MARINE TROPHIC INTERACTIONS BY DYNAMIC SIMULATION OF FISH SPECIES

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ABSTRACT

A mathematical model was developed for performing dynamic simulations of groups of interacting animal species. The energy balance of the individual animal was modeled so that growth and reproduction respond to food consumption after metabolic expenses are met. Populations change in response to recruitment (based on parental spawning) and mortality from natural causes, predation, starvation, and (where applicable) human exploitation. The forms of the various component mathematical functions were derived from the available ecological sources. Functions and parameters are especially applicable to marine fish species. Trophic webs of any size or form can be constructed using this basic species model. Computer solution of the essentially continuous differential model gives a time history of trophic and population variables for all species in the web.

Models of trophic webs of 2, 3, and 4 levels were constructed and exercised. These were used to examine effects of age class structure, reproductive time lag, and population regulation by starvation mortality and fecundity control. Competition between species and the effects of a top predator on competitors, with and without human exploitation, were studied.

Thus far in the history of trophic ecology there has been little effort to bring together the important results of the diverse studies which provide the components of the total trophic system into a construct that will permit analyzing the effects of metabolism, food consumption, reproductive effort, and the structure of the trophic web upon the weight, population, and biomass of the various species involved. Perhaps the most complete and useful approaches in the literature are those of Menshutkin and Kislyakov (1967, 1968), Menshutkin (1968), Menshutkin and Prikhodko (1968, 1969, 1970), Karpov et al. (1969), Krogius et al. (1969), Menshutkin and Umnov (1970), Lassiter and Hayne (1971). The present work is an attempt to create a complete model for fish in the natural environment and to employ it for the stated type of total trophic analysis.

The mathematical "trophic anatomy" of the generalized species modeled contains certain functions which represent trophic interactions with other species. The trophic web consists of an arbitrary number of such interacting species, coupled in this way into any arbitrary design; e.g., with any number of trophic "levels" (or coupled across levels), any number of species at each level, any number of predator species on a single prey species, etc. The trophic properties of the generalized, modular species are established by specifying a set of equations which define its various ecological functions, such as respiratory metabolism, feeding, natural mortality, and reproduction. The composite nature of the model species' trophic anatomy permits considerable structural flexibility in model development. A particular ecological function, such as feeding rate as a function of prey abundance, may be expressed differently in different simulation runs by changing a single component equation. The separate identity of each species is determined primarily by the numerical values of the parameters in its component functions, but the form of functions may be different in different species where the data dictate.

The model approach used allows a number of different levels of approximation. In the simulations performed here, no differentiation is made between sexes in the populations. The sexes could easily be represented separately at the cost of more computing time and a larger data base. A common and convenient simplification that is used in most of the present simulations is construction of an entire species population of identical individuals. Thus, the individual must be given a set of characteristics and parameter values that are in some sense representative of the entire life history after recruitment. A population with separate age classes has also been created explicitly with the present model.

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The model was employed in a number of simulations for a variety of trophic webs. There were not sufficient data at hand for all the species of a real trophic web to permit simulation of such a web in this way. The parameters and initial values used in these simulations are, therefore, reasonable illustrative values for fish in the natural environment, based mostly on the literature.

Despite the scarcity of the real data that would be required to use the model effectively for quantitative prediction of real systems at present, models of this sort have considerable immediate value. Representing and interrelating animal functions analytically enforces a discipline in thinking which tends to clarify perceptions of the trophic relations. Formulation of a system in mathematical functions makes clear the nature of the data required, so that effort in gathering data can be applied efficiently. Component functions for a single species can be collected from a variety of sources and fused. The trophic behavior of the resulting model species can be studied, at least qualitatively, to see if the model behaves as the animal appears to behave. If the species model appears to represent the animal reasonably well, and if a trophic web is constructed from such animals, some confidence may be placed in its predictions of the behavior of the real system—a system which may be much more difficult to evaluate independently of the model.

THE MODEL

The basic model used for each species in every trophic web was developed from an energy balance of the individual and a formulation of the population dynamics of the species. Table 1 contains a glossary of symbolic notation used in the model.

(A) The Energy Balance

The energy balance was written by equating assimilated food intake, kC, to the sum of the three physiological uses of the assimilated food: respiratory metabolism, Q, reproductive material produced for spawning, S, and growth, G.

$$kC = Q + S + G \tag{1}$$

Similar expressions are found in Winberg (1956:210, 1962), Ivlev (1961a), Warren and Davis (1967), Mann (1967, 1969), Davis and Warren (1971), and elsewhere. Mann (1965) has made one of the very few attempts to include the S term quantitatively in the balance. Most workers (e.g., Winberg 1956:209; Mann 1967, 1969) find that to a very acceptable ecological approximation, most fish under most circumstances assimilate a fairly constant fraction, $k \approx 0.8$, of the food, C, consumed (C, the feeding rate, is commonly called the ration and will be so designated herein). Ten (1967) should be consulted for a minority opinion on the effective constancy of k. Kostitzin (1939:180) and Beverton and Holt (1957:113) also deal with the form of possible variation.

All the above terms are time rates. In the present simulations, the time unit used is the year. Since G is dW/dt, the instantaneous value of body weight, W, can be found by integration of G. Each term in Equation (1) can be expressed as energy or as the equivalent weight of body tissue, wet (live) or dry. In these simulations, all terms for all species are expressed in wet weight of tissue, based on a standard conversion factor of 1 kcal/g wet weight (Winberg 1956; Mann 1969). Recent results (Davis 1968; Kausch 1968; Brett et al. 1969) on changes in water content of fish tissues at various nutritional states suggest that a dry weight basis may be noticeably more accurate where data are available. The use of different conversion factors for different species or conditions, when known, introduces no conceptual problems. That Equation (1) can be balanced using experimental values of k, C, Q, and G determined simultaneously in the laboratory for a group of fish over a range of sizes, ambient temperatures, and nutritional states, has been demonstrated by Kausch (1968), using the carp, *Cyprinus carpio*.

The results of many investigations indicate that respiratory metabolism can be expressed approximately as a function of body weight, W, by the relation

$$Q = \alpha W^{\gamma}, \tag{2}$$

where γ is some fractional power. For most fish species a value of $\gamma = 0.8$ appears to be sufficiently reliable for ecological purposes (Winberg 1956:149, 1962; Mann 1965, 1969; Paloheimo and Dickie 1966). Where a more accurate value of γ is known for a particular species, the model will accept it readily.

For the purpose of the present simulations, a level of α for a constant (or long-term average) temperature of 10°C is used. Based on a large

TABLE 1.–Glossary of symbolic notation used in the model. [Notation defined in referenced literature, when different from that of the present model, is not repeated here.]

Symbol	Definition
a	Numerical parameter in the Beverton and Holt reproductive function
B	Species biomass
B_i	Biomass of the *i*th species
B_I	Biomass of the food base
b	Numerical parameter in the Beverton and Holt reproductive function
C	Actual ration; actual rate of food consumption by an individual
C_{max}	Maximum ration when feeding to satiation
$Cp = Cp_{Total}$	Ration of a predator
Cp_i	Consumption of the *i*th prey species by a predator
c_{s1}	Numerical predation parameter in the linear feeding function
c_I	Instantaneous coefficient of natural increase of an "exponential growth" type food base
D_{FISH}	Rate of change of population due to fishing mortality
D_{NAT}	Rate of change of population due to natural mortality
D_{PRED}	Rate of change of population due to predatory mortality
D_{STARV}	Rate of change of population due to starvation mortality
E	Total egg production rate of a population
e	Base of natural logarithms
F	Coefficient of instantaneous fishing mortality
G	Actual growth rate of an individual
G_{max}	Maximum growth rate; growth rate when $C = C_{max}$
G_{VB}	Growth rate predicted by the von Bertalanffy growth function
g_m	Fraction of the species population that is sexually mature
g_1, g_2	Numerical parameters in the linear sexual maturity function for g_m
I_1	Constant of integration for critical starvation mortality time
J	Convenience combination of variables in Equation (A-2), Appendix
K_1	Recruit body weight coefficent
k	Ration assimilation coefficient; fraction of the ration assimilated
L_∞	Numerical parameter (theoretical maximum body length) in the von Bertalanffy growth function for length
M	Coefficient of instantaneous natural mortality
m	Numerical parameter in the starvation mortality function
m_{mc}	Numerical predation parameter in the Holling feeding function
N	Species population
N_{Fish}	Population of a fish species
N_i	Population of the *i*th species or age class
N_m	Sexually mature species population
N_0	Initial population
N_p	Predator population
N_s	Standard equilibrium value of species population
n	Numerical parameter in the starvation mortality function
P	Prey abundance
P_I	Rate of food base biomass input to the system in a "constant input" model
Q	Rate of respiratory metabolism of an individual
Q_{max}	Rate of respiratory metabolism of an individual at maximum ration
R	Rate of reproductive recruitment
R_s	Standard equilibrium recruitment rate
r	Fraction of the maximum ration actually consumed
S	Fecundity: actual rate of production of reproductive material by an individual
S_{max}	Maximum fecundity at current body weight
s	Computed numerical parameter in the starvation mortality function
t	Time
t_c	Critical time to 100% starvation mortality
u	Fecundity coefficient of an individual
v_i	Coefficient of predator preference for the *i*th prey
W	Body weight of an individual
W_{Fish}	Body weight of an individual fish
W_i	Body weight of an individual of the *i*th species or age class
W_0	Initial body weight of an individual
W_{prey}	Body weight of a prey individual
W_s	Standard equilibrium body weight of an individual
W_∞	Numerical parameter (theoretical maximum body weight) in the von Bertalanffy growth function
α	Respiratory metabolism coefficient
α_{max}	Respiratory metabolism coefficient at maximum ration
α_{starv}	Respiratory metabolism coefficient at zero ration
γ	Numerical parameter (weight exponent) in the respiratory metabolism function
κ	Numerical parameter in the von Bertalanffy growth function
ξ	Numerical predation parameter in the Ivlev feeding function

collection of data from the experimental literature, a level of α appropriate to an average spontaneous activity level was chosen. The instantaneous value of α is allowed to vary in response to ration according to the equation

$$\alpha = \alpha_{\mathrm{starv}} + (\alpha_{\max} - \alpha_{\mathrm{starv}}) \frac{C}{C_{\max}}, \qquad (3)$$

where C is the actual instantaneous ration, α_{starv} is the value corresponding to minimum metabolic rate at complete starvation, and $\alpha_{\max}$ corresponds to the maximum metabolic rate when feeding to satiation at ration $C_{\max}$. Equation (3) is a linear expression that generally approximates the best results from the few applicable long-term fish feeding and growth experiments (Davis and Warren 1965, 1971; Paloheimo and Dickie 1965, 1966; Beamish and Dickie 1967; Warren and Davis 1967; Brett et al. 1969). Use of Equation (3) in Equation (2) gives Q for any size fish at any feeding level.

Fecundity of fish must be dependent on size and, at least in some limiting sense, on nutrition. A number of workers have noted reduced fecundity in overcrowded, undernourished fish populations and have speculated on how this reduced fecundity might tend to regulate the population (Woodhead 1960; Nikolskii 1961, 1962; Scott 1962; Bagenal 1967; Mackay and Mann 1969). There is good evidence (Simpson 1951; Bagenal 1957, 1967; Beverton 1962; Pitt 1964; LeCren 1965; Bagenal and Braum 1971) that in most fish with adequate food supply above metabolic demands, fecundity is strongly dependent upon body weight. Regressions on weight usually fit better than regressions on length or age (Bagenal 1957, 1967; Nikolskii 1962). It seems reasonable to represent the rate of production of reproductive material, S, (or accumulation of body stores for that purpose) as a simple function of weight. Although more general functions have been proposed (Bagenal and Braum 1971), apparently most regressions so far fitted using data from specimens have been quite close to the linear expression.

$$S = uW, \tag{4}$$

where u is a constant. In the present simulations, $u = 0.1$ in all cases, based on average values for several species and both sexes (Bagenal 1957, 1967; LeCren 1958, 1962; Mann 1965; Norden 1967; Phillips 1969). The linear function is truncated near its lower end at a weight corresponding to sexual maturity. This is consistent with the general observation that the onset of sexual maturity in fish appears to be a function of size rather than age (Beverton and Holt 1959; LeCren 1965). Exceptions for individual species are noted in Bagenal (1957).

Trophic factors regulate the animal's fecundity through their effect on body weight. Also, when food intake becomes sufficiently low, there must not be enough energy above metabolic demands for normal fecundity. The scanty field data available suggest that usually fish sacrifice growth for reproduction, so that as food intake decreases, fecundity stays at or near normal (with decreased growth) until the net energy above metabolic expenditures is less than the normal fecundity requirements, after which fecundity decreases (Mackay and Mann 1969). The model operates in this way.

The ration, C, under any instantaneous set of conditions, is obtained from the maximum ration, $C_{\max}$, and the current abundance of the prey which constitutes the food supply. $C_{\max}$ is dependent on body weight, and its current value can be determined from Equation (1) if the maximum growth rate, $G_{\max}$, is known. Since $G_{\max}$ is a function of the current size of the individual, this function is required. Data from appropriate ad libitum feeding experiments with a particular species of interest could be fitted to the appropriate function to give continuous values of $G_{\max}$. The von Bertalanffy growth function is a convenient one to which growth data from a large number of fish species have been fitted (e.g., Beverton and Holt 1959; Ursin 1967). In its differential form it expresses growth

$$G_{\mathrm{VB}} = \kappa(W_\infty{}^{1/3}W^{2/3} - W), \tag{5}$$

where κ and W_∞ are numerical fitting parameters (κ corresponds to the ${}_1k$ of Ursin 1967, and to 3 times the K of Beverton and Holt 1959). W_∞ corresponds to a theoretical maximum weight, asymptotically approached. Values of κ and W_∞ for the present simulations are taken for certain illustrative species from Beverton and Holt (1959) and Ursin (1967:2421-2423). Equation (5) is employed in the model with a constant coefficient of 4.0 as an arbitrary standard adjustment to represent the highest feeding conditions. This gives a relationship between values over the full feeding range (e.g., zero, maintenance, and maximum ration) consistent with those observed in long-term feeding and growth experiments. With the $C_{\max}$ term thus expressed, the $Q_{\max}$ term is simply Equation (2) with $\alpha = \alpha_{\max}$ and using the current weight, W. The $S_{\max}$ term comes from Equation (4). Thus

$$C_{\max} = \frac{Q_{\max} + S_{\max} + G_{\max}}{k}. \tag{6}$$

There is a considerable and developing body of theory, for which evidence continues to accumulate, that where environmental conditions are fairly stable, a predator's ration may be expressed as a fraction, r, of its maximum ration, r being a simple function of the abundance of prey, P. This approach is taken as a useful long-term ecological approximation, in which short-term behavioral factors, factors affecting the accessibility of the prey, etc. are smoothed out. Several expressions for this relationship have been proposed.

Three alternative expressions for simple predation with no explicit competitive effect between predator individuals were used in the model in different simulation runs. These are:

Linear: $r = c_{s1}P$ (7A)
Ivlev: $r = 1 - e^{-\xi P}$(Ivlev 1961b) (7B)
Holling: $r = \dfrac{P}{m_{mc} + P}$(Holling 1959) (7C)

where c_{s1}, ξ, m_{mc} are numerical parameters. For prey species modeled as described here, expressing P in terms of prey numbers rather than biomass seems to have system stability advantages. It is through Equation (7) that this species interacts with the next lower species in the trophic chain (web).

The instantaneous rate of production of reproductive material and growth at the current body weight and prey abundance can be determined by use of the above terms in Equation (1). Using $r = \frac{C}{C_{\max}}$ from Equation (7) in Equation (3) gives the current value of α to be used in Equation (2) to give the current value of Q. When food supply is adequate; i.e., when $kC - Q > S_{\max}$, "fecundity" is

$$S = S_{\max},$$

and, from Equation (1), positive growth is

$$\frac{dW}{dt} = G = kC - Q - S_{\max}. \quad (8)$$

When food supply is so low that $0 < kC - Q < S_{\max}$, growth is zero and fecundity is

$$S = kC - Q. \quad (9)$$

In more extreme food shortage, when $kC - Q < 0$, fecundity is zero and growth is

$$\frac{dW}{dt} = G = kC - Q. \quad (10)$$

(Note that in the last case, growth is negative; i.e., dystrophy occurs). Equations (8) and (10) are in differential form, representing rates of change of body weight. Numerical integration of these equations gives "continuous" values of body weight over the entire time span of the simulations. Figure 1 shows the relationships between the component equations which describe a single species.

(B) Population Dynamics

Numerical changes in the population of any species are the net result of gains through reproduction (recruitment) and losses through the various sources of mortality. Therefore, the dynamics of any species population can be summarized in the expression

$$\frac{dN}{dt} = R + D_{\text{NAT}} + D_{\text{PRED}} + D_{\text{STARV}}. \quad (11)$$

The rate of change of population is the algebraic sum of four terms: reproductive recruitment, R, natural mortality, D_{NAT}, mortality due to predation, D_{PRED}, and starvation mortality, D_{STARV} (the sign of the reproductive term is positive; all the other terms have negative signs). Equation (11) is used in essentially this form for the representative individual model. For the age class model, the last three terms appear for all age classes. Instead of including the first term, the appropriate number of recruits is simply introduced as a pulse into the youngest age class at the appropriate times in the simulation.

The recruitment rate, R, is expressed as a function of the rate of egg production, E, by the Beverton and Holt (1957:49) reproductive function

$$R = \frac{1}{a + \frac{b}{E}}, \quad (12)$$

where a and b are numerical parameters. A simple relationship such as Equation (12) is appropriate for the present model where the response of a system of essentially adult populations to purely trophic variables is of interest. The egg production rate, E, is the cumulative spawn of the entire mature population, N_m; i.e.,

$$E = N_m S. \quad (13)$$

For the age class model, this involves summing over all mature age classes and over the entire year. All real species have some reproductive time lag or "generation time." In all except the simplest animals, this lag is significant and can have important influence on the dynamics of the population. Such lags of any desired length are introduced in the simulations by properly coding the programs so that the E produced in 1 yr is stored and used in Equation (12) to compute the R for the appropriate later year.

Except for fishing mortality, natural mortality is the only kind expressed in most fishery models. The position taken is that all mortality not due to fishing is "natural" and may be measurable in an unexploited stock or by eliminating the fishing mortality from statistics on an exploited stock by some analytical technique. Thus defined, natural mortality is almost invariably represented in

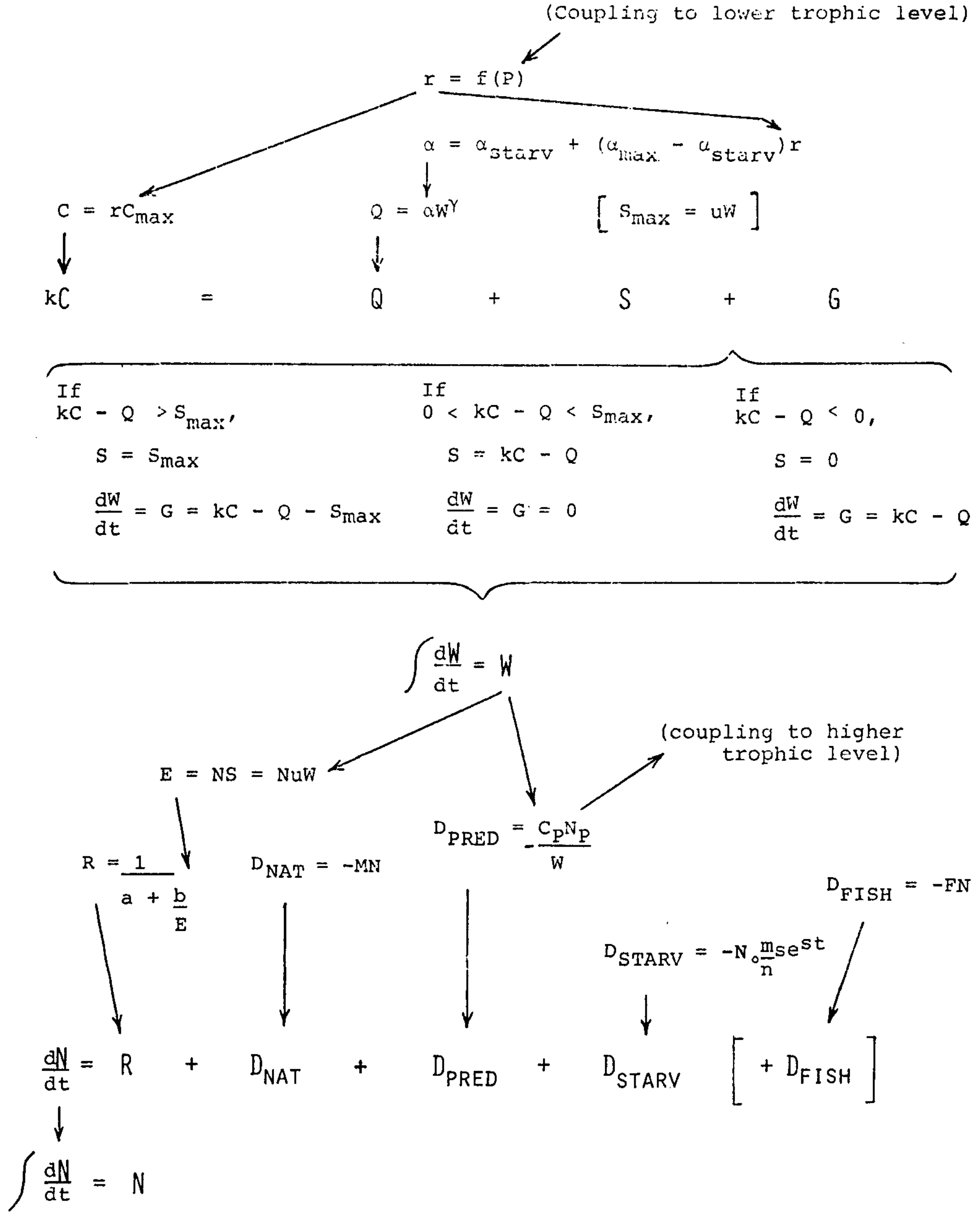

FIGURE 1.—Relationships between principal component equations describing a single species.

fishery works by the simple decaying exponential function

$$D_{NAT} = -MN, \qquad (14)$$

where M is a numerical parameter, the "coefficient of instantaneous natural mortality." The function has been applied very widely, whatever the predation rate may be (even where it is zero) and in situations where starvation probably does not occur. Lacking data to support another assumption, it seems reasonable to use Equation (14) to express the more limited category of natural mortality of the present model also. In the model, then, natural mortality is all mortality not due to predation or starvation (the trophic controls) or fishing, and would include death due to disease, senility, accident, environmental stress, etc. Field data for this limited class of mortality are rather scarce. For the hypothetical species in these simulations, approximate conventional M values were taken from Beverton and Holt's (1959) tables, and for species under predation, these were at times modified. In the age class models, different values of M are used for different age classes. Beverton and Holt (1959) discussed the variation of mortality with age more fully.

The expression for mortality due to predation, D_{PRED}, comes directly from the ration of the predator species, C_P, modeled as described in the preceding discussion of energy balance. Thus, the rate of change of prey population due to predation, D_{PRED}, is

$$D_{\mathrm{PRED}} = -\sum \frac{C_P N_P}{W_{\mathrm{prey}}}, \tag{15}$$

where N_P is the number of predators, each with ration, C_P, W_{prey} is the weight of a prey individual, and the summation is over all predator species which consume the particular prey. Equations (15) and (7) provide the coupling between each model species and the other species with which it interacts in the trophic web.

Despite the scarcity of knowledge on starvation in fish, it would seem that a complete model for a system controlled by trophic variables should include some reasonable attempt at a formulation of this source of mortality. An expression was developed that can approximate the general form of the survival versus time curves from Ivlev's (1961b:266) starvation experiments with fish. This expression states that under pressure of starvation alone, the surviving number, N, of an initial population, N_0, after time, t, will be

$$N = N_0 \frac{1}{n}(m + n - me^{st}). \tag{16}$$

The m and n are numerical parameters, and the parameter, s, comes from the boundary condition at 100% mortality, after the critical time, t_c, to extinction has been found from the integrated form of the energy balance equation under starvation conditions (see Appendix). The form of the function of Equation (16) is plotted in Figure 2. Use of Equation (1) in computing t_c and s provides an appropriate curve for any ration. The model uses the differential form of Equation (16),

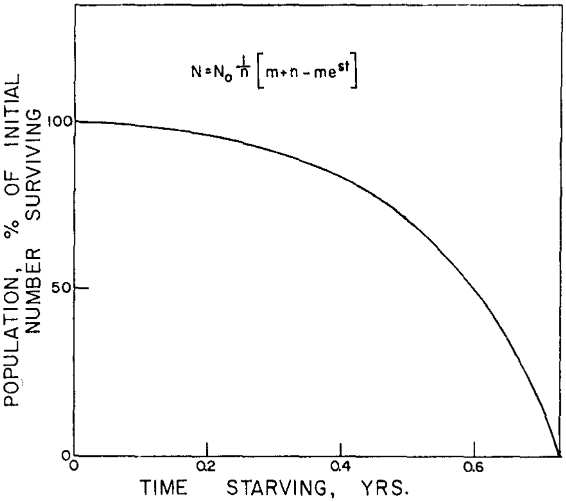

FIGURE 2.—Survival curve of a population undergoing only starvation mortality at zero ration.

$$D_{\mathrm{STARV}} = -N_0 \frac{m}{n} s e^{st}, \tag{17}$$

as the fourth term in Equation (11).

When exploitation by man is included in the system, the only modification is the addition of another term to Equation (11). In accordance with conventional fishery theory and the concept of chance encounter between fish and fishing gear, this term is exactly like Equation (14); i.e., fishing mortality, D_{FISH}, is

$$D_{\mathrm{FISH}} = -FN. \tag{18}$$

The numerical parameter, F, is an expression of the intensity of fishing effort and the vulnerability of the prey to the fishing gear.

Equations (12), (14), (15), (17)—and (18) where appropriate—provide all the terms for determining rate of change of population from Equation (11). (Figure 1 summarizes their relationships.) Numerical integration of Equation (11)—less the first term for the age class model—gives "continuous" values of population of the species over the entire time span of the simulation. Biomass of an entire species population at any instant is the product of instantaneous values of W and N (summation of a group of such products in age class models). Production over any desired period is obtained by integrating the incremental growth rates, G, and reproductive products, S (if desired), over that period.

(C) The Trophic Web

All the fish species in a trophic web can be modeled more or less as described above. Many invertebrates that serve as fish food can be modeled in much the same way, with some appropriate changes in individual component functions and by use of the proper parameter values (see Winberg 1962, and Mann 1969 for discussion relative to invertebrates). Since this model uses feeding functions based on prey abundance, an operational limitation is imposed that the ultimate resource base–the lowest item in the food chain–cannot be modeled fully in this way. In terms of total ecosystems, this is natural enough. Although the ultimate autotroph might be thought to "prey" upon inorganic nutrients, and models for plant growth as a function of nutrient abundance exist, the present model is obviously not appropriate for autotrophs.

Thus, any trophic web modeled in this way must have at its base an arbitrarily defined species or group of species. The purpose of this first exercise with the model is to explore trophic interactions among fishes. Therefore, the cause of clarity seems best served by modeling all the species of interest as fishes. The level(s) below the lowest fish species–the food base for the fish community–is then given only the simplest representation.

Two types of food base have been used in these simulations: 1) the "constant input", and 2) the "exponential growth." Properties of the constant input base are that biomass, B_1, enters the system at a constant rate, P_1, and is reduced only through predation by the higher level, fully modeled species. Thus, the rate of change of food base biomass is

$$\frac{dB_1}{dt} = P_1 - \Sigma C_P N_P, \tag{19}$$

where the summation is over all predators with their individual rations, C_P, and populations, N_P. Ecologically, this system might correspond to a fish community whose base prey enters the community feeding area at a constant rate; e.g., as brought in by water circulation or by migration as prey individuals continuously reach a particular life stage. Because of its extreme simplicity, this type food base model is preferred for studying the trophic relationships of fishes higher in the web.

Properties of the exponential growth food base are that biomass is produced at a rate directly proportional to the current standing crop of biomass and is reduced only through predation by the higher level species. Thus

$$\frac{dB_1}{d_t} = c_1 B_1 - \Sigma C_P N_P, \tag{20}$$

where c_1 is a numerical parameter corresponding to the "instantaneous coefficient of natural increase" of classical population growth theory. Again the summation is over all predator species preying on the food base. Without predation, B_1 would of course increase exponentially and indefinitely. This makes stability of such a system precarious, a fact borne out by experimentation with the model.

For these simulations, numerical values of P_1 and c_1 were selected arbitrarily to be compatible with the standard equilibrium state of the trophic webs constructed.

SIMULATION TECHNIQUE

Combination of the previously described functions produces the basic species model. A single such model species, with one of the food base models described above as prey, was exercised over a range of conditions and with some variety in certain component functions, in an effort to become familiar with some of the dynamic properties of the basic species model. Groups of such model species were then interconnected in various ways to explore the behavior of various trophic webs. Interactions between species occur through Equations (7) and (15). Where a predator feeds on more than one prey species, P in Equation (7) for that predator is the total abundance of all the n species. For each of the n prey species, the predation mortality imposed by that predator is given by Equation (15) in which the C_P upon the ith prey is

$$C_{P_i} = C_{P_{\text{TOTAL}}} \frac{v_i N_i}{\sum^{n} v_i N_i}, \tag{21}$$

where N_i is the current population of the ith species, and v_i is a coefficient expressing predator preference and availability (vulnerability) of the prey. The two (or more) elements contained in v can be separately expressed by making v a product of separate coefficients. By Equation (21), the predator tends to adjust the makeup of its diet proportionately to the abundance of the various prey, but bias is allowed for known preferences or differences in the ease with which various prey can be taken. These features, together with the basic structure of the age class model, allow that predators and prey interacting with any species may be different for different age classes of the species or may change in their degree of importance.

All the model species created for these simulations are hypothetical. To avoid resorting to pure fantasy and to get some consistency among certain species properties, each model fish species was based on a real fish species (see Table 2). Real species were selected which are sympatric, and in fact, each of the predator/prey relationships modeled has been reported in the literature in a nonquantitative way. A major simplification in

TABLE 2.–Values of parameters and of basic variables at standard equilibrium state as used in simulations. [Values shown in parentheses are alternate values used in some simulations.]

Parameter or standard equilibrium variable	Units	Source	Namesake species				
			Clupea sprattus	*Clupea sprattus*	*Clupea sprattus*	*Scomber scombrus*	*Sarda sarda*
			Model species				
			E	A	B	C	D
α_{starv}	$g^{0.2}$-$yr^{-1.0}$	See MODEL section (A)	1.0	1.0	0.7	1.0	1.0
α_{max}	$g^{0.2}$-$yr^{-1.0}$		7.0	7.0	4.9	7.0	7.0
u	yr^{-1}	See MODEL section (A)	0.1	0.1	0.1	0.1	0.1
γ		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
k		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
κ	yr^{-1}	Ursin (1967): 2421-2423	1.75	1.75	1.75	1.2	0.539
W_∞	g	Ursin (1967): 2421-2423	30.6	30.6	30.6	516.0	9,400.0
M	yr^{-1}	Beverton and Holt (1959)	1.0	1.076 [0.1169]	1.076 [0.1169]	0.9 [0.0325]	0.9
$W_{\bar{s}}^*$	g		10.0	15.16106	15.16106	150.0	600.0
N_s^*			1.0×10^5	0.61032×10^5 (1.22064×10^5)	0.61032×10^5 (1.22064×10^5)	5,000	500
R_s^*			1.0×10^5	0.65680×10^5 (1.31360×10^5)	0.65680×10^5 (1.31360×10^5)	4,500	450
a		Computed based on R_s	0.66667×10^{-5}	1.09232×10^{-5} (0.54616×10^{-5})	1.09232×10^{-5} $(0.54616 \times 10^{-5}$	0.13333×10^{-3}	0.13333×10^{-2}
b	g-yr^{-1}	Computed based on R_s	0.33333	0.39808	0.39808	6.66667	26.66667
ζ		See SIMULATION TECHNIQUE section.	0.49584×10^{-7}	0.60178×10^{-7}	0.60178×10^{-7}	0.37902×10^{-5}	0.79657×10^{-4}
c_{st}				0.45217×10^{-7}	0.45217×10^{-7}	3.03435×10^{-6}	0.65706×10^{-4}
m_{mc}				1.21158×10^{7}	1.21158×10^{7}	0.20750×10^{6}	0.10219×10^{5}
m		Selected to fit form of Ivlev (1961b: 266)	1.0	1.0	1.0	1.0	1.0
n			40.0	40.0	40.0	40.0	40.0
v		See SIMULATION TECHNIQUE section		1.0	1.0		
g_1		See RESULTS section (A)		−1.02147	−1.02147	−1.00000	−0.71428
g_2	g^{-1}	See RESULTS section (A)		0.13333	0.13333	0.013333	0.00286
F	yr^{-1}	See RESULTS section (D)		0.05 to 0.90	0.05 to 0.90	0.05 to 0.20	

*Values of variables at standard equilibrium state.

the simulations is the extremely limited range of diet of the model species; their factual namesakes have rather catholic tastes.

For these hypothetical species, a set of values for an arbitrary standard equilibrium condition was established as follows. Populations for all species were arbitrarily set at values that seemed reasonable relative to each other and in respect to the various body weights and reproductive rates. Using the various parameters selected, for each species, the r value corresponding to the standard equilibrium state was then computed. From this r and the equilibrium population of the prey, the predation parameters of Equation (7) were computed. Using this procedure for each fish species, working up the trophic chain, a complete set of equilibrium values for all species became available. A compatible trophic web was thus created arbitrarily, having at least static stability; i.e., dN/dt and dW/dt were zero for all species. Table 2 provides the values of parameters and of basic variables at standard equilibrium state for the model species used in these simulations. Where a consistent set of laboratory and field data on species in a real trophic web were available to be used in the model for predictive purposes, some of these procedures would be unnecessary.

Like all simulations, those run with the model require that initial conditions be specified. Typically in these runs, the initial conditions were those of the standard equilibrium state with the exception of some single variable value which was displaced so as to perturb the system. For example, a simulation run started with all variables at equilibrium except B_1 might be analogous to the natural occurrence of sudden catastrophic mortality in a prey species. Initial conditions are discussed further under RESULTS. In each case, the simulation was allowed to run for an arbitrary length of time, or until automatically terminated when some variable reached a prescribed limiting value. Usually runs were continued until a stable state (the original standard equilibrium or otherwise) was approached, or until a distinct monotonic trend with a predictable outcome was detected.

All the simulations were programmed using the IBM[2] System/360 CSMP (Continuous System Modeling Program) (International Business Machines Corporation 1969, 1971) and run on an IBM 360/50 Data Processing System.

RESULTS

A limitation of the approach taken here, as with any simulation model for numerical solution, is that mathematically exact and general solutions are not obtainable. A full solution of the system represents a very complex multidimensional response surface. In the very simplest case of one modeled fish species and a food base species, there are three basic dependent variables whose integrated values appear in the solution; viz., N_{Fish}, W_{Fish}, and B_1. In a "representative individual" model with n fish species and the food base, there are $2n + 1$ basic dependent variables, and in a similar model with x explicit age classes per species, there are $2nx + 1$ basic dependent variables.

A system with the complexity and nonlinearities of this type of model is capable of behaving quite differently in different regions of the state space. Since it is impossible to explore the entire response surface thoroughly, measures must be taken to limit simulation effort to regions of interest. Eventually a detailed and systematic exploration of regions of known interest using established optimization techniques (e.g., Box et al. 1953; Box 1954; Box and Hunter 1957) may be useful with the model.

For the present, the scope of simulation effort has been limited by selecting parameter values that seem reasonable and compatible for each of a small group of rather common fish species and by building out from a system already investigated to a larger system of which the original is a subset. In a number of cases where moderate changes to values of parameters or even to the form of component functions have been made, system dynamics have been somewhat altered or the system has even moved toward a new stable state. Usually, however, in a system with any regulatory capacity (stability) at all, the change has not been drastic. Rather large perturbations in initial values of the basic dependent trophic variables of such a system have not usually displaced the system to a distant stable region or resulted in breaking the trophic web (eliminating one or more species). This behavior of most of the systems simulated gives evidence that there is at least one region of some useful size in the total state space—i.e., the region in which the arbitrary

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

equilibrium state has been placed—in which the system models are fairly stable. For these reasons, it is believed that the basic form of the behavior of systems demonstrated in these simulations has some generality beyond the specific cases tested. However, in all cases, the results shown here are simply examples of interest from an infinite number of possibilities.

The simulation technique used here is amenable to use in sensitivity analyses; i.e., for determination by a systematic program of successive trials how sensitive the result is to the numerical value of a parameter or an initial variable value. Such analyses not only help define useful regions for particular results; they also give an indication of how accurately particular parameters must be measured in the field or laboratory, so that effort is applied where it is important to the system result.

In describing the following results, the shorthand notation used to reference the trophic webs has the following form:

P 1 2 1 0 0
1st 2nd 3rd 4th 5th
Trophic level

The digit in each column indicates the number of species at that trophic level. Where two species appear at a common level, they compete for prey at the next lower trophic level and are preyed upon equally by the next higher trophic level. The lowest level is always occupied by the food base with biomass B_1.

(A) Regulation of Body Weight and Population

The basic species model seems to have a considerable capacity for self-regulation; i.e., it can return to an equilibrium state after sizable displacements of some of the variables in the system. The return usually involves a series of oscillations above and below the equilibrium values, with the degree of damping depending on the exact structure and parameter values.

One of the most common and interesting perturbations involves displacement of prey abundance. Figure 3 illustrates a P11000 trophic web with a representative individual model of a species A fish preying on an exponential growth type food base with an Ivlev feeding function. The system responded to an initial condition in which the fish population was at the standard equilibrium value and the prey abundance was initially about 71.4% of the standard equilibrium value. The system returned to the standard equilibrium state with damped oscillations. The purely population controls, natural mortality and reproduction (D_{NAT} vs. R), were satisfied initially, but the system was unbalanced trophically because of the scarcity of prey. Regulation resulted from the response of body weight and resulting fecundity to food consumption, balanced by natural mortality responding to the changing population level.

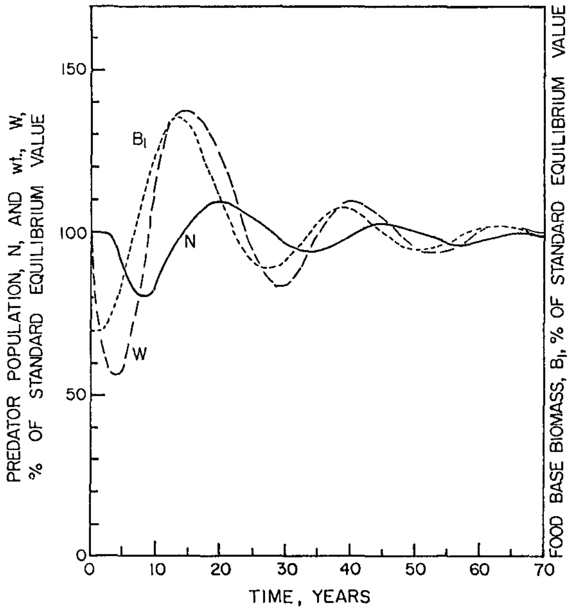

FIGURE 3.—Response of a single species to an initial perturbation in the abundance of its prey. N = predator population; W = predator body weight; B_1 = prey (food base) biomass.

Similar stable responses were demonstrated with the model for cases of initial perturbation due to high prey abundance, B_1, high predator population, N, and high predator body weight, W.

At sufficiently low values of prey abundance and production, substantial starvation mortality can occur. This is particularly true when the prey abundance decreases suddenly, since the normal population response of the predator through reduced fecundity is delayed by the reproductive time lag. Figure 4 shows such mortality for a population for four age classes modeled explicitly. The abundance of each year class decreased with time until those which had become 4-yr-olds were decimated at about 1.6 yr after the start. The

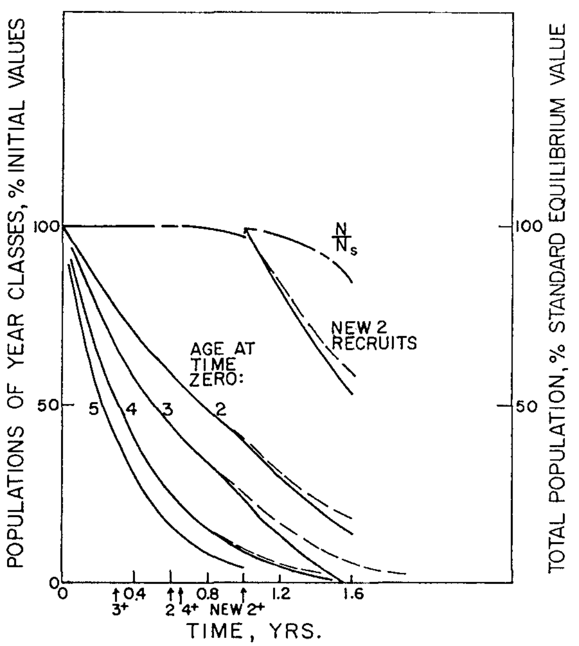

FIGURE 4.–Effects of starvation mortality on the 4 age classes of a species population and on the total population. A new class of recruits entered one year after the start of the simulation. Arrows indicate when starvation mortality began for each year class. (——— actual population of an age class; — — — population of an age class in the absence of starvation mortality; —— – —— N/N_S, where N = total species population, N_S = standard equilibrium value of total species population.)

dashed lines indicate the course of natural mortality. As interesting as the fate of individual year classes is the substantial effect on the total population (shown by the upper broken line in Figure 4).

Theoretically, starvation mortality should be capable of regulating the population. However, based on a considerable range of simulation runs, it appears that with the usual sets of reasonable parameter values for the species considered here, body weight and fecundity normally respond to produce regulation so that a starvation condition is not reached. With longlived, slowly growing species, starvation would tend to become a more important factor. In some of the cases simulated, where trophic conditions were sufficiently extreme to produce heavy starvation mortality, total extinction occurred. Figure 4 represents such a case, in which the food base biomass, B_1, was initially 20% of the standard equilibrium value and c_1 was 10%. Extinction occurred during the initial 2-yr reproductive time lag before fecundity changes could be reflected in recruitment. Some simulations were run in which fecundity was made unresponsive to actual body weight so that the effects of starvation could be better observed. With the nutritional control on fecundity thus removed, starvation occurred for some systems and started with B_1 at 50% of standard equilibrium and c_1 at 90%. With normal nutritional control on fecundity, these systems had survived.

Experience with the model indicates that for the types of species used, where extreme trophic conditions exist, disruption of the system is more likely to result from excessive stunting of growth and resultant failure of spawning than from starvation mortality. In age class models, the stunting can be observed directly in the failure of individuals of a year class to grow normally while in the recruited population. Where food supply is extremely low, actual weight loss by an individual can also be observed. In representative individual models, these separate effects are combined in the single continuous variable, W. A smaller-than-standard W represents a population that, on the whole, is undersize. If the population as a whole becomes sufficiently stunted, at some point, egg production will be reduced to zero. This corresponds to a population unable to reach sexual maturity. If the entire population fails to spawn for enough successive years, extinction of the local species population must result. It is difficult to see how a species could persist if it failed to spawn for a continuous period as long as its lifespan.

In most of the results shown here, no effort has been made to impose a sexual maturity limit on fecundity; i.e., Equations (4) and (13) with $N_m = N$ determine the egg production, E, at any body weight.

$$E = N_m u W = N u W. \tag{22}$$

For exploring the limits of stability of systems against perturbations, it seems useful to represent the attainment of sexual maturity in the model. A "knife-edge" representation–one in which fecundity has a substantial positive value or functional form above some age, length or weight, and zero below it–has been used for simplicity in much fishery work. This may be a justifiable approximation of nature for some species, especially those with short lives, fast growth, and infrequent spawning. However, a smoother and more realistic representation seems desirable. For some species, data exist on the fraction of all individuals mature as a function of age, length, or weight. In some cases (e.g., Bagenal 1957) the weight function appears reasonably linear. This means that in Equations (13) and (22) the mature spawning population, N_m, can be expressed as

$$N_m = g_m N, \tag{23}$$

and

$$g_m = g_1 + g_2 W, \tag{24}$$

where g_1 and g_2 are numerical parameters, for all values of W between that which gives $g_m = 0$ and that which gives $g_m = 1.0$. At lower and higher values of W, g_m is 0 and 1.0 respectively.

For species A and C, information from Bigelow and Schroeder (1953) permitted a rough fitting of this function. The length corresponding to the body weight at which all were mature agreed reasonably well with the ratio: length at maturity/theoretical maximum length (L_∞) of Beverton and Holt (1959) for both species. The same sort of weight limits for the function were assumed for species D, in the absence of better data. The standard equilibrium weight and the 100% sexual maturity weight were made to coincide in each species. This means that in this particular modified model, any reduction below standard equilibrium weight decreases the number of mature spawners. The effect of the linear sexual maturity of Equation (24) on the total population egg production is shown in Figure 5.

Figure 6 illustrates the response of a single P11000 trophic web with sexual maturity of species A modeled in this way. For the first 4 yr of the simulation run, input production at the food base level was about 20% of the standard equilibrium value; subsequently it was always at the standard equilibrium value. The reduced food supply resulted in stunting the population so much that from year 6 through 9 there was no recruitment. The subsequent reduced total food consumption by the greatly reduced population tended to bring the system into balance. If it survived, it would eventually return to standard equilibrium conditions. However, for this species with a lifespan of 6 yr or less, an interruption of recruitment for 4 yr is very dangerous. This, combined with a minimum population of about 1.4% of the standard at one point in the simulation, suggests that the condition reached here was very near a critical one for survival of the local species population. This

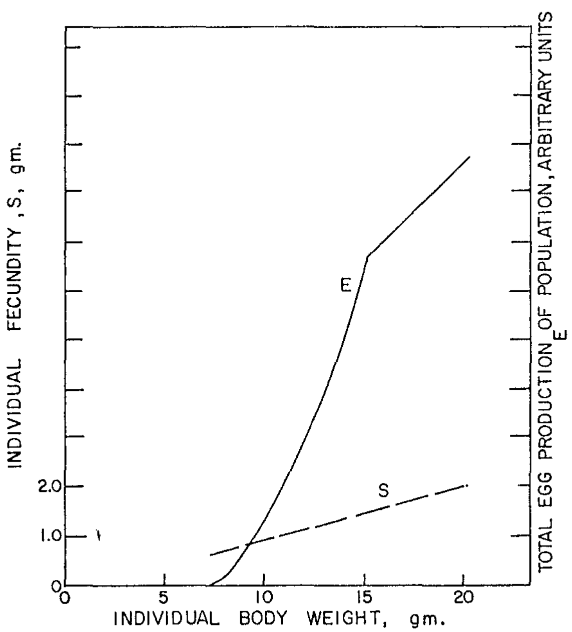

FIGURE 5.—Relationship between individual fecundity, S, and body weight and between total population egg production, E, and body weight. Sexual maturity is a linear function of body weight.

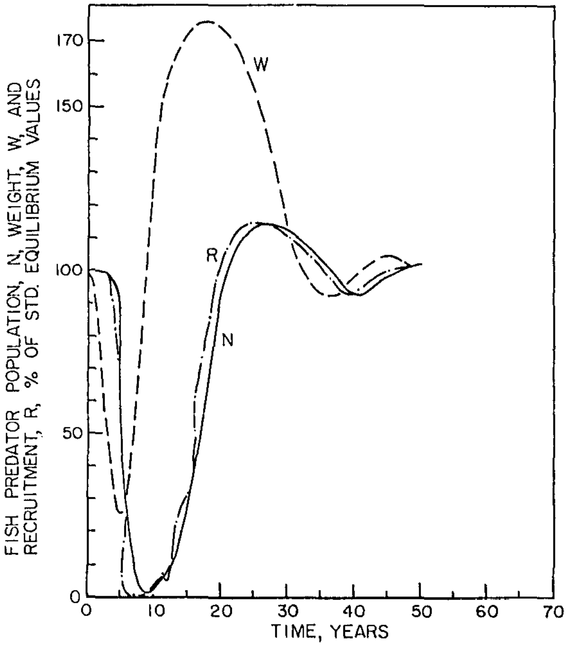

FIGURE 6.—Response of a single species, with sexual maturity a linear function of weight, to an initial 4-yr perturbation of low production by its prey. (P_1 = 20% of standard equilibrium value for the first four years.) Reproduction ceased between years 6 and 9. N = predator population; W = predator body weight; R = predator recruitment.

approach seems to offer a means of predicting the limits of stability of trophic webs against perturbation.

(B) Reproductive Time Lag

A limited study of the effects of the length of reproductive time lag was made using a representative individual model of the simplest trophic web, P11000 (a food base and the fish predator, species E). The food base was of the exponential growth type and the predator employed an Ivlev feeding function. Reproductive lags of 0, 2.50, and 6.25 yr were tried with a model that was otherwise basically the same. These three alternatives correspond respectively to the assumptions: 1) that offspring are mature when spawned, 2) that they take 2.50 yr to reach the "representative" stage, 3) that they take 6.25 yr to reach this stage. The second assumption is reasonable for species E.

The system was initially perturbed by starting with species E at 20% above its standard equilibrium population. The results for the biomass of species E are shown in Figure 7. It is clear that with increasing reproductive lag, the regulation of the system about its standard equilibrium becomes weaker; i.e., the biomass of species E, and other variables (not shown), reach more extreme oscillatory amplitudes. Larger amplitudes always incur greater risk of disaster. For example, in the runs shown here, a different sexual maturity criterion was used—knife-edge maturity at 80% of the standard equilibrium body weight. In the 6.25-yr lag run, this weight was reached at about 59 yr into the simulation, and after the 6.25-yr lag, it so reduced recruitment and the species E population that the system became unstable. This instability, which did not occur in the other runs, was due to the long lag in recruitment response to change in fecundity with changing food availability.

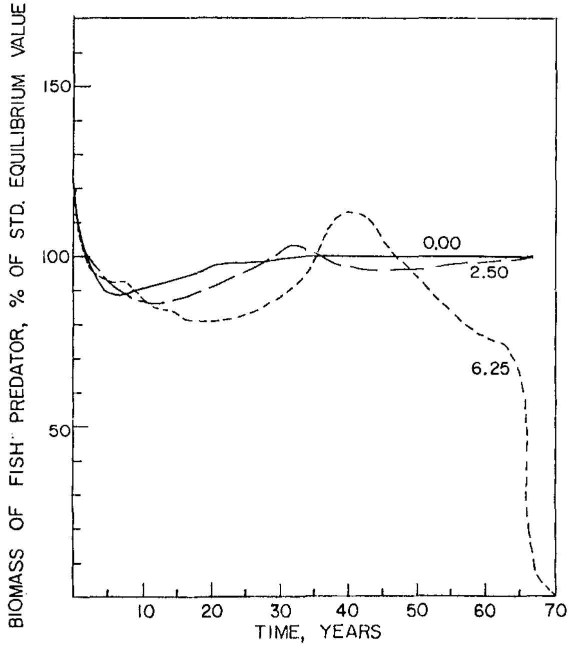

FIGURE 7.—Effects of reproductive time lag on the response of a single species to an initial perturbation in its population. The three cases illustrated have reproductive time lags of 0.00, 2.50, and 6.25 yr, respectively.

Except where otherwise stated, all the results presented here are for representative individual models having 2.50-yr lag and age class models having 2.00-yr lag. These are reasonable for the species involved. They are mutually consistent because in the age class model, reproductive products are summed over a full year and produce recruits 2.00 yr after the end of the year. Thus the average lag is about 2½ yr for the age class model also.

(C) Age Class Effects

A number of simulations were run with an explicit 4-age class model. Some results involving starvation have been shown above. Other exercises investigated the capabilities of this more accurate type of population model to regulate in the normal manner. Figure 8 illustrates the response of a simple food base-fish predator P11000 system with Ivlev feeding function to an initial perturbation of the fish predator population. The "mean total population" is a variable obtained by summing the populations of all the age classes, $\sum_{i=1}^{4} N_i$, during each computational increment of the year and taking the arithmetic average of these values. "Population mean annual biomass" is obtained by similarly summing and averaging the biomass values, $\sum_{i=1}^{4} N_iW_i$. These variables are shown in Figure 8 as percents of their standard equilibrium

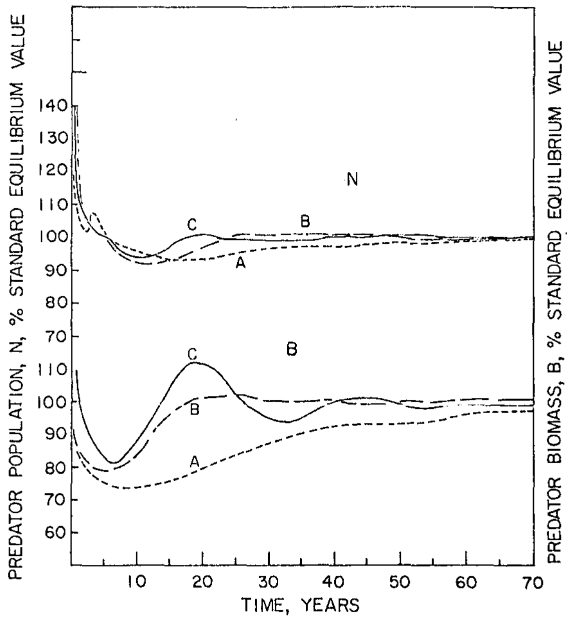

FIGURE 8.—Effects of age class structure and condition of recruits on the response of a single species to an initial overpopulation. (Curve A - 4-age class model with recruitment at standard recruit weight; curve B - 4-age class model with K_1 recruitment; curve C - representative individual model.) The three upper curves represent total species population, N; the three lower curves represent total species biomass, B.

values. In curve A, the system was represented by an explicit 4-age class model in which recruitment occurred at "standard recruit weight" (standard equilibrium weight for recruitment age). In curve B the model was identical except that recruitment occurred at K_1 times "standard recruit weight." The coefficient, K_1, is the ratio of the weight of the class ending its first recruited year to its standard equilibrium weight. Its use makes recruitment weight more consistent with current conditions. In curve C the system was represented by the corresponding representative individual model. Because of the way weight at recruitment is expressed, curves B and C are most directly comparable.

It is clear that there are some real differences in dynamics among all three models. These simulations and others indicate that for some detailed studies of the dynamics of trophic systems, age class models can provide additional information not available through representative individual models. However, much of the information of basic interest is contained in the representative individual solution. The final stable state is predicted accurately. Because of its lower damping, this model gives a conservative (maximum) estimate of the time required for the system to return to within any given range of this state, and this maximum is close enough to the actual time to be useful. For most variables and most perturbations, the maximum amplitudes of the age class model tend to be less than those of the representative individual model, so that the latter tends to predict an envelope of reasonable size within which the actual values will lie. These characteristics make the representative individual model especially useful for predicting stability.

The results shown and others suggest that the representative individual model can be used to approximate the behavior of the much more difficult and expensive age class model sufficiently well to justify use of the simpler model for many purposes. However, the quality of the approximation depends upon the characteristics of the particular system to be simulated. Where species are included that display a large range of sizes and ecological differences among the age classes of the recruited population, the representative individual approximation is likely to be less acceptable.

(D) Competition and Predation in More Complex Webs

A major purpose of the model developed here is to serve as a tool for study of more complex trophic systems. A few examples of particular interest are presented below.

In Figure 9 the trophic chain is extended by one link in the simplest possible manner to make a P11100 web. Species C preys on species A which preys on a constant input food base. Both interactions employ Holling feeding functions. The populations of all three trophic levels oscillated as the system returned from the initial perturbation of low food base biomass. Within about 3½ to 4 cycles (≈35 to 40 yr), all variables were within about 1% of standard equilibrium values again. The phase sequence of population and biomass rapidly became level 1, level 2, level 3 as would be expected. The population phase displacement was complicated by the 2½-yr reproductive lags and the effect of predation on the species A population (as species A lost weight, species C ate more species A individuals to meet its energy demands).

Such an extremely simple trophic web would be

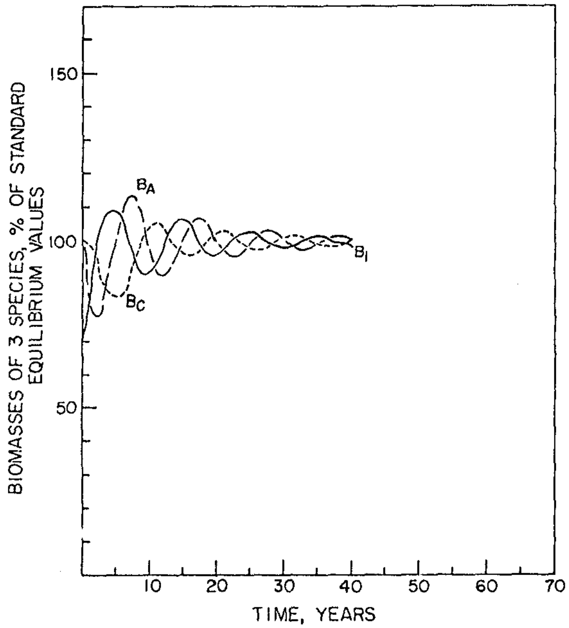

FIGURE 9.—Response of a simple 3-level trophic web (P11100) to an initial low prey abundance. (—— food base; — — — 2nd level fish species; ----3rd level fish species.)

rare indeed in nature, but it is interesting for at least two reasons. The various species might be thought of as representing in some sense whole trophic levels of more extensive natural systems, each level consisting of a rather homogeneous group of species. If all the species at a single level have identical trophic parameters, this simple web in fact represents them exactly. This follows logically and has also been verified in simulation. Thus, the P11100 web model provides a base line for comparison for later unequal competition runs in a 3-level system. It represents the behavior of any n equally competing species at a trophic level, each with a population of $1/n$th the total population. The P11000 web model provides the same kind of base line for competition in 2-level systems.

Figure 10 illustrates the simplest web, P11110, with four trophic levels: the food base and three fully modeled fish species. It consists of the P11100 web with species D added as a top predator. Again, an initial perturbation of low food base biomass caused oscillation of trophic variables of all species. After about 8 to 9 cycles (≈70 yr), all were within a very few percent of standard equilibrium values again. The same population and biomass phase sequence appears. Predation by species D caused quicker response of the species C population, reducing the phase displacement between species A and species C. The large phase displacement now occurred between species C and species D. The basic period of oscillation was also shortened from about 10 yr to about 8 yr. In all the above cases, maximum oscillation amplitudes of variables were less than the initial perturbation, and they rapidly became substantially less.

Effects produced on the system by feeding competition between species were of particular interest in these studies. No attempt was made to formulate explicit (interference) competition. Implicit competition was studied by constructing models with two predator species utilizing a common prey species. The P11000 and P11100 models above represent exactly equal competition at the second level in 2- and 3-level webs respectively.

The abstraction of exactly equal competition is not likely nor very interesting ecologically. A simple type of unequal competition is modeled by replacing one of the two species A-type competitors with species B, which is identical except that it has the advantage that its α_{starv} and α_{max} are 70% of the species A values. Thus it has lower metabolic requirements and grows more for a given food intake. Figure 11 illustrates a simulation of this

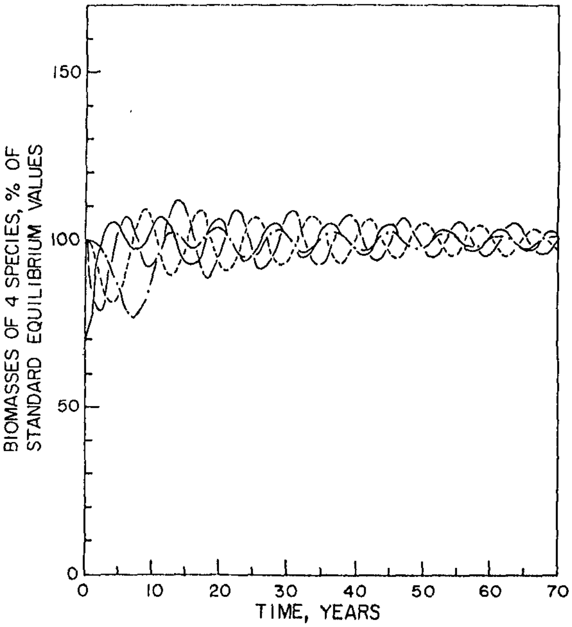

FIGURE 10.—Response of a simple 4-level trophic web (P11110) to an initial low prey abundance. (—— food base; — — — 2nd level fish species; ----- 3rd level fish species; — · — 4th level fish species.)

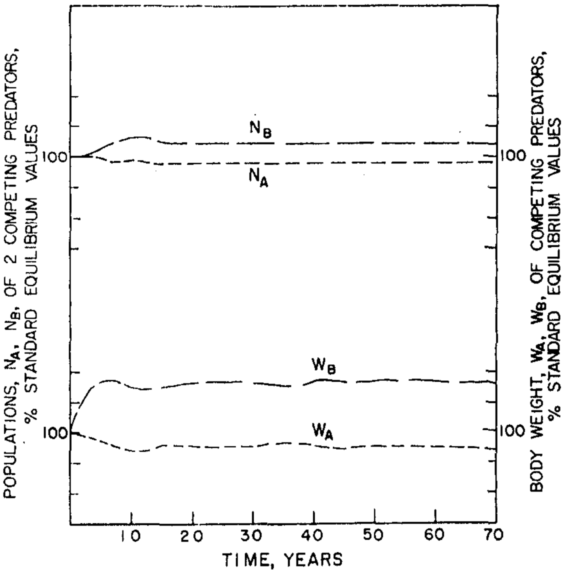

FIGURE 11.–Course of competition between two fish species with unequal metabolic demands, competing for a common food base. Species B is favored, since $\alpha_B = 0.7\,\alpha_A$. N_A = population of species A; N_B = population of species B; W_A = body weight of species A; W_B = body weight of species B.

2-level P12000 web started without initial perturbation, with identical body weights and populations of the two species. This situation is somewhat analogous to the simultaneous entry of the two competitors into an environment where the prey biomass and input are fairly close to the standard equilibrium values. The system moved away from the even start with oscillations which were firmly damped toward an apparent new steady state. In this state, the population and weight of the more capable competitor were increased relative to those of the less able contender. Their final relative positions might be characterized by the biomass ratio $B_B/B_A = 1.30$.

It is interesting to compare this prediction with that derived from the simpler graph theory analysis (Saila and Parrish 1972). This was accomplished by using the variable values from the present model for Q, B, and M to calculate the parameters q, h, a, b, and m for the graph theory model. These parameter values were then used in Equation (18) of Saila and Parrish (1972) to compute the biomass ratio $B_2/B_3 = 1.56$ of the competitors. This ratio is directly comparable with the ratio $B_B/B_A = 1.30$ from Figure 11. In view of the considerable differences in the two approaches, the agreement seems too good to be entirely fortuitous.

The above simulation represents simple unequal competition with the competitors' populations controlled by natural mortality and fecundity. Considerable theoretical and practical interest attaches to the influence of predatory mortality on such a system. Questions arise concerning whether more competing species can coexist, or whether competitors can coexist on a more even basis, where they are utilized by a common predator than in an otherwise similar environment without such top predation. Paine (1966) dealt with these questions by observation and field experiment and suggested that some intertidal systems seemed able to support more competing species when a top predator was present. Parrish and Saila (1970) explored a small number of cases by dynamic simulation of systems using Lotka-Volterra type interactions. Some competitive situations were found in which two unequally competing species persisted longer in more equal numbers when utilized by a top predator. Subsequently, May (1971) did a neighborhood stability analysis of the same systems and determined stability criteria in terms of competitive and predatory coefficients. Using coefficient values picked on this basis, Cramer and May (1972) used the Parrish and Saila model to demonstrate a case where an unstable two-species competition became stable when a common top predator was added to the system.

Figure 12 illustrates the behavior of a system with species C added as a top predator on the P12000 web of Figure 11. After some oscillation, the system moved to a new stable state with species C reduced to a level such that the competitors could support the total mortality. The stable relative biomasses of the competitors still reflect the competitive advantage of species B, but the ratio $B_B/B_A = 1.23$ is less than in the comparable 2-level system; i.e., the competitors occur in more nearly equal numbers. The result obtained by using the graph theory parameter values in Equation (19) of Saila and Parrish (1972) is $B_2/B_3 = 1.39$. When compared with the $B_2/B_3 = 1.56$ for the P12000 web, this also represents a more even standing among the competitors. Table 3 summarizes the B_B/B_A values obtained by dynamic simulation and by graph theory.

The same trend toward more equal biomasses of two species competing in the q coefficient when a common predator was present was found (Saila and Parrish 1972) using an independent set of "rough coefficients" provided by Menshutkin (1969). These comparisons of biomass ratios are

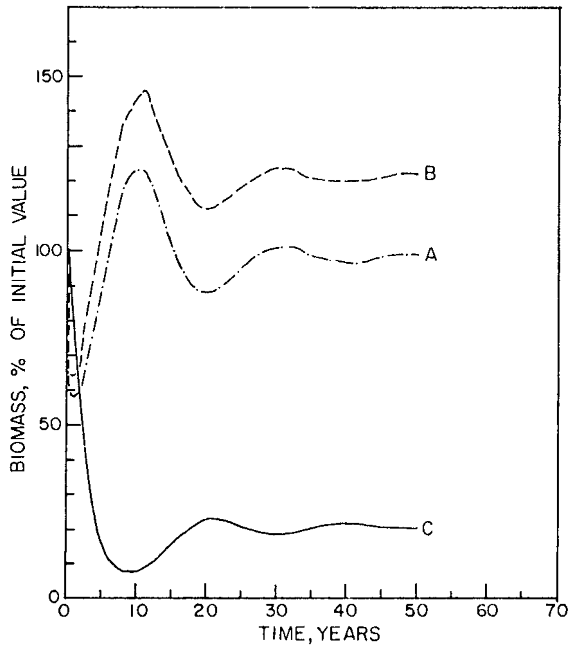

FIGURE 12.—Course of competition between two fish species, A and B, with unequal metabolic demands, competing for a common food base and utilized equally by a common predator, C. ($\alpha_B = 0.7\alpha_A$).

TABLE 3.—Biomass ratios for competing species.

Trophic system	Biomass of species with lower α / Biomass of species with higher α — Dynamic model prediction, B_B/B_A	Graph theory prediction, B_2/B_3
P12000 web	1.30	1.56
P12100 web	1.23	1.39

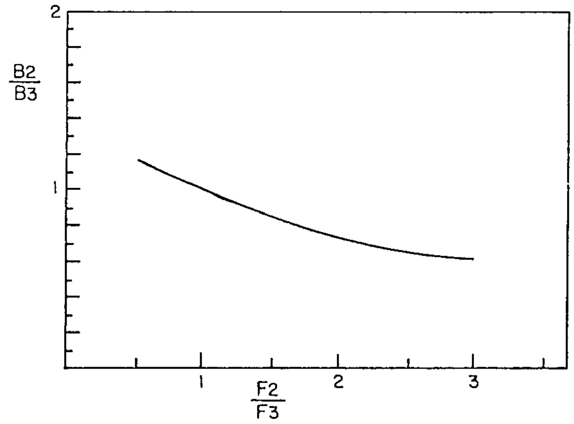

FIGURE 13.—Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: dynamic simulation prediction. The coefficient of instantaneous fishing mortality for species 3 is always $F_3 = 0.3$.

related to the concept of equitability diversity (Lloyd and Ghelardi 1964).

Some effects of human exploitation on systems of this kind have been briefly examined. Human exploitation on any species in any trophic web is expressed by the addition of Equation (18) to Equation (11) for that species (see MODEL section). Exploitation has been applied to two identical competitors in simple P12000 webs which were initially at standard equilibrium. It has produced the expected result of reducing both populations. Since the system is energy-controlled, there is always an accompanying increase in the competitors' body weights (which are always equal), and an increase in food base biomass, B_1. The total biomass of the competitor trophic level remains essentially constant. Differential exploitation of the two competitors affects the ratio of their numbers, and therefore also their biomass ratio. Figure 13 shows an example, using identical species A-type competitors that have arbitrarily been designated species 2 and species 3. This is the kind of curve produced by graph theory analysis for exploitation situations by Saila and Parrish (1972); e.g., their Figure 6, curve B. Parameter relationships are considerably different in the two papers. Natural mortality, M, in the present case is about 10 times its value in the Saila and Parrish paper. For another set of parameter values and a particular series of values of the exploitation coefficient, F, the stable B_2/B_3 ratio was predicted by both the dynamic simulation and the linear graph theory technique, as shown in Figure 14.

Exploitation of a comparable 3-level trophic web has also been simulated. A common predator, similar to species C except smaller, was added preying equally on two competitors almost identical with species A. A stable state for this unexploited system was found. Exploitation was applied to the competitors at various F values that had been used previously with the P12000 web. At sufficiently low values of F (in the range of Figure 14), in the new exploited steady state, the food base biomass, B_1, increased with exploitation of the competitors. The competitor with the lower F value increased in absolute population and biomass, while the more heavily exploited competitor decreased in both. Again, total biomass at the second trophic level remained essentially constant. In all cases, population and body weight of the predator decreased markedly when the competi-

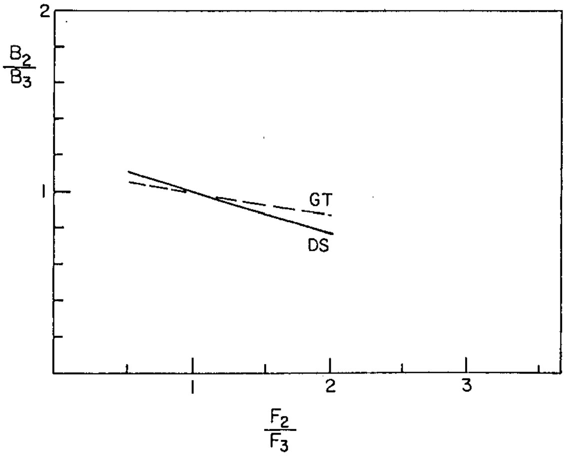

FIGURE 14.–Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: predictions of dynamic simulation (DS) and graph theory (GT). The coefficient of instantaneous fishing mortality for species 3 is always F_3 = 0.1.

tors were exploited. The ratio B_2/B_3 from the simulation at a given F_2/F_3 ratio was slightly less extreme than in the P12000 web. However, the difference was too slight to permit a meaningful check against graph theory calculations.

The top predator in this system could also be exploited using low values of F. The results were qualitatively similar to the last case above. The B_2/B_3 ratio changed only very slightly in this particular system to values intermediate between those of the last case above and those obtained with the P12000 web. At even the lowest F values for the competitors in Figure 14, if exploitation of the top predator was carried above about $F = 0.2$, the top predator was lost from the system. The same result occurred with $F \leq 0.2$ on the top predator if slightly higher F values than those in Figure 14 were applied to the competitors. The two lower trophic levels persisted stably. This vulnerability of the top predator represents another limit to the stability of the larger system. Although it has not been explored, it appears to have implications for possible effects of exploiting real multispecies fisheries.

The particular combinations used in this brief investigation were far from optimum for exploring a large range of exploitation intensities in multilevel webs (The choices were made primarily for similarity to other cases studied previously). The low permissible levels of predation and exploitation that the 3-level system would tolerate, together with the high natural mortality, made for difficulty in comparing results with those of trophic systems previously examined; e.g., by graph theory. However, the considerable similarity of the predictions in Figure 14 and Table 3 by these very different approaches seems highly suggestive.

AVAILABILITY OF MODEL AND COMPUTING DETAILS

Written descriptions of various portions of the model and their sources in somewhat more detail are available from the author. The basic computer software package used (IBM 1969) and a more advanced version (IBM 1971) are described in the manufacturer's literature with enough detail in the former case for ready use by the reader. The CSMP package is sufficiently user-oriented that no further interface program is required; the model is written directly into the CSMP structure using simplified FORTRAN-like statements. Program listings and card decks for sample trophic models are available from the author, together with tables of input values used and a glossary of code names of variables and parameters.

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APPENDIX

The parameter, s, in the starvation mortality Equations (16) and (17) is found as follows:

During starvation, since $kC < Q$ and $S = 0$, Equation (1) simplifies to

$$G = \frac{dW}{dt} = kC - Q = kC - \alpha W^{\gamma} \qquad \text{(A-1)}$$

At any constant level of ration, C, this integrates to give

$$t = \frac{5j}{4\alpha}\left[\ln\left|\frac{j + W^{0.20}}{j - W^{0.20}}\right| + 2\tan^{-1}\frac{W^{0.20}}{j}\right] - \frac{5W^{0.20}}{\alpha} - I_1, \qquad \text{(A-2)}$$

where: $j = \left(\frac{kC}{\alpha}\right)^{0.25}$,

I_1 is a constant of integration. Taking the boundary condition that $W = W_0$; i.e., the initial weight of each original N_0 individual, at time $t = 0$, the constant I_1 can be evaluated any any level of ration.

The boundary condition at 100% mortality is taken to correspond with a critical fraction—0.6—of the body weight of a normal, well-fed individual (the critical fraction is estimated from a variety of sources, including: Dawes 1930; Lawrence 1940; Phillips 1954; Adelman et al. 1955; Brett 1962; Brett et al. 1969). Using this critical lethal body weight for W, Equation (A-2) can be solved to give the critical time, t_c, to 100% mortality. Using this t_c in Equation (16) when $N/N_0 = 0$ gives the value of s.