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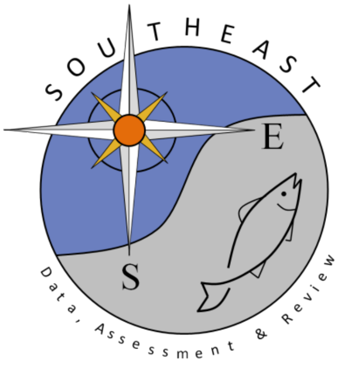

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Introduction

Because of the substantial economic value of fisheries, population dynamics of fish (here taken to include similarly exploited living resources such as crustaceans, mollusks, reptiles, and marine mammals) is one of the oldest realms in quantitative population ecology. For over 100 years, scientists have been developing mathematical models of fish populations.

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Any such field will have specialized terms. In fish population dynamics, this includes the term ‘stock’, which for practical purposes is synonymous with the biological term ‘population’. In this article, the terms stock and population are used interchangeably.

The goals of much work in fish population dynamics are to evaluate the effects of fishing and to provide advice for policy makers on whether fishing should be increased or decreased. For that reason, special attention has been given to estimating the fishing mortality rate and whether it is above or below some optimal value. This focus is also relevant biologically because in many exploited stocks, the strongest force of mortality on adult fish is fishing.

Basic Forces

The simplest representation of the dynamics of a fish stock, represented in units of biomass, is that due to Russell:

$$B_{t+1} = B_t + (G_t + R_t) - (Y_t + D_t) \qquad [1]$$

where B is stock biomass, t denotes time (conventionally measured in years), G is somatic growth of individuals, R is biomass increase due to recruitment (addition of young individuals to the stock), Y is yield (catch in weight) from fishing, and D is loss of biomass from deaths due to other causes. These are the four basic forces considered in models of fish population dynamics.

An equation parallel to eqn [1] can be written for stock size in numbers. Notably, it would omit the term expressing somatic growth.

Generally, external influences such as environmental forcing are either assumed unimportant or modeled as modifying one of the four basic forces. Because eqn [1] models a closed stock, migration in or out is excluded by definition. Stock mixture is usually modeled as exchange between otherwise independent stocks.

Time

Treatment of time in fish population dynamics is flexible. By convention, stock size in number or weight N_t or B_t refers to the start (however defined) of year t. Yield Y_t and catch in numbers C_t are annual sums. Recruitment R_t is usually an annual number or biomass, and is typically modeled as occurring at a discrete point during the year, rather than as a continuous process. This practice may reflect the origin of much fish population dynamics theory in higher latitudes, where seasonality is pronounced, as are the corresponding biological processes.

Models of individual growth (see section ‘Growth of Individuals’) are usually continuous in time, but size at age is often simplified to an annual average, rather than a continuously varying measure. In modeling mortality, instantaneous – rather than simple – rates are used, with the notable exception of some salmon models, or in simplified models written in discrete time. Reflecting the conventions above, a detailed fish population model may combine continuous-time processes (fishing and natural deaths) with discrete-time processes (recruitment and growth). Considerable variation in approach is found among applications; here, equations typically will be given with implied 1-year time steps.

Equilibrium, Sustainability, and Maximization

These three concepts are widely used in fishery models. In the context of a deterministic analysis, a sustainable yield Y_e is one that can be taken every year, the result being a population in equilibrium. Under models with density dependence, a population can reach equilibria at various levels of removals; therefore, each equilibrium stock size has a corresponding sustainable yield, $Y_e \geq 0$.

A particularly durable concept is that of maximum sustainable yield (MSY), which is often conditioned on some pattern of removals (e.g., taking fish starting at a certain age). In general, $Y_e = \mathrm{MSY}$ occurs at some intermediate stock size.

Biological Reference Points for Management

Biological reference points (BRPs) are benchmarks for gauging the status of a stock or fishery (Table 1). Using a metric such as fishing mortality rate (F) or standing biomass (B), BRPs provide an avenue for rational guidance of fishery management. Their estimation is a primary goal of most fishery models.

Common BRPs come in two varieties: limit reference points (LRPs) and target reference points (TRPs). An LRP represents the maximum degree of safe exploitation, and a TRP represents the degree of exploitation sought by management. Given uncertainties in fishery modeling and management, the difference between a limit and target provides a buffer to prevent frequent overexploitation.

Maximum sustainable yield is the basis for several BRPs, such as F_{MSY} or B_{MSY}, often preferred on theoretical or legal grounds. When data are not sufficient to estimate MSY reliably, other BRPs are commonly used as proxies for MSY reference points. Probably the most widely applied proxies are those based on per-recruit analysis (see section ‘Per-Recruit Analyses’). Almost all common BRPs require equilibrium assumptions.

Table 1 Common biological reference points (BRPs) and typical applications as target (TRP) or limit (LRP)

BRP	*Description*	*Application*
Mortality-based biological reference points		
F_{MSY}	Fishing mortality rate (F) at maximum sustainable yield	LRP
$X\%\ F_{\mathrm{MSY}}$	F equal to $X\%$ of F_{MSY}; $X<100$	TRP
F_{crash}	F giving stock extinction	LRP
F_{mbp}	F at maximum biological production	TRP
F_{max}	F giving maximum yield per recruit (YPR)	LRP
$F_{0.1}$	F where slope of YPR curve is 10% that at the origin	TRP
$F_{X\%}$	F giving $X\%$ of spawning biomass per recruit at $F=0$	LRP
F_{low}	F giving >50% of years with stock replacement	TRP
F_{med}	F giving 50% of years with stock replacement	LRP
F_{high}	F giving <50% of years with stock replacement	LRP
F_{loss}	F giving replacement of lowest observed biomass	LRP
Biomass-based biological reference points		
B_{MSY}	Biomass (B) at maximum sustainable yield	TRP
$X\%\ B_{\mathrm{MSY}}$	B equal to $X\%$ of B_{MSY}; $X>100$	TRP
$X\%\ B_{\mathrm{MSY}}$	B equal to $X\%$ of B_{MSY}; $X<100$	LRP
B_{loss}	Lowest observed B	LRP
B_{pa}	B below which expected recruitment is decreased	LRP
$B_{50\%\mathrm{R}}$	B at which recruitment is one half its maximum	LRP
$B_{X\%}$	B corresponding to $X\%$ of B at $F=0$	LRP

Source: Adapted from Collie JS and Gislason H (2001) Biological reference points for fish stocks in a multispecies context. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2167–2176, with permission from NRC Research Press.

Article Structure

The rest of this article is structured as follows: First, each of the four basic forces of stock dynamics (eqn [1]) is considered in turn. Then, models that include various combinations of those forces are described, starting with relatively simple models, and progressing to more detailed ones. Finally, we discuss extensions of conventional models. Selected content reflects a decided emphasis on marine systems.

Growth of Individuals

Growth is of interest both as the mechanism by which fish add weight (thus increasing the stock's biomass) and because growth is the link between size and age. The most common growth model is the von Bertalanffy model of length at age (henceforth, VBGF):

$$L_a = L_\infty\left(1 - \mathrm{e}^{-\kappa(a-a_0)}\right) \qquad [2]$$

where L_a is length at age a; model parameters are L_∞ (asymptotic length), κ (growth rate), and a_0 (theoretical age at length zero). This model fits most observed data on fish growth reasonably well, especially when the youngest ages are excluded.

The relationship between fish weight (W) and length (L) is commonly modeled with the allometric function

$$W = gL^b \qquad [3]$$

where g and b are constants. Weight would be expected to be proportional to body volume, and indeed in most data sets, it is found that $\hat{b} \approx 3$. (We use the notation $\hat{x}$ throughout to refer to an estimate of quantity x.)

Equations [2] and [3] can be combined to form a model of weight at age:

$$W_a = W_\infty\left(1 - \mathrm{e}^{-\kappa(a-a_0)}\right)^b \qquad [4]$$

Here, $W_\infty \equiv g(L_\infty)^b$ is the asymptotic weight of a fish; other parameters are as in eqns [2] and [3].

Growth – Other Considerations

The statistical distribution of size at age is usually modeled as normal; however, no single error structure is used universally when fitting the VBGF. Multiplicative error is assumed most frequently, reflecting the observation that variability of size at age typically increases with age. Additive error is sometimes preferred in cases where variability seems relatively constant with age; for example, when modeling narrow age ranges.

Several modifications to the VBGF allow seasonal variation in growth. One example is due to Hoenig and Hanumara:

$$L_a = L_\infty \left(1 - \mathrm{e}^{-\kappa(a - a_0 - \phi(a) + \phi(a_0))}\right) \qquad [5]$$

where

$$\phi(a) = \frac{\delta}{2\pi}\sin\left(2\pi(a - a_1)\right) \qquad [6]$$

The scale of seasonal variation is determined by δ; the starting point of the seasonal cycle, by a_1. Growth becomes negative seasonally if $\delta > 1$.

In fitting the VBGF, estimates of κ and L_∞ tend to be highly correlated, which makes comparison of growth rates difficult between populations or over time. Hotelling's T^2 statistic has been suggested for testing such comparisons.

The Gompertz model is often considered superior to the VBGF in modeling growth of young fish. Its parameterization is similar to that of VBGF:

$$W_a = W_\infty \mathrm{e}^{-(1/\kappa)e^{-\kappa(a - a_0)}} \qquad [7]$$

where W_∞ is the asymptotic weight and κ the growth coefficient. The same form is used in modeling weight or length.

Bioenergetic Models

Bioenergetic models describe the factors affecting the growth of an individual over its lifetime. The rate of change in average individual biomass (B') is modeled as the sum of weight-specific rates of physiological processes: consumption (C'), respiration (R'), egestion (F'), excretion (U'), and reproductive loss (G'):

$$\frac{\mathrm{d}B'}{\mathrm{d}t} = C' - \left(R' + F' + U' + G'\right) \qquad [8]$$

These process rates in turn are considered functions of other variables, such as water temperature or food availability. A population model based on bioenergetics must also consider mortality and recruitment, two forces not included in eqn [8].

Recruitment

The term 'recruitment' in fish population dynamics denotes, generally, addition of fish to the stock or to some part of the stock (e.g., the part vulnerable to fishing). In this broad sense, recruitment could be caused by growth, migration, or spawning. Here, we use recruitment in the narrower sense of addition due to reproduction.

Most fish species (cartilaginous fishes being a notable exception) are highly fecund, a property related, in an evolutionary sense, to a period of high mortality in the life cycle. This period generally is early in life, usually before age 1. In most species, early mortality is quite stochastic from year to year, as is the resulting recruitment. To simplify population models, the age at which recruitment occurs in a stock is conventionally defined as an age soon after year-class strength has been fixed.

Recruitment models postulate a relation between recruitment and total egg production. In most species, egg production of a mature female is highly correlated to her body mass. Thus, in practice, many recruitment models predict recruitment R_t from spawning biomass S_t, the total body mass of all spawning females. In species with ontogenetic sex change, both males and females may be counted. Either way, recruitment models are central to prediction of future stock trajectories and also to estimation of many management benchmarks.

Linear Recruitment Model

The simplest spawner-recruit model assumes a linear (density-independent) relationship between spawning biomass and recruits:

$$R_t = \alpha S_t$$

Under this model, recruitment has no upper limit, which could allow population growth to infinity. For that reason, the linear model is seldom applied to real populations, but its simplicity retains value in theoretical studies.

Spawning Success and Density Dependence

The quantity $\psi \equiv R/S$, termed spawning success, is useful in describing and understanding recruitment models. In the linear model above, spawning success is assumed constant at $\psi = \alpha$. More typical recruitment models assume a nonlinear (density-dependent) relationship between S and R, in which ψ declines as S increases (**Figure 1**).

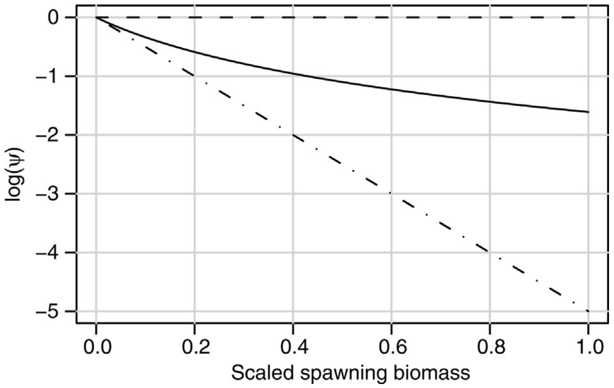

Figure 1 Examples of spawning success (ψ), in terms of recruits per spawner, from three spawner-recruit models: linear (dashed), Beverton–Holt (solid), and Ricker (dash-dot).

Beverton–Holt Recruitment Model

Under the Beverton–Holt model, recruitment approaches an asymptote as spawning biomass increases:

$$R = \frac{\alpha S}{\beta + S} \quad \text{or} \quad R = \frac{S}{\alpha' + \beta' S} \qquad [9]$$

The versions are equivalent, given $\alpha = 1/\beta$ and $\beta = \alpha'/\beta'$. Here α is the asymptotic level of recruitment; β, the level of S at which recruitment is half its asymptotic level.

Unfortunately, spawner-recruitment data rarely fit models well, leading to considerable uncertainty. An alternative form of the Beverton–Holt model uses external data to constrain or fix recruitment parameters. In this form (**Figure 2(a)**), the two parameters are the recruitment R_0 from the stock when unfished and steepness h, defined as the proportion of R_0 produced by 20% of S_0, the spawning biomass of the unfished stock. (The value of 20% is arbitrary but conventional.) In this parametrization, the model becomes

$$R = \frac{0.8 R_0 b S}{0.2 \Phi_0 R_0 (1 - b) + (b - 0.2) S} \qquad [10]$$

with $0.2 < h < 1.0$. Steepness quantifies resilience to exploitation, and its values have been estimated by several authors through meta-analysis. Although R_0, like α, is a scaling parameter, it scales recruitment to a specific stock size, not to an asymptotic recruitment that may occur only at infinite population size.

A third apparent parameter in eqn [10] is Φ_0. This is the unfished spawning biomass per recruit (see section '**Per-Recruit Analyses**') corresponding to R_0, and it is completely determined by the stock's mortality, maturity, and growth schedules (when weight is used to quantify S). With recruitment at age $a = 1$, and given spawning contribution at the beginning of each year

$$\Phi_0 = \sum_{a=1}^{A} W_a \mu_a e^{-M(a-1)} \qquad [11]$$

where W_a is weight at age, μ_a is the proportion mature at age, M is the natural mortality rate, and A the oldest age considered.

Ricker Recruitment Model

Under the Ricker recruitment model, the largest recruitment occurs at an intermediate level of spawning biomass. The usual form of the Ricker model is

$$R = \alpha S e^{-\beta S} \qquad [12]$$

Here, α is a scaling factor, $\alpha = \lim_{S \to 0} (\psi)$, and β controls the level of density dependence. The Ricker model (**Figure 2(b)**) can be written in terms of R_0 and h as

$$R = \frac{S}{\Phi_0} \exp\left\{ b \left(1 - \frac{s}{\Phi_0 R_0} \right) \right\} \qquad [13]$$

but here, $0 < h < \infty$.

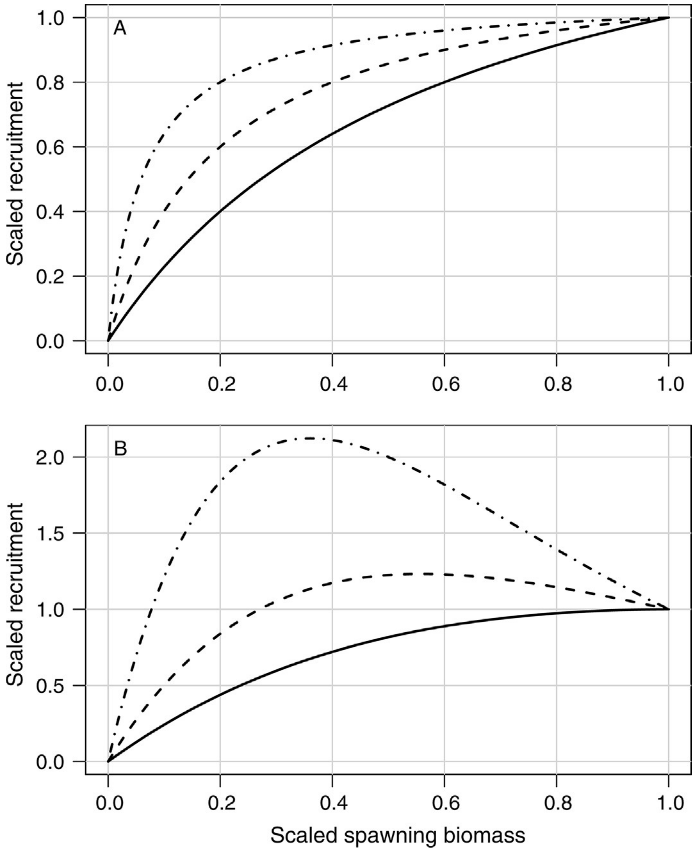

Figure 2 Spawner-recruit curves for various levels of steepness, with *x*-axis scaled to virgin spawning biomass and *y*-axis scaled to virgin recruitment. (a) Beverton–Holt model with steepness $h = 0.4$ (solid), 0.6 (dashed), or 0.8 (dash-dot); (b) Ricker model with steepness $h' = 0.98$ (solid), 1.79 (dash), or 2.77 (dash-dot). These values satisfy $h' = \log(4h) - \log(1 - h)$, the intrinsic population growth rate.

Recruitment – Other Considerations

Although the Beverton–Holt and Ricker models are most widely used, other density-dependent models have been proposed, such as the Deriso–Schnute, Shepherd, and gamma models. Many are generalizations of the Beverton–Holt or Ricker models or both. The following generalization of the Beverton–Holt model allows for depensation (or Allee effect: a decline in spawning success (see section '**Spawning Success and Density Dependence**') as S becomes small):

$$R = \frac{\alpha S^{\gamma}}{1 + \beta S^{\gamma}} \qquad [14]$$

Here, depensation occurs for $\gamma > 1$.

In the recruitment models described above, recruitment and spawning success ψ are considered a function purely of S. More detailed models add explanatory factors such as environmental forcing or trophic interactions. Still other models rely less on functional form, using non-parametric or semi-parametric approaches.

Mortality

Total Mortality Rate

Mortality includes all factors reducing abundance of a closed population. In fish models, mortality is typically modeled as an instantaneous rate Z. Thus, abundance decreases by a constant fraction in each instant of time:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -ZN \qquad [15]$$

The solution to eqn [15] at time t is

$$N_t = N_0 \mathrm{e}^{-Zt} \qquad [16]$$

given initial abundance N_0 at $t = 0$. The instantaneous mortality rate Z carries units inverse to those of t; for example, when t is expressed in years, Z has units year^{-1}. The annual proportion that dies is $1 - \exp(-Z)$.

If the population is structured by age, eqns [15] and [16] apply to each portion of the population, so that

$$N_{a+1,t+1} = N_{a,t}e^{-Z_{a,t}} \quad [17]$$

where $N_{a,t}$ is abundance at age and time, and $Z_{a,t}$ is annual mortality rate at age.

The total mortality rate Z (age-specific or otherwise) is often partitioned into components, usually into natural mortality rate M and fishing mortality rate F, assumed noncompensatory. A property of instantaneous rates is that mortality from various sources is additive:

$$Z = F + M \quad \text{or} \quad Z_a = F_a + M_a \quad [18]$$

This allows the fishing mortality rate, a primary focus of fishery management, to be considered separately from other sources of mortality.

Catch-curve analysis

Catch-curve analysis is a heuristic method of estimating Z. Consider a cohort exploited at constant F_a for all ages $a \geq a_r$. When the logarithm of relative abundance at age is graphed against age, the right-hand portion of the graph, representing $a \geq a_r$, should be a straight line with slope $-Z$. Due to stochasticity and sampling error, the decline will not be precisely linear, but a straight line can be fitted to estimate Z. A major assumption of this method is that a_r is chosen correctly. To make the analysis easier, a 'synthetic cohort' is often used, that is, relative abundance at age in a single year is graphed; this entails the additional strong assumption of constant recruitment. The method has fallen into relative disuse because estimates are quite sensitive to violations of assumptions, and those violations are difficult to detect without additional information.

Natural Mortality Rate

The natural mortality rate of a fish stock is notoriously difficult to estimate. Tagging studies are used, but in large or open systems, such as the ocean, tagging studies are often infeasible or provide hopelessly imprecise estimates. When both the total mortality rate and the fishing mortality rate can be estimated, M is known by subtraction in eqn [18]. More commonly, a natural mortality rate is approximated indirectly by drawing on empirical relationships between M and observable life-history characteristics.

Many of these relationships have been derived through meta-analysis. For example, Hoenig estimated a linear relationship giving the total mortality rate Z as a function of maximum age A. The work was based on data from 134 stocks, comprising 79 species of lightly exploited fish, mollusks, and cetaceans:

$$\hat{Z} = 1.709 - 1.084 \log(A) \quad [19]$$

For small sample sizes ($n < 200$), Hoenig recommended this variant:

$$\hat{Z} = \frac{\log(2n+1)}{A - a_r} \quad [20]$$

where a_r is the earliest age fully represented in the sample. When using either equation, the result is an estimate of the total mortality rate Z, from which an estimate of M can be obtained by subtracting F, if known. Another possibility is applying the method to an unfished or lightly fished stock and considering the result an estimate of M.

Alverson and Carney developed an empirical estimator of M based on the age at which an unfished cohort reaches its maximum weight, sometimes called the critical age a^*:

$$\hat{M} = \frac{3\kappa}{e^{\kappa a*} - 1} \quad [21]$$

where κ is the growth coefficient of VBGF (eqn [2]). Their analysis further suggested $a^* \approx 0.38\, A$.

Pauly examined data from 84 species of marine and freshwater fishes, linking M to average water temperature (T) in celsius and the VGBF growth parameters of eqn [2] or [4]:

$$\begin{aligned}\log(\hat{M}) = &-0.015 + 0.463 \log(T) \\ &+ 0.654 \log(\kappa) - 0.279 \log(L_\infty)\end{aligned} \quad [22a]$$

or

$$\begin{aligned}\log(\hat{M}) = &-0.485 + 0.463 \log(T) \\ &+ 0.676 \log(\kappa) - 0.082 \log(W_\infty)\end{aligned} \quad [22b]$$

In the above, L_∞ is in centimeters; W_∞, in grams.

Natural mortality at age

In many stocks, natural mortality appears to decrease with age. Several studies have suggested that M_a can be estimated from weight at age W_a. Lorenzen concluded that the relationship differs among ecosystems. For oceanic ecosystems, his model is

$$\hat{M}_a = 3.69 W_a^{-0.305} \tag{23}$$

Charnov later proposed a relationship between natural mortality and length, $M = K(L/L_\infty)^{-1.5}$, which can be converted to age-based mortality, given size at age. Despite questions about estimating M_a, the assumption of M decreasing with age is increasingly preferred to the alternative of M constant with age. To estimate M_a, equations such as those of Lorenzen or Charnov can be used directly or their estimates scaled to other information on mortality over the lifespan.

Fishing Mortality Rate, Fishing Effort Rate, and Catch

The instantaneous rate of fishing mortality F denotes the force of the fishery on the stock. The F and abundance N determine the rate of catch:

$$\frac{dC}{dt} = FN \tag{24}$$

The fishing mortality rate generally must be estimated from data, often including data on the fishing-effort rate E, a measure of the amount of fishing gear used per unit time. The theoretical relationship between the two is $F = qE$, where q, the 'catchability coefficient', is constant and specific to the gear, vessel, location, and possibly other factors. Much effort in fishery modeling is devoted to estimating q and standardizing E for a particular fishery.

Catch C_t over period t can be found by integrating catch rate (eqn [24]) with respect to time. Because N_t depends on M as well as F, the solution requires knowing the natural mortality rate. A formulation that does not require M explicitly (though it does implicitly) is

$$C_t = F_t \overline{N}_t \tag{25}$$

where F_t is the (constant) fishing mortality rate during period t, and $\overline{N}_t$ the average population size in the same period.

For an age-structured population, eqn [24] is applied to each age class:

$$\frac{dC_a}{dt} = F_a N_a \tag{26}$$

Given M_a, eqn [26] can be solved by integration to obtain catch at age over the year (or any time interval). The result is the Baranov catch equation, a cornerstone of fishery models:

$$C_a = \frac{F_a}{Z_a} N_a \left(1 - e^{-Z_a}\right) \tag{27}$$

Given annual catch at age $C_{a,t}$, annual total catch is simply the sum across ages, $C_t = \Sigma_a C_{a,t}$. The annual yield (catch in weight) is

$$Y_t = \sum_a W_a C_{a,t} \tag{28}$$

where the W_a are the average weights at age during the period.

Landings, discards, and removals

The ideal fishery model recognizes several categories of fish encountered by fishing gear and accounts for all resulting mortality. 'Catch' means the fish taken by the gear. 'Landings' means all the fish brought to land. The difference between landings and catch forms the 'discards': fish caught and thrown back. The probability of death of a discarded fish (P_d) depends on many factors, including its biology and the mode of fishing. If 100 fish are discarded, the removals (total deaths due to fishing) are then the landings plus 100 P_d. Discarding occurs for numerous reasons, such as management regulations, market conditions, or undesirability of by-catch (i.e., non-targeted or unintended catch).

Reliable estimation of discards and the discard-mortality fraction P_d is difficult. The former may require an at-sea observer program, and the latter, field and laboratory experimentation. Because of these difficulties, models that theoretically require data on total removals often are used with landings data instead. This imparts a bias, which is most troublesome when the fraction of the catch discarded changes over time, as under changing regulations, increasing abundance, or highly variable recruitment.

Selectivity

An age-specific fishing mortality rate is often treated as the product of a full ('fully selected') fishing mortality rate F and selectivity at age s_a. Selectivity measures both availability (presence of fish in the fishing area) and vulnerability (susceptibility to fishing gear). Its value is typically scaled to that of the most selected age or ages, for which $s_a \equiv 1$. Selectivity may be estimated for each age, but often a parametric function of age or length is used, such as the logistic equation

$$s_a = \frac{1}{1 + e^{-\eta_1 (a-\eta_2)}} \qquad [29]$$

with parameters η_1 controlling the slope and η_2 determining the location of inflection (age at 50% selection). If selectivity is not monotonically increasing, but rather dome shaped, it can be described by the double-logistic equation,

$$s_a = \left(\frac{1}{1 + e^{-\eta_1 (a-\eta_2)}}\right)\left(\frac{1}{1 + e^{-\eta_3 (a-\eta_4)}}\right) \qquad [30]$$

with parameters η_1 and η_3 controlling slopes of ascending and descending portions of the curve, respectively, and η_2 and η_4 determining the locations of inflection (Figure 3).

Many parametric and non-parametric functions have been developed for estimating selectivity, ranging widely in the number of parameters. Selectivity models also may include time dependence, to account for changes in fishing methods. For example, in eqn [30], location parameters (η_2 or η_4) could be treated as functions of time. A more common approach lets selectivity vary among blocks of years, yet remain constant within each block, to account for changes in fishing regulations or practices.

Models of Population Dynamics

Per-Recruit Analyses

Recruitment in many fish stocks is highly stochastic. To evaluate fishery management measures in spite of this characteristic, 'per-recruit' analyses were developed. By computing the utility (in some sense) expected from a typical fish from recruitment through death, such analyses sidestep the uncertainty associated with recruitment. Per-recruit analyses are widely used to model yield (catch in weight) and spawning contribution. However, other measures of utility, such as economic value, can be modeled equally well.

Yield per recruit (YPR) expresses yield as a function of overall fishing mortality rate, conditioned on the selectivity pattern (Figure 4). It is calculated as

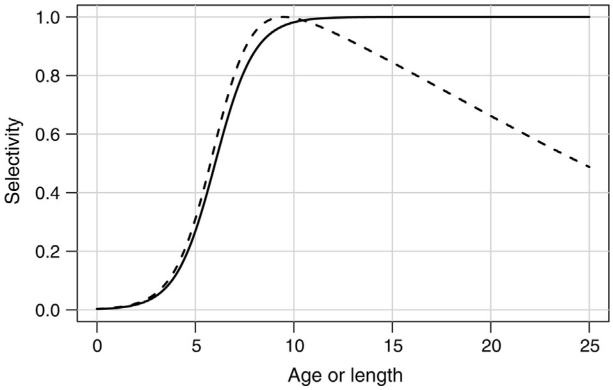

Figure 3 Example of logistic (solid) and dome-shaped (dashed) selectivities.

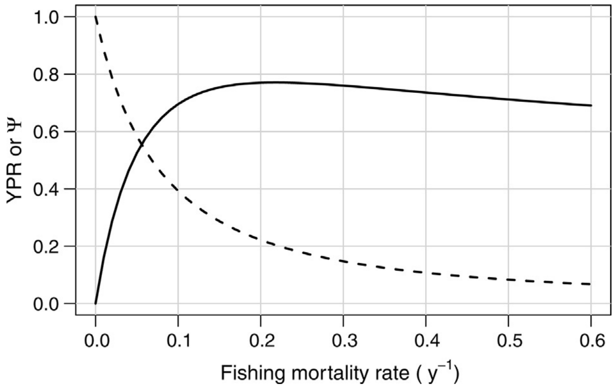

Figure 4 Example of per-recruit analysis, based loosely on tilefish (*Lopholatilus chamaeleonticeps*) off the southeastern United States. Solid line represents yield per recruit (YPR; weight per fish); dashed line represents spawning potential ratio (Ψ; unitless).

$$\mathrm{YPR} = \frac{1}{R}\sum_{a} Y_a \tag{31}$$

where Y_a is yield at age (eqn [28]), and R is an arbitrary recruitment used to initialize abundance at the first exploited age. If selectivity shifts to older fish, YPR increases due to greater opportunity for somatic growth, but decreases due to the prolonged force of natural mortality.

As stocks have become more heavily exploited, focus has broadened from maximizing yield to maintaining stock viability through adequate spawning biomass. This is the motivation for analysis of spawning biomass per recruit (SPR or Φ_F). Specifically, SPR quantifies the amount of reproductive output per recruit expected under different fishing regimes. Computation is similar to that of unfished SPR (eqn [11]), with the same assumptions and fishing mortality included:

$$\Phi_F = \sum_{a=1}^{A} W_a \mu_a \mathrm{e}^{-Z(a-1)} \tag{32}$$

It is often convenient to express SPR relative to that with no fishing (Φ_0), a ratio known as spawning potential ratio (**Figure 4**). Here, we propose the notation $\Psi_F = \Phi_F/\Phi_0$. This ratio scales SPR to a species' reproductive potential, which allows more meaningful comparison across stocks and species than does SPR alone. Unfortunately, the abbreviation SPR has been used by different authors to mean either Φ or Ψ, leading to considerable confusion.

Indices of Abundance

In rare situations, field surveys can estimate absolute population abundance. More typically, indices of abundance are used. Indices ideally are proportional to abundance, either of the entire population or of the fraction sampled, such as a range of length or ages. Applications range from using the index alone as an indicator of stock status to incorporating indices into formal assessment models.

Abundance indices are developed from catch per unit of standardized effort U. The underlying relation is a variant of eqn [25]:

$$C_t = qE_t\overline{N}_t \text{ and thus } U_t \equiv C_t/E_t = q\overline{N}_t \tag{33}$$

where C_t is catch in numbers, E_t is standardized fishing-effort rate (e.g., tows, hauls, or sets per unit time), $\overline{N}_t$ is average population abundance, and q, the catchability coefficient, is often assumed constant.

The assumption of constant q is reasonable in a designed study, where methods remain constant and are based on random sampling. In contrast, when abundance indices are developed from fishery-dependent data, removing variation in q (a step known as 'effort standardization') can be difficult. Catchability may vary for biological or nonbiological reasons. If fishing effort is mainly along the edge of a stock's range, U computed from fishery data may decline more quickly than abundance. Conversely, if catches saturate at some level due to finite fishing capacity, U may not increase when abundance does. Such hyperstability of U can occur also when abundance decreases, because skillful fishermen often maintain their catch rates at lower stock sizes. This phenomenon is especially pronounced in schooling species, where aggregations may be easy to locate. A related issue is the increase in q over time due to improvements in fishing gear, vessel efficiency, and navigation technology. Studies have estimated compounding efficiency increases in several fisheries at around 2% per year.

Surplus-Production Models

Surplus-production models (production models) were the first fishery models to consider all four forces of population dynamics (eqn [1]) together with density dependence. In contrast to yield-per-recruit or early catch–age models, the population is modeled as persisting across years and generations by means of recruitment. Production models are not detailed: the population is considered an undifferentiated biomass, without age structure, and dynamic forces are combined into few parameters.

Schaefer model

In all production models, production (rate of increase) per unit biomass is highest at low population sizes and decreases at larger ones, becoming zero at the carrying capacity K. A simple way to express this is with the equation

$$\frac{1}{B}\frac{\mathrm{d}B}{\mathrm{d}t} = r - rB/K \tag{34}$$

which implies

$$r = \lim_{B\to 0} \frac{1}{B}\frac{\mathrm{d}B}{\mathrm{d}t} \tag{35}$$

defining r, the 'intrinsic rate of increase'. From eqn [34], the population production without fishing is that of logistic growth:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = rB - rB^2/K \qquad [36]$$

which forms a parabola. Population production is typically called 'surplus production', meaning the surplus of recruitment and growth above mortality. If the surplus is caught in the fishery rather than contributing to population growth, it is denoted 'equilibrium' or 'sustainable' yield (Y_e), synonyms for the annual yield that can be taken from a population at equilibrium. Each population has many possible sustainable yields, depending on the biomass level at which it attains equilibrium. That level in turn is controlled by the steady-state fishing mortality rate. Maximum sustainable yield (MSY) is found at the peak of the parabola formed by eqn [36] and is related to model parameters by $\mathrm{MSY} = rK/4$ (**Figure 5**). The biomass from which MSY can be taken is $B_\mathrm{MSY} = K/2$, and the corresponding fishing mortality rate is $F_\mathrm{MSY} = \mathrm{MSY}/B_\mathrm{MSY} = r/2$.

For nonequilibrium analyses, an instantaneous rate of fishing mortality per unit time is added to eqn [36]:

$$\frac{\mathrm{d}B}{\mathrm{d}t} = (r - F)B - \frac{B^2}{K} \qquad [37]$$

By integrating with respect to time over the period t to $t+1$, a population projection equation is obtained:

$$B_{t+1} = \begin{cases} \dfrac{(r - F_t)B_t\mathrm{e}^{r-F_t}}{r - F_t + (r/K)B_t(\mathrm{e}^{r-F_t} - 1)}, & F_t \neq r \\ \dfrac{B_t}{1 + (r/K)B_t}, & F_t = r \end{cases} \qquad [38]$$

Integration can of course give the biomass at any time during an interval of constant F_t. That makes possible the integration of $\mathrm{d}Y/\mathrm{d}t = F_tB$ in the time interval t to $t+1$ to obtain the yield (catch in weight) during that interval:

$$Y_t = \begin{cases} \dfrac{F_tK}{r}\log\left[1 - \dfrac{(r/K)B_t(1 - \mathrm{e}^{r-F_t})}{r - F_t}\right], & F_t \neq r \\ \dfrac{F_tK}{r}\log\left(1 + \dfrac{rB_t}{K}\right), & F_t = r \end{cases} \qquad [39]$$

Applying the model to a typical data set (records of removals and relative abundance) results in estimates of MSY, F_MSY, B_MSY, E_MSY, and of the trajectories of biomass and fishing mortality rate through time.

Pella–Tomlinson model

In the Schaefer production model, the production curve is symmetrical about B_MSY. In the Pella–Tomlinson (generalized) production model, the production curve may be symmetrical or skewed in either direction (**Figure 5**). Fletcher's form of that model replaces eqn [36] with

$$\frac{\mathrm{d}B_t}{\mathrm{d}t} = \gamma m\frac{B_t}{K} - \gamma m\left(\frac{B_t}{K}\right)^n \qquad [40]$$

where m is MSY, n determines the shape of the production curve, and γ is a function of n:

$$\gamma = \frac{n^{n/(n-1)}}{n-1} \qquad [41]$$

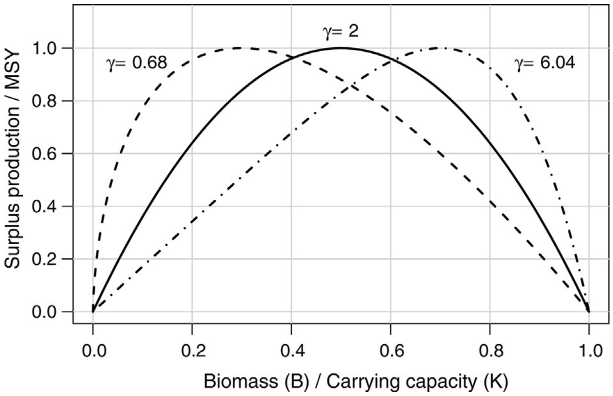

Figure 5 Maximum sustainable yield (MSY) from a generalized production model with different values of n. The Schaefer model of logistic population growth corresponds to $n = 2$. Other values of n chosen so that $B_\mathrm{MSY}/K = \{0.3, 0.7\}$.

At $n = 1$, where eqn [41] has a removable singularity, the Pella–Tomlinson model is known as the Fox model. At $n = 2$, it is the Schaefer model.

In the Pella–Tomlinson model, yield (the analog to eqn [39]) must be solved by numerical approximation, as no analytical solution to the corresponding catch equation is known. The parameterization of eqn [40] does not include r, because when $n \leq 1$, r is infinite, implying an extremely resilient population. The consequences of that theoretical property in modeling actual populations is unknown.

Use of production models

Production models are typically used in stock assessment when the catch cannot be aged, sometimes in the continuous time forms shown above, and sometimes in discrete-time versions, where the time step is typically 1 year. They are also used as complements to more detailed age-structured models. They generally perform reasonably well if the abundance index is informative and recruitment is not highly stochastic.

Delay-Difference Models

Delay-difference models provide intermediate detail between (age-aggregated) production models and age-structured models. They are similar to production models, but allow a lag between birth and maturity. This lag accounts for an effect of age structure on reproduction, at least implicitly.

In simplest form, delay-difference models predict the number of adults in the next time period (N_{t+1}) based on current abundance, survival, and recruitment:

$$N_{t+1} = \ell_t N_t + \mathcal{F}_N(N_{t-T+1}) \qquad [42]$$

where ℓ_t is the proportion of adults that survives year t, $\mathcal{F}_N$ is a function describing the relationship between numbers of adults and recruits (see section '**Recruitment**'), and T is the lag from birth to maturity. Survival rate ℓ_t can reflect fishing, if one assumes that the exploited part of the population is the same as the mature part.

Equation [42] is based on numbers of fish, but the framework can also be based on biomass (B) to allow for effects of individual growth. Assuming von Bertalanffy growth, Deriso derived a delay-difference model in biomass:

$$B_{t+1} = \ell_t B_t + \ell_t(B_t - \ell_{t-1}B_{t-1})\mathrm{e}^{-\kappa} + \mathcal{F}_B(B_{t-T+1}) \qquad [43]$$

where κ is from the VBGF and $\mathcal{F}_B$ is a function describing the relationship between biomass of adults and biomass of recruits. Equation [43] states that new biomass is the sum of surviving biomass, growth, and biomass of recruits.

Data requirements of delay-difference models are greater than those of production models. Besides time series of catches and relative abundance or biomass, additional information is needed on growth, natural mortality, and the spawner–recruit relationship. Many generalizations of delay-difference models have been proposed, for example, to allow for individual growth patterns other than the VBGF.

Fully Age-Structured Methods

Population models that trace cohort abundance and mortality through time are widely used in contemporary stock assessments. So-called catch–age analyses were made possible by large-scale research programs of aging fish through analysis of hard parts, usually scales or otoliths.

Virtual population analysis and cohort analysis

The term 'virtual population' was used originally to mean the sum of catches from a single cohort through its lifespan. Thus, the virtual population provides a minimum estimate of initial cohort strength, but it neglects losses from natural mortality. That concept of virtual population has become obsolete.

Today, virtual population analysis (VPA) refers to a family of methods that account for losses to a cohort from fishing and natural mortality. In its simplest realization, VPA is a solution of the Baranov catch equation applied backward in time, starting from the oldest age (A) of each cohort at a time near the present. It is due independently to Murphy and Gulland, who pointed out that given catch at age, this procedure (under constant M) involves a system of $A-1$ equations with $A+1$ unknowns, and that the need for two additional pieces of information could be filled by a value for the natural mortality rate M and an estimate or guess of the final cohort size N_A or, more typically, the corresponding fishing mortality rate F_A. If M is thought to vary with age, M_a at each age must be provided.

Typically, VPA applies the Baranov catch equation, rearranged to calculate abundance from catch, to the oldest age of a cohort:

$$N_A = \frac{Z_A C_A}{F_A(1-\mathrm{e}^{-Z_A})} \qquad [44]$$

From N_A and the known C_{A-1}, F_{A-1} is calculated:

$$F_{A-1} = \frac{C_{A-1}Z_{A-1}}{N_A(\mathrm{e}^{-Z_{A-1}}-1)} \qquad [45]$$

where eqn [45] is derived from the ratio of catch at age (eqn [27]) to abundance at age (eqn [17]). With F_{A-1} computed, eqn [44] can be applied to the next younger age ($A-1$) to calculate N_{A-1}, and eqn [45] to estimate F_{A-2}. This procedure is repeated until reaching the youngest age for which catch data are available. Thus, F_a and N_a are calculated for each age.

Equation [45] must be solved iteratively. To ease calculation, Pope provided an approximation for backward calculation of population number,

$$N_a \approx N_{a+1} e^{M_a} + C_a e^{M_a/2} \qquad [46]$$

whose application he termed 'cohort analysis'. MacCall later provided a slightly more accurate approximation:

$$N_a \approx N_{a+1} e^{M_a} + \frac{C_a M_a}{1 - e^{-M_a}} \qquad [47]$$

Although calculations for VPA or cohort analysis can also be done forward in time, when the backward algorithm is used, calculated values of F and N at young ages are relatively insensitive to choice of F_A; that is, estimates of younger ages would be quite similar from a wide range of values for F_A, with this insensitivity applying to older ages if the total mortality rate is high. This insensitivity (sometimes described as convergence) is a valuable property when estimates of recruitment are desired – as they frequently are. However, the convergence property applies only to cohorts that have been subject to high cumulative mortality; when incomplete cohorts are analyzed, calculated F for younger ages is sensitive to the assumed F_A.

Because the basic VPA algorithm treats each cohort independently, F_A must be supplied for each cohort. That requirement can be eased by postulating, for example, that $F_{A,t} = F_{A-1,t}$ for all A. Then after computations for the oldest cohort are completed, the calculated value of F_{A-1} can be used to initialize F_A of the next youngest cohort.

In simple VPA, the starting values and catch at age completely determine the calculated values of $N_{a,t}$ and $F_{a,t}$. Although this attribute removes the need for statistical optimization, it also means that simple VPA provides no estimates of variance. When errors occur in the catch at age, patterns of F_A can fluctuate in unrealistic ways between adjacent cohorts or ages.

Although the convergence property of basic VPA provides stable values of initial year-class strength, the estimates of present-time cohort strengths are highly sensitive to assumptions of final-year F or N. This was one of the major motivations for the numerous generalizations of VPA that have been developed. Other major motivations are to allow for error in the observed data and to provide estimates of precision.

Extensions to catch–age analysis

Many developments in catch–age analysis since basic VPA have aimed at reducing the number of estimated parameters and thus allowing a statistical error structure. A common approach has been to consider $F_{a,t}$ as the product of a time factor and an age factor. The age factor is often parameterized as a selectivity curve (e.g., eqn [29]). This approach has been called 'separable VPA', reflecting the separation of F into those factors, assumed independent. This separability assumption has been maintained in many more detailed catch–age models.

A second common extension to basic VPA is use of auxiliary data, such as indices of abundance, to help shape the estimates. This 'tuning' can increase the ability of VPA to stably estimate current population status.

Other common extensions include conditioning estimates on a spawner-recruitment function; modeling error in the catch-at-age data; and partitioning selectivity, catch, and fishing mortality by fleet. Standard errors of estimates are derived through analytical approximations or resampling procedures, including the bootstrap.

Statistical catch–age models

Recent highly detailed evolutions of VPA are sometimes termed statistical catch–age (SCA) models. Here, we use that term to refer to generalizations of VPA that use a forward solution of the catch equation. Most such models also differ from basic VPA in assuming that catch at age is subject to sampling error.

The major advantage of using a forward solution of model equations is the ease with which stock-specific detail can be added to the model structure. In SCA models, initial abundance of each cohort is typically estimated by a stochastic spawner-recruit model, and subsequent abundances are estimated using an age-structured population model, usually eqn [17]. The Baranov catch equation provides estimates of catch at age.

Growth in computing power and the advent of specialized software packages have fostered increased detail in SCA models. A typical stock-specific model includes some of the following extensions: migration, changing selectivity or catchability over time, simultaneous estimation of growth from data on length and age composition, distinct modeling of different gears, explicit treatment of discarded fish, and sex-specific submodels. A complex SCA model may have hundreds of parameters. A strength of the SCA approach is the synthesis of multiple and varied kinds of data on the stock and fishery. This unified approach of bringing together the population model and any relevant data is often called 'integrated analysis'.

Statistical catch-age models typically use a compound objective function, in which appropriate objective functions for each type of data are merged into a weighted sum. Estimation has usually been least squares or maximum likelihood, with either being conditional on the weights chosen. Estimates can be sensitive to the choice of weights, and this is an important research topic, with some recent progress on determining likelihood weights objectively.

Although fishery models have become far more detailed and optimization techniques have improved, the basic theory of population dynamics has changed very little since VPA was introduced in the mid-1960s. In many cases, the limiting factor in analyses is still uncertainty in the data. Even in well-studied species, some population parameters may be unknown, and if known, may change surprisingly when aging and other biometric techniques improve.

Population Models – Other Considerations

Data-poor methods

Many fish stocks worldwide lack the data to support conventional stock assessment methods, a situation that has attracted research on alternative analyses for data-poor situations. Two modeling approaches that require data only on catches are depletion-based stock reduction analysis and depletion-corrected average catch analysis. Even simpler methods attempt to provide management advice without explicitly modeling population dynamics of the stock, instead looking at life-history characteristics, scaling of current or historic catch patterns, or using assessment of a more data-rich stock (or an assemblage of stocks) as an indicator. All such approaches use assumptions or expert judgment in place of the detailed data that are not available.

Uncertainty

When fitting models to data, the usual goal is to estimate parameters such that modeled dynamics match observations. In practice, estimates are always uncertain, due to stochasticity in population dynamics and error in fishery data. Quantifying this uncertainty has motivated extensions of each model described above to include various versions of process error, observation error, or both. As in other fields, Bayesian methods have also gained popularity. In many cases, estimates have been found more precise when normalized to their respective biological reference point, for example, B_t/B_{MSY} and F_t/F_{MSY} are usually more precise than the corresponding absolute estimates, B_t and F_t.

Length-based models

In some fisheries, catch–age information is unavailable or unreliable, yet catch–length information is obtained readily. For such cases, length-based models may be appropriate. These models typically combine a growth model with a statistical distribution to estimate transition probabilities from one length category to another. Under deterministic growth, length- and age-based models are equivalent in the sense that one is deducible from the other.

Spatial models

In many respects, population dynamics of actual stocks are more complex than those described by simple VPA or statistical catch–age models. For example, many stocks exhibit migratory patterns that vary from year to year. In some cases, the spatial scale of migration may be such that effects on population dynamics are negligible, and in other cases, migration is a valid consideration. Many migration models have been proposed; their implementation usually requires detailed information to characterize the migratory pattern, as migrations often depend on age, size, density, or environment.

Multispecies and ecosystem models

Another complexity often ignored or simplified is interaction among species (e.g., competition or predation). Multispecies fishery models have been developed to incorporate predator–prey interactions. Such models require additional data to characterize interactions, a difficult undertaking even under laboratory conditions. Most attempts have surmised interactions from analysis of stomach contents. Some scientists have advocated developing full ecosystem models, despite information needs that others consider unattainable. As well, environmental forcing and effects of climate change have drawn increased attention. Like all mathematical models, fishery models make simplifying assumptions in an attempt to provide useful information.

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