APPENDIX III. CHARACTERISTICS AND RELATIONSHIPS FOR TWO TYPES OF RECRUITMENT CURVE, EACH EXPRESSED IN TWO DIFFERENT FORMS

Characteristics and relationships for two types of recruitment curve, each expressed in two different forms. For curves 1 and 3 the items marked by an (*) are valid regardless of the units in which R and P are expressed; for the remaining items it is necessary that R and P be in the same units and that R = P at replacement abundance.

P	abundance of parents (stock)
R	abundance of progeny (recruits)
C	catch, in numbers
Y	mean number of fertilized eggs produced per mature fish (males and females together)
Z	total mortality rate (eggs to mature fish)
α, β	parameters (different for the two types of curve)
a, A	parameters
r	as subscript, indicates the condition of replacement abundance and recruitment
m	as subscript, indicates the condition of maximum recruitment
E	as subscript, indicates steady-state conditions (mortality balanced by recruitment)
s	as subscript, indicates the condition of maximum sustainable yield (MSY)
c	as subscript, indicates the compensatory component of natural mortality
i	as subscript, indicates the density-independent component of natural mortality

Most of the expressions are as given in Ricker (1973c), where their derivation is described; see also Paulik et al. (1967). Item 16 is a rearrangement of 13. Items 20 and 21 are from expressions A22 and A24 of Ricker (1958a), the former being a simpler form of No. 19 of the 1973 paper.

Appendix III *(continued)*

Curve No.	1	2	3	4
1.* Equation	$R = \alpha P e^{-\beta P}$	$R = P e^{a(1-P/P_r)}$	$R = \frac{P}{\alpha P + \beta}$	$R = \frac{P}{1 - A(1-P/P_r)}$
2.* Slope of the curve	$(1 - \beta P)\alpha e^{-\beta P}$	$(1 - aP/P_r)e^{a(1-P/P_r)}$	$\frac{\beta}{(\alpha P + \beta)^2}$	$\frac{1 - A}{(1 - A[1-P/P_r])^2}$
3.* Slope at the origin	α	e^a	$\frac{1}{\beta}$	$\frac{1}{1 - A}$
4. Slope at maximum sustainable yield (MSY)	1	1	1	1
5.* Slope at maximum recruitment	0	0	0	0
6. Slope at replacement level of stock	$1 - \log_e \alpha$	$1 - a$	β	$1 - A$
7.* Slope at maximum level of stock	0	0	0	0
8. Replacement level of stock	$P_r = R_r = \frac{\log_e \alpha}{\beta}$	$\frac{P_r}{P_r} = \frac{R_r}{P_r} = 1$	$P_r = R_r = \frac{1 - \beta}{\alpha}$	$\frac{P_r}{P_r} = \frac{R_r}{P_r} = 1$
9.* Spawners needed for maximum recruitment	$P_m = \frac{1}{\beta}$	$\frac{P_m}{P_r} = \frac{1}{a}$	$P_m = \infty$	$\frac{P_m}{P_r} = \infty$

10.* Maximum recruitment	$R_m = \frac{\alpha}{\beta e}$	$\frac{R_m}{P_r} = \frac{e^{a-1}}{a}$	$R_m = \frac{1}{\alpha}$	$\frac{R_m}{P_r} = \frac{1}{A}$
11. Ratio of replacement spawners to maximum recruitment spawners	$P_r/P_m = \log_e \alpha$	$P_r/P_m = a$	not applicable	not applicable
12. Sustainable yield	$C_E = P_E(\alpha e^{-\beta P_E} - 1)$	$C_E = P_E(e^{a(1-P_E/P_r)} - 1)$	$C_E = P_E\left(\frac{1}{\alpha P_E + \beta} - 1\right)$	$C_E = P\left(\frac{1}{1 - A(1-P/P_r)} - 1\right)$
13. Equilibrium rate of exploitation	$u_E = C_E/R_E = 1 - \frac{1}{\alpha e^{-\beta P}}$	$u_E = C_E/R_E = 1 - e^{-a(1-P_E/P_r)}$	$u_E = C_E/R_E = 1 - \alpha P - \beta$	$u_E = C_E/R_E = A(1 - P/P_r)$
14. Limiting equilibrium rate of exploitation (when $P \to 0$)	$1 - \frac{1}{\alpha}$	$1 - e^{-a}$	$1 - \beta$	A
15. Limiting equilibrium rate of fishing (when $P \to 0$)	$\log_e \alpha$	a	$-\log_e \beta$	$-\log_e(1 - A)$
16. Spawners required to sustain an equilibrium rate of exploitation u_E	$P_E = \frac{\log_e(\alpha[1-u_E])}{\beta}$	$\frac{P_E}{P_r} = 1 + \frac{\log_e(1-u_E)}{a}$	$P_E = \frac{1 - u_E - \beta}{\alpha}$	$\frac{P_E}{P_r} = 1 - \frac{u_E}{A}$
17. Spawners needed for MSY	P_s is found by solving: $(1 - \beta P_s)\alpha e^{-\beta P_s} = 1$	P_s/P_r is found by solving: $(1 - aP_s/P_r)e^{a(1-P_s/P_r)} = 1$	$P_s = \frac{\sqrt{\beta} - \beta}{\alpha}$	$\frac{P_s}{P_r} = \frac{A - 1 + \sqrt{1-A}}{A}$
18. Recruitment at MSY	R_s is found by substituting P_s in (1)	R_s/P_r is found by substituting P_s/P_r in (1)	$R_s = \frac{1 - \sqrt{\beta}}{\alpha}$	$\frac{R_s}{P_r} = \frac{1 - \sqrt{1-A}}{A}$

Appendix III *(concluded)*

Curve No.	1	2	3	4
19. Maximum sustainable yield (MSY)	$C_s = P_s(\alpha e^{-\beta P_s} - 1)$	$C_s = P_s(e^{a(1-P_s/P_r)} - 1)$	$C_s = \frac{(1-\sqrt{\beta})^2}{\alpha}$	$\frac{C_s}{P_r} = \frac{(1-\sqrt{1-A})^2}{A}$
20. Rate of exploitation at MSY	$u_s = \beta P_s$	$u_s = aP_s/P_r$	$u_s = 1-\sqrt{\beta}$	$u_s = 1-\sqrt{1-A}$
21. Curve parameters when u_s is known	$\log_e\alpha = u_s - \log_e(1-u_s)$ $\beta = u_s/P_s$	$a = u_s - \log_e(1-u_s)$	$\alpha = (1-\beta)/P_r$ $\beta = (1-u_s)^2$	$A = 1-(1-u_s)^2$
22. Rate of recruitment (a) actual	$R/P = \alpha e^{-\beta P}$	$R/P = e^{a(1-P/P_r)}$	$\frac{R}{P} = \frac{1}{\alpha P+\beta}$	$\frac{R}{P} = \frac{1}{1-A(1-P/P_r)}$
(b) instantaneous	$\log_e\alpha - \beta P$	$a(1-P/P_r)$	$-\log_e(\alpha P+\beta)$	$-\log_e(1-A[1-P/P_r])$
23. Rate of recruitment at minimal stock (a) actual	$R_0/P_0 = \alpha$	$R_0/P_0 = e^a$	$R_0/P_0 = \frac{1}{\beta}$	$R_0/P_0 = \frac{1}{1-A}$
(b) instantaneous	$\log_e\alpha$	a	$-\log_e\beta$	$-\log_e(1-A)$
24. Rate of recruitment at maximum recruitment (a) actual	$R_m/P_m = \alpha e^{-1}$	$R_m/P_m = e^{a-1}$	not applicable	not applicable
(b) instantaneous	$\log_e\alpha - 1$	$a-1$		

25. Rate of recruitment at replacement				
(a) actual	$R_r/P_r = 1$	$R_r/P_r = 1$	$R_r/P_r = 1$	$R_r/P_r = 1$
(b) instantaneous	0	0	0	0
26. Instantaneous rate of compensatory mortality	$Z_c = \beta P$	$Z_c = aP/P_r$	$Z_c = \log_e(1 + \alpha P/\beta)$	$Z_c = \log_e\left(1 + \frac{AP}{P_r(1-A)}\right)$
27. Instantaneous rate of density-independent mortality	$Z_i = \log_e Y - \log_e \alpha$	$Z_i = \log_e Y - a$	$Z_i = \log_e Y + \log_e \beta$	$Z_i = \log_e Y + \log_e(1-A)$

1.2. Definitions, Usages, and Glossary

The list below includes only a part of the varied terminology which has been used in fish population analysis. More extended descriptions of some terms are given in later sections. If a special symbol is associated with a term, it is shown in parentheses. Terms marked with an asterisk are not used in this book, at any rate not in a context where strict definition is called for.

Absolute Recruitment: The number of fish which grow into the catchable size range in a unit of time (usually a year).

Age: The number of years of life completed, here indicated by an arabic numeral, followed by a plus sign if there is any possibility of ambiguity (age 5, age 5+)[1].

Annual (or seasonal) growth rate (h): The *increase* in weight of a fish per year (or season), divided by the initial weight.

Annual (or seasonal) total mortality rate (A): The number of fish which die during a year (or season), divided by the initial number. Also called: actual mortality rate, *coefficient of mortality (Heincke).

Availability: 1. (r): The fraction of a fish population which lives in regions where it is susceptible to fishing during a given fishing season (Marr 1951). This fraction receives recruits from or becomes mingled with the non-available part of the stock at other seasons, or in other years. (Any more or less completely isolated segment of the population is best treated as a separate stock.)

2. (C/f or Y/f): Catch per unit of effort.

Biomass (B): The weight of a fish stock, or of some defined portion of it.

Catchability (q): The fraction of a fish stock which is caught by a defined unit of the fishing effort. When the unit is small enough that it catches only a small part of the stock — 0.01 or less — it can be used as an instantaneous rate in computing population change. (For fractions taken of various portions of the stock, see "vulnerability.") Also called: catchability coefficient, *force of fishing mortality (Fry 1949, p. 24; in his Appendix, however, Fry defines the force of fishing mortality as equivalent to our rate of fishing, F).

Catch curve: A graph of the logarithm of number of fish taken at successive ages or sizes.

Catch per unit of effort (C/f or Y/f): The catch of fish, in numbers or in weight, taken by a defined unit of fishing effort. Also called: catch per effort, fishing success, availability (2).

Conditional fishing mortality rate (m): The fraction of an initial stock which would be caught during the year (or season) *if* no other causes of mortality

[1] While the above is recommended, other usages exist. Roman numerals are frequently used in North America, but their cumbersomeness seems to outweigh any advantage. Some have used either roman or arabic numerals to indicate year of life, rather than years completed. For anadromous fishes both the actual age and the age at seaward migration are frequently indicated. Several conventions are employed for this purpose, and it seems necessary to specify each time which one is being used.

operated ($= 1 - e^{-F}$). Also called: annual fishing mortality rate, seasonal fishing mortality rate.

CONDITIONAL NATURAL MORTALITY RATE (n): The fraction of an initial stock that would die from causes other than fishing during a year (or season), *if* there were no fishing mortality ($= 1 - e^{-M}$). Also called: annual natural mortality rate, seasonal natural mortality rate.

CRITICAL SIZE: The average size of the fish in a year-class at the time when the instantaneous rate of natural mortality equals the instantaneous rate of growth in weight for the year-class as a whole. Also called: *optimum size.

EFFECTIVE FISHING EFFORT (F/q): Fishing effort adjusted, when necessary, so that each increase in the adjusted unit causes a proportional increase in instantaneous rate of fishing.

EFFECTIVENESS OF FISHING: A general term referring to the percentage removal of fish from a stock, but not as specifically defined as either rate of exploitation or instantaneous rate of fishing.

EQUILIBRIUM CATCH (C_E): The catch (in numbers) taken from a fish stock when it is in equilibrium with fishing of a given intensity, and (apart from the effects of environmental variation) its abundance is not changing from one year to the next.

EQUILIBRIUM YIELD (Y_E): The yield in weight taken from a fish stock when it is in equilibrium with fishing of a given intensity, and (apart from effects of environmental variation) its biomass is not changing from one year to the next. Also called: sustainable yield, equivalent sustainable yield. (See also SURPLUS PRODUCTION.)

EXPLOITATION RATIO (E): The ratio of fish caught to total mortality ($= F/Z$ when fishing and natural mortality take place concurrently). Also called: *rate of exploitation.

FISH STOCK: See STOCK.

FISHING EFFORT (f): 1. The total fishing gear in use for a specified period of time. When two or more kinds of gear are used, they must be adjusted to some standard type (see Section 1.7).

2. Effective fishing effort.

*FISHING INTENSITY: 1. Effective fishing effort.

2. Fishing effort per unit area (Beverton and Holt).

3. Effectiveness of fishing.

*FISHING POWER (of a boat, or of a fishing gear): The relative vulnerability of the stock to different boats or gears. Usually determined as the catch taken by the given apparatus, divided by the catch of a standard apparatus fishing at nearly the same time and place.

FISHING SUCCESS: Catch per unit of effort.

INSTANTANEOUS RATES (in general): See Section 1.4. Also called: logarithmic, exponential, or compound-interest rates.

INSTANTANEOUS RATE OF FISHING MORTALITY (F): When fishing and natural mortality act concurrently, F is equal to the instantaneous total mortality rate, multiplied by the ratio of fishing deaths to all deaths. Also called: rate of fishing; instantaneous rate of fishing; *force of fishing mortality (see under CATCHABILITY).

INSTANTANEOUS RATE OF GROWTH (G): The natural logarithm of the ratio of final weight to initial weight of a fish in a unit of time, usually a year. When applied collectively to all fish of a given age in a stock, the possibility of selective mortality must be considered (Section 9.4).

INSTANTANEOUS RATE OF MORTALITY (Z): The natural logarithm (with sign changed) of the survival rate. The ratio of number of deaths per unit of time to population abundance during that time, if all deceased fish were to be immediately replaced so that population does not change. Also called: *coefficient of decrease (Baranov).

INSTANTANEOUS RATE OF NATURAL MORTALITY (M): When natural and fishing mortality operate concurrently it is equal to the instantaneous total mortality rate, multiplied by the ratio of natural deaths to all deaths. Also called: *force of natural mortality (Fry).

INSTANTANEOUS RATE OF RECRUITMENT (z): Number of fish that grow to catchable size per short interval of time, divided by the number of catchable fish already present at that time. Usually given on a yearly basis: that is, the figure just described is divided by the fraction of a year represented by the "short interval" in question. This concept is used principally when the size of the vulnerable stock is not changing or is changing only slowly, since among fishes recruitment is not usually associated with stock size in the direct way in which mortality and growth are.

INSTANTANEOUS RATE OF SURPLUS PRODUCTION: Equal to rate of growth plus rate of recruitment less rate of natural mortality — all in terms of weight and on an instantaneous basis. In a "balanced" or equilibrium fishery, this increment replaces what is removed by fishing, and rate of surplus production is numerically equal to rate of fishing. Also called: *instantaneous rate of natural increase (Schaefer).

MAINTAINABLE YIELD: "The largest catch that can be maintained from the population, at whatever level of stock size, over an indefinite period. It will be identical to the sustainable yield for populations below the level giving the MSY, and equal to the MSY for populations at or above this level" (Gulland).

MAXIMUM EQUILIBRIUM CATCH (see MAXIMUM SUSTAINABLE YIELD).

MAXIMUM SUSTAINABLE YIELD (MSY OR Y_s): The largest average catch or yield that can continuously be taken from a stock under existing environmental conditions. (For species with fluctuating recruitment, the maximum might be obtained by taking fewer fish in some years than in others.) Also called: maximum equilibrium catch (MEC); maximum sustained yield; sustainable catch.

*MECHANICAL INTENSITY OF FISHING: Fishing effort (1).

NATURAL MORTALITY: Deaths from all causes except man's fishing, including predation, senility, epidemics, pollution, etc.

NET INCREASE (OR DECREASE): New body substance elaborated in a stock, less the loss from all forms of mortality.

PARAMETER: A "constant" or numerical description of some property of a *population* (which may be real or imaginary). Cf. statistic.

PIECES: Individual items, as in the expression "two dollars a piece" (German *Stück*). Individual fish.

PRODUCTION: 1. (sense of Ivlev). The total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time. Also called: *net production (Clarke et al. 1946); *total production.
2. *Yield.

RATE OF EXPLOITATION (u): The fraction, by number, of the fish in a population at a given time, which is caught and killed by man during the year immediately following ($= FA/Z$ when fishing and natural mortality are concurrent). The term may also be applied to separate parts of the stock distinguished by size, sex, etc. (See also "rate of utilization.") Also called: *fishing coefficient (Heincke).

RATE OF FISHING (F): INSTANTANEOUS RATE OF FISHING MORTALITY.

*RATE OF NATURAL INCREASE: INSTANTANEOUS RATE OF SURPLUS PRODUCTION.

RATE OF REMOVAL: An inexactly-defined term that can mean either rate of exploitation or rate of fishing — depending on the context (see Section 1.4.3).

RATE OF UTILIZATION: Similar to rate of exploitation, except that only the fish *landed* are considered. The distinction between catch and landings is important when considerable quantities of fish are discarded at sea.

RECRUITMENT: Addition of new fish to the vulnerable population by growth from among smaller size categories (Section 11.1).

RECRUITMENT CURVE, REPRODUCTION CURVE: A graph of the progeny of a spawning at the time they reach a specified age (for example, the age at which half of the brood has become vulnerable to fishing), plotted against the abundance of the stock that produced them.

SECULAR: Pertaining to the passage of time.

STATISTIC: The estimate of a parameter which is obtained by observation, and which in general is subject to sampling error.

STOCK: The part of a fish population which is under consideration from the point of view of actual or potential utilization.

SUCCESS (of fishing): Catch per unit of effort.

SURPLUS PRODUCTION (Y'): Production of new weight by a fishable stock, plus recruits added to it, less what is removed by *natural* mortality. This is usually estimated as the catch in a given year plus the increase in stock size (or less the decrease). Also called: natural increase, sustainable yield, equilibrium catch (Schaefer).

SURVIVAL RATE (S): Number of fish alive after a specified time interval, divided by the initial number. Usually on a yearly basis.

SUSTAINABLE YIELD: Equilibrium yield.

USABLE STOCK: The number or weight of all fish in a stock that lie within the range of sizes customarily considered usable (or designated so by law). Also called: *standing crop.

UTILIZED STOCK, UTILIZED POPULATION (V): The part, by number, of the fish alive at a given time, which will be caught in future.

VIRTUAL POPULATION: Utilized stock.

VULNERABILITY: A term equivalent to CATCHABILITY but usually applied to separate parts of a stock, for example those of a particular size, or those living in a particular part of the range.

YEAR-CLASS: The fish spawned or hatched in a given year. In the northern hemisphere, when spawning is in autumn and hatching in spring, the calendar year of the hatch is commonly used to identify the year-class (except usually for salmon). Also called: brood, generation.

In the above, only the kinds of "rates" are defined which are most frequently used. In general, for any process there will be an *absolute* rate, a *relative* rate and an *instantaneous* rate (Sections 1.4, 1.5).

1.3. SYMBOLS

The symbols used are those of the "international" system (Gulland 1956a) as far as possible, but quite a number of additional ones are required, of which those more frequently used are shown below. The predecessors of this bulletin (Ricker 1948, 1958a) used essentially the system recommended by Widrig (1954a, b), and their symbols are indicated below in square brackets.

- a 1. a coefficient used in the Ricker recruitment curve (Section 11.6.2)
  2. the multiplier in the functional weight–length relationship (Section 9.3.1)
- b 1. the slope of any line
  2. the exponent in the functional weight–length relationship (Section 9.3.1)
- e 2.71828 . . .
- f fishing effort
- h annual growth rate
- k 1. Ford growth coefficient (Section 9.6.4)
  2. a rate; used in various connections
- l length of a fish
- m conditional rate of fishing mortality
- n conditional rate of natural mortality
- q catchability [c]

r 1. availability (1).
2. rate of accession (Section 5.3)

s standard deviation

t 1. a point in time (often used as a subscript)
2. an interval of time (also Δt)
3. age

u 1. rate of exploitation of a fish stock, or expectation of capture by man (μ of Ricker 1948)
2. the ratio of number of recoveries to number of marked fish released (= R/M)

v expectation of natural death (ν of Ricker 1948)

w weight of a fish

y instantaneous rate of emigration

z 1. instantaneous rate of immigration
2. instantaneous rate of recruitment

A annual (or seasonal) mortality rate [a]

A′ annual (or seasonal) rate of disappearance of fish

B weight (biomass) of a group of fish; for example of a year–class, or of an entire stock

C 1. catch, in numbers — usually for a whole year
2. number of fish examined for tags or marks

E 1. escapement (of salmon, etc., past a fishery)
2. number of eggs
3. exploitation ratio (= F/Z)
4. (as subscript) an equilibrium level (see Appendix III)

F instantaneous rate of fishing mortality [p]

G instantaneous rate of growth [g]

K 1. Brody growth coefficient (Section 9.6.1)
2. any rate
3. cumulative catch (Chapter 6)

L mean length at recruitment, in Baranov's yield equation

L_∞ asymptotic length, in the Brody–Bertalanffy growth equation

M 1. instantaneous rate of natural mortality [q]
2. number of fish marked or tagged (also M′)

N number of fish in a year–class, population, or sample

P 1. abundance of a parental stock or generation
2. level of statistical probability

Q the constant which appears in the integration of Baranov's yield computation

R 1. number of recruits to the catchable stock
2. number of recaptures of marked or tagged fish
3. multiple correlation coefficient

S rate of survival ($= -\log_e Z$) [*s*]

S′ apparent survival rate ($= -\log_e Z'$)

U instantaneous rate of "other loss" (includes emigration and, for tagged fish, the shedding of tags)

V 1. utilized stock, virtual population
2. variance

W_∞ the mean asymptotic weight which corresponds to L_∞

Y yield, catch by weight

Z instantaneous rate of (total) mortality [*i*]

Z′ instantaneous rate of disappearance (total losses) from a stock ($= F + M + U = Z + U$)

— (over a symbol) a mean value

Σ summation symbol

1.4. Numerical Representation of Mortality

1.4.1. Total mortality rate. The mortality in a population, from all causes, can be expressed numerically in two different ways.

(a) Simplest and most realistic perhaps is the *annual expectation of death* of an individual fish, or *actual mortality rate*, expressed as a fraction or percentage. This is the fraction of the fish present at the start of a year which actually die during the year.

(b) If the number of deaths in a small interval of time is at all times proportional to the number of fish present at that time, the fraction which remains at time t, of the fish in a population at the start of a year ($t = 0$), is:

$$\frac{N_t}{N_0} = e^{-Zt} \tag{1.1}$$

The parameter Z is called the *instantaneous mortality rate*. If the unit of time is 1 year, then at the end of the year (when $t = 1$):

$$\frac{N_1}{N_0} = e^{-Z} \tag{1.2}$$

But $N_1/N_0 = S = 1 - A$; hence $1 - A = e^{-Z}$, or $Z = -\log_e (1 - A)$; hence the instantaneous mortality rate is equal to the natural logarithm (with sign changed) of the complement of the annual expectation of death.

The instantaneous rate Z also represents the number of fish (including new recruits) which would die during the year if recruitment were to exactly balance mortality from day to day, expressed as a fraction or multiple of the steady density of stock.