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NOTITIAE COLLATI
Pertaining to biomass based fisheries ecosystem simulation models

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NOTITIAE COLLATI

(pertaining to biomass based ecosystem models)

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NOTITIA I

1. INTRODUCTION AND REVIEW OF PRODUCTION AND DYNAMICS OF ORGANIC MATTER IN THE MARINE ECOSYSTEM.
   - 1.1 The purpose of the Notitiae collati and the manner of presentation.
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1.1 The purpose of the Notitiae Collati and the manner of presentation.

These Notitiae Collati (collected notes) attempt to give the pertinent biological and ecological background for quantitative numerical reproduction of processes in the marine ecosystem. Some general knowledge is briefly summarized and approaches suitable for use in the simulation are selected, indicating also reasons for selection such as availability of data, quantitative sufficiency in relation to quantitative knowledge, the most accurate and well validated approach, etc. It should be remembered that there are few matters in science where there is unanimous consensus. Obviously several slightly different approaches are possible in several subjects and different individuals (simulators) might prefer different approaches. In fact, the use and

test of different approaches, including their comparison, is desirable for the advancement of the science and technology.

No long explanations are given in these notes as it is assumed that users and readers are knowledgeable and experienced scientists with wide backgrounds. The whole subject of ecosystem simulation is not a suitable subject for students to attack at the present stage, as proper textbooks and university training are not available.

The references are kept to an absolute minimum and are given only in cases where more detailed descriptions are necessary and/or available or a more controversial subject needs validation. Many subjects have been investigated by many researchers and to list them all fairly would be a difficult (nearly impossible) task. References are given in some cases for data sources, and for numerical values of constants when these were derived in an empirical way--however, data and the values for coefficients used in the models are given in the documentation of individual model applications.

Most of the mathematical formulas given in these notes are usually given in their empirical form, as used in the models; exceptions are in the introductory part where some of the mathematical derivation is briefly discussed. A few of the formulas are graphed to demonstrate the numerical behavior of them.

It should be borne in mind that the models discussed here are computed in small time steps with finite difference approaches. Thus many constants are adjusted to the time step used in particular models.

In some cases the estimates of the error limits are approximately given. In other cases these limits have been, and will be, studied quantitatively with the models--"sensitivity studies".

The actual formulas used in the models and the manner of using the coefficients in these formulas are given in the description of the model in other reports and in programme documentations.

It has become a nearly impossible task to establish the authority to individual statements, due to the growing amount of scientific literature and due to never ending repetitions. Thus in a summary like the following notes, the readers can take or leave (disagree with) the statements, depending on their backgrounds. Ones own thoughts and experiences are necessary today to evaluate any statement made by anyone.

Furthermore, it should be pointed out that the summary below is not meant for indoctrination of anyone. It is merely a documentation of methods used in the holistic, fisheries oriented ecosystem simulation and the evaluation of direct and derived data availability.

1.2 Dynamics of organic matter and biomasses in the marine ecosystem.

Henri Pointcaré has pointed out that clarity in arguments cannot be achieved before it is introduced into definition.

The term production has been widely used (mostly misused) in connection with the dynamics of organic matter in the marine ecosystem. First, the term implies dynamics; thus we must always define the subject of the production and quantify the production as a rate, i.e. define the unit of time, amount, and subject (a single organism of given age and size, a group of organisms in defined 3-D space).

The most common use of the term production is in the production of organic matter by plants (mainly phytoplankton) ("basic organic production").

The organic production depends first on the type of producers and their production capacity (rate to produce). Thus in order to estimate production we must know: the type (species) and their quantity present at the initial time or at any given time step, i.e. we must know the standing stock or standing crop of all the producing species. The standing stock is in itself a dynamic property and depends on the production (thus a nonlinear second order interaction exists). Furthermore, the producers are being eaten and die from other causes, creating secondary nonlinear effect.

The production capacity depends (under otherwise identical conditions) often also on the age of the individuals in the population. The production capacity furthermore depends on the following conditions:

—Availability of matter (nutrients) from which to produce (i.e. carbon, oxygen, and other minor constituents). Besides the available quantities of these substances which should be measured at given locations and times, their availability is dynamic, depending on transport and regeneration of the produced matter in the past. The required density of measurements in space and time are not available for any region of the ocean.

—Energy is required for each production. In basic organic production light energy is required. This depends on the energy available on the surface (which besides position and time is also dependent on very variable cloudiness). The availability of light energy in the depth depends, besides the depth and location (distribution of producers in it), on the turbidity of the water and its change with time. Furthermore, the dynamics of the producers themselves influences largely the turbidity. Furthermore, different organisms utilize different wave lengths of light. The energy utilization (or the production capability) depends also partly on temperature. The space and time variation of light

energy can only be approximated at present (re. rapid variation in cloudiness, etc.).

The above could be put into a general mathematic form. In order to establish "manageable" (realistic and to our knowledge corresponding) formulas of the organic production and production of biomasses of other components of biota, some idealized assumptions are necessary in order to keep the model realistic.

If we designate the condition or state vector of basic organic production to be - $\underline{P}(t)$, then the rate of change of this state vector would be:

$$\underline{P}(t) = \underline{P}(t) = \frac{dP(t)}{dt} = f(\vec{W}_{(t)}(B_{i-n}, Z_{i-n}, R_{i-n}, Q_z, Q, N, G))$$

where: $R_i = f(b, z, Q, Q_z, A, N)$

Where:

P - phytoplankton production

B_{i-n} - biomass of individual species (i-n)

b - type of organisms

Z - depth distribution of the species

R - production rate of the species

Q - surface light

Q_z - distribution of light with depth

z - extinction coefficient

N - nutrients availability level

G - grazing

W - transport vector

A - age of the species

Every one of the above parameters can be a function of many other parameters not mentioned here and can in turn affect other rates in operation in the nature. Some processes and conditions can be presented as rate parameters (k_i) if they are slowly varying or nearly constant. Our present quantitative knowledge of most of the above parameters and their changes is rather limited.

Various other formulations of primary production are available, such as the one by Andersen and Ursin, 1977, based on earlier works by Steele (1958, 1962) and Lassen and Nielsen (1972). With the notation described below, the rate of primary production per m^2 and day is expressed by Andersen and Ursin (1977) as:

$$p = p_m \hat{H} f(c_p).(e-e^{A})/xz \quad \text{days}^{-1}$$

$$\hat{A} = \begin{cases} -1 \text{ for } I/\hat{H} \geq 150 \text{ kcal m}^{-2} \text{ hours}^{-1} \\ 1 - I/\hat{I} \text{ for } I/\hat{H} < 150 \text{ kcal m}^{-2} \text{ hours}^{-1} \end{cases}$$

$$f(c_p) = \begin{cases} 1 & \text{for } c_p \geq .018 \\ 55.5556\ c_p & \text{for } c_p < .018 \text{ (pure number)} \end{cases}$$

p_m is a proportionality constant (hours^{-1}).

$\hat{H}$ is length of day (hours days^{-1})

c_p is the concentration of phosphorus accessible to plants (g m^{-3}).

1 is the total radiation (kcal m^{-2} days^{-1}).

$\hat{I}$ is half the value of the radiation at the time of the year when $I/\hat{H}$ = 150 kcal m^{-2} hours^{-1}.

x is the coefficient of extinction of the light (m^{-1}).

z is the depth of the euphotic zone (m).

$f_{(cp)}$ is analogous to the feeding level of animals.

As seen above, many quantities and rates must be available and the rates of changes known or possibilities for prediction must be at hand (radiation, light extinction--i.e. the prevailing turbidity, concentration of phosphorus, etc.). These data are seldom available in desired space and time scales and very approximate estimations must be made. These estimates do not warrant a complex formulation of the process and do not allow that the process would be terminant for other (following) processes.

Most of the parameters necessary for the computation of basic organic production can only be estimated at any given location and time to the order of magnitude. Thus it is senseless to base quantitative ecosystem computations on the estimation of basic organic production and its utilization. Furthermore, the pathways of the produced organic matter in the marine ecosystem are greatly variable in space and time (i.e. the utilization and regeneration of organic matter is very variable).

Thus we can use organic production measurements and estimates only in large space and time scales for comparison of different regions as to their "productivity" (large scale

carrying capacity). It has become fashionable to attempt to evaluate "production" in the marine ecosystem in terms of energy and "energy flow". This procedure only adds considerable uncertainty of conversion and makes the comparison with reality a virtual impossibility.

We can often find in the literature a term of "secondary production" which usually refers to the dynamics of the biomass of zooplankton and sometimes even fish. Even a more nebulous term, "surplus production", is found in the fisheries literature. Examination of the biomass dynamics below (or above) the basic organic production could indicate whether we can really talk about production or only of biomass conversion from one form or species to another. It may be that we can define and talk about production utilization, utilization efficiency, and/or conversion efficiency. The first step in the utilization of biomass is the process of eating (predation), live or dead.

The second process is the digestion of the eaten matter which results in the conversion of some into new biomass, breakdown of some to basic nutrients and organic compounds (non-living) to obtain energy for activity as well as other living processes, and excretion of some of the eaten matter undigested, which can be used by other organisms including bacteria.

The conversion of the digested matter into a new form of biomass thus results in growth via katabolic processes and the breakdown of organic matter (metabolism). The utilization of organic matter for energy release is also a process of regeneration of basic nutrients. Thus from the point of view of dynamics of organic matter we must consider the processes of predation, growth, and reutilization (disposal) of growth.

Predation (dealt with more fully in another Notitia) depends on many conditions of the prey and predator as well as general ecosystem conditions at large. Among these determining factors are: suitability (preference), predator prey size relations, availability (encounter-density dependent), and avoidance behavior. Thus mobility and distribution of predator and prey in space and time are important predation determining factors.

Growth is described in detail in another Notitia in this collection. Growth is a complex process affected by many factors. First, it is dependent on the efficiency of digestion (i.e. how much of the eaten material is converted to tissue), thus dependent on the organism and on some physical factors, such as temperature. Furthermore, it depends also on the biomass of the growing organism present. As a population consists of individuals with different age and size, the growth rate of an individual is different than

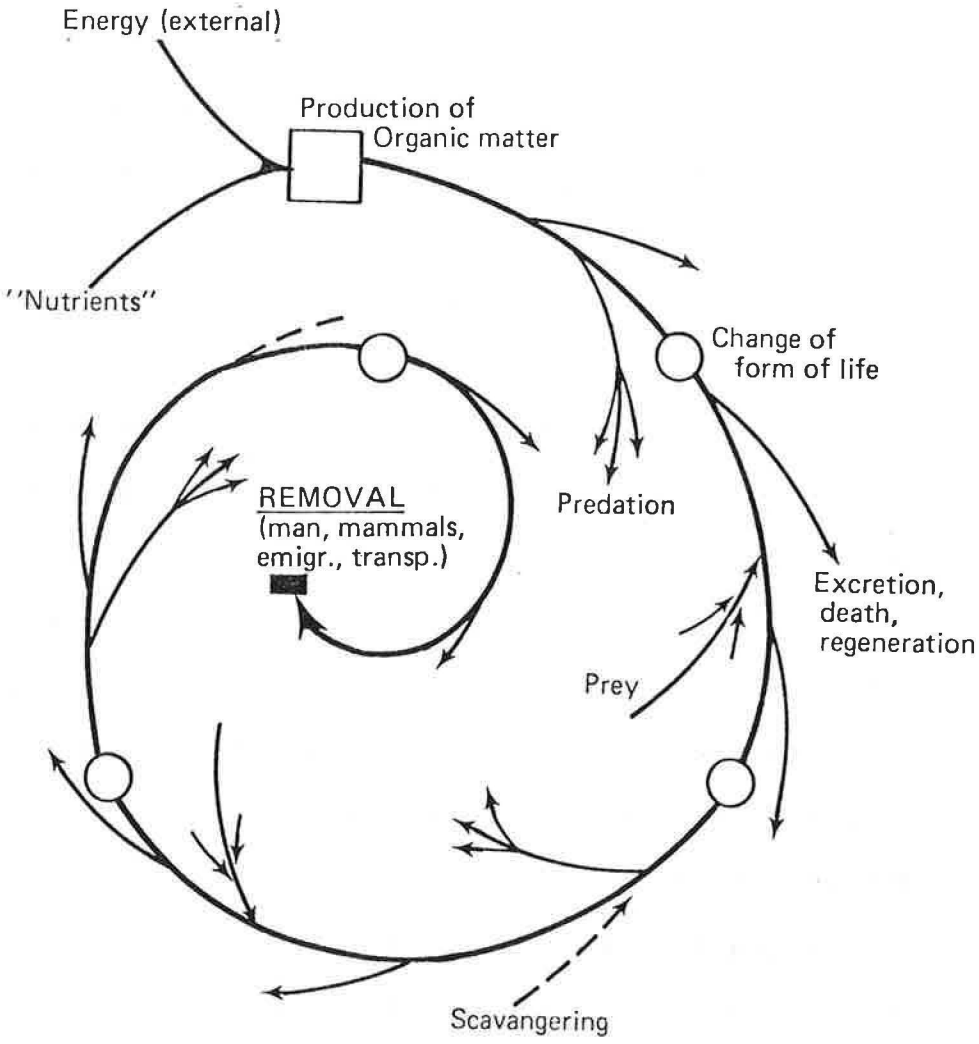


Figure 1-1.--The biomass spiral.

the average growth rate of a biomass. Obviously the amounts of food available and taken are additional important growth determinants. Thus growth is a complex dynamical process with many nonlinear terms. (The possible simplifications of computation of predation is given in corresponding Notitia later.)

Finally, we must consider the disposal (utilization) of growth and come by necessity to an "inward" decreasing circulation system. (See schematic figure 1-1--"the production spiral".) The utilization encompasses also predation (in this case by others) and includes other mortalities such as from diseases and old age. However, the organic matter does not end with the death of an organism--the carcasses are utilized to a large extent by many other biomasses, specially demersal fish and benthos. In summa summarum we can conclude that there is no defineable surplus production in the marine ecosystem. Furthermore, there are no clearly defined food chains and trophic levels--these have been gross oversimplifications in the past.

Considering the above, we must also conclude that no single or simple theory, and no simple primitive equation formulations are possible for the marine ecosystem. This system must be presented and simulated with a set of equations of considerable size, which reproduce individual processes

and distributions. However, three important processes dominate quantitatively, controlling the abundance and distribution of individual components--growth, predation, and migration. Each of these processes is in turn controlled by a relatively complex set of conditions. The above can be demonstrated in mathematical notation with simplified assumptions.

The biomass of any given population is a function of time and location ($P = f(t,x,y,x)$). The individual time change of this population ($\frac{dP}{dt}$) is:

$$\frac{dP}{dt} = \frac{\partial P}{\partial t} + \frac{\partial P}{\partial x} V_x + \frac{\partial P}{\partial y} V_y + \frac{\partial P}{\partial z} V_z$$

The first term on the right side ($\frac{\partial P}{\partial t}$) is the local time change and the following three terms represent migrations and advection. These migration terms comprise several processes, such as spawning and feeding migrations, dispersal and aggregation, migrations caused by unfavorable environmental conditions, and transport by currents. The migration terms determine largely the spatial distribution of most species/ecological groups. These terms never vanish; however, if we consider a large region (such as the Bering Sea), we may assume that the migrations into and out of this large region are negligible and that the migration term is 0. In this case individual change equals local time change. The local

time change is largely a function of biomass growth (G) and its removal (R), the latter comprising mainly predation, mortality, and the fishery.

$$\frac{\partial P}{\partial t} = f(G,R)$$

If we consider that an equilibrium might exist (which, however, is very unlikely) in an ecosystem over one year, then $\frac{\partial P}{\partial t} = 0$ and

$$dG = dR$$

The above is the criterion for finding "equilibrium biomasses" with a deterministic Bulk Biomass Model (BBM) (also PROBUB).

Biomass growth of any given species is a function of the age of the species, time of the year (also in relation to e.g. spawning), food availability, and environmental conditions.

$$\frac{\partial G}{\partial t} = f(A_1, t, F, T)$$

The removal is a complex space-time function of many variables, such as food requirements of many components of the ecosystem, mortalities from various causes, etc.

$$\frac{\partial R}{\partial t} = f(t,x,y,z,q_1..q_n,m,s,k,f_f...)$$

Thus it becomes apparent that quantitative computation of changes in the ecosystem requires the use of numerous explicit equations. Consequently the numerical ecosystem simulation becomes, to a large extent, the accounting of growth, removal

(predation and mortalities), and the changing biomass imbalance in nature. Thus we can define the ecosystem simulation (avoiding the word modeling) as quantitative reproduction of the marine ecosystem dynamics (i.e. including all pertinent processes), based on the best available quantitative knowledge of this system.

1.3 References

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NOTITIA II

2. DISTRIBUTION OF BIOMASS PARAMETERS WITH AGE IN A FISH POPULATION

The subject matter of this note has been recently summarized in two NWAFC Processed Reports by Granfeldt (1979 a and b). This Notitia contains only general remarks on the subject as details are found in abovementioned reports.

Cushing (1973) noted that the age structure of a marine fish population and the age-variable mortality had not been described in full. Many rates of processes altering the biomass of a given population change with age of the species. Therefore the computation of age-dependent biomass parameters requires quantitative knowledge of biomass distribution with age within a given population. A numerical method for computation of these parameters is outlined in the above cited reports, showing also some results and their applications.

The method mentioned above allows the extrapolation of juvenile (pre-fishery) biomasses, using turnover rate and a mean number distribution with age as auxiliary data. Empirical input data consist of average growth rates of individual year classes (age groups) and long-term mean age composition of exploitable part of the population.

The growth rate of a population is different from the growth of the species. (The computation of biomass growth rate is discussed in Notitia III.) Furthermore, the distribution of average biomass with age varies considerably from species to species and is at the same time also a function of growth rate.

Many parameters and rates, such as growth and mortality rates and food requirement, are functions of fish size/age. Thus we must know the size/age distribution in order to compute biomass based parameters. Examples of distribution of biomass, numbers, and growth with age are shown on Figures 2-1 to 2-4.

Quite different considerations of age structure with age and its change apply to biomass based models than to number based models. The number based models consider the reduction of the numbers with time and are thus, among other considerations, very sensitive to the variations in recruitment. Furthermore, in trophodynamic computations in number based models one has to know rather exactly the ages of species subject to predation and other mortalities in order to subtract these from the numbers. This information is very approximate and requires that individual populations (species) must be divided into year classes and/or other age groups. On the other hand, in the biomass based models the biomass can increase and decrease with the age of the population, and the distribution of biomass with age can be determined computationally which provides realistic possibilities of various age dependent computations, such as predation, without the necessity of dividing the biomass into age groups.

If biomass distribution changes with time, due to e.g. fishery, changing recruitment, etc., the corresponding size/age dependent biomass parameters such as growth rate must also change. On the other hand, if one of the biomass distribution with age dependent parameters

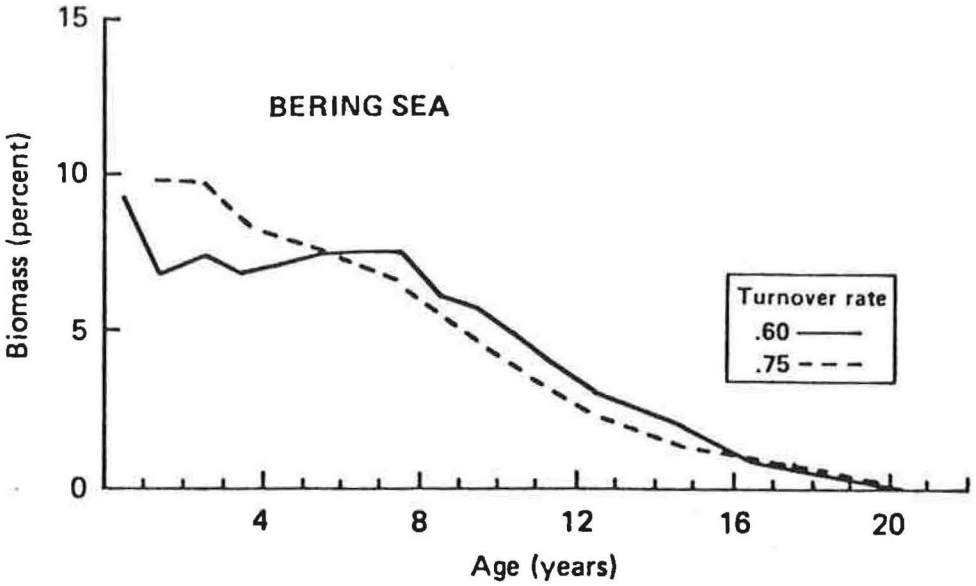


Figure 2-1. Distribution of biomass with age of Pacific ocean perch from eastern Bering Sea.

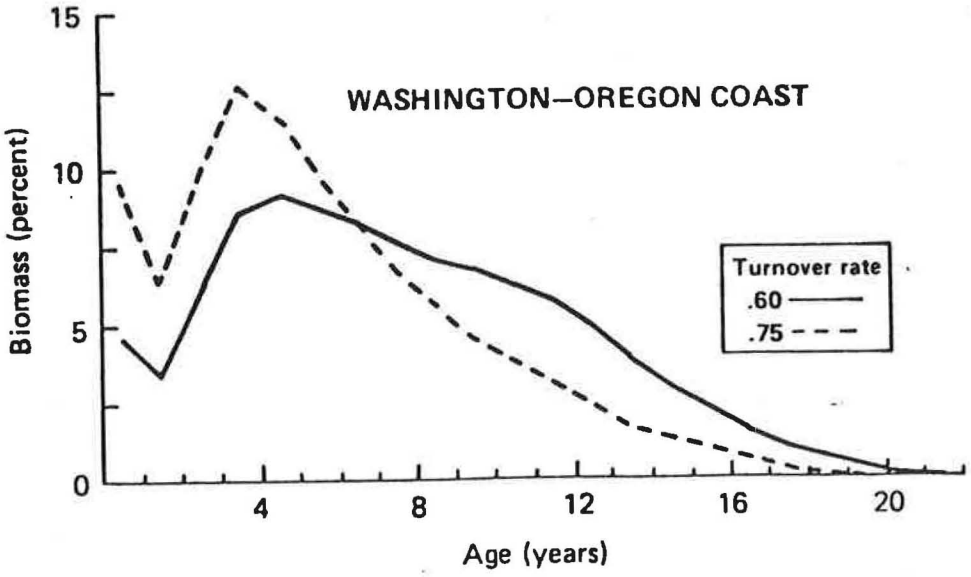


Figure 2-2. Distribution of biomass with age of Pacific ocean perch from Washington-Oregon coast.

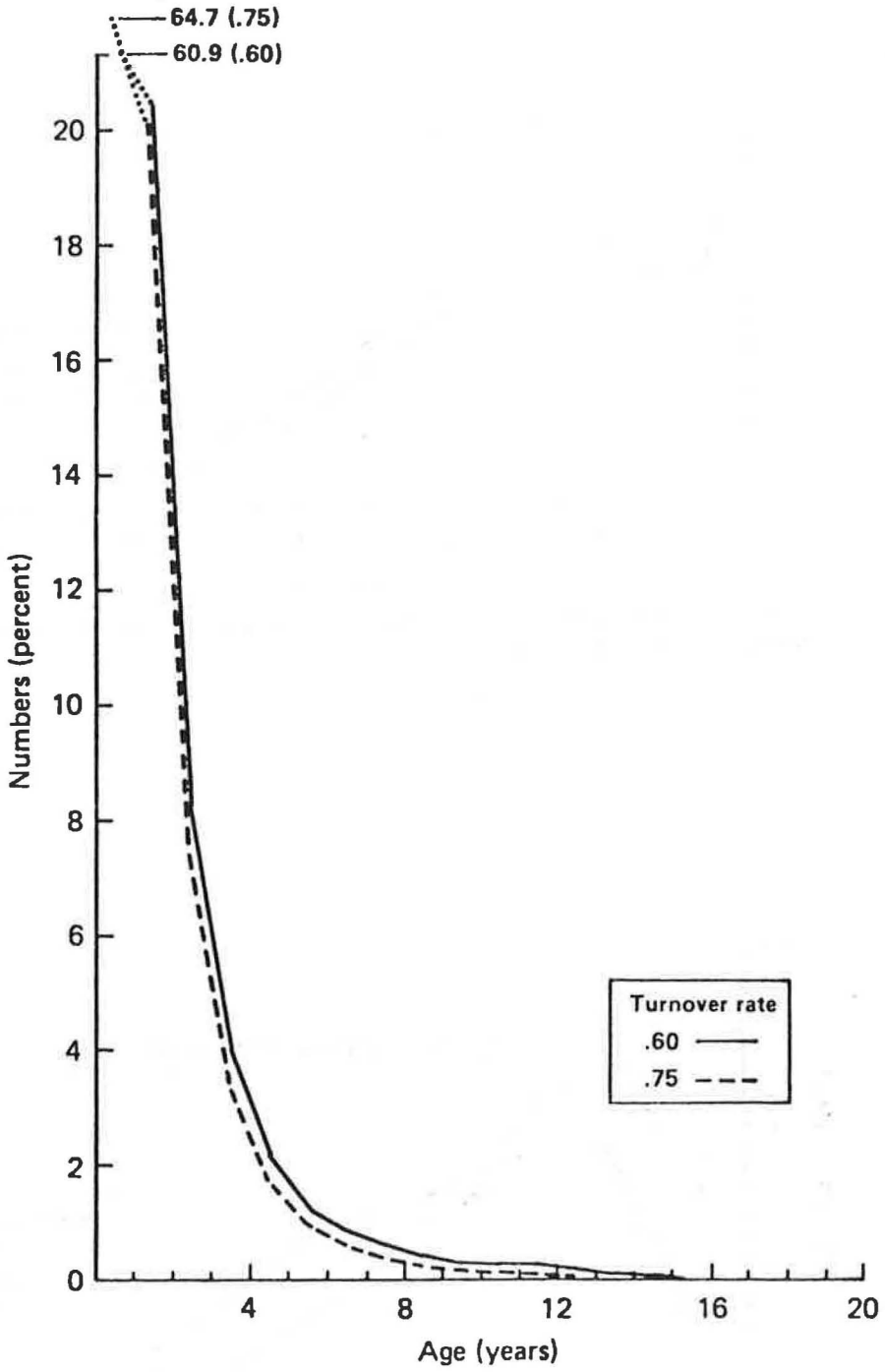


Figure 2-3. Distribution of numbers with age of Pacific ocean perch from eastern Bering Sea.

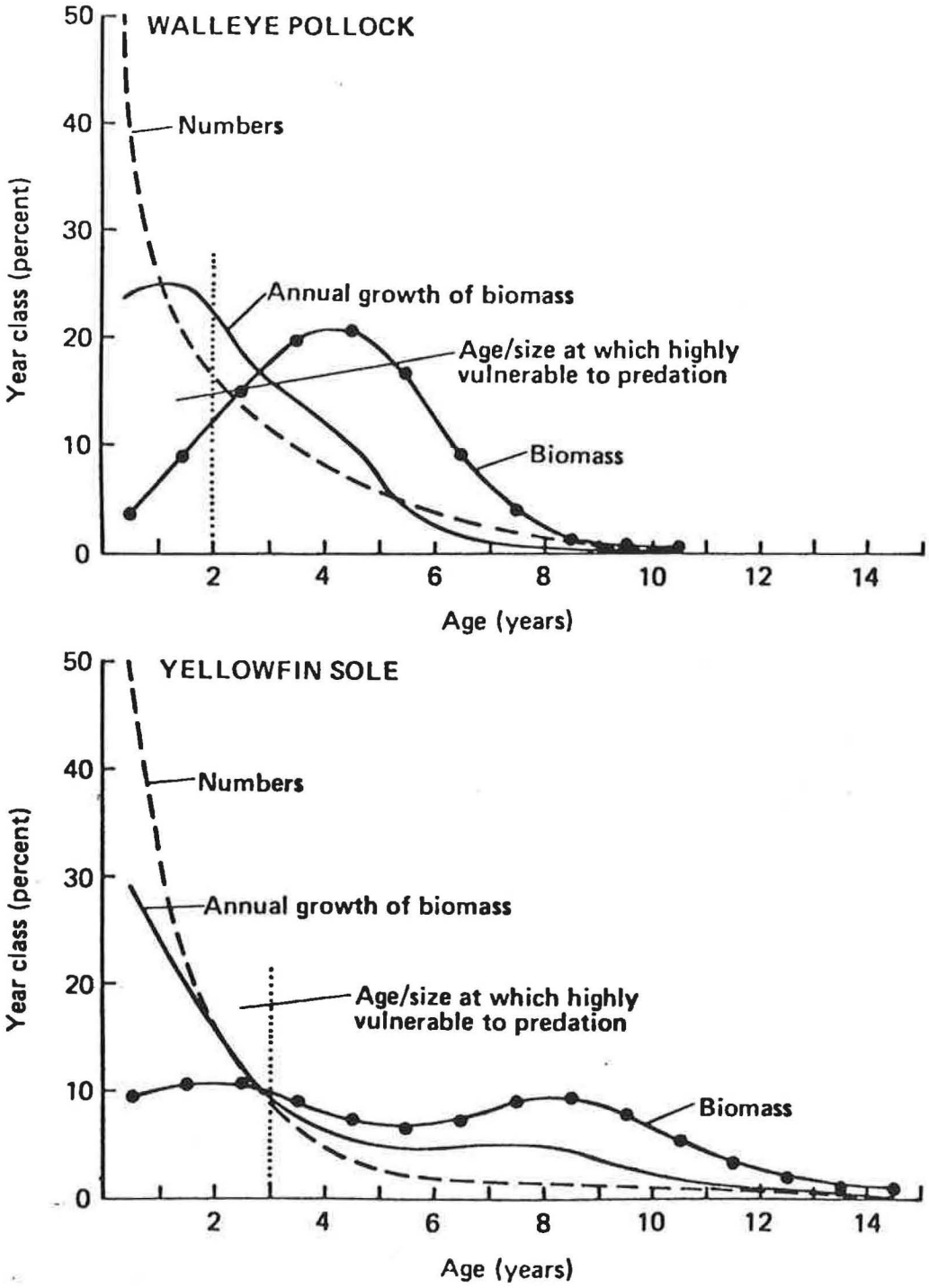


Fig.2-4. Mean biomass and its annual production distribution with age in pollock and yellowfin sole. The portion of biomass highly vulnerable is indicated.

(such as growth or mortality rate) changes, the distribution of biomass with age will also change. This change of biomass distribution must be implicit in the ecosystem simulation. Thus the changes of biomass are computed indirectly in changes of growth and mortalities (g-m). We must, however, know and/or assume, based on evidence, on which part of the biomass does various mortality rates apply (predation, fishery, spawning stress mortality). Furthermore, we must also be able to compute the fraction of exploitable and the juvenile biomasses for variety of reasons (e.g. fishing/yield computations, comparison of computed results to survey results, etc.).

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NOTITIA III

3. GROWTH OF FISH BIOMASS AND FACTORS AFFECTING IT.

3.1 Growth of individual fish.

3.2 Growth of biomass as function of its distribution with age.

3.3 Seasonal growth and the effect of temperature on growth.

3.4 Effect of food availability and partial starvation on growth.

3.5 Effects of variations in recruitment, spawning and fishery on the growth rate of biomass.

3.6 References

3.1 Growth of individual fish

Paloheimo and Dickie (1965) have summarized the processes of growth of individual fish. The growth rate (in terms of weight per unit time) is highest in larvae and juveniles and decreases considerably with age (Fig. 3.1). The growth rate is known to vary with seasonal changes of temperature and with the availability of food. The growth rate of individual fish is not used directly in the biomass based ecosystem models, but is used for computation of the growth rate of the biomass of the population which is also a function of biomass distribution with age.

Instantaneous growth rate (G) of a fish is usually computed as:

$$G = (\log_e W_T - \log_e W_t) / (T-t) \qquad (1)$$

where: W_T - final weight (g) at time T; W_t - initial weight (g) at time t; T - final time (in e.g. days); t - starting time.

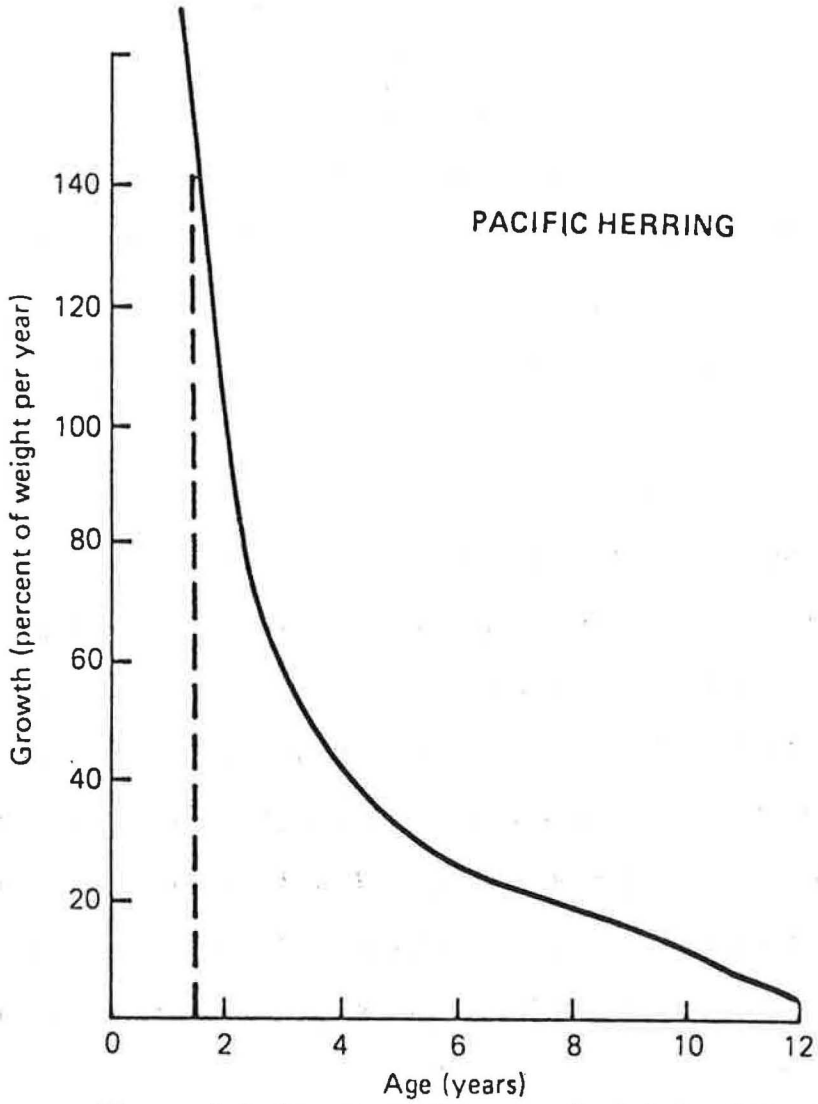


Figure 3-1. Growth of biomass (weight) of Pacific herring at different ages, as percent per year.

Annual growth rate (in percent per year) is computed with the following formula:

$$G_{an} = \left[(W_{n+1}/W_n \ .100)\right] - 100 \qquad (2)$$

The corresponding monthly growth rate is computed with the well-known compound interest formula:

$$G_{mn} = (10^a - 1) \ .100 \qquad (3)$$

where $a = \log (W_{n+1}/W_n)/12$

The corresponding instantaneous coefficients are:

$$g = \ln (1-G/100) \qquad (4)$$

The symbols in the above formulas are:

g - instaneous growth coefficient

G_{an} - annual mean growth rate (in %)

G_{mn} - monthly mean growth rate (in %)

W_n - weight of the fish in year n

W_{n+1} - weight of the fish in year n+1

3.2 Growth of biomass as a function of biomass distribution with age

The computation of growth rate of a biomass of a given species requires the knowledge of the distribution of the biomass with age, as the growth of individual fish changes rapidly with age (see Fig. 3.1). The method of computation of biomass distribution has been described by Granfeldt (1979a, Notitia II) (see also Fig. 3.2 as an example).

The annual mean growth rate of a population is:

$$G_A = \sum^{n} (G_{an} \times B_{pn}/100) \qquad (5)$$

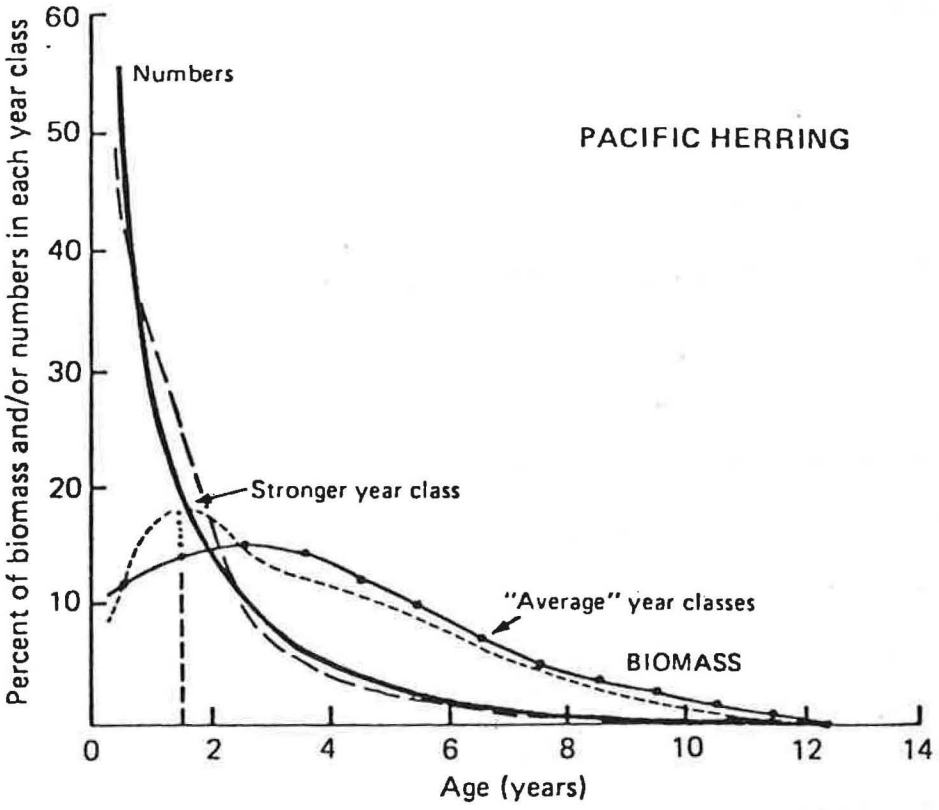


Figure 3-2. Distribution of biomass of Pacific herring within different year classes (% of total).

where: B_{pn} - percent fraction of biomass in year class n

G_A - annual mean growth rate of a population

G_{an} - annual mean growth rate of year class n

The BIODIS model (Laevastu 1978, Granfeldt 1979a, ref. Notitia II) computes separate growth rates of biomass for: whole population, prefishery juveniles, exploitable biomass, and the biomass deceased during the year.

The biomass based ecosystem models require the use of monthly growth coefficient, which is derived by multiplying the annual growth rates of the species (derived from empirical data on weight-at-age) with the decimal fraction of the biomass in given year-class plus the growth coefficient of the deceased biomass times half fraction of this deceased biomass and divided by two:

$$G_o = \sum^{n} ((G_{an} * G_{pn}/100) + (G_{an} * B_{dn}/2*100))/2 \qquad (6)$$

where: B_{dn} - percent fraction of the decased biomass of year class n

G_o - growth rate of the biomass in percent per year

The corresponding instantaneous monthly growth rate is computed with formula 4 above.

Another formulation for computation of mean growth rate is:

$$g_o = \frac{B_h}{B_h + 0.5\ B_d}\ g_h + \frac{0.5\ B_d}{B_h + 0.5\ B_d}\ g_d \qquad (7)$$

where: B_h - whole biomass, B_d - deceased biomass, g_h - growth rate for whole biomass and g_d is growth rate for deceased biomass. (The study of the validity of either formula 6 or 7 is in progress in general simulation validation task.)

If several species are grouped together in the simulation into an ecological group, the growth rate of this group must be a function of relative abundance of the species in the group.

3.3 Seasonal growth and the effect of temperature on growth

The growth rate varies seasonally in most species in medium and high latitudes. This seasonal variation can be reproduced either as a harmonic function of time or as a function of environmental temperature. A simple harmonic function is:

$$g_t = g_o + g_m \cos(\alpha t - \kappa) \qquad (8)$$

where:

g_t - monthly growth rate for month t

g_o - monthly mean growth rate

g_m - magnitude of annual change of growth rate

α - phase speed (depends on time step; 30^o for monthly computations)

t - time (months)

κ - phase lag

One of the main causes of the seasonal changes of growth is the change of temperature of the water. Thus the growth can be made a function of temperature (either surface or bottom temperature, depending on whether the species is pelagic or demersal). Several formulas for computation of changes in growth as affected by temperature are available in literature, such as:

$$g = ab^{\frac{-1}{T+c}}$$

where a, b, and c are constants and T is temperature;

$$g = g_o e^{0.081T} \qquad g = g_o e^{(-1/T)} \qquad g = g_o e^{\frac{-1}{T+c}}$$

and others.

The growth rate maximum can be at different temperatures in different species. In some species growth ceases already at $4^{o}C$. Nearly every species in higher latitudes has a specific optimum (acclimatization) temperature. In some species the optimum temperature range can be quite wide.

In comparative study of the temperature effect formulas, the following has been found best (Krueger 1964):

$$g = g_o e^{\left(\frac{1}{T_o} - \frac{1}{T}\right)} \qquad (9)$$

where T_o is optimum (acclimatization) temperature for the species and T is actual temperature (see Fig. 3.3).

This formula (9) permits the assignment of optimum temperature for each species/group of species and does not give abnormally high growth at high temperatures, as some formulas do.

3.4 Effect of food availability and partial starvation on growth

A linear relation between growth in weight and food intake has been found to be applicable to growth of fish (Jones and Hislop 1979). If fish obtains full daily ratio of food, no changes of growth coefficient are necessary. If, on the other hand, growth is made a harmonic function of time, the food requirement must also be made a harmonic function of time. In order to account for the effects of changes in growth caused

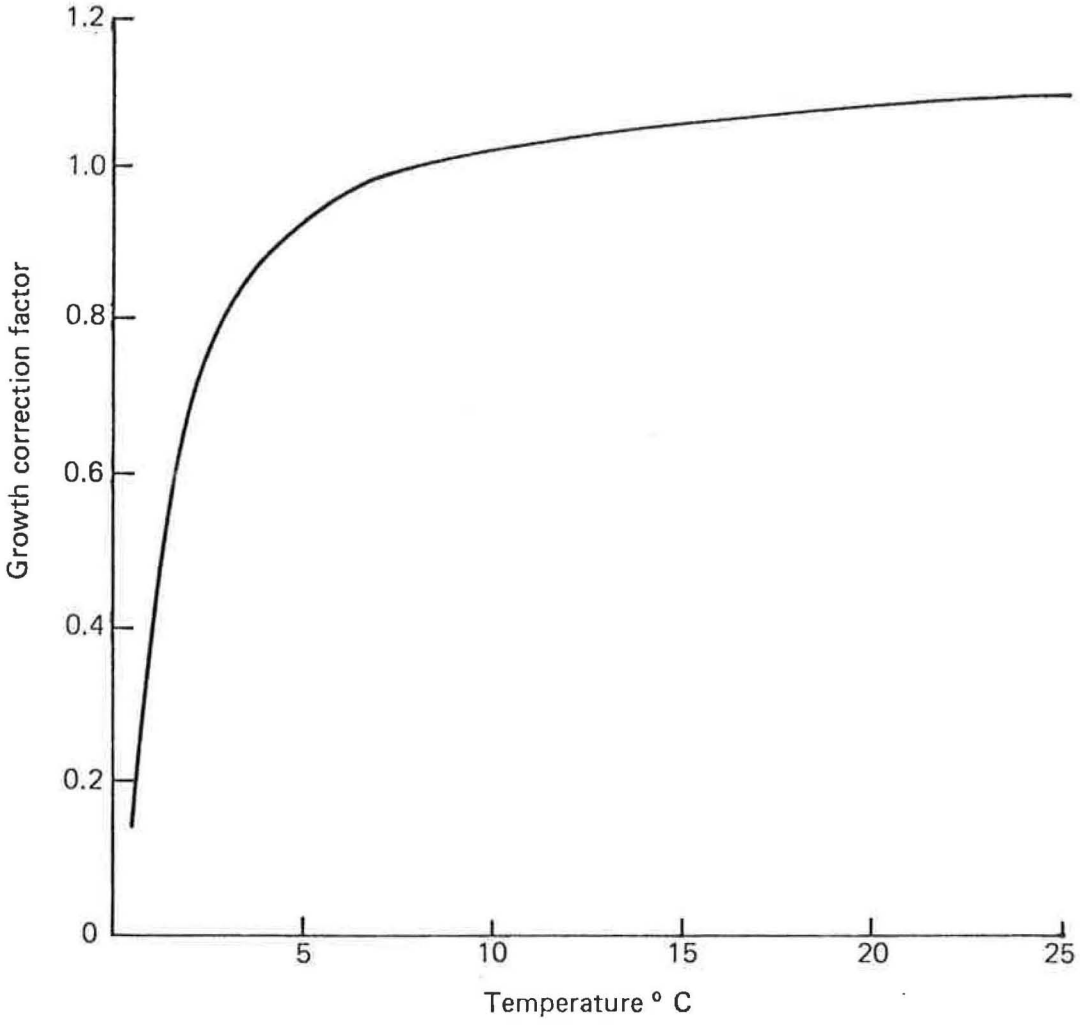


Figure 3-3.--Effect of temperature on growth rate (Formula 9); acclimatization temperature 8°C.

by temperature on food intake, the food requirements must be computed in two steps: food requirements for maintenance and food requirements for growth (see further Notitia IV).

As availability of food might determine growth of fish population, it is imperative to test the food availability and possible food substitution at each time step (and grid point) (see also Notitia IV). If full substitution is not possible, or is unlikely, partial starvation occurs.

There are several subjective ways to compute the effect of starvation on the growth. The actual (complex) method used in simulation will be described in model documentation (see subroutine FOOCON in programme PROBUB). The following description serves only as an example for computation of food composition change and starvation: First, the fraction of biomass of a given species consumed in previous time step (month) (p_a) is compared to the maximum allowable fraction (p_j) (predetermined). If the actually consumed fraction exceeds the allowable fraction, then the prescribed mean fraction of this species in the food of the species under consideration is decreased ($\pi_{i,j} = p_j/p_z * \pi_{i,j}$). The new food composition for the species i is summed and the missing fraction of food requirement is divided between those food items which had an ample supply in proportion of their occurrence in the mean food composition (prescribed at the start of the computations). However, if the missing fraction is large (e.g. in excess of 30% of food requirements), part of this missing fraction is recorded as starvation (i.e. subtracted

from the normal food requirement). The latter part of this approach requires several subjective decisions and can require a lengthy computer program (see subroutine FOOCON).

The effect of starvation on growth rate is assumed to be linear:

$$g_t = g_o * \frac{S_a}{S_r} \qquad (10)$$

Where S_a is the amount of food the species eats at a given timestep and location and S_r is the full food requirement (see Formula 1 in Notitia IV).

3.5 Effects of variations in recruitment, spawning, and fishery on the growth rate of biomass

Biomass distribution with age changes with the intensity of fishery (see Notitia XII). Thus the growth coefficient increases with the increase of fishing intensity (re. rejuvenation of population a la Dementjeva). Detailed computations of the change of growth coefficient due to change of fishing intensity are not practicable, as the exact age composition of exploitable biomass is seldom accurately known. Instead an approximate "correction" with the following empirical formula could be made:

$$g_t = g_o \, a \, \frac{F_a}{F_s} \qquad (11)$$

where a is an empirical constant, F_a is old fishing mortality coefficient and F_s is new fishing mortality coefficient.

The recruitment (and spawning) can be considered either as a continuous function of biomass in time or a semi-continuous function of biomass in time. The recruitment in biomass based models is more fully described in Notitia VIII.

Considering a continuous recruitment to all age/size groups and assuming that there are no exceptionally strong or weak year classes of postlarval juveniles, the recruitment would be proportional to the biomass present. The variations in postlarval recruitment would be depicted in biomass based models in the variations of growth coefficient of the species biomass (if the species is treated as one unit). This is shown in Figures 3.1 and 3.2 where high growth rate in postlarval juveniles (dotted line in Figure 3.1) and an increase in biomass of these postlarval juveniles (dotted curve in Figure 3.2), would result in increased overall mean growth coefficient for the species. (A strong year class of older fish would lower the mean growth coefficient.)

On the other hand, large spawning biomasses are known to produce proportionally smaller year classes and small spawning biomasses are known to produce proportionally large recruitment (year classes). Therefore, the recruitment could be regulated (controlled) in biomass based models, making the growth coefficient inversely proportional to biomass present.

$$g_c^o = g_i^o \times \sqrt{B_i^E / B_{i,t-1}} \qquad (12)$$

where B_i^E is the equilibrium or mean biomass of species i. This computation can be done in the models in prognostic mode after the determination of the equilibrium biomasses.

3.6 References

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NOTITIA IV

4. FOOD REQUIREMENTS OF FISH

4.1 Food requirements for maintenance, growth, and sex products development, and the effect of partial starvation.

4.2 Food requirements in relation to size, age, and growth rate of fish.

4.3 Change of food requirements throughout the year and the effect of temperature on the food requirements.

4.4 References.

4.1 Food requirements for maintenance, growth, and sex products development, and the effect of partial starvation.

The information in the literature on the food requirements by fish is quite diverse and at times contradictory, thus requiring serious evaluation as to reality and applicability in the ecosystem simulation models. Most of the empirical information pertains to fish culture with fast growing fish and its direct applicability to natural populations is often questionable.

Some reports pertaining to trophodynamics have used the energy content of the food as well as predators as bases, rather than biomass. The reasons for the use of caloric values in these studies is unclear and quite artificial. The caloric value of the diverse and in time and space variable prey items is very superficially known. The stomach content is not measured by its caloric content but by volume of biomass. Furthermore, the "caloric value" of the fish varies with age, season, and location.

(For the benefit of conversion it could be mentioned that some reports give the "natural food" caloric contents as 330 kcal/kg; others report a value of 500 kcal/kg. Lindeman (1942) proposed a mean caloric conversion of 4.9 kcal/g dry matter. Some reports state that ca 3500 kcal of food is required to produce 1 kg fish. There is at present no reliable way to confirm the data presented above.)

Further confusing and scarcely usable expressions in the literature are gross conversion efficiency (K_1) and net conversion efficiency (K_2) which are supposed to present the ratio of growth (in g cal) to mean monthly ratio (usually undefinable), and growth ratio to mean monthly ratio minus ratio for maintenance of body weight (also in practice undefinable).

The majority of the research on food requirements by fish has expressed these requirements as function of maintenance and growth requirements plus food requirements for sex products development.

$$S = aG + bW(+cW)_d \qquad (1)$$

where: S is total food requirement; aG is food requirement for growth (G being growth of biomass and a is a coefficient (food coefficient for growth)); bW is maintenance ratio, which is a function of biomass (weight) (W) and basic maintenance requirement per unit time (b, e.g. 0.7 percent body weight daily). The factor b is also a function of the activity of fish. The last term (cW) is food requirement for sex product development, which can be (and often has been) included in first term (aG) under certain conditions.

There are various considerations which use a single food requirement in terms of fraction of body weight daily. Zar (1968) proposes for birds:

$$M_{(k\ cal/bird\text{-}day)} = aW^b;\ a \approx 100\ b = 0.7 \text{ and } W \text{ is in kg}$$

In analog Jones and Hislop (1979) (ref. in Notitia II) found that there is a linear relation between food uptake and growth and proposes a net conversion factor:

$$= 0.79W^{-0.15} g/kcal$$

The food demand for growth/demand for sustenance is estimated in fish culture $\approx$ 1:2.3. Often used estimate of food conversion is that ca 30% of food fed is converted to tissue (i.e. "food coefficient" ca 1:3). The best fish culture results with high-caloric food (fish pellets) is that 3.3 kg food is required to produce 1 kg fish (Halver 1972). The above data originates from experiments in fish culture.

On the other hand, Last (1979) reports a conversion efficiency of 10 to 20% and that young fish can take up food to 28% of body weight daily (BWD).

Most commonly used annual food consumption is 3 to 4 times the mean biomass (standing crop) (i.e. about 1% BWD). Some earlier data on respiration (assimilation-growth) and assimilation (ingestion-defacation) rates and fish food requirements are summarized in Tables 4.1 and 4.2 (references given in Laevastu, 1963, "Evaluation of the Sea").

During about half a century the marine ecosystem has been assumed to consist of definite "trophic levels" and a trophic level "conversion factor" of 10:1 has been commonly used. In reality the trophic levels

Table 4.1

RESPIRATION AND ASSIMILATION RATES

Species or Group of Species	% of food taken up which is assimilated (digestion)	Respiration loss in % of assimilated food	% of assimilated food converted to tissue	Author
Zooplankton	ca 50	75	25	Kalle, 1950
	50 - 90	30	70	Harvey, 1950 Marshall and Orr 1957
Artemia (nauplii)	38 - 55		64 - (100)	Gibor, 1957
Veliger larvae			60 - 70	Jorgensen, 1952 (from Teal, 1957)
Benthos (av.)		71	11	Harvey, 1950
(well growing)			29	Teal, 1957
Benthos (slowly growing)			5	Harvey, 1950
Herbivores		75	25	Teal, 1957
Carnivores		37	59	Teal, 1957
Mytilus			11 - 54	Jorgensen, 1952 (from Teal, 1957)
Tubifex larvae		38.4	61.7	Ivlev, 1939 (from Hanaoka, 1955)
Fish		90 - 95	5 - 10	Harvey. 1950
Plaice			(5.6)[1/]	Peterson, 1918
Carp (K_1)		58.3	41.6	Ivley, 1939 (from Hanaoka, 1955)
Fish (av.)	25	25	(15)[2/]	Hagmeier, 1951

1/ % of food taken up

2/ Recalculated

Table 4.2

FOOD REQUIREMENT AND FOOD COEFFICIENTS OF FISH

Species or Biological Group	Food requirement % of body weight daily	Uptake of food % of body weight daily	Average % food needed for respiration	Rest food coefficient	Author
Fish	1.1 - 2.2%		25	1:5	Hagmeier, 1951
Plaice, small		3.6 - 5.4 %			Hempel, 1956
medium		3.3 - 4.2 %			(recalculated)
Herring	3 (theoretical)	0.7 (cut contents)			Horwood and Cushing, 1978
Tuna	3				Tiews, 1978
Flounder	1		75	1:4	Tyler and Dunn, 1976

are undefinable in real ecosystem and in case some definition would be possible, most fish change the "trophic level" throughout their life history, throughout the year, and from area to area (re. space-time variation of food composition).

After considerable review of the literature and after experimentation with single food requirement (defined as fraction of body weight daily), it was decided to use Formula 1 in the ecosystem simulation. (Single food requirement formula has several shortcomings, such as: it must vary with growth (coefficient), it varies with age (size) of the fish, and it does not allow an easy presentation of "irregular" seasonal changes of food requirement).

Daan (1973) found from stomach content and food uptake studies that cod in the North Sea required an average 0.5 to 1.5 percent body weight of food daily (BWD). Dann's data converted to mean value for cod biomass is ca 0.75 percent of BWD, which includes food for maintenance as well as for growth (it could be mentioned that Tyler and Dunn (1976) estimated that flounders require 1% BWD for maintenance, and other authors have estimated the total food uptake by fast-growing salmon up to 2% BWD). We can compute the food requirements as

$$S = bW + aG \qquad (2)$$

where S is food requirement per unit time, b is food requirement for maintenance in terms of percent BWD, W is biomass (weight), a is food requirement for growth (including sex products development) in terms of growth, and G is growth of biomass. The coefficient of a and b varies

from species to species and coefficient b varies also with temperature.

Although the mean value for coefficient b is about 0.75, if we use a single food requirement factor, in above formula it is about 0.55 (varying from species to species). Furthermore, it is same function of temperature as the growth (see further Formula 3 in this Notitia).

The coefficient a is about 1.2, varying from species to species. Growth (G) is already a function of temperature (see Notitia II).

A numerical example of the above paragraph would be as follows:

Biomass, (monthly mean) 100 (kg/km^2)	
Growth-6% per month	= 6 (kg/km^2)
Food requirement for maintenance at equilibrium temperature and with 0.55% BWD (x 30 days)	= 16.5%
Body weight per month	= 16.5 g
Food requirement for growth (6x1.2)	= 7.2 g
Total food requirement	= 23.7 g
Food requirement in terms of BWD (growth + maintenance)	= 0.79% BWD

Total food uptake is, besides food requirement, also a function of availability of suitable food items (by size and by species) at given time and location. Thus a check has to be made in the simulation at each time step and location (grid point/region) whether sufficient food is available to a given species (age group, if so divided) so that the fish can obtain the optimum ration. If a given food item is not present in sufficient quantity (or has been "overconsumed" in previous time step), possibilities of substitution with other food items,

specified in diet for the given species, must be attempted. If, however, a full substitution is not possible, it must be assumed that partial starvation occurs, the measure of which is the difference between full ration required and that which can be taken. The growth rate of the biomass must consequently be adjusted if partial starvation occurs (linear dependency assumed).

There are some other consequences of partial starvation: Tyler and Dunn (1976) found that partial starvation of flounders in Passmaquaddy Bay occurred and that the fish seemed to sacrifice egg production and maintain body weight. Flüchter and Trommsdorf (1974) also found that malnutrition was the reason for incomplete development of eggs in the common sole.

4.2 Food requirements in relation to size, age, and growth rate of fish

Extensive stomach content studies by Daan (1973) show that fish (cod) eats about 0.5 to 1.5% BWD; the lower value is for older, the higher value for younger fish. Other studies on young fish (e.g. salmonids) show that young fish eat 5 to 40% BWD.

As the young fish grows faster than the older ones (see Notitia II), it can be concluded that food uptake for growth must be proportional to growth of the biomass.

In some reports in the literature an average production to food ratio of 0.2 is used, whereby this ratio is assumed to be 0.2 to 0.25 for younger fish and 0.1 to 0.15 to older fish. No empirical data validating the above ratios are available.

It can be assumed that the maintenance ratio is a function of the activity of fish. Both the activity of fish and metabolism are functions of temperature. As the temperature is taken into consideration for growth computation (see Notitia III), it can be neglected for computation of food requirement for growth if Formula (1) is used. Quantitative empirical data for the effect of temperature on maintenance rate is scarce. Jones and Hislop (1979) presented the following formula:

$$\text{Maintenance requirement} = 0.0080W \; e^{0.081T}$$

where T is in ^{o}C and W is in g.

As growth varies with age (size), thus total food requirement would vary with age (size) of the fish. As the growth rate of a population changes with its age composition, the "rejuvenation" of a population would result in higher food consumption if the biomass would remain constant. However, "rejuvenation" involves usually a decrease of total population. Thus it could be concluded that if a population does not vary within wide limits, its food consumption is quasi-constant on an annual basis.

The growth rates and food requirements are main determinants of the "equilibrium biomass" (the unique solution in PROBUB model). Thus to obtain a "minimum equilibrium biomass", highest plausible growth rates and lowest plausible food requirements should be used in the model.

4.3 Change of food requirements throughout the year and the effect of temperature on the food requirement

Many environmental factors are known to influence the behaviour of fish and its feeding. One of the factors is the seasonal temperature. Both too high and too low temperatures decrease the feeding rates. Different species have different optimum temperature where the feeding is at maximum. It is also known that "abnormal" temperatures hinder fish from migrating into areas where the food might be abundant.

In high latitudes the growth varies with season. This seasonal growth rate change can be simulated either with a harmonic formula or with seasonally changing temperature (see Notitia II). As growth rate is related to food requirement, the food requirement must be made a harmonic function or function of temperature (see Formula (3).

In our simulation growth is a function of temperature (which varies with seasons) and as food requirement is a function of growth, thus food requirement becomes also a function of temperature (and season).

Furthermore, in our simulation we have assumed that the effect of temperature on metabolism (and maintenance food requirement, which reflects also the activity of fish) is the same as for growth, and have used the following formula:

$$S_m = C\ W\ e^{(\frac{1}{T_o} - \frac{1}{T})} \qquad (3)$$

where S_m is food requirement for maintenance, C is food requirement in terms of decimal fraction of body weight per unit time step (usually given as body weight daily), varying from species to species (see input

data documentations for individual models). W is biomass of the species, T_o is "acclimatization temperature" and T is actual temperature.

4.4 References

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NOTITIA V

5. COMPOSITION OF FOOD OF FISH

5.1 Predator/prey size ratio

5.2 Average food composition

5.3 Opportunistic food availability dependent feeding

5.4 Description of a feeding subroutine

5.5 References

5.1 Predator/prey size ratio

The average composition of food of individual species (which serves also as vulnerability to predation index) is given with input data in the simulations (see input data documentation for given programmes). Only general notes on the composition of food and its spatial and temporal changes are given in this Notitia.

The composition of food of any species in any specific time and location depends on the availability of preferred food items of proper size (and of other size dependent quantities, such as escapement speed).

The predator weight/prey weight ratio varies from species to species and the mode is in general >100. The corresponding length ratio is >30. A general weight-length relation in marine ecosystem is given in Figure 5-1.

Due to age dependent growth and mortalities the availability of proper size food decreases with increasing predator size so that larger predators must start to feed on smaller than optimum size prey. The generalized prey-size consumption of prey by numbers and biomass is shown on Figure 5-2.

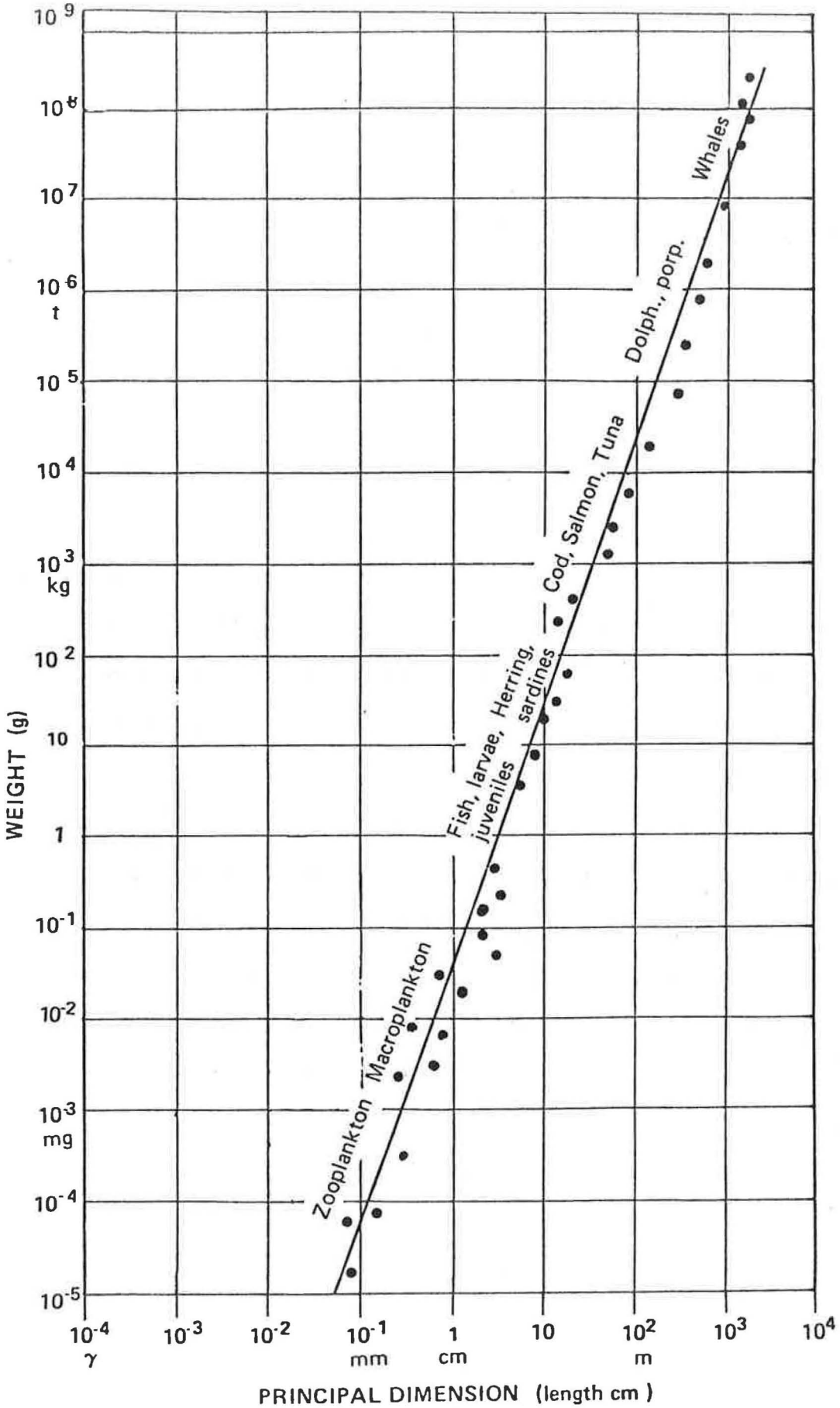
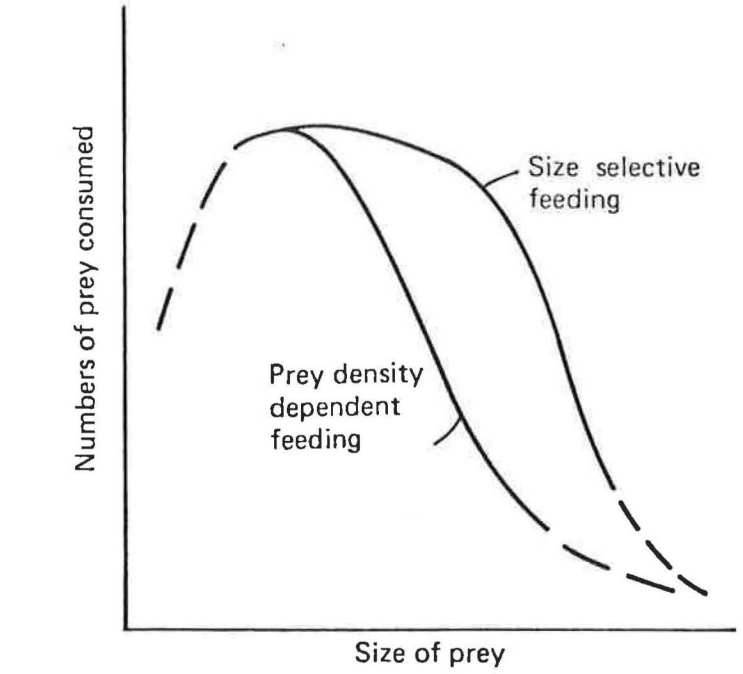


Figure 5-1. Weight-length relations in marine ecosystem.



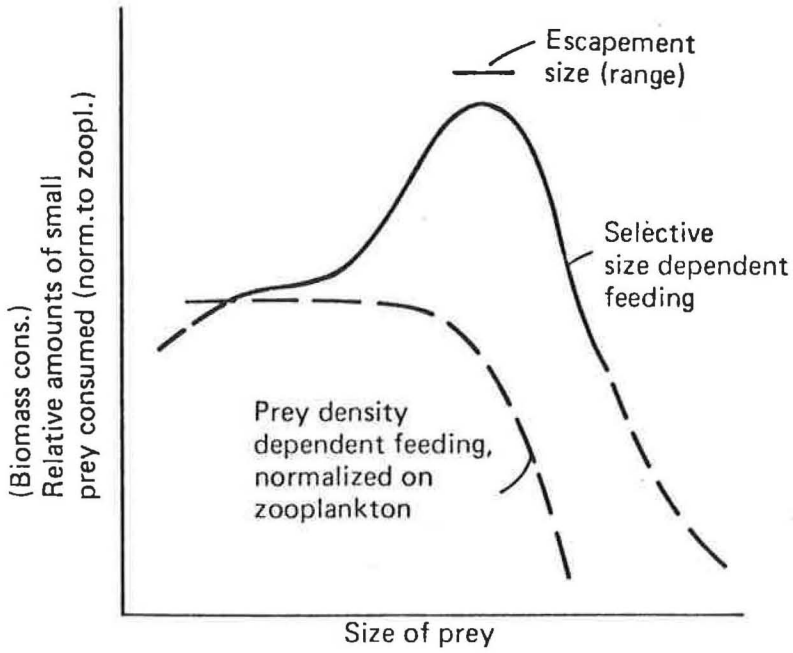


Figure 5-2.--Generalized size-dependent consumption of prey.

The effect of growth rate on the predation mortality of species is shown in Figure 5-3 where also the size range of fish most vulnerable to predation is schematically shown.

Using the last figure computed for different species and other considerations such as size distribution of biomass, one can derive a criterion and method for limitation of predation on a given size of a given species per unit time and space. When the composition of biomass by age/size and the computed age-dependent predation mortality (Notitia II, Granfeldt 1979) are computed, one can arrive at a realistic limit of the amount of predation allowed from a given species per unit time. This limit varies usually from 3 to 10% of mean biomass per month and can be higher during a few months after spawning.

5.2 Average food composition

Average food composition of a species (considering the size distribution with age and the corresponding food composition with size/age) indicates also the vulnerability of different food items in respect to the given species.

Extensive quantitative food composition studies are few. Additional information on average food composition must thus be obtained by considering the feeding regime (pelagic or demersal), the diurnal mobility of the species, and their seasonal migrations. As known, fish do not feed continuously and several species migrate diurnally between the surface layers where the food is abundant and the bottom where they usually spend the daytime.

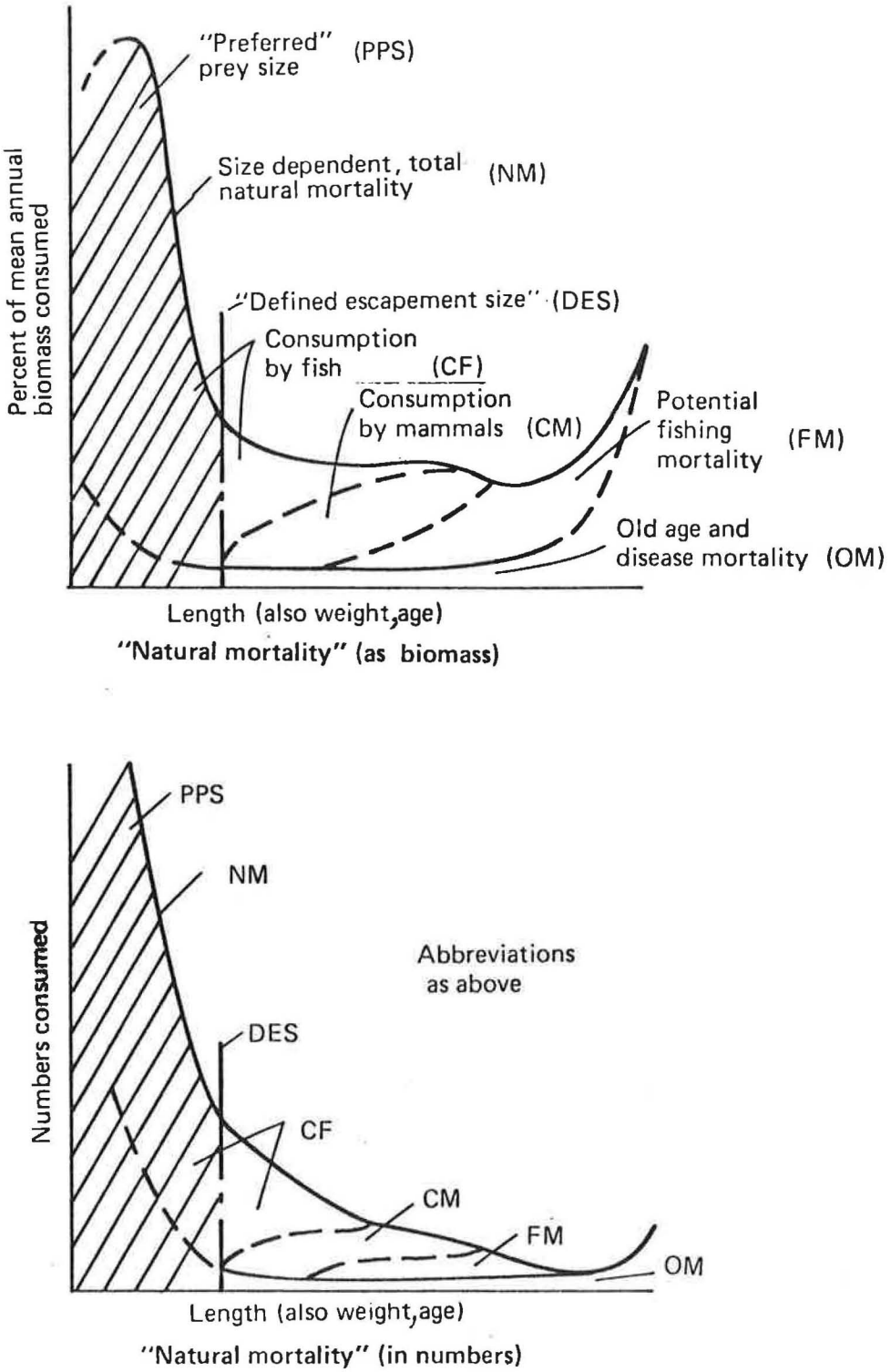


Figure 5-3.--Preferred prey size and defined escapement size.

It has to be borne in mind that average food composition indicates mainly the vulnerability of species (food items) to particular species-specific predation. Actual food composition would vary in space and time, depending on the availability of food items. Thus the average composition of food would serve as only a "vulnerability index".

5.3 Opportunistic food availability dependent feeding

At present relatively few data are available on the feeding behavior of fish, especially on the strategy of food finding. It is known for example that the feeding behavior varies with the changing availability of the quantities of food as well as with the availability of specific food items prefered by different species. Generally it is accepted that fish aggregate when the food is abundant and disperse when the food is scarce. No quantitative criterions have, however, been established. It is assumed that fish aggegate in areas where the food is most abundant.

In general an opportunistic, availability dependent, "regime defined" (i.e. pelagic or demersal), and size dependent feeding with some preference (selection) for food items prevails in the fish ecosystem.

Availability dependent feeding implies that if one preferred food item becomes more abundant, its consumption would increase. On the other hand, if there is a lack of a preferred food item, substitution with similar size item, either lower or higher on the food composition list, might be made. If no substitution is possible, partial starvation will occur which would affect the growth rate. Thus food uptake is not necessarily a function of particular food density because substitution occurs.

Another fact about food composition plays an extraordinarily important role, but has been relatively little recognized as such--cannibalism. There are few examples of it in the literature such as Daan (1976) found that, "The most important food item by weight is for the herring its own offspring, but in numbers it is surely the fish eggs". Mito (1972) gave the maximum cannibalism in pollock in the Bering Sea by the size of pollock: 24-37 cm - 71%; 42-55 cm - 84%; >55 cm - 100%.

5.4 Description of a feeding subroutine

There are various ways to simulate space and time variable food availability dependent food composition of a given species in marine ecosystem. The following is one of the examples used in PROBUB.

R_o is the "maximum percentage" of any food item allowed to be consumed at a given time step (e.g. month). R_{t-1} is the percentage actually consumed in previous time step.

If $R_{t-1}/R < 1$

then $p_{(i,j,t)} = p_{(i,j,o)} = p_{vj}$

where:

$p_{(i,j,t)}$ is the decimal fraction of food item j in the food of species i at the time step t.

p(i,j,o) is the above quantity as prescribed with input (i.e. the average composition of food).

p_{vj} = the unchanged composition (= $p_{(i,j,o)}$).

If $R_{t-1}/R > 1$

then the changed decimal fraction (p_{mj}) is:

$$p_{(i,j,t)} = p_{(i,j,o)} * R_{t-1}/R_o = p_{mj}$$

and the missing decimal fraction of food (f_m) is:

$$f_m = p_{(i,j,o)} - p_{(i,j,t)}$$

After the determination of equilibrium biomasses with the PROBUB model, the food composition as determined at the equilibrium condition will be changed as the food density changes, i.e. the term R_{t-1}/R_o will be replaced with B_t/B_e where the B_t is the actual biomass and B_e is the equilibrium biomass (both referring to the food item).

The sum of unchanged food composition (P_{si}) is:

$$P_{si} = \sum^{j} p_v$$

and the sum of the missing decimal fraction (F_{si}) is

$$F_{si} = \sum^{j} f_m$$

If $P_{si} \times 100 > 85$ (this is a subjective decision)

then the adjusted decimal fraction ($p_{(i,j,t,a)}$) is:

$$p_{(i,j,t,a)} = p_{(i,j,t)} + ((p_{(i,j,t)}/P_{si}) * F_{si})$$

If $P_{si} \times 100 < 85$, then some starvation can be assumed to occur and some subjective decisions must be made about how much of the food could be taken from food items present (V_p) and how much "starvation" should occur (S) (V_p and S are in decimal fraction).

If $P_s \times 100 < 85$ but > 50; $V_p = 0.80$; $S = 0.20$

If $P_s \times 100 < 50$; $V_p = 0.68$; $S = 0.32$

Final food composition (i.e. fraction taken) ($p_{(i,j,t,f)}$) is

$$p_{(i,j,t,f)} = p_{(i,j,t)} + ((V_p(p_{(i,j,t)}/P_s) \times F_{si})$$

and

$$S_n = S * F_{si}$$

5.5 References

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NOTITIA VI

6. AVAILABILITY TO PREDATION AND PREDATION MORTALITY

Size dependent feeding and the size dependent vulnerability to predation is briefly described in previous Notitia. Literature contains many references, examples, and notes on the increase of food size with increase in the size of the predator (e.g. Werner, 1979, Ref. Notitia VII). The speed of escape ability of the prey changes also with size. Thus the predation mortality (and survival rate) is also size dependent and decreases rapidly with increasing size (the survival rate increasing).

It can be argued that predation might control recruitment (ref. from Pred.-Prey Symp., summary by Rotschild - see ref. to Werner in Notitia VII). Consequently if predation in given area and year is below average or "equilibrium predation", an increased survival and increased biomasses would result. This is well demonstrated with ecosystem simulations.

The apex predators (marine mammals and birds) have considerable mobility and can thus search concentration of preferred food easier than many fish species. Thus they are more selective in respect to food than the rest of the ecosystem. Their food composition varies in the model only from one region to another.

The "maximum predation" is controlled in the ecosystem simulation by considering the size distribution of the given prey item biomass and the availability of the smaller, to the predation most vulnerable, size

group (see previous Notitia). This fraction is determined from the output of BIODIS model in terms of maximum monthly fraction of biomass available for predation. This availability can vary throughout the year, depending on the spawning season as well as on the transport and migration (spatial distribution) of larvae and small fish. The latter aspect can be treated in the DYNUMES model which has spatial resolution.

The predation of eggs and early larval stages is treated as consumption of zooplankton at present.

General procedure for the determination of fraction of biomass available for predation from BIODIS computations is as follows: a) determine the first mortality "inflex point" (see Figure 5-3 in Notitia V); b) determine how much biomass growth is occurring in the biomass to the right of this inflection point per year and divide the amount by 12. Thus the resultant is directly proportional to growth rate: the faster the growth of larvae and juveniles, the faster they pass the to predation vulnerable phase. The relations between predation mortality and fecundity enters mainly via vulnerability in specifying average food composition.

Additional notes on predation morality are found in the next Notitia. Cushing (1973, ref. Notitia VII) pointed out that Ricker and Foerster (1948) and Beverton and Holt (1957) have also pointed out the effect of speed (rate) of growth on the time of passing the most vulnerable predation age (size).

NOTITIA VII

7. SENESCENT, DISEASE, AND SPAWNING STRESS MORTALITIES

Mortalities have in general been unknown quantities in fisheries population work in the past. Lots of assumptions have been made, many of which are inconsistent with present state of knowledge. Mortality and growth have in general been assumed to be "density dependent".

Ricker stock-recruitment curve is dome-shaped because a stock dependent mortality is used. This mortality could only be cannibalism (Harris, 1975, ref. Notitia VIII), which is in most cases entirely unrealistic.

Lett and Kohler (1976, ref. Notitia VIII) have been among the first to recognize the importance of predation mortality which, tempered by available food density, is assumed to be a major population stabilizing and fine-tuning mechanism for year class formation.

The mortalities in the first year (mainly predation mortalities) are about 50% per month and more (Cushing, 1973, found that the mortality of plaice larvae in the first months is about 80% per month). Furthermore, Cushing estimates that during the first year the increment of weight of a population is on the order of 10^5 but the decrement of numbers is 10^4 so that the gain of the biomass can be one order of magnitude (obs. fish larvae can grow 10% a day).

Methods for computation of age dependent mortalities have been described by Granfeldt (1979a, ref. Notitia II). Examples of some of his results are given in Figures 6-1 to 6-5. Figures 6-1 and 6-2 show

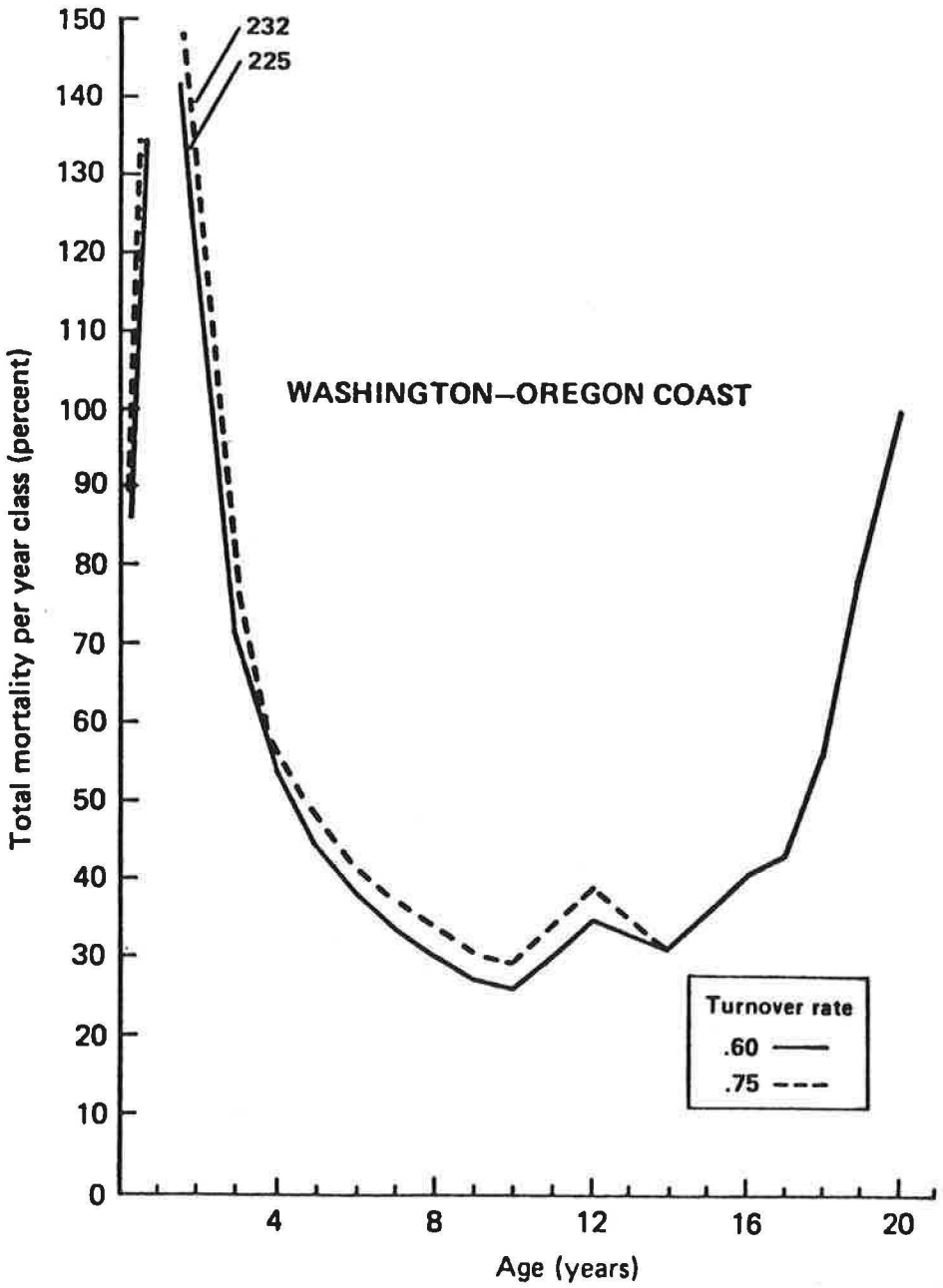


Figure 6-1. Total mortality of biomass in percent per year class with reference to annual mean biomass in the year class, Pacific ocean perch from Washington-Oregon coast.

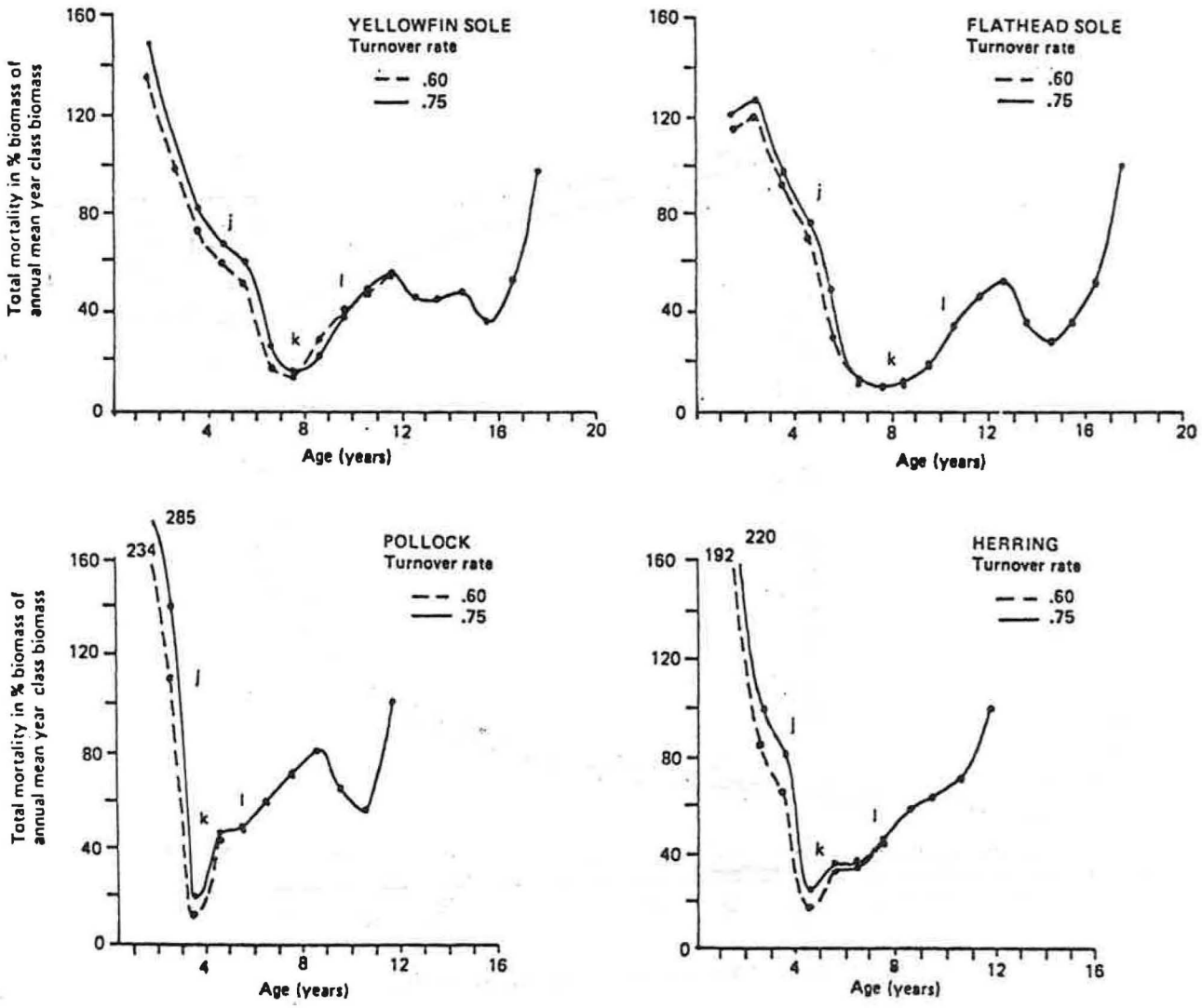


Figure 6-2. Distribution of total mortality with age (in percent of biomass of the annual mean biomass of given year class) for four species from the eastern Bering Sea.

the mortality in terms of % of mean year class (biomass) in five species, showing the high predation mortality in the first years and the increase of spawning stress and senescent mortality after a given age which varies from species to species.

Figures 6-3 and 6-4 show the mortality in terms of the total biomass mortality as a function of age and different locations (mainly affected by different growth rates).

The mortalities are classified by various causes in the ecosystem simulation.

1. Predation mortality. In most cases this is the largest mortality component (the main component of the earlier used term "natural mortality"). This component is computed in detail in the ecosystem simulation with the trophodynamic approach (see previous Notitiae).

2. Spawning stress (and senescent) mortality is discussed by Granfeldt (1979b, ref. Notitia II) in detail. There is an upward trend of mortality in older animals (senescent mortality). Lately it has been considered that in fish the main component of this senescent mortality is spawning stress mortality (see notes on its possible quantitative treatment below). Figure 6-5 shows the relative uniform increase of spawning stress mortality with age (re. number of spawning).

3. The fishing mortality is determined from catches and from exploitable biomasses present. Its computation in biomass based models is described in Notitia XII and XIII.

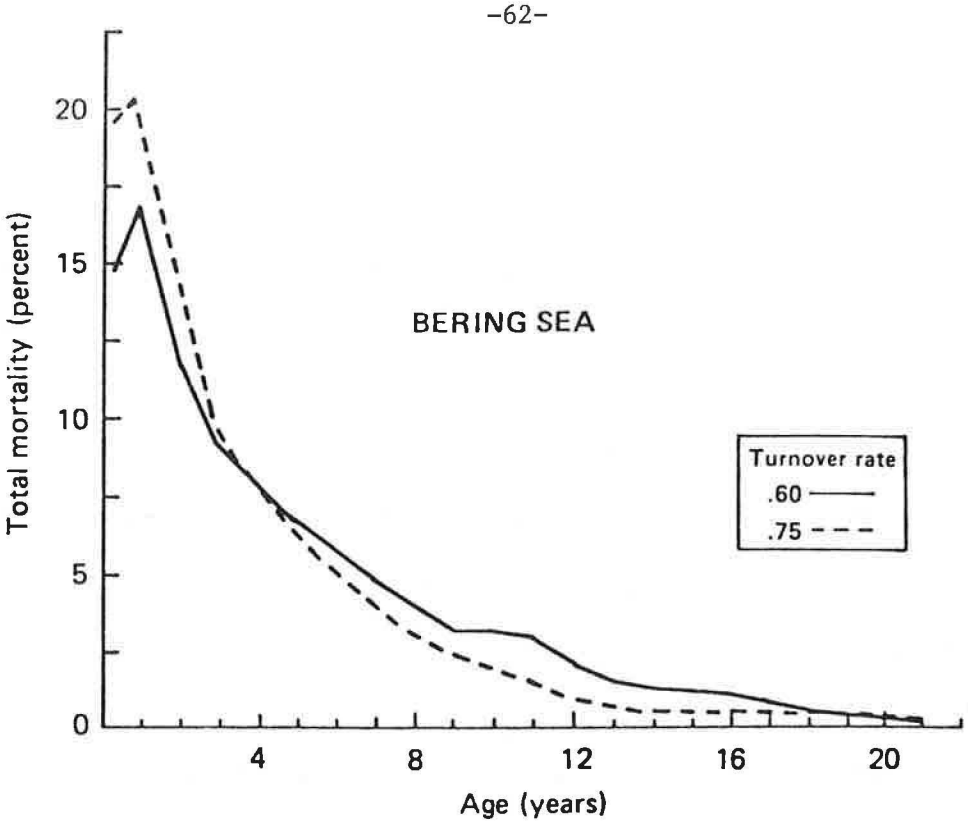


Figure 6-3. Distribution of total annual mortality of biomass with age (in percent of total mortality) of Pacific ocean perch from eastern Bering Sea.

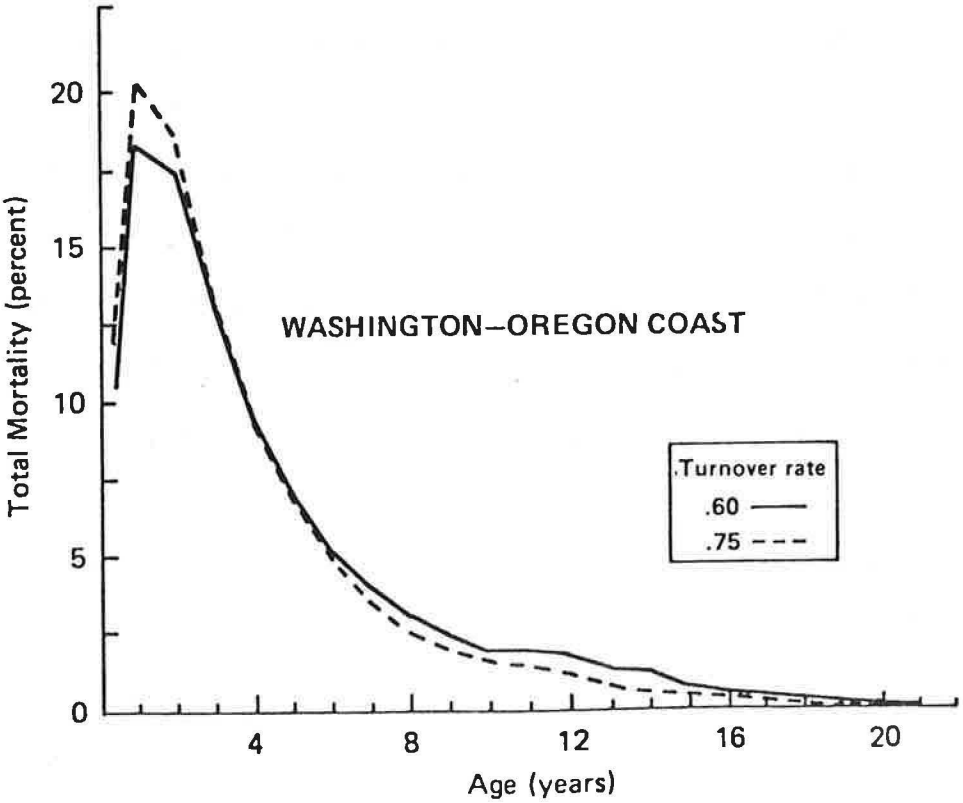


Figure 6-4. Distribution of total annual mortality of biomass with age (in percent of total mortality) of Pacific ocean perch from Washington-Oregon coast.

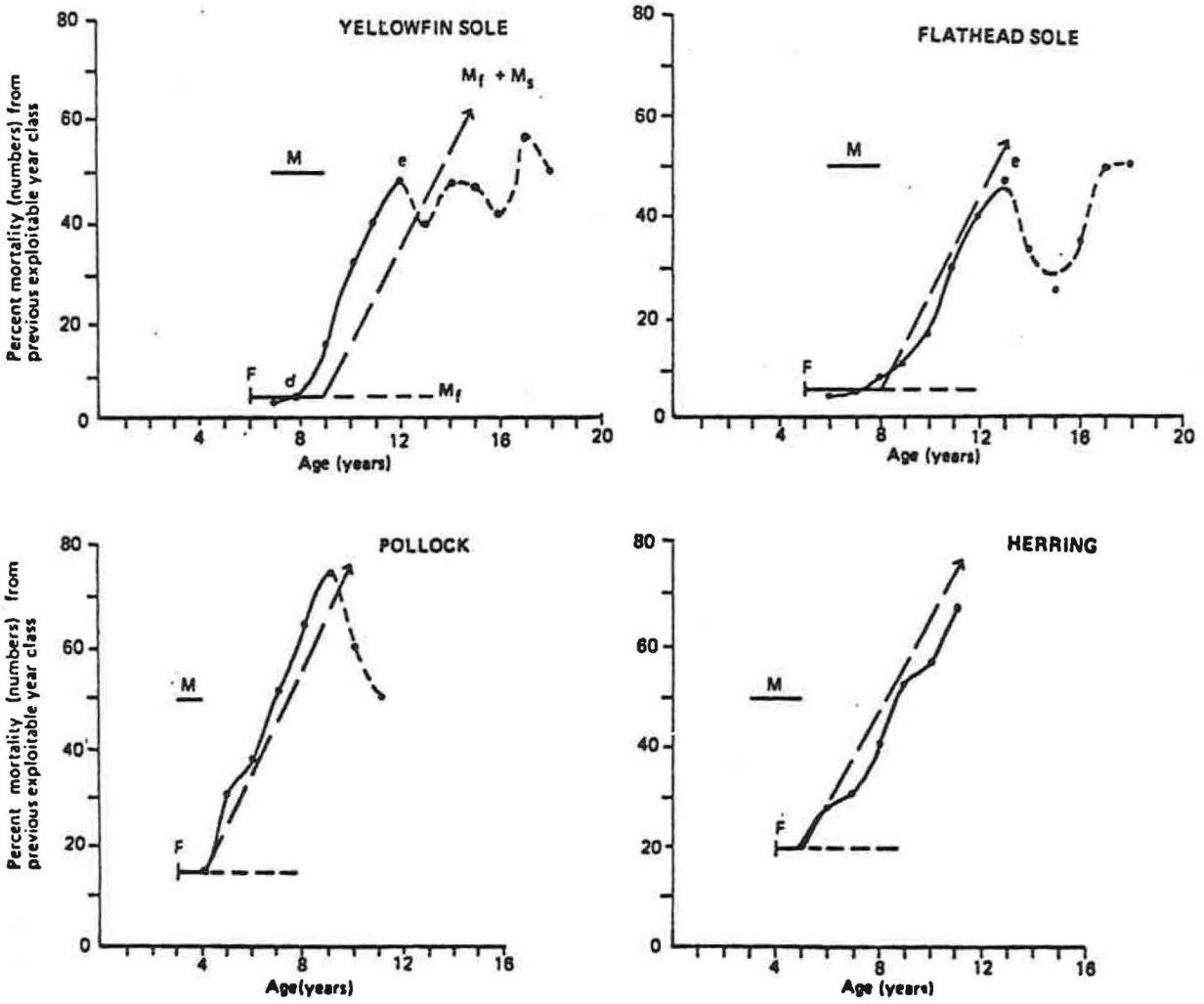


Figure 6-5. Percent mortality (in numbers) from previous fully recruited year class, for four species from the eastern Bering Sea (explanations see text).

4. There can be a residual "natural mortality" which might be caused by diseases and infestation by parasites (disease mortality). The magnitude of this mortality is at present unknown, but can be assumed to be small in "normal" conditions. A small "natural mortality" coefficient is therefore prescribed for all species to account for this mortality. (This coefficient is assumed to be higher in species which are not subject to fishery.)

5. There are some additional "special mortalities": the mortality from exceptionally cold conditions (known and often described as "cold's mortality") is treated in the ecosystem simulation by increasing the "natural mortality" subjectively in areas and times when specially cold anomalies occur. Some "starvation mortality" is assumed to occur if computed partial starvation is above a predescribed level. The "natural mortality" coefficient is also slightly increased (at times and locations) when this occurs.

As the mortalities change with age, consequently if the biomass distributions change with age, there must be corresponding changes in mortalities.

Biomass distribution is assumed to be in balance with:

present fishery - recruitment to fishery =

removal + spawning stress mortality.

Spawning stress mortality (M_s) operates on exploitable part of biomass. Original exploitable biomass would be in new equilibrium in 5 years (see Figure in Notitia XIII).

Approximation: $M_{s,new} = M_{s,orig} + 0.5\ (F_o - F_n)$

F_o - original fishery; F_n - new fishery

B_a - adult biomass fraction; f_a - fraction of adult biomass deceased.

M_s - spawning stress mortality

$$M_{tot,old} = (f_a B_a)/12$$

$$M_{tot.,inst.} = n\ (1-M_{tot}) \qquad M_s = M_{tot} - F$$

Growth rate changes also with fishery. Approximation:

$$0.5\ (F_n - F_o)\ B_a + g_o = g_n$$

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NOTITIA VIII

8. RECRUITMENT IN THE BIOMASS BASED ECOSYSTEM MODEL

The recruitment problem in fisheries prediction and management has been of paramount importance. Unfortunately relatively little progress has been made over the decades to explain quantitatively the processes affecting it.

The term recruitment itself is ambiguous; it applies to the recruitment as larvae as well as recruitment to exploitable portion of stock. There is a variable number of years between these two "entry points" and several processes reducing the numbers and increasing the biomass are in action.

The earlier single species population dynamics approaches applied an assumed stock recruitment relation. The Ricker stock-recruitment curve is dome-shaped, implying stock dependent mortality, which can only be cannibalism (Harris 1978), which scarcely occurs with such intensity. Thus Ricker's stock-recruitment curve cannot be applied to multi-age stocks and Beverton Holt curve should not be applied to gadoid stocks (Cushing 1973). Furthermore, Cushing (1973) states a paradox: "Until the stock/recruitment problem is solved, fisheries will fail".

The only sure knowledge about stock-recruitment relations at present is that large spawning stocks have been known to produce proportionally small recruitment and small spawning stocks are known to have produced proportionally large recruitment. Often a relatively ambiguous statement is made: "Recruitment per unit stock decreases when stock increases". On the other hand, many stocks are remarkably stable. This stability is partly caused by the presence of several year classes, which can be different in strength.

Spawning may be considered (and treated) either as a discontinuous or a semi-continuous process in time (Figure 8-1).

There are several justifications for treatment of the recruitment as a continuous process in the biomass based models.

First, the "biomass internal recruitment" (e.g. the recruitment to the exploitable biomass) is continuous because of the growth (and size) diversity within a population.

Second, the spawning time can be several months long, especially if a number of species are included in an ecological group.

Third, the growth of biomass commences immediately after hatching. However, in most considerations the larvae are accounted for in the species biomass at the age of four to six months; eggs and early (small) larvae are consumed at the same rate as zooplankton.

In fact, the treatment of spawning as a discontinuous process is more "artificial" than the continuous treatment.

The continuous recruitment in biomass based models is mainly regulated by time change of growth coefficient. The change of growth coefficient is also indicative of relative year class strength variation (see Notitia II).

When a given biomass is abnormally low, there is a justification of slightly increased growth coefficient, partly as recruitment compensation (density dependent) and partly because of possible increased availability of food (density dependent feeding).

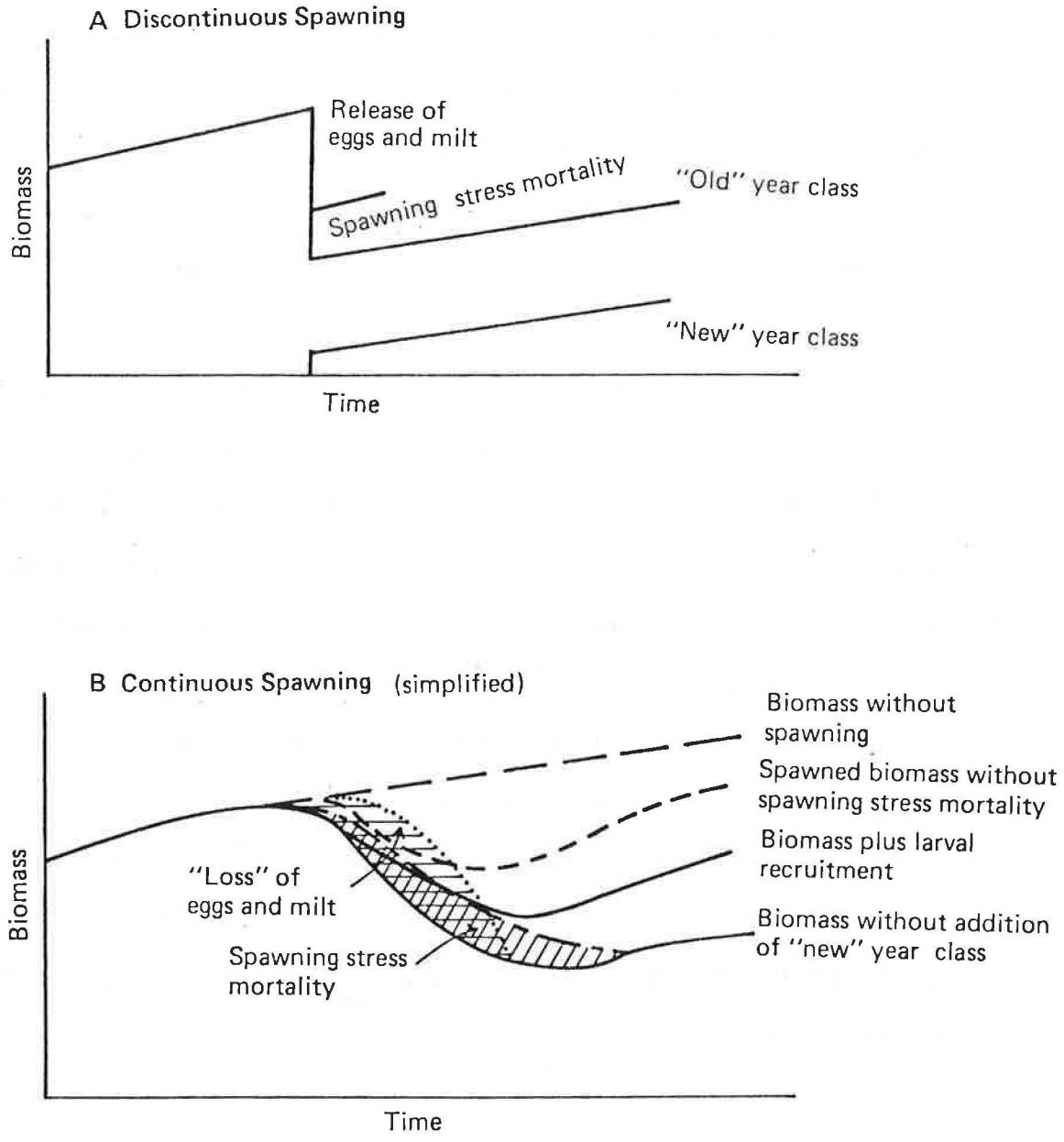


Figure 8-1.--Schematic presentation of A-discontinuous spawning (which requires the separation of a given species biomass into several age groups), and B-continuous spawning (which can be treated with a given species biomass as a unity).

The following paragraphs contain suggestions on the treatment of semi-discontinuous spawning in biomass based models. The last paragraphs describe the fully continuous treatment of recruitment as applied at present in PROBUB.

1. Determine the period (months) of spawning of the species. Note that the spawning can occur over a period of several months in most species. If a number of species are grouped into an ecological group, the spawning period of this group might be long indeed (one of the justifications for treatment of spawning as a continuous process).

2. Subtract 1 to 3% of biomass per month, presenting the release of eggs and milt. (The amount subtracted depends on the length of spawning period and the biomass distribution with age. The eggs constitute about 10% of the body weight of average spawner; milt is less. An average percentage of 8% can often be assumed.)

3. Increase the basic growth coefficient (g_o) in the second (and third) month after first month of spawning (percentage increase depends among others on life span, fecundity, and growth rate of the species) and decrease it gradually in subsequent 5 to 9 months to reach its "normal" value. This change of growth coefficient change simulates the "uptake" of the larvae (larval recruitment) into the biomass of the species.

4. If a species spawns in a relatively restricted area, the released eggs (and the early larvae) can be added to zooplankton and assumed to be consumed at the same rate (in DYNUMES MODEL). If a special ichthyoplankton group is considered in the model, about 1/3 of the released egg mass is added to this group, grown fast, and consumed fast.

Another suggested spawning and recruitment subroutine is as follows:

1. Determine the two to three months when peak spawning occurs in SPEPRE (species preparation) and call SKUDEM (spawning) subroutine during these months.

2. Introduce percent of adult (exploitable) biomass (f_a) as a parameter in the simulation (obtained from BIODIS programme).

3. Assume that sex products are about 8% of body weight of spawning population (i.e. of the adult biomass f_a).

4. Subtract $f_a B_e$ 0.04 of biomass each of <u>two</u> spawning months from the biomass.

5. Apply spawning stress mortality during the two months (see notes on this mortality in Notitia VII).

6. Increase growth coefficient for second month and allow this coefficient to return to "normal" during the following six months.

The recruitment is usually depicted in number based models as a time dependent discontinuity, relating it to discrete spawning period. In the biomass based model the spawning can be treated as a continuous process. This consideration is more acceptable if we think in terms of size groups rather than age groups, a long spawning period, and consider variations in growth of individuals belonging otherwise to the same age group.

Considering a continuous recruitment to all size groups and assuming that there are no exceptionally strong or weak year classes of postlarval juveniles, the recruitment would be proportional to the biomass present, then the variations in postlarval recruitment would be depicted in biomass based model by the variations of growth coefficient in the species biomass (if the species is treated as one unit).

On the other hand, large spawning biomasses are known to produce proportionally smaller year classes and small spawning biomasses are known to produce proportionally large recruitment (year classes). Therefore, the recruitment is regulated (controlled) in biomass based PROBUB and DYNUMES models, making the growth coefficient inversely proportional to biomass present.

$$g_c^o = g_i^o \times B_i^E / B_{i,t-1}$$

where B_i^E is the equilibrium or mean biomass of species i. This computation can be done in the models in prognostic mode after the determination of the equilibrium biomasses. In determination of the "equilibrium biomasses" (i.e. finding a unique solution to the set of biomass balance equations), the recruitment problem is eliminated because of the annual adjustment of biomasses (see Notitia X).

The factor $B_i^E/B_{i,t-1}$ dampens the possible fluctuations of recruitment rather heavily so that the much above or below average recruitment does not appear. It has been found somewhat more acceptable to use the term $B_i^E/B_{i,t-1}$ instead. It could be generally noted that in contrast to number based models, the biomass models are not oversensitive to errors in recruitment computation.

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NOTITIA IX

9. SIMULATION OF MIGRATIONS

The migrations can be classified into several categories by their periodic occurrence and by cause.

Seasonal migrations which can occur regularly are either caused by fish desire (instinct) to find proper and abundant food, or by its search for optimum environmental conditions.

Life cycle dependent migrations are spawning migrations to "traditional" spawning grounds, predation avoidance migrations such as outmigration of adults from own spawning grounds, migration of juveniles either into coastal or offshore regime, and others, and life cycle dependent feeding migrations (with reference to availability of proper size food and food composition changes with age).

Environment dependent migrations can be affected by seasonal changes and profound environmental anomalies, such as too cold water. The advection by currents and the response of fish to currents belong to this category of migrations.

There are numerous reports and some books on fish migrations. However, the migrations of fish in the NE Pacific are ill known, as very few tagging experiments have been carried out. Often one has to estimate the migrations (especially seasonal migrations and their speeds) from the known summer and winter distributions.

Fish are transported also by currents. Furthermore, they can take advantage of tidal currents during their migrations (Harden Jones et al. 1979). Many environmental factors can affect and "force" migrations. Koto and Maeda (1965) demonstrated that cold bottom water affects the migrations of flatfish (including aggregation at the boundaries).

Migrations through the boundaries of the models must be treated in an empirical way, adding or subtracting a given conservative amount each time step. These estimates can be based on the knowledge of seasonal migrations. Furthermore, some regions are source regions and some are sink regions which must be taken into consideration in estimating seasonal migrations through the boundaries. In an advanced state of modeling the boundary values for smaller, detailed models can be obtained from a large scale (ocean-wide) gridded model.

The procedure of through-the-boundaries migration computations involves the removal of predetermined fraction of biomass in the months in which migration occurs from one region (box) and adding it to another region. The return migration at a later month must be adjusted by the amount of growth and predation during intervening period in the region where the migration was previously directed.

The static conditions usually implied in past studies of ecosystem productivity, as well as in respect to the effects of fishing, will not give quantitative answers when prey is quasi-stationary and predators migrate or vice versa. Some of these migration effects are shown schematically (Fig. 9-1). Consider that there is a given benthos biomass

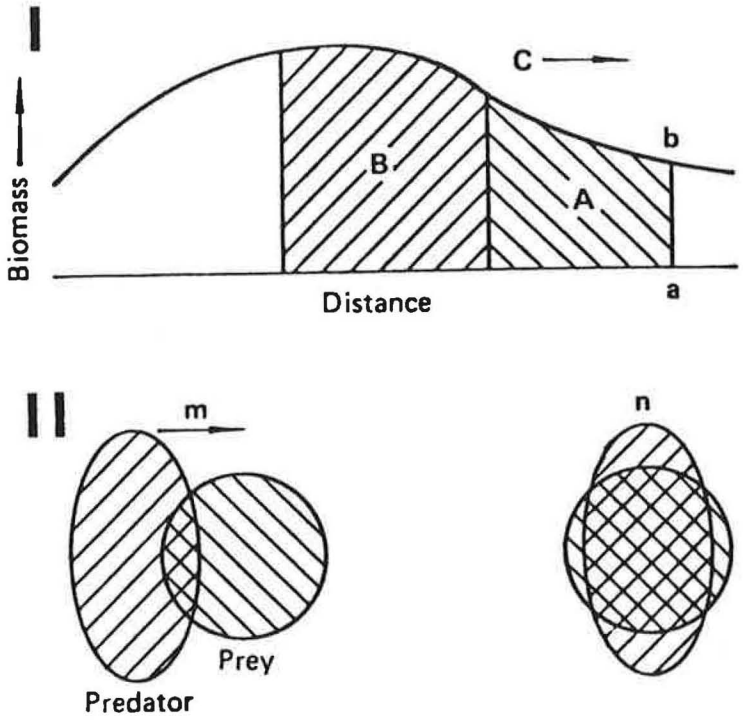


FIG. 9-1. Schematic presentation of two effects of migration.

I. With a given migration speed c the biomass A passes through the section a-b. Doubling either the speed or time, biomasses A+B pass through the same section.

II. Schematic example of the migration of predator into the region of a given prey.

as a fish food resource at the section a-b. Under stationary conditions this benthos biomass is grazed by the stationary predator biomass (a-b) at this location. However, if the predator moves with a speed C through this section, the "upmigration" of biomass A can prey on the same standing stock of benthos at the section a-b during migration. If the speed is doubled, the biomass A+B can prey on the same benthos biomass (time factor must also be considered above). This applies also to fishing: in the stationary case, the fish is caught (and sampled) as representing the biomass present at all times. However, with varying migration speeds and quantities of biomass passing through the section, the effect of a constant fishery for different segments of the population would be different. This difference becomes more complex if the biomass age composition also varies with time as the fish biomass moves through section a-b. The second part of the Figure shows the self-explanatory effect of predation caused by separation and/or overlap of predator and prey. These concepts are simulated numerically in the model.

The effects of migration on predator-prey interactions is especially important in gridded models, such as DYNUMES, and is one of the main reasons for the use of gridded models.

Some of the dynamic aspects of predator-prey "overlap", pertaining especially to benthos and to seasonal migrations of flatfish, have been presented in Figure 9-1. The effects of spatial distribution of different prey items on the composition of food of a predator are schematically shown in Figure 9-2 which depicts a vertical section with predator-prey distribution. Not only does the food composition of the predator vary in space, but the predation pressure on the prey varies as well.

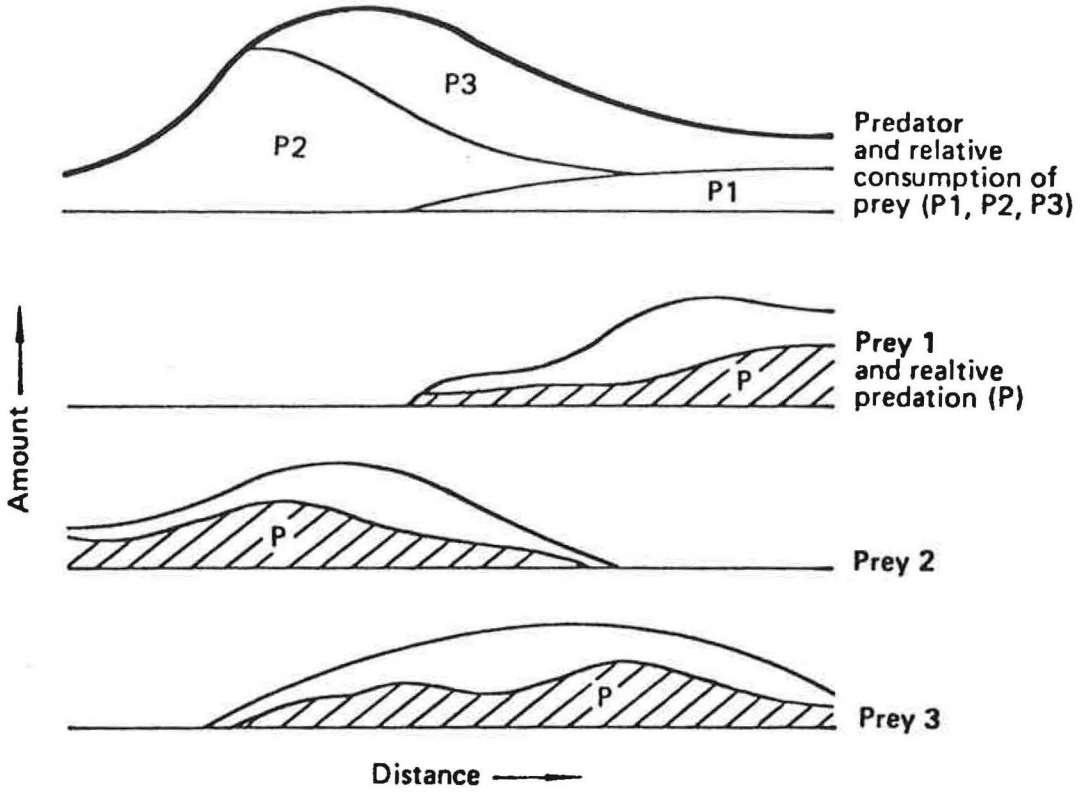


FIG. 9-2. Schematic presentation of the predation by one predator on three prey items with different spatial distributions (presented as a section).

Not all of the biomass participates in a given migration. Thus, before computing migrations, the portion of migrating biomass must be estimated. The migration speed must be ascertained and separated into u and v components, which must be prescribed or simulated.

The computation of migrations are done with an "upcurrent interpolation and advection" method, which is quasi-conservative. However, the conservation of biomass must be checked after each time step. The migration formulation has a stability criterion and might require smaller time step than the routinely used monthly time step:

$$t_d < \frac{\ell}{|u,v|} \qquad (1)$$

where: t_d is time step, ℓ is grid length and u and v are migration speed components.

Migration computation is carried out in two steps. First, the linear gradient of biomass in "upcurrent" (upmigration) (UT and VT) are determined:

u positive:

$$UT_{(n,m)} = (B_{n,m} - B_{n,m-1}) / \ell$$

u negative:

$$UT_{(n,m)} = (B_{n,m} - B_{n,m+1}) / \ell \qquad (2)$$

v positive:

$$VT_{(n,m)} = (B_{n,m} - B_{n-1,m}) / \ell$$

v negative:

$$VT_{(n,m)} = (B_{n,m} - B_{n+1,m}) / \ell$$

In the second step, the gradient is advected to the grid point under consideration.

$$B_{(t,n,m)} = B_{(t-1,n,m)} - (t_d|u_{(t,n,m)}|UT_{(n,m)}) - (t_d|v_{(t,n,m)}|VT_{(n,m)}) \quad (3)$$

After each time step a smoothing (diffusion) operation is performed, which also simulates the random migration of fish:

$$B_{(n,m)} = \alpha B_{(n,m)} + \beta (B_{n-1,m} + B_{(n+1,m)} + B_{n,m-1} + B_{n,m+1}) \quad (4)$$

The migrations due to unfavorable environment and/or search for food is done by checking surrounding grid points for various prescribed unfavorable-favorable criteria (and or presence of optimum conditions) and corresponding to the finding of this search a portion of the biomass is moved towards optimum conditions:

$$B_{i(n,m)} = B_{i(n,m)} - k_o B_{i(n,m)}$$
$$B_{i(n\pm1,\ m\pm1)} = B_{i(n\pm1,\ m\pm1)} + k_s B_{i(n,m)} \quad (5)$$

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NOTITIA X

10. EQUILIBRIUM BIOMASSES AND THE UNIQUE SOLUTION TO THE SET OF ECOSYSTEM DYNAMICS EQUATIONS

Equilibrium biomass is defined as the biomass of a given species (or group of species) where the growth (plus recruitment which is among others a function of growth rate and biomass present), equals the sum of mortalities (including predation and fishery) and consequently the biomass would be the same in a defined month from one year to another. This requires that growth as well as mortalities (especially predation) remains the same each year (although seasonal fluctuations occur). The equilibrium biomass concept is obviously an unnatural one, but is required as a "standard" (basis) for the assessment of the long term mean resources and their internal relations (in respect to biomass). It is determined as a unique solution to the basic ecosystem equation:

$$B_{e,(const.)} = B_{(adj.)} \ (2-e^{-(g-z)}) \qquad (1)$$

In other words:

If the biomasses of all species in the ecosystem do not change over a year (i.e. previous January biomass is the same as actual January biomass), then we can say that the biomasses are in equilibrium. This implies that the growth of the biomass equals its removal by mortalities (especially by predation). If we want to achieve this equilibrium, we can change either growth rate, mortality rate, or biomass level itself. The growth rate is determined by empirical data (and other factors such as temperature) and are assumed in the equilibrium case to be the same

from one year to another (although seasonal changes can occur). Fishing and other mortality rates are also assumed to remain the same from one year to another. The predation mortality (consumption) must then balance (together with other mortalities which remain unchanged) the growth rate. This balancing can be achieved if the biomass levels of the biomasses are adjusted in the simulation model at the end of each year so that at the end of the iterations biomass of one January is the same as in the next January. This adjustment can be done by finding a unique solution to the biomass equations of all species (or groups of species) in the ecosystem. This unique solution exists when one of the biomasses and the consumption by that biomass is predetermined (assumed to be known and fixed). In this case an iterative solution can be applied to adjust the biomasses of other species once after each year's computation:

$$B_{i,t12,0} = B_{i,t12,a} + \frac{(B_{ib} - B_{i,a})}{k} \qquad (2)$$

where $B_{i,t12,0}$ is the new (adjusted) biomass for December, $B_{i,t12,a}$ is the previous December biomass, $B_{i,b}$ is the biomass of previous January (computed as next step from $B_{i,t12,a}$), $B_{i,a}$ is the computed biomass in January one year later and k is an iteration constant (3.5 to 10, depending on the state of convergence). Forty years or more of computation is usually needed before the solution converges to a unique (equilibrium) solution. The speed of convergence is among others dependent how close equilibrium values were to the initial guess biomasses at the start of computation.

We can define three basic equilibrium biomasses which among others are useful for determination of our numerical assessment error limits. The minimum equilibrium biomasses are computed with lowest plausible food requirements and highest plausible growth rates. The maximum equilibrium biomasses are obtained with lowest plausible growth rates and highest plausible food requirements. The mean equilibrium biomasses use plausible mean values for both.

Errors in initial (first guess) input of biomasses do not affect the results (but affect the time (number of iterations) required for conversion). However, in order to obtain a unique solution, part of the predation mortality must be known (fixed, constant). This can be done by keeping a major species biomass (whose magnitude is better known) constant, or by predescribing marine mammal biomasses (and obtain their constant predation).

There must be a trophic relation between the biomasses in the system if the system is a unit ecosystem (Figure 10-1 below; we have one system in Figure A whereas in Figure B we have two independent systems).

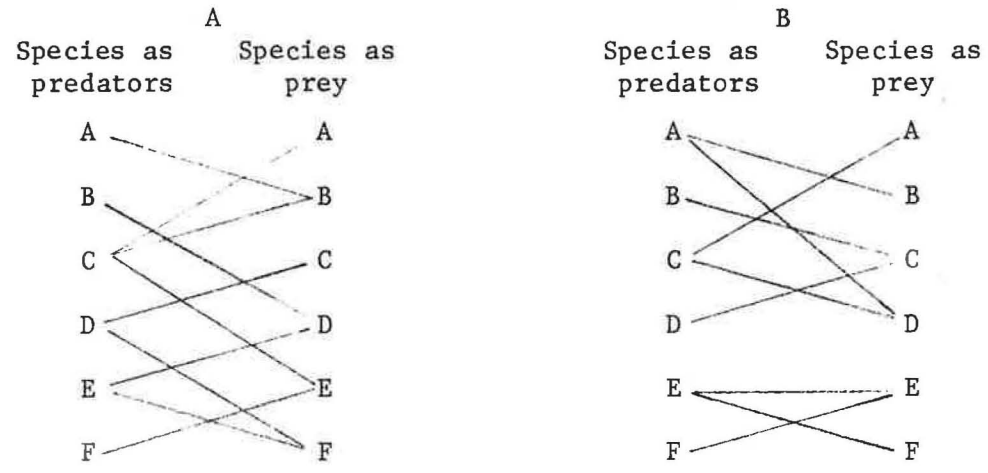


Figure 10-1.--Trophic interactions in ecosystem as determinant of the system dependence.

As mentioned above, the food requirements and growths are determining factors of biomass levels in the ecosystem. Food composition determines the "bond" of the species to the system and largely also its predation.

If the biomass is in equilibrium with growth and fishing and other mortalities:

$$B(1-e^{-g}) = B - Be^{-(f+\frac{C}{B})}$$

where C is predation and f is fishing mortality.

Then:

$$Be^{-g} = Be^{-(f+\frac{C}{B})}$$

if f = 0 then:

$$g = \frac{C}{B}$$

However, if g remains constant and f increases, $\frac{C}{B}$ must decrease (which is partly true to "density dependent feeding). However, if f increases, g also increases a little (rejuvenation of populations).

NOTITIA XI

11. TOTAL PRODUCTION CONTROLLING FACTORS AND INTERACTIONS OF FISH BIOTA WITH ZOOPLANKTON AND BENTHOS

The direct quantitative utilization of phytoplankton in the marine ecosystem is very variable in space and time. However, it is the main production of organic matter and thus determines to a large scale the level of marine ecosystem and is thus one of the "buffers" of the marine production. The phytoplankton produces the bulk of the organic matter for remineralization process, for burial in sediments and for use as detrital food for benthos.

However, the most important direct food source (and food buffer) for marine biota is the zooplankton (which includes euphausids and epibenthic crustaceans) about which our present knowledge is very deficient. The quantitative knowledge on zooplankton at large, and especially about its production, is also badly lacking in many areas and seasons. The reported values of phytoplankton and zooplankton standing crop are relatively few. The reported values by various authors vary more than one order of magnitude. The estimations of production are still fewer (see further model input documentation). Thus it is virtually impossible to start any ecosystem model computations with basic organic or zooplankton production values. Furthermore, the pathways of plankton production through the food chain are extremely variable in space and time and quantitatively nearly unknown.

Therefore, the best approach to use zooplankton in ecosystem computations is to simulate its standing stock (see model description in NWAFC processed reports) based on empirical data and compare (and limit) its consumption, if necessary, in space and time in the same manner as limiting consumption of other ecological groups.

One of the most important factors in respect to the zooplankton availability to fish is its patchiness, about which our knowledge is at best qualitative.

The quantitative data on benthos are still more deficient than the data on plankton. Nearly nothing is known on the annual production of different components of benthos from the Bering Sea. Thus we cannot fully evaluate the benthos in respect to fish productivity in simple models of J. Petersen's type. Considering the very slow progress made in benthos research in the past 50 years, it might take hundreds of years before we could start a quantitative ecosystem model from primary production, zooplankton and benthos as "producers". It seems that all the quantitative computations which we can make at present in respect to benthos are good for the order of magnitude only. Available quantitative data on the benthos in the Bering Sea and the simulation of its standing stock and production are described in model input documentation.

Benthos distribution and dynamics are as complex as that of fish; its detailed treatment would require a programme larger than the present DYNUMES and PROBUB--which would be a practical impossibility (computer size limitations). Furthermore, the quantitative composition of benthos, especially that of the mobile epibenthos, is badly known.

For the purpose of the fish ecosystem simulation where benthos is the second "production buffer", it is sufficient to treat benthos in three ecological groups--predatory benthos, infauna and epifauna.

Fish and other mobile marine organisms seem to be in constant search for food; by contrast most of the benthos and plankton have limited or no mobility at all. There seems to be a migration by fish into high food density areas and when the food is grazed down, the grazers move into other areas, leaving former ("grazed down") areas for recovery.

The zooplankton and benthos control the productivity in large space and time scale and should be used as such in the ecosystem models.

NOTITIA XII

12. THE EFFECTS OF FISHERY ON THE BIOMASS OF THE TARGET SPECIES

The simplest formulation of the theory of fishing, Russell (1931) (from Cushing 1968) is:

$$P_2 = P_1 + G + R + Z^1 \qquad (1)$$

P_2 - stock at time t_2

P_1 - stock at time t_1

G - growth between t_1 and t_2

Z^1 - mortality between t_1 and t_2

R - recruitment

This formula, as many other fishing theory formulations, does not unfortunately include the recruitment to exploitable stock. Furthermore, the losses and/or gains of biomass of a given species due to fluctuations of fishery are not linearly dependent on the magnitudes of these fluctuations. Thus, if we remove e.g. 10,000 tons by fishery of the biomass of a species, the annual decline of the biomass of that species is usually considerably more, as will be briefly demonstrated in this Notitia. This fact has been difficult to appreciate as it is not apparent from conventional number-based computations.

If the fisheries dynamics computations of the effect of fishery have been made on number bases, annual time step has been customarily used, assuming that this does not cause appreciable errors, as computing is done "downhill", i.e. only losses of numbers occurs and no numbers can be added except by recruitment from the "uphill" side (which is unfortunately neglected in most cases). However, if we need to convert the numbers

to biomass for trophodynamic computations, errors rise with annual timestep as growth is nonlinear function of time. Thus much smaller time step than one year must be used to minimize the error.

The production models, however, require the computation of the biomass growth ("surplus production") as well as accounting for the recruitment "uphill". Thus age-dependent mortality coefficient as well as age and biomass distribution dependent growth coefficients are required for these computations but have not been used in the practice, invalidating these models.

Biomass based models require the computation of growth, mortality, and fishery which are all age and biomass distribution dependent as well as dependent on the biomass present. Therefore, the effect of the fishery on the biomass does not necessarily become linearly dependent on time nor on initial exploitable biomass present. This is demonstrated with the following special model.

The biomass dynamics is computed in monthly time steps with the following well known formula:

$$B_t = B_{t-1} e^{Z} \qquad (2)$$

where t is time step (one month)

B - biomass (initial biomasses 3600, 4200, 4800 and 5400 kg/km^2 assumed in the enclosed examples). It can be used as biomass of whole population, biomass of a cohort, or groups of cohorts. The coefficient Z (below) must be adjusted (selected) correspondingly:

$$Z = G - FM - F - CL \qquad (3)$$

where:

G - instantaneous growth coefficient (per month) = 0.10 (must correspond to group of cohorts or whole biomass being computed)

FM - instantaneous mortality coefficient from old age and diseases = 0.003 (per month)

F - instantaneous fishing mortality coefficient = 0.015 (per month)

CL - instantaneous predation mortality coefficient (prescribed in the example below and converted with Formula 4)

The instantaneous predation mortality coefficient is computed from known (and/or assumed) predation C_t

$$CL = -\ln \left(1 - \frac{C_t}{B_{t-1}}\right) \qquad (4)$$

C in our example has been assumed to be 360 kg/km^2 per month.

The level of predation on a given species is mostly dependent on the density of the prey. The exact density dependent function cannot be determined, but can be assumed to be linear or approximately linear. Furthermore, the predation is expected to contain also a density independent part, due to selective feeding. Thus the following predation functions were computed with all assumed biomass levels:

$$C_t - C_{cons.}$$
$$C_t = A + B \frac{B_{t-1}}{\bar{B}} \qquad (5)$$

where constants A and B in the examples below are: A = 100 and B = 260, the constant A being density independent predation. The density dependent predation is presented with the equation: actual biomass of prey (B_{t-1}) divided by the mean biomass (equilibrium biomass) ($\bar{B}$), which is the initial (input) biomass.

The fully density dependent predation was computed as:

$$C_t = C \frac{B_{t-1}}{\bar{B}} \qquad (6)$$

The corresponding partially and fully density dependent predation (at computation range only slightly nonlinear) functions tested were:

$$C_t = A + B \sqrt{\frac{B_{t-1}}{\bar{B}}} \qquad (7)$$

and

$$C_t = C \sqrt{\frac{B_{t-1}}{\bar{B}}} \qquad (8)$$

The old age and disease mortality (including spawning stress mortality) coefficient FM has been assumed constant in the example, unless fishery is considered to operate on older year classes and biomass recruitment to exploitable stock is smaller than yield, in which case the FM should decrease and growth coefficient for the whole biomass should increase.

If the fishing mortality coefficient F remains constant, it is a fishing intensity coefficient and the catches decrease with decreasing biomass. This might be the case with trawl fishery for e.g. flatfishes:

$$F = \text{constant} \qquad (9)$$

In most cases the annual catch is known or there might be a need to simulate the effect of a given annual catch on the biomass of target species. In this case the fishing mortality coefficient is computed (tuned) on "equilibrium biomass" and must change if the biomass changes. This represents also an example of targeted fishery on schooling species:

$$F_t = F \frac{\bar{B}}{B_{t-1}} \qquad (10)$$

The following figures 12-1 to 12-6 illustrate the change of biomass with fishery, computed with a combination of density dependent and density independent predation and fishing mortality coefficients and other formulsas described above.

As seen from these figures, the relation between fishery removal and the change of biomass is not strictly proportional to fishery (nonlinear). Reasons for this unproportionality in biomass decline are:

1. Mathematically they (growth, fishery) are exponential coefficients, thus biomass is a nonlinear function of these coefficients. Furthermore, the whole process is a finite difference approach, thus dependent on the length of time step.

2. Growth of biomass is a function of biomass present and its growth coefficient (positive in the type of presentation in this Notitia).

It should also be pointed out that changes in predation are more important in biomass change than changes in fishery.

Finally, it should be pointed out that there is a relationship between fishing mortality and biomass growth coefficient (re. rejuvenation of populations) and senescent (and spawning stress) mortality coefficient.

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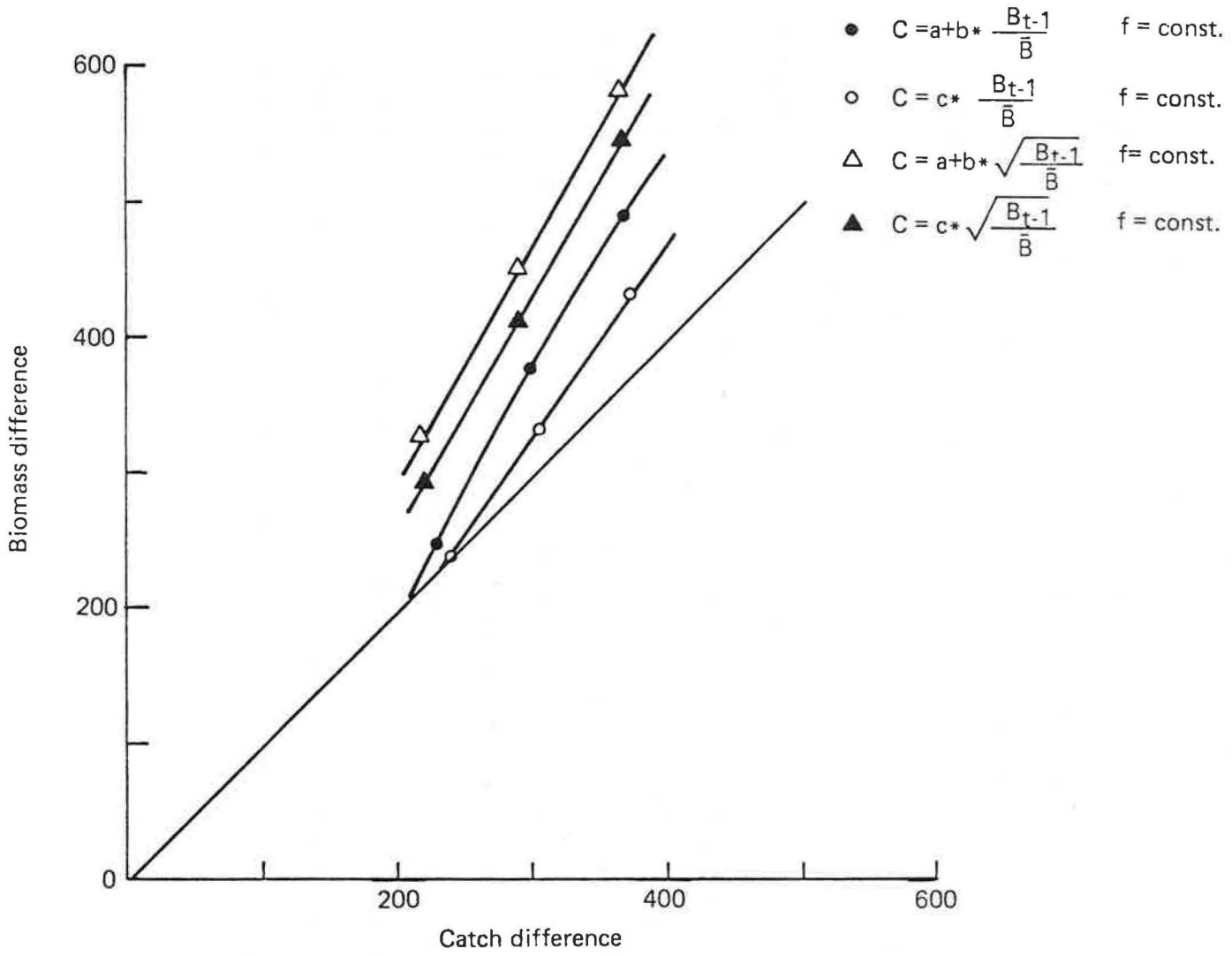


Figure 12-1.--Difference in biomass resulting from differences in catch with various variations in consumption (predation) (constant fishing mortality coefficient).

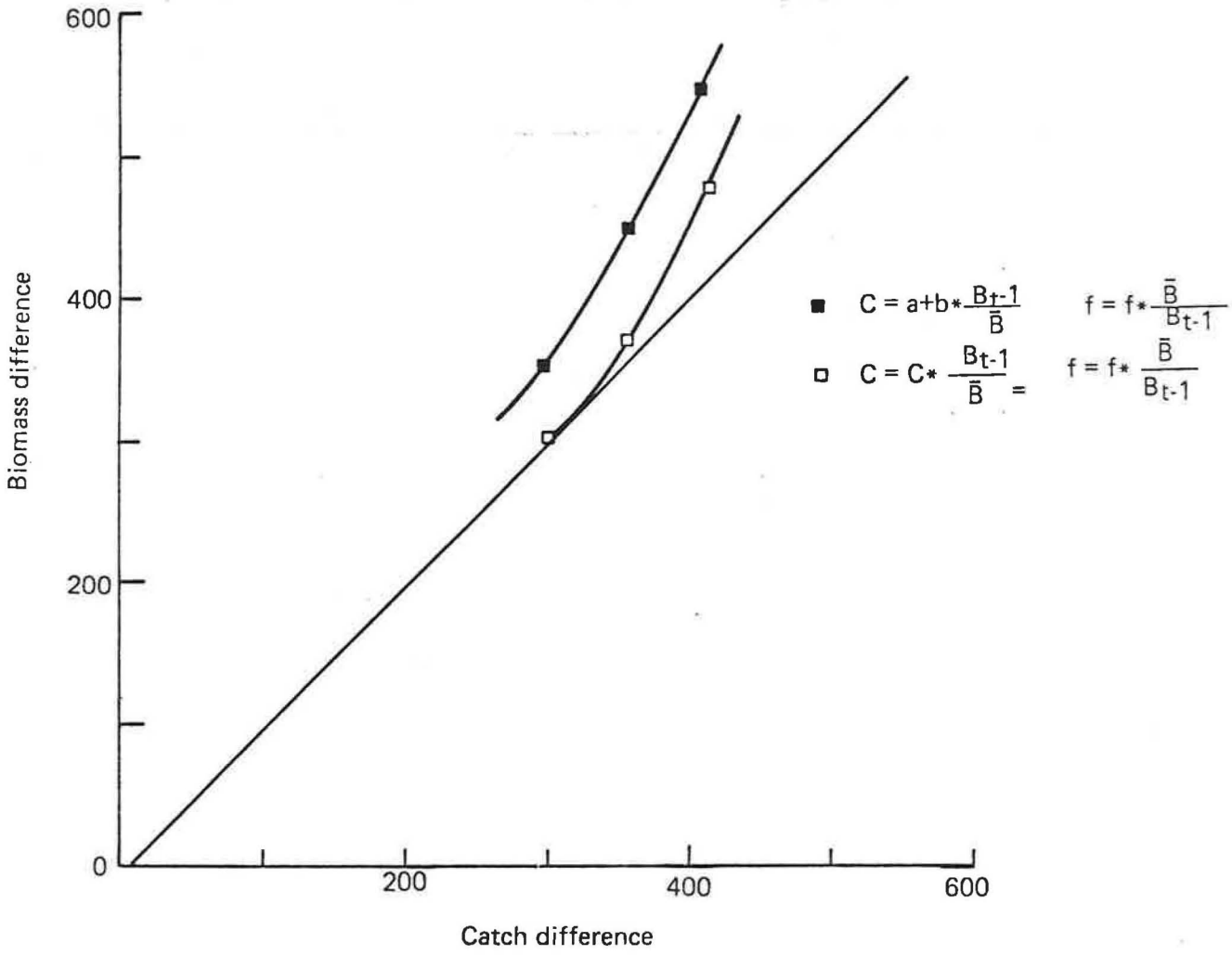


Figure 12-2.--Differences in biomass resulting from differences in catch with different consumption (predation) (constant yield).

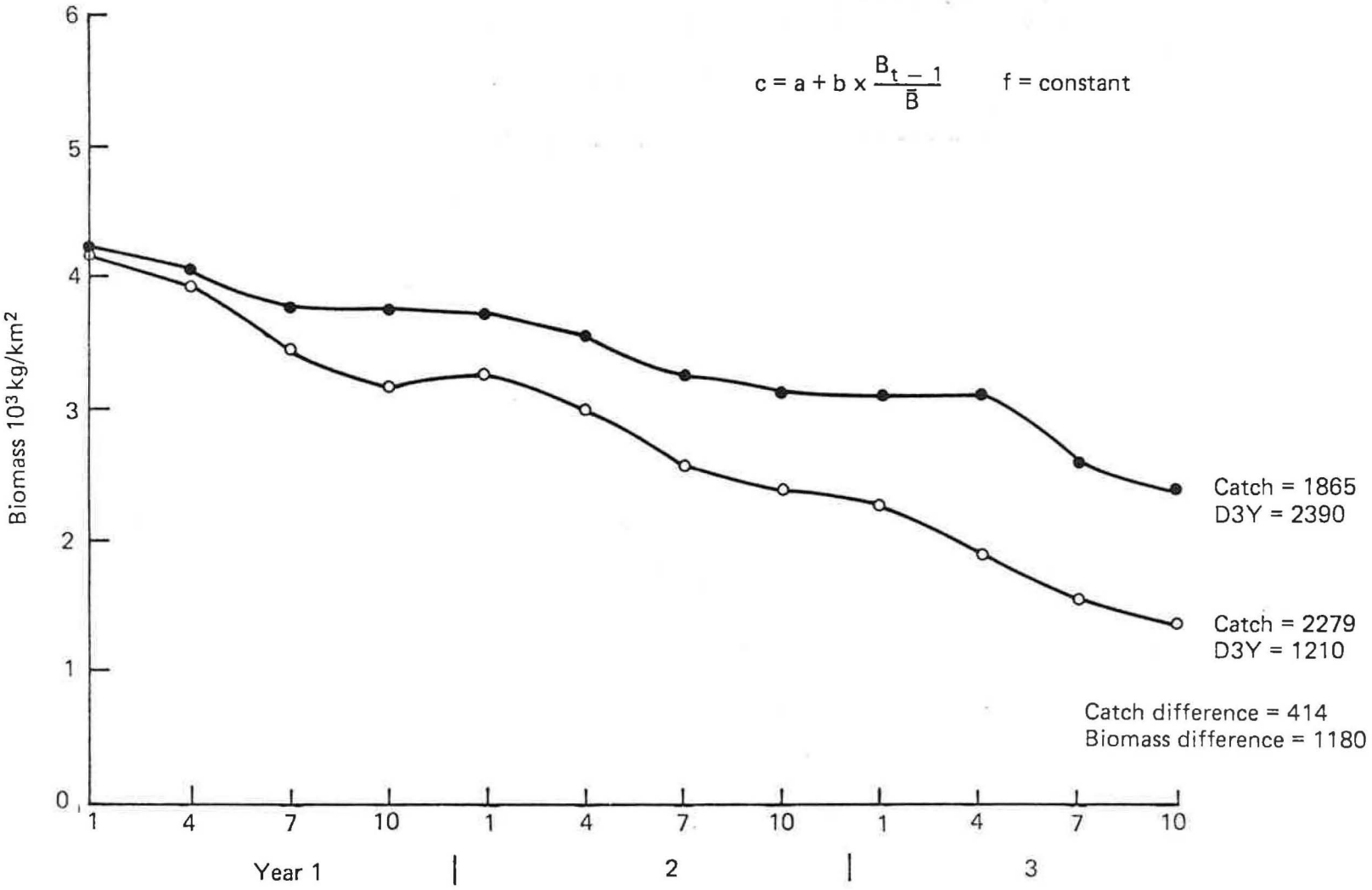


Figure 12-3.--Change of biomass with time with two different fishing intensities (seasonally variable fishery).

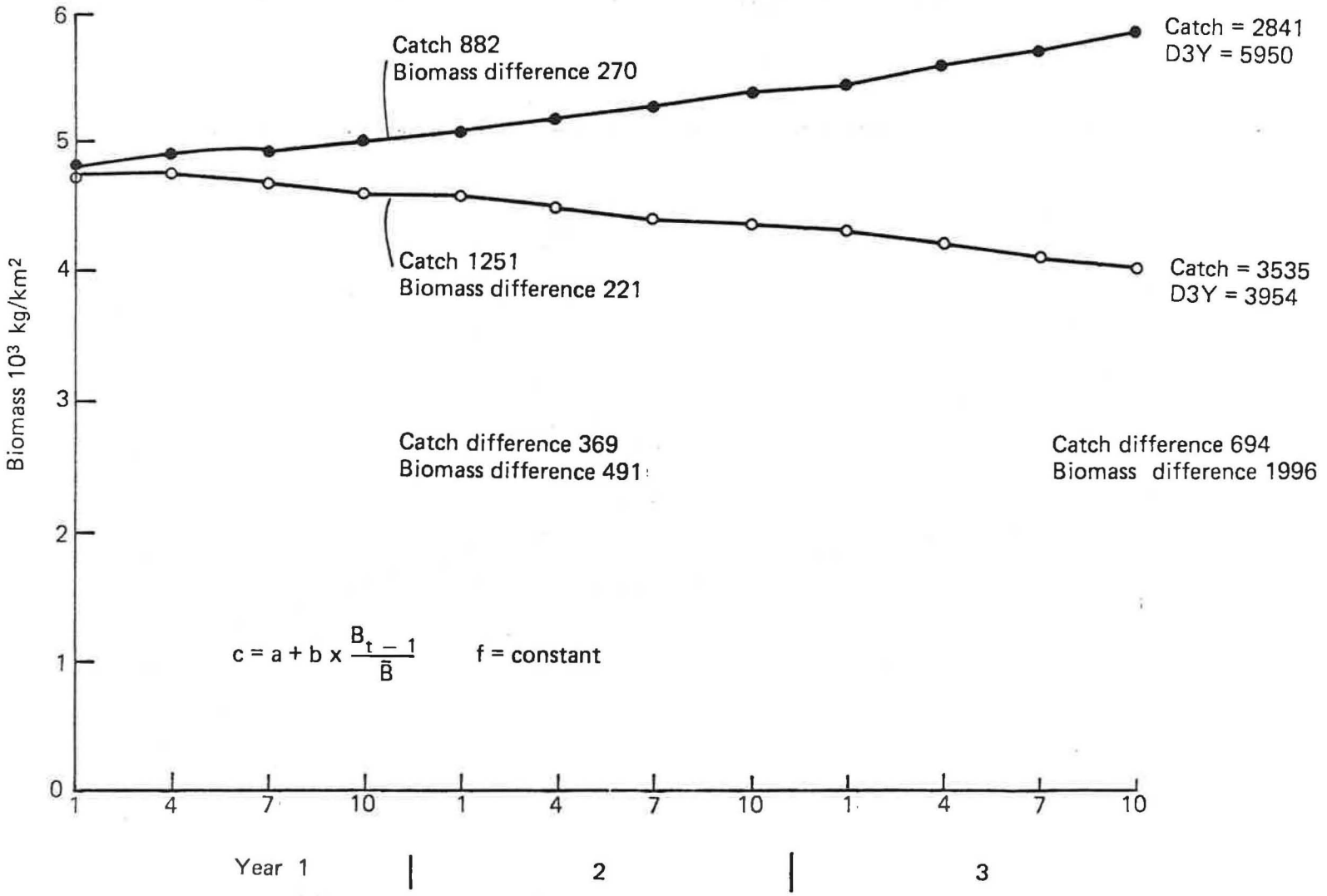


Figure 12-4.--Change of biomass with time with two different fishing intensities.

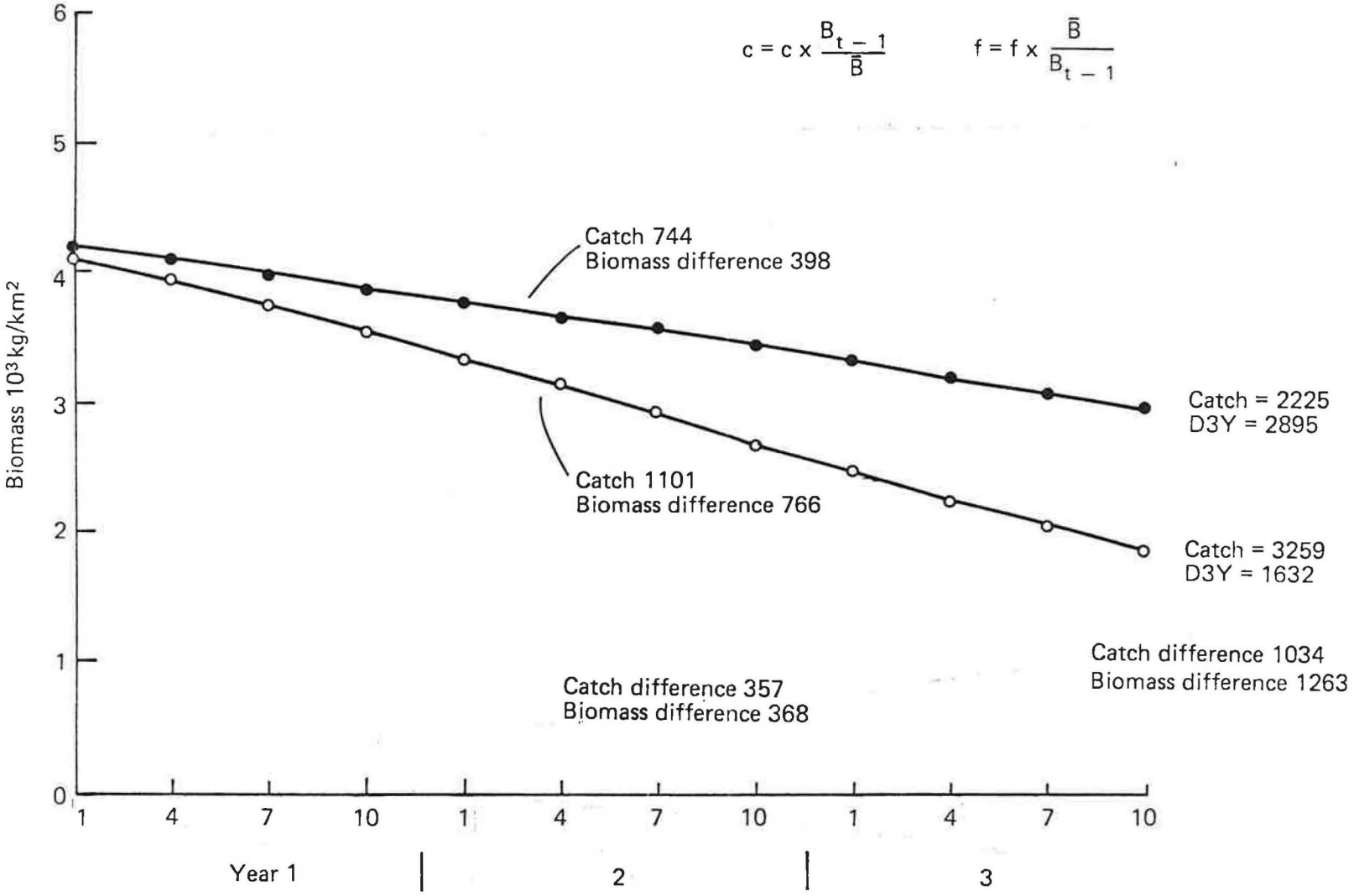


Figure 12-5.--Changes of biomass with time with two different fishing intensities.

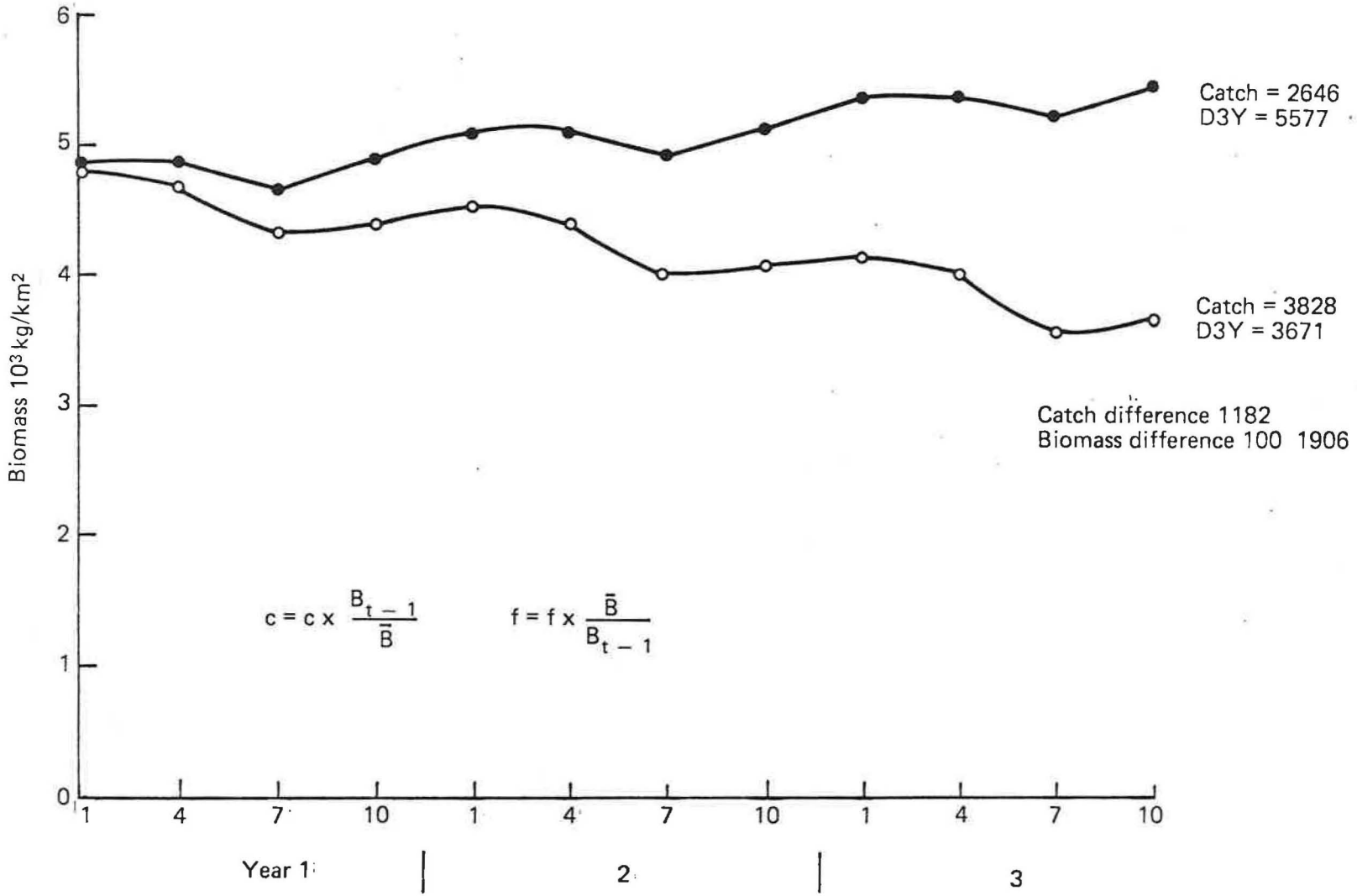


Figure 12-6.--Changes of biomass with time with two different fishing intensities (seasonally varying fishery).

NOTITIA XIII

13. ACCEPTABLE CATCH (AC) AND ITS FIRST GUESS (ACG) ESTIMATION FOR INPUT INTO THE ECOSYSTEM SIMULATION, AND THE SIMULATION OF CATCH AND YIELD

1. Need for and use of the first guess input of AC.
2. The epitaph to MSY, the uprising of its ghost and the present practices with MSY and its related "alphabet soup".
3. Criteria for ACG and processes affecting it.
4. The indices and formulation of AC guess, and the use of fishing and yield equations in ecosystem models.
5. References

1. Need for and use of the first guess input of ACG

One of the main objectives of the ecosystem simulation modeling is to determine quantitatively the response of the ecosystem to exploitation and to determine how much of any given species can be taken from the ecosystem of a given region without causing changes of undesirable nature and extent. The decision of what are "undesirable changes" in the ecosystem must be based on many criteria, most of which have little to do with science proper. However, science must show the nature and extent of the changes and make suggestions as to which changes are acceptable from the ecosystem point of view.

The effects of fishery on the ecosystem can only be determined in a full (complete) ecosystem simulation model where all species and all fisheries are included. Any removal of some quantities of fish

will cause changes in the biomass of the target species as well as in other species. The criteria of which changes in the ecosystem are acceptable from the ecosystem "health" point of view, considering especially its capacity to reproduce harvestable species biomasses, must usually be established on regional bases, with the knowledge that these criteria should vary in time with changing economical conditions. The establishment of these criteria are outside the scope of the ecosystem simulation task at present.

The estimation of the acceptable catch is not part of ecosystem simulation proper, but rather an auxiliary approach to facilitate the use of the simulation model. Although in this notitia we attempt to produce with simple indices some numbers as guidance for acceptable catch, we do not intend to give a definite and simple answer to a very complex problem. The first guess estimate derived from the approach described below will merely serve as first guess input of fishing intensity (and/or yield) into the ecosystem simulation to determine the response of the ecosystem to these yields and to provide background for management decisions. The first guess estimate is merely necessary to reduce the trial-and-error inputs for testing of the effects of fisheries with these models. The complex and complete simulation models enable us to evaluate the changes in the stocks due to "natural fluctuations" as well as those fluctuations in abundance caused by fishery.

The term Maximum Sustainable Yield (MSY) was conned from the report of the Select Committee of the Imperial Parliament (The House of Commons) in 1893. This report described the need for and the purpose of fisheries conservation as: "...to enable fishermen to obtain from a stock of fish the highest yield, consistent with that yield being maintained in the future...". In recent years a number of closely related terms have been conned, such as optimum yield (OY), equilibrium yield (EY), allowable biological catch (ABC) and others, the definition of which often depends on the state of the mind of their definers/users.

In order to distinguish our estimated number (quantity of possible catch from a given region) from earlier used terms, we are calling our estimated number "Acceptable Catch". What is acceptable catch depends on the extent and nature of the changes in the ecosystem as a result of any catch and a great number of considerations of economic and social nature, and will usually be debated and determined by a concerned populus (fishermen) and the fishing industry.

2. The epitaph to MSY, the uprising of its ghost and the present practices with MSY and its related "alphabet soup".

Larkin (1977) wrote an epitaph to MSY and related concepts (of which there are many) which have been defined and described in many versions. He also described all the objections and difficulties involved in quantification of any of these terms, as well as the fallacies and wrong expectations connected with these concepts, which are neither fully biological nor economical concepts.

However, as the managers and politicians require a number or quantity which might show how much of any species they will allow to be taken by fishery from any given area, and as mathematicians seem to love, at times, to manipulate numbers which have no meaning in the real world, the religion of MSY is unfortunately not dead. Temples for it are being erected in such prominent places as fisheries management plans and elsewhere. It is time that these temples be provided with proper inscriptions from the words of Horacius: Laude esse animus stolidus.

Reference to and use of is often made of a method of MSY computation which is based on an empirical (and not mathematically or biologically defined) simple equation:

$$MSY = K \cdot M \cdot B_o$$

where K is assumed to be an empirical constant (mostly used value is 0.5, but can range from 0.3 to 0.6); M is "natural mortality", which is usually an unknown quantity and can vary between 0.2 and 1.0; B_o is the size of "virgin biomass", which is in most cases also an unknown quantity and can at best be estimated to the order of magnitude with the past available methods.

Thus, according to this formula:

MSY = Unknown * Unknown * Unknown

Thus we must find another method of estimation of acceptable catch, which would be based on known biological and ecological concepts.

3. Criteria for ACG and processes affecting it.

Berfore establishing the criteria for the estimation of ACG we will review briefly the dynamics of the marine ecosystem in response to the fishery with the help of a few graphical illustrations.

The total finfish biomass in a given region fluctuates but little in the course of time (Fig. 13-1), but individual members (species) can fluctuate considerably, one decreasing, the other increasing. These individual species fluctuations are not always caused by fishery, but may be caused by other factors such as environmental anomalies. Thus the determination of the causes, magnitudes, and periods of these "natural fluctuations" is one of the important tasks in modern fisheries science.

The total finfish biomass (the carrying capacity of finfish) is determined by the production of organic matters, its turnover, and the benthos and zooplankton. The true carrying capacity is always smaller than the theoretical carrying capacity, computed with the assumption of full utilization of organic production plus the circulation of the biomass of the smaller members of the finfish community.

The following figures will help to realize that the dynamics of a single species biomass varies considerably from species to species, and that no simple concept (MSY or others) can be fully valid for all species. Figure 2-4 shows some aspects of the biomass dynamics of two species. The comparison of individual species growth rates (Fig. 13-2) with the corresponding biomass growth distribution with

age (shown on Fig. 2-4) shows the necessity of using the dynamics of the stocks rather than individual species parameters in any resource assessment and management problems. Figure 13-3 shows the change of mortality with age (relative to the biomass present in each year class). The high predation mortality in larvae and in young fish decreases rapidly with the growth of the fish and reaches a minimum at a given age (size) which usually coincides with the size where the fish comes under the fishery. Thereafter the spawning stress mortality starts to increase with age.

Figure 13-4 illustrates schematically what happens to biomass distribution with age when a virgin stock comes under the fishery. Within about five years the older part of the biomass (exploitable biomass) which was originally in balance with spawning stress mortality (i.e. its distribution with age was determined by spawning stress mortality), will decrease until it is in balance with the sum of fishing mortality and spawning stress mortality. This results in the rejuvenation of the population, which has been observed in many fish stocks. The corresponding changes in landings and "CPUE" are shown in Figure 13-5. Thus the landings of a given stock which has been taken under exploitation will reach a maximum within a few years, so will the "CPUE". Both will decline rapidly thereafter, reaching a given plateau. This decline does not mean "overfishing" as it has been interpreted often in the past. Finally, Figure 13-6 illustrates schematically the changes in number and biomass distribution with age if a "stronger than normal" year class occurs in a given stock. This rather normal "abnormality" occurs as a "disturbance" in the normal reduction of numbers in the population (e.g. from 200,000 eggs of a pollock to 2 fish at the age of 4).

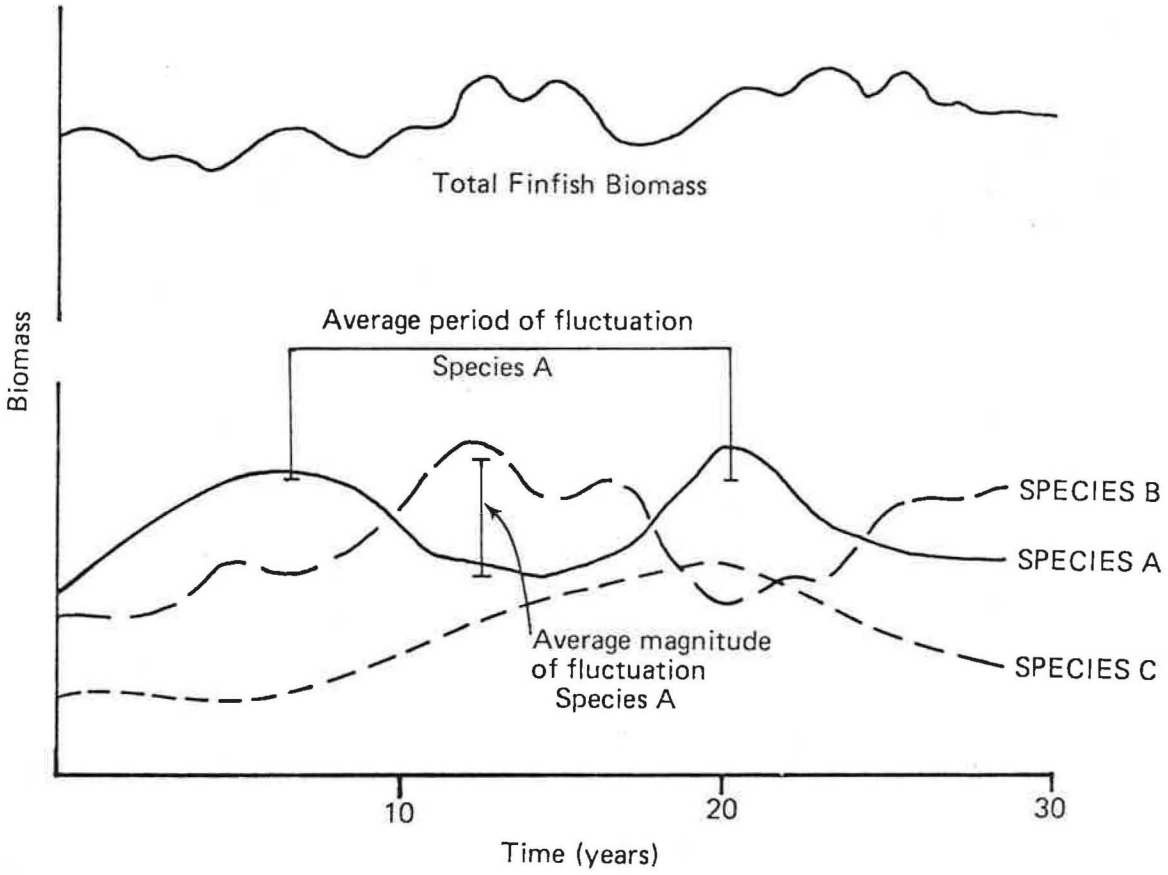
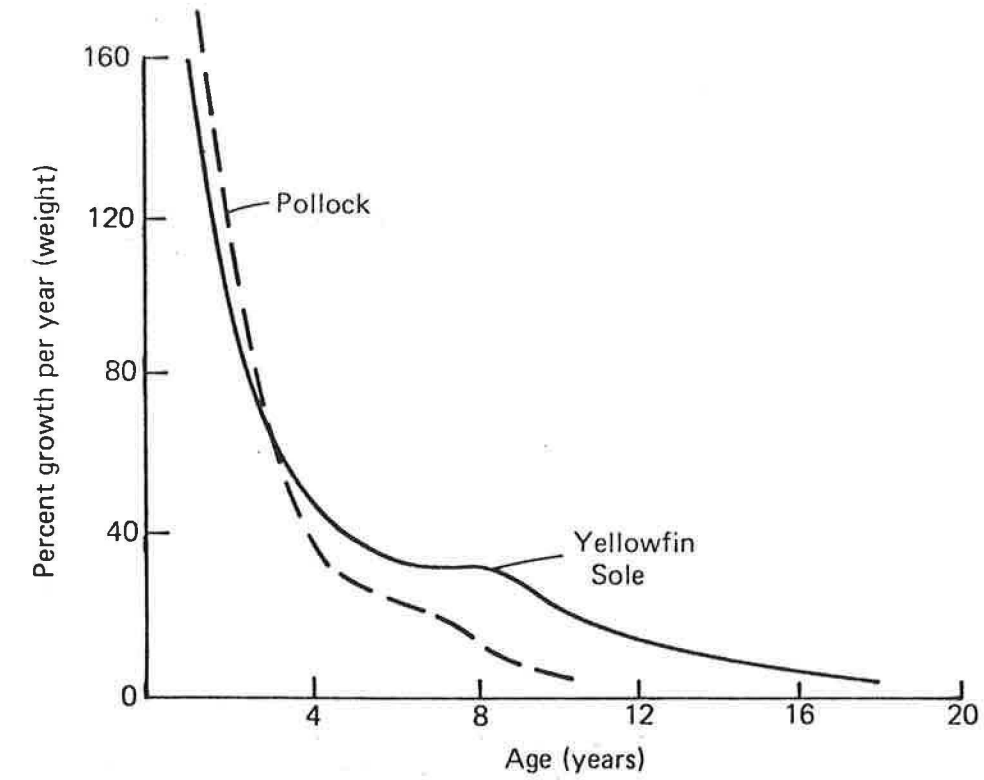


Figure 13-1.--Schematic presentation of fluctuations of total finfish biomass and biomasses of individual biomasses with time.



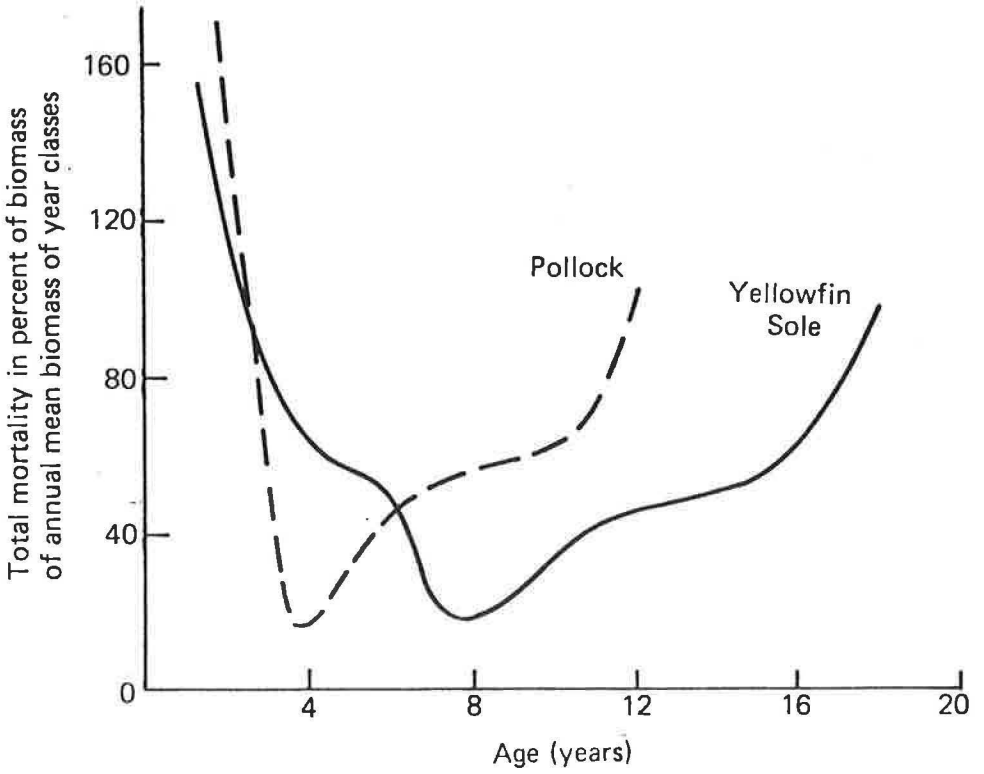


Figure 13-3.--Distribution of total mortality with age in pollock and yellowfin sole.

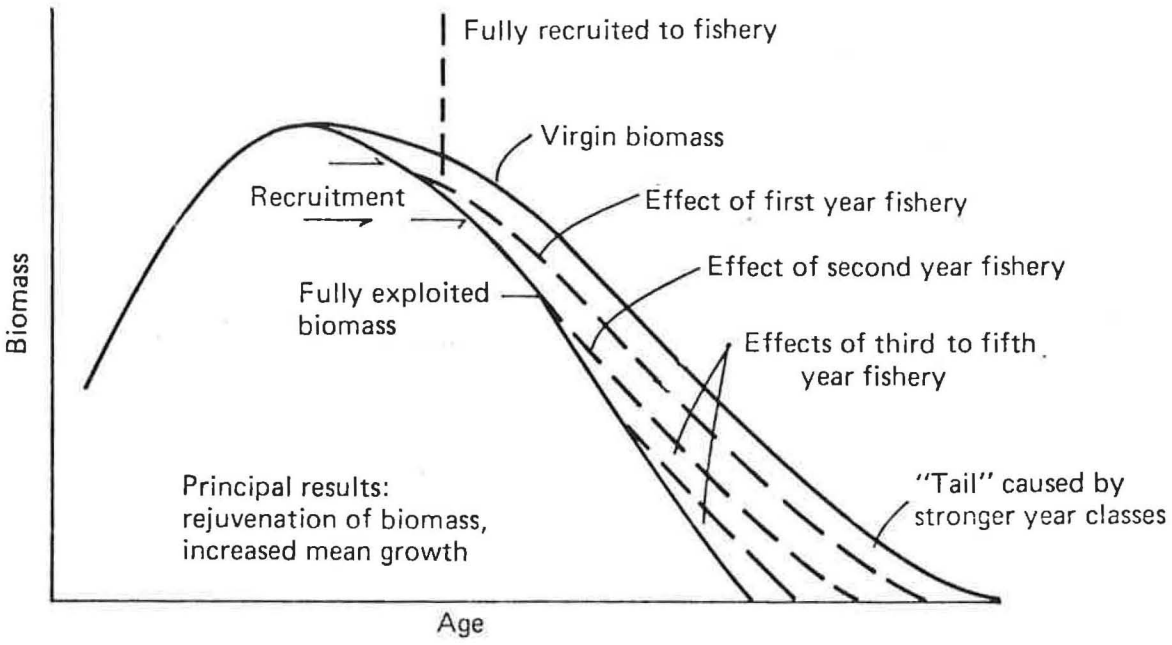


Figure 13-4.--Schematic presentation of the effect of fishery on age composition of biomass, assuming recruitment remains constant and fishing intensity is constant.

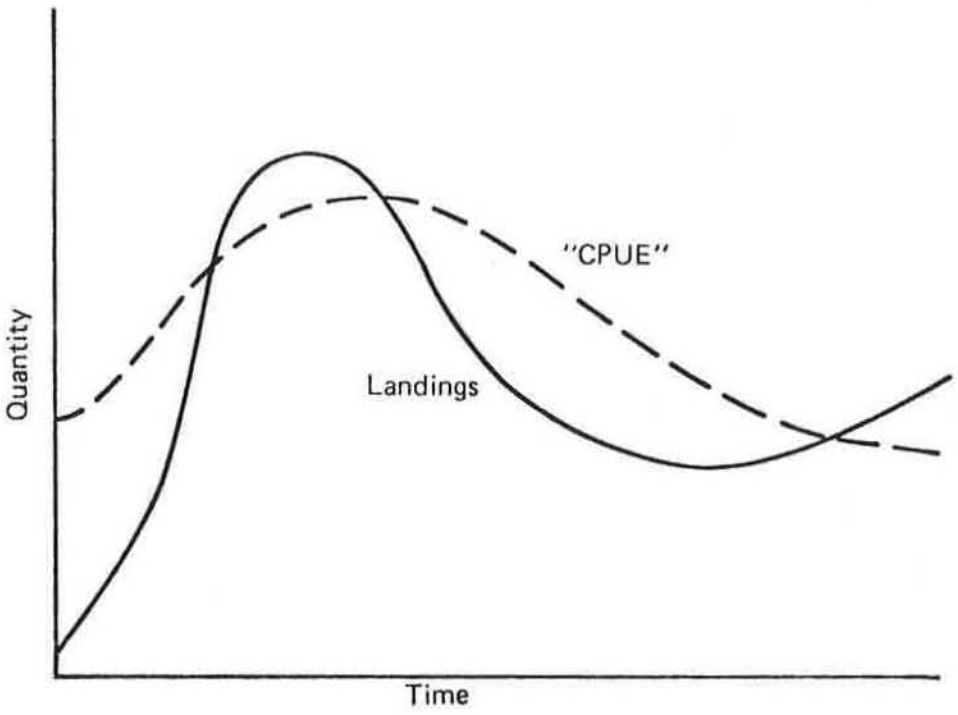


Figure 13-5.--Changes in landings (catches) and "CPU" with time when a "virgin" stock is taken under exploitation.

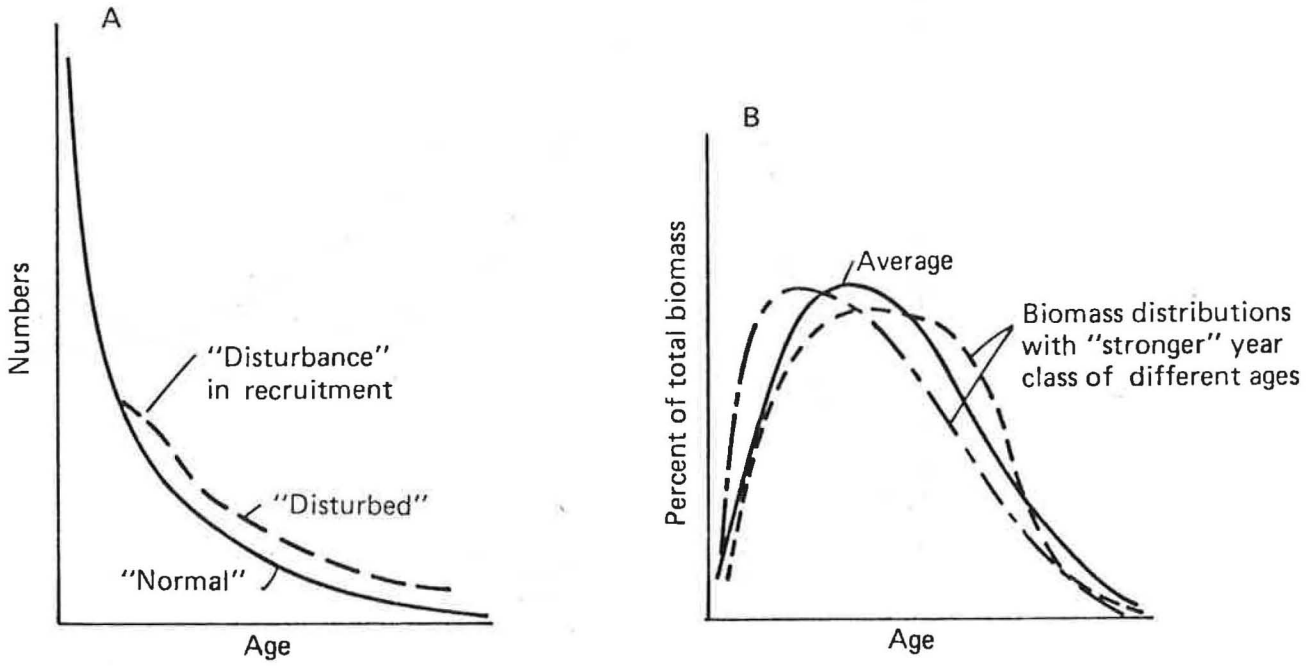


Figure 13-6.--The distribution of numbers with age and "disturbances" in this distribution (A), and average biomass distribution with age and two distributions with stronger year classes at different ages.

Three basic criteria are useful in establishing the procedures for estimation of ACG:

1. Maintenance of a reasonably high potential to reproduce in a commercially desireable species, i.e. to keep the biomass at a level where recruitment is not appreciably affected by occasional "recruitment failures" and especially by too low a spawning biomass. Thus we must know the state of the resource (i.e. the level of the biomass) and consider in addition: age of maturity in relation to fishery (i.e. fully exploited year class) and spawning stress mortality, fecundity, fishery in relation to spawning period (assuming fishery can be regulated in space and time), the life span of the species, and also must have a good idea of the magnitudes and periods of recruitment variations.

2. Minimization of any adverse effect on the other resources and ecosystem at large. This requires the knowledge of the ecosystem response to fishery which can be evaluated only in large simulation models. One of the less considered aspects is the shrinking of the resource distribution (and spawning areas) with the decrease of biomass. Of concern also are the indirect effects of the fishery on other economically important species (other than "target species"). Here the economic aspects enter into consideration, and the task of the biologist is to advise what might happen or what is expected to happen.

3. The harvesting and economic aspects - i.e. maintaining the resource at a level where harvesting is profitable. Although some "maximization" or "optimization" of the production would be possible, it is seldom economically and politically possible--i.e. to achieve Maximum Sustainable Yield in an economic sense.

Additional consideration must be given to the following factors and processes which are expected to affect ACG:

4. Can the "natural fluctuations" which occur in the ecosystem without the influence of fishing be separated from the effects of fishing, and what are the interactions between fishing and "natural fluctuations"? The magnitudes and periods of these "natural fluctuations" caused by a variety of factors, such as temperature anomalies, must be determined with the ecosystem models before introducing high intensity fishing.

5. What is the process of "recovery" of a stock, what are the factors determining it, and what are the "recovery" speeds (relatively sudden or slow and gradual)? Again, the recovery process must be investigated with a full ecosystem model.

6. What is the state of a given stock in relation to equilibrium biomass (to be determined from the model)?

During the iterative procedure in determining the changes in the ecosystem caused by different estimated ACG's, additional consideration must be given to the following:

7. Quantitative changes taking place in pricipal predator-prey relations in the ecosystem.

8. Changes in age distribution and recruitment to exploitable stock.

9. Changes of growth rate and age of maturity.

10. Changes in bycatch composition in mixed fishery.

4. The indices and formulation of AC guess, and the use of fishing and yield equations in ecosystem models.

The estimation procedure, described below, uses indices, the numerical values of which are derived from past knowledge and experiences as well as from PROBUB and BIODIS models. Examples of the selected values and their boundaries are given, together with the explanation of the terms.

The estimated AC is only advisory and used as first guess input into the ecosystem model. The actually recommended acceptable catches or optimum yields can only be determined by management bodies after the plausible multitude of changes which will take place in the ecosystem are determined in a complete ecosystem model and presented to the management body for evaluation and consideration. The management body, consisting of a variety of interests, have then to decide which changes are acceptable in relation to different catches and exploitation strategy.

Indices

I. Direct species indices

B_e - Exploitable equilibrium biomass (from PROBUB simulation)

B_t - Actual exploitable biomass present at time t (from PROBUB)

C - "State of the biomass" index = $\frac{B_t}{B_e}$

A_s - Age at which 50% of the population has reached maturity

A_r - Age at full recruitment to fishery

a - "Spawning biomass saving" index = $A_s - A_r$

If >2, a = 1; if 0, a = 0.7; if -1, a = 0.55, if -2 or smaller, a = 0.45

- "Effective" life span (age after which the catches are insignificant; maximum value $A_s + 7$)

M_s - Spawning stress mortality index = $\infty - A_s$ (minimum value 2, maximum 7)

g - Growth rate of biomass (in % per month of whole biomass, normally between 4.5 and 15)

f - Fecundity index (relative, highly fecund 1.5 to very low fecundity 0.9)

M_p - Predation mortality index (indicating the importance of the species as "forage fish" in the ecosystem; consideration includes prefishery juveniles) = $1 + (\frac{g}{5A_r})$

r - Recruitment variability index (year-class strength variability; highly variable 3; relatively uniform 2)

n - Index of vulnerability to environmental changes (anomalies) (0.8 vulnerable, 1.0 least vulnerable)

h - Index of "stationarity" of biomass (nonmigratory 1.5, highly migratory 1)

y - Index of fishery in relation to spawning season and area (no or very little fishery in spawning grounds and in spawning season 1.2; fishery mainly in spawning season and on spawning grounds 0.8)

u - Cannbalism index (older species very cannibalistic 1.4, minimal cannibalism 1.0)

II. "Combination indices"

d - "Mixed fishery" index (species also caught as bycatch in other fisheries 0.8, species caught mainly in mixed fishery 1.0, species caught mainly as "targetted species" 1.1)

p - "Predatory index" (species is important predator on other commercially caught species 0.8, species does not prey on other commercial species to any considerable extent 1.1)

s - "Prey substitution" index (species can be substituted easily with ecologically and in size/growth similar species 1.1, species substitution possible only from juveniles of dissimilar species 0.9)

The acceptable catch first guess (ACG) is computed with the following formula:

$$ACG = \underbrace{\frac{AcB_e}{rM_s}}_{\text{"Basic ACG"}} \cdot \underbrace{\frac{M_p fnyu}{h}}_{\text{"Species specific effects"}} \cdot \underbrace{\frac{ds}{p}}_{\text{"Combined effects"}}$$

It could be mentioned for general guidance that MSY has varied in the past between 5 and 40% of the exploitable biomass of target species.

The computation of catch in the ecosystem model is done with "fishing intensity" (fishing mortality) coefficient. This coefficient F is computed for desired time step (e.g. month), using equilibrium biomass (B_e) and the acceptable catch guess (ACG) (or actual landings for a given year).

$$F = n\left(1 - \frac{ACG}{12B_e}\right)$$

$$Y_t = B_t e^{-G}$$

In the last formula the yield fluctuates with the fluctuating biomass. However, if a given yield is desired, the following formula must be used:

$$Y_t = B_t e^{-F B_t/B_e}$$

5. References

Larkin, P. A.

1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106 (1):1-11.

NOTITIA XIV

14. SENSITIVITY ANALYSES, VERIFICATION, AND VALIDATION

Sensitivity analyses

A simple sensitivity analyses of complex ecosystem simulations is not possible due to the great number of variables involved and the great expenses in running the model. Thus other approaches must be devised to study the sensitivity and accuracy of the model and its results. The first method is the verification of individual formulations (submodels) used in the simulation. This task is usually accomplished during the design of the model and during the preparation of the inputs.

The second "sensitivity analyses" of the simulation is conducted via a number of changes in input parameters in the process of updating the inputs. First change might involve the updating of marine mammals and birds and their food composition. The first input usually includes conservative estimates of marine mammals whereas the revision will include plausible amounts.

The third sensitivity test involves the updating of food composition of fish and the fourth sensitivity test concerns the change of fisheries. These latter are the main tests with the model for management purposes.

Verification and validation

Verification refers to the checking of logic and the correctness of individual models and formulas used in the simulation. The models and formulas are verified with available empirical data. Verification also

includes the testing of the simulation at large, using various impulses as input whereby the expected response of the ecosystem to the inputs must be at least qualitatively known.

It could be pointed out that the variations in results of deterministic simulations (models) depend also on accuracy and reliability of the input data, but to a much lesser degree than the "parameterized" models.

Validation of simulation refers to the comparison of principal results from simulation with direct observations in the field. One of the main validations of the simulation results is the comparison to good survey results. The latter must, however, be converted to total biomass, using catchability coefficients. The latter have, unfortunately, errors of the same magnitudes as the simulations themselves.

There are a number of indirect validation possibilities which vary from one area (region) of model application to another and are limited to one or a few species at a time. Some of the validations are described in recent NWAFC processed reports.