surplus production model. The maximum sustainable yield ( $Y_{\max}$ ) theoretically occurs at a stock size equal to one-half of the maximum biomass ( $B$ ) that the habitat can support.

Dynamic-pool models are useful for predicting yield where fishing effort and the minimum size (or age) of capture can be regulated. Mesh size restrictions in a commercial fishery or minimum length limits in a recreational fishery would affect the age at which a cohort is first exploited. Regulations that influence fishing effort, such as restrictions on numbers of licenses issued, or those that otherwise influence fishing mortality, such as closed seasons or refuge zones, would affect  $F$ . By simulating the effects of different levels of  $F$  and age at first harvest, one can evaluate the extent to which yield is influenced and determine levels that produce maximum yield.

Implementation of the model requires mathematical expressions for changes in numbers and average weight of a cohort during its life span. The formulation most commonly used follows that originated by Beverton and Holt (1957):

$$Y = FR e^{-M(t_c - t_r)} W_\infty \sum_{n=0}^3 \left[ \frac{U_n}{F + M + nk} e^{-nK(t_c - t_0)} \right], \quad (6.57)$$

- $t_r$  = the age, in years, when fish reach a size at which they could be harvested;
- $t_c$  = the age at which fish actually are first harvested ( $t_c \geq t_r$ );
- $t_0$  = a constant introduced upon integration of equation (6.56), usually interpreted as the age at which fish length is 0;
- $F$  = annual instantaneous rate of fishing mortality, assumed equal for all fish older than age  $t_c$ ;
- $M$  = annual instantaneous rate of natural mortality, assumed constant over time and equal for all fish older than age  $t_r$ ;
- $R$  = recruitment, the number of fish alive in a cohort at age  $t_r$ ;
- $W_\infty, K$  = parameters of a von Bertalanffy growth model, assumed constant over time; and
- $U_n$  = a mathematical term used to simplify equation (6.57), where  $U_0 = 1, U_1 = -3, U_2 = 3,$  and  $U_3 = -1.$

The model includes three distinct periods during a cohort's life span. The first period is the prerecruitment phase, when the fish are too young (small) to be harvested. This stage begins at age  $t_0$  and ends at  $t_r$ , when the fish reach a size at which they could be harvested. The postrecruitment stage in the life cycle can include a preexploited phase as well as an exploited phase. The age at which the fish are first harvested ( $t_c$ ) sometimes exceeds  $t_r$  because of economic or social factors. For example, fishing technology may be available to harvest small fish commercially, but dollar value per unit biomass may be low for these fish, and it thus would be more profitable to harvest fish at a larger size (older age). In a recreational fishery,  $t_r$  would correspond to the age at which fish reached a size that anglers would harvest in the absence of length limits, whereas  $t_c$  would correspond to the age at which fish reached a legally imposed size limit.

The rate of fishing mortality ( $F$ ) and the age at first harvest ( $t_c$ ) can be manipulated by fisheries managers, and the influences of these on yield can be predicted using equation (6.57). Estimates of the number of recruits entering the

fishery are rare, and it has become customary to divide both sides of equation (6.57) by  $R$  so that the prediction of yield actually is yield per recruit rather than an estimate of total yield. Yield-per-recruit estimates ( $Y/R$ ) can be used as an index of actual yield for stocks that have relatively stable (albeit unknown) levels of recruitment. Gulland (1983) suggested that yield-per-recruit models are best suited to providing guidance on how to manage specific cohorts in stocks that have variable, environmentally regulated recruitment levels. In these cases, data from some index of cohort abundance at the time of recruitment could be used to define appropriate timing and levels of harvest.

In practice, fisheries managers are often more interested in how the yield-per-recruit predictions would vary across a range of management options, as opposed to obtaining point estimates for specific combinations of parameters. In the dynamic-pool model, it is possible to have many combinations of  $F$  and  $t_c$  that would produce the same  $Y/R$ . After calculating yield for ranges of  $t_c$  and  $F$  in a given fishery, the results can be summarized by plotting isopleths that connect the same  $Y/R$  estimates (Figure 6.8). The plots then can be used to choose desirable levels of  $F$  and  $t_c$  for the fishery.

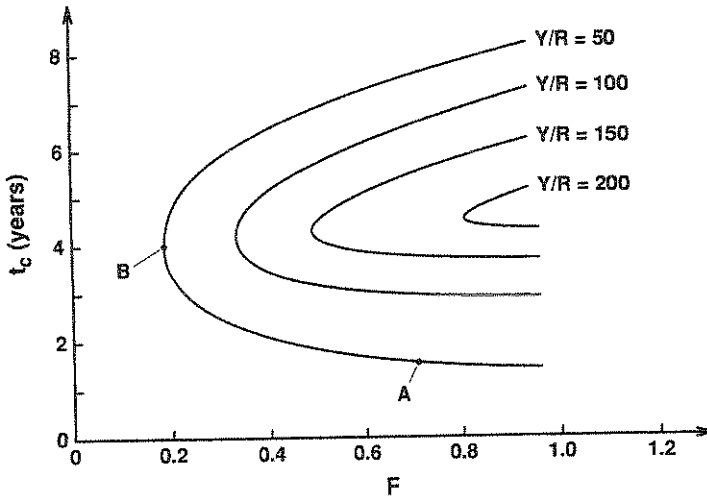
For example, suppose that the fishery represented in Figure 6.8 has been operating at point A, where  $F$  is 0.7,  $t_c$  is 1.5 years, and  $Y/R$  is 50. If our goal is to increase  $Y/R$ , it is clear that we could accomplish the most by altering  $t_c$  rather than increasing  $F$ . If  $F$  is maintained at 0.7,  $t_c$  should be increased to about 4.5 years to maximize yield. Thus, by delaying the age at first harvest by about 3 years, we would expect a three- to fourfold increase in  $Y/R$ .

If, however, the fishery was presently operating at point B on Figure 6.8,  $Y/R$  still equals 50, but  $F$  is 0.2 and  $t_c$  is 4. In order to increase  $Y/R$  from this point, the most effective approach will be to increase  $F$ , possibly by allowing or promoting increased effort or improved harvest techniques. An approximate fourfold increase in  $F$  would be required to approach the maximum yield.

Despite the inclusion of the adjective dynamic in the name dynamic-pool model, the suitability of using the yield predictions for making management decisions is dependent on several assumptions of stability or constancy of the stock's vital statistics. For example, the model assumes that natural mortality and growth rates remain constant over time and are independent of stock size. This may be a reasonable assumption for stable environments or for stocks where postrecruitment survival and growth are relatively constant from year to year. The model also assumes that the fishery has an equal influence on all ages of fish older than  $t_c$  and that rates of growth and natural mortality are not influenced by changes in the level of harvest.

### 6.4.3 Age-Structured Models

The basic structural unit of a fish population is the age-group. Each age-group has rates of growth, natural mortality, fishing mortality, and reproduction that can vary with time and differ from those of other age-groups. Age-structured models incorporate these differences in an attempt to provide realistic predictions of population behavior.



**Figure 6.8** Summary of yield predictions obtained from the Beverton-Holt dynamic-pool yield model across a range of age at first capture ( $t_c$ ) and fishing mortality ( $F$ ). Lines are isopleths indicating combinations of  $t_c$  and  $F$  expected to produce the same yield per recruit ( $Y/R$ ). Points A and B are discussed in text.

Population processes most frequently included in age-structured models are illustrated in Figure 6.9. This graph shows that the number of fish alive at any age is a function of the number alive in the previous year, less the numbers lost to fishing and natural causes. The number alive at age 0, however, is a function of the reproductive rates and age structure of the entire population; this feature is not included in the surplus production or yield-per-recruit models discussed earlier. Age-structured models of population number can be converted to biomass models by including a predictor of size at age, such as a von Bertalanffy or Gompertz growth model, or by using observed size-at-age data for a given population.

Walters (1969) formulated an age-structured model for fish population studies and illustrated its application for making management decisions in a brook trout fishery. He used an exponential model to predict the number ( $N$ ) of brook trout in a year-class that would survive from year to year, given observed age-specific rates of instantaneous natural mortality ( $M$ ) and hypothetical rates of instantaneous fishing mortality ( $F$ ):

$$N_{i+1} = N_i e^{-(F_i + M_i)}. \quad (6.58)$$

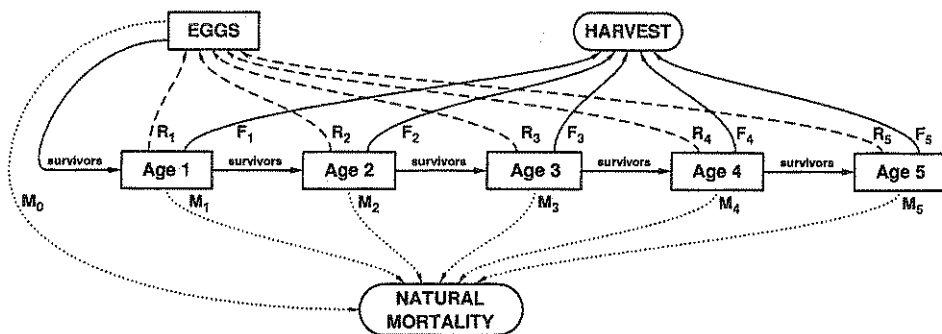
The model was used to predict total population size and yield under conditions of either no fishing, a constant rate of fishing over time and among ages, or a periodic fishery.

Taylor (1981) claimed that fisheries models available prior to the 1980s were either too simplified or too complicated to be useful to inland fisheries managers, and he attempted to solve this problem by developing a computerized population simulator specifically aimed at inland fisheries. His model, termed a generalized inland fishery simulator, is fundamentally similar to the one proposed by Walters (1969), but it uses a different mathematical approach and can incorporate a num-

ber of population processes not considered by Walters. Examples of the application of Taylor's model have been reported by Taylor (1981) for rainbow trout, Zagar and Orth (1986) for largemouth bass, Johnson et al. (1992) for walleye, and Luecke et al. (1994) for lake trout.

Greater versatility for addressing management options of inland fisheries is achieved from age-structured models. However, a great deal of information is needed to estimate model parameters, and, in many cases, data are inadequate to develop the model for a specific fishery. According to Taylor (1981), the minimum data requirements are (1) the initial age structure or number of fish in each age-class, (2) the average length-at-age relationship for the population, (3) weight-length regression coefficients, and (4) natural and fishing mortality rates.

During the 1990s, there has been increased use of mathematical models that follow large numbers of individual animals simultaneously to describe population dynamics. Unlike the previously described population models, which implicitly assume that all individuals in the modeled population respond identically, individual-based models allow the study of individual variation as well as calculation of the average dynamics for a population (DeAngelis and Gross 1992; Chambers 1993). Actually, the development of individual-based models is an endpoint reached by the reduction of a population into its component parts. We may initially think that a population needs to be categorized according only to age-group but then find that the distinction of gender, size, or other subdivision is necessary to represent dynamics adequately (Crowder et al. 1992). Ultimately, this process leads to the modeling of each individual separately and using the results of numerous simulations to develop generalities about the subdivisions or the population as a whole. Some recent applications of individual-based models include evaluations of population dynamics of young-of-the-year striped bass (Rose and Cowan 1993), growth of young bluegills (Breck 1993), and contaminant accumulation in stocked lake trout (Madenjian and Carpenter 1993).



**Figure 6.9** Representation of an age-structured population with maximum fish age of 5 years. Age-specific rates of reproduction ( $R_i$ ), fishing mortality ( $F_i$ ), and natural mortality ( $M_i$ ) regulate survival from one age to the next.