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A Numerical Simulation Model of the Population Dynamics of Walleye Pollock, *Theragra chalcogramma* (Pallas 1811), in a Simplified Ecosystem

Part I, Model Description

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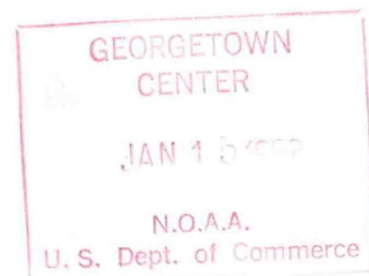
PART I, MODEL DESCRIPTION.

by

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ABSTRACT

This report is a description of an age-structured energetics and population model of walleye pollock, _Theragra chalcogramma_ (Pallas 1811), in a simplified Bering Sea ecosystem consisting of phytoplankton, copepods, and euphausiids. The objective of the model is to study the theoretical effects of linkages among energy flow, recruitment, mortality (particularly due to cannibalism), and fecundity on the population dynamics and potential fishery yields of walleye pollock.

The model pollock populations are driven by primary production in the form of phytoplankton. The model is principally defined using ordinary differential equations in an age-structured array approximating the integro-differential equation formulation for population dynamics. Equations, parameter values and initial conditions are given with their bibliographic sources. The model includes processes of diet selection, consumption rate, assimilation, respiration, starvation mortality, predatory mortality (due to cannibalism), reproduction, and fishing mortality. A subsequent report will describe the dynamics of the model pollock populations and other emergent properties.

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I.   INTRODUCTION

1.1.   The Problem

When managing or regulating a fishery resource, it is necessary to be able to predict what effects implementing various management decisions (for example, changing the fishing effort) will have on the resource and its surrounding ecosystem. The environment and biology of the fish largely determine their response to the implementation of management and regulatory decisions. Although different theories and hypotheses may have been proposed, the environment and biology of any given fish species are imperfectly understood. Mathematical simulation modeling is one useful tool for predicting the consequences of different management or regulatory decisions, assuming the validity of a given set of hypotheses or theories about the environment and biology of the exploited fish. It is also useful for contrasting the consequences of alternative hypotheses.

Mathematical simulation of animal populations has shown that many different recurring population levels can plausibly exist in a population (for example, see May and Oster 1976). In contrast, some of the most commonly used models of exploited fish populations, such as the Beverton and Holt (1957) model, and its extension, the Ricker

(1958) model, predict only one nontransient population level for a given set of parameters. In these models, mortality and fecundity are independent of energy flow and recruitment.

This study examines the problem of simulating and describing (within practical limitations) the possible population dynamics of walleye pollock, <u>Theragra chalcogramma</u> (Pallas 1811), that result from hypotheses linking energy flow, recruitment, mortality, and fecundity. This problem was approached by taking a theoretical mathematical model of an animal population (described in Bledsoe 1979), and modifying it to more closely represent walleye pollock and its biological environment, while implementing the model as a computer program using numerical methods. It was thought that this problem might provide insights into ways to improve fishery yields of walleye pollock, as well as give insight into the population dynamics of walleye pollock and similar fish and animal species.

1.2.   Problem Background

Walleye pollock, which is often referred to simply as "pollock" in this study, is in the family Gadidae and reaches a maximum fork length (FL) of about 90 cm. Pollock form perhaps one of the most important components

of the Bering Sea ecosystem, representing a large portion of the total biomass. For example, in a survey in the eastern Bering Sea from August to October 1975, pollock represented 40.3% of the total catch (per unit effort) of all fish and invertebrates (Pereyra et al. 1976: table IX-12). The yearly total organic production of pollock biomass is large because pollock consume large amounts of food and grow rapidly. Pollock is important both as a predator and prey species. The distribution of pollock is shown in Figure 1. In 1979, commercial trawl fisheries operating in the eastern Bering Sea harvested 913,881 metric tons (t) of pollock (Bakkala et al. 1980: table 1). In 1979, the dockside (exvessel) value of the United States domestic catch of walleye pollock was about $185 per t (Pileggi and Thompson 1980: 1). Assuming the entire 1979 eastern Bering Sea harvest of pollock had a similar dockside (exvessel) value, it was worth approximately $169 million. In the eastern Bering Sea, large pollock are cannibalistic, as shown in Figure 2. Pollock are described as semidemersal over the continental shelf of the eastern Bering Sea, tending to form schools near the bottom in the daytime, then dispersing up into the water column at night (Smith 1981). Pelagic populations of pollock are found over deep water in the central Bering Sea (Okada 1979).
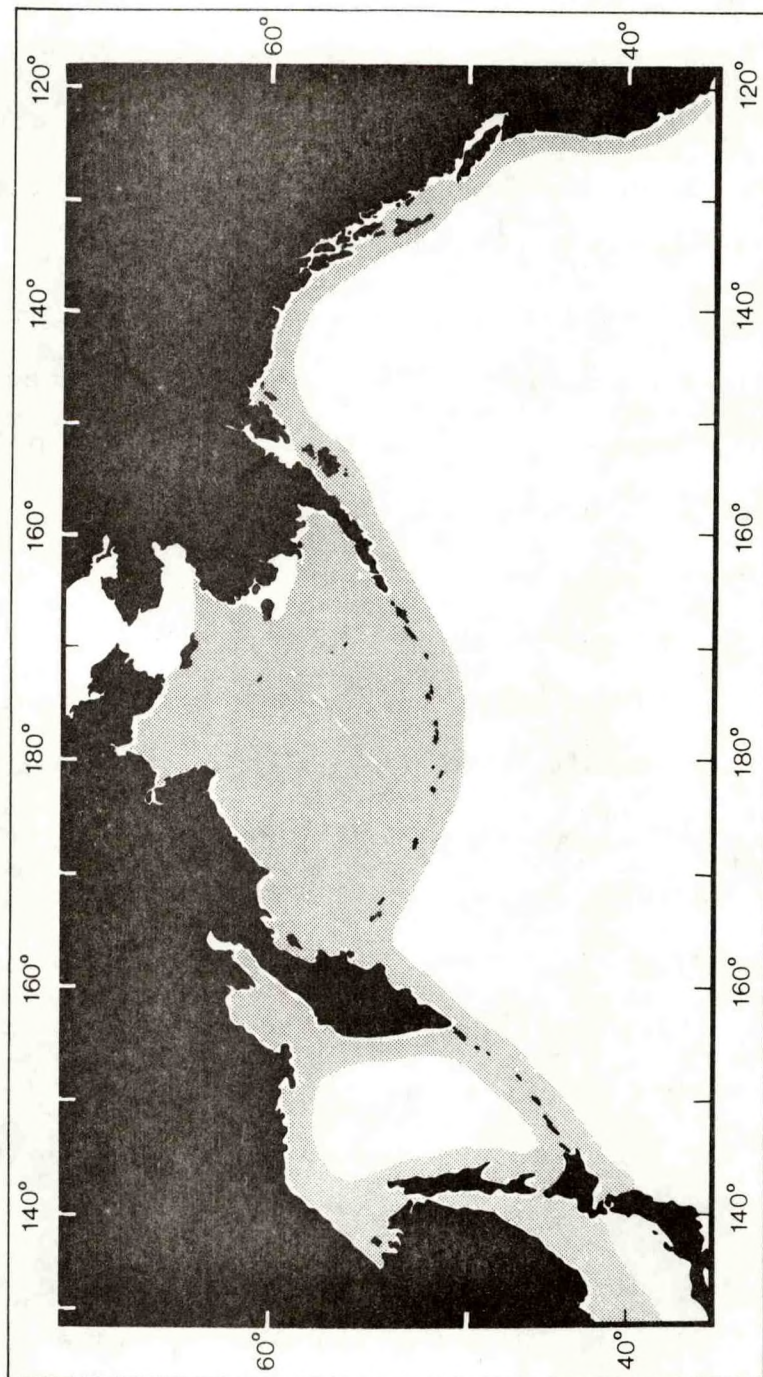
Figure 1. The distribution of walleye pollock, _Theragra chalcogramma_, in the
northern Pacific Ocean (shaded area). (Smith 1981).

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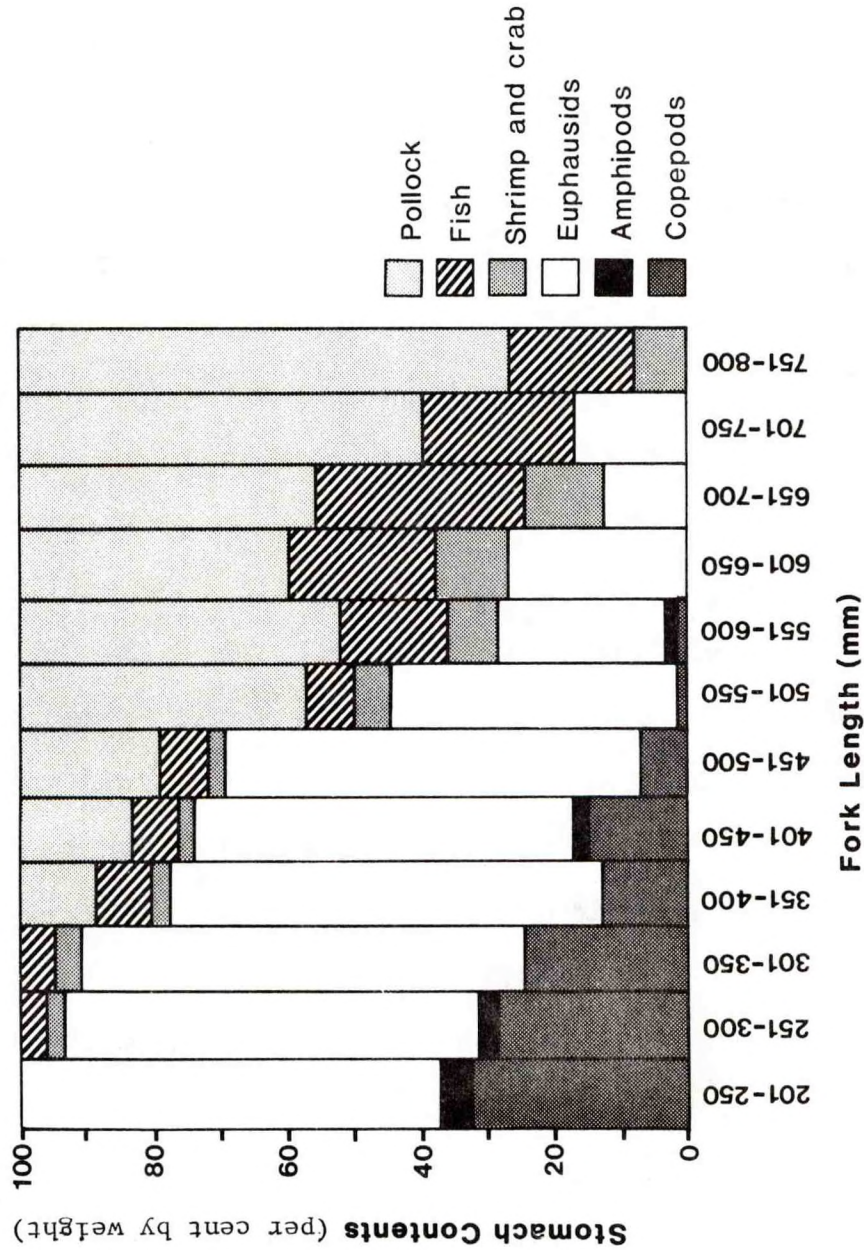
Figure 2. Changes in the prey selection of walleye pollock as a function of walleye pollock length in July-August 1970, in the eastern Bering Sea (after Smith 1981, and Takahashi and Yamaguchi 1972).

The Bering Sea is a large continental sea with an area of about 2,258,000 km^2 (Lisitsyn 1966: 1) with a broad continental shelf underlying 45% of its total area. From November through May, most of the sea over the shelf is covered by ice. Breakup of the sea ice begins in March or April, and continues through June (McRoy and Goering 1974). However, due to the influence of relatively warm (3-4° C) subarctic water, temperatures above freezing exist throughout the year in the southeastern part and along the central and eastern continental slope areas, where major concentrations of commercially important fish species occur (Favorite and Laevastu 1981). Overall, the total annual primary production of the Bering Sea is very high (McRoy and Goering 1975), however, secondary productivity is poorly known. Dominant species and the regional distribution of copepods and euphausiids in early to midsummer are shown in Motoda and Minoda (1974: figures 10.3 and 10.6). The yield from fisheries indicates high productivities at upper trophic levels, although this may also be a result of the concentration of fish production from a large area (i.e. the extended continental shelf area and the near surface [0-200 m] waters of the Aleutian Basin) over the shelf edge harvesting sites. Some important fisheries are for demersal fish, crab, shrimp, snails, Pacific salmon (Oncorhynchus spp.), Pacific

herring (<u>Clupea harengus pallasi</u>), northern fur seal (<u>Callorhinus ursinus</u>), and whales. Pollock form the bulk of the demersal fish catch. Other demersal fish caught include yellowfin sole (<u>Limanda aspera</u>), Pacific halibut (<u>Hippoglossus stenolepis</u>), other pleuronectids, Pacific cod (<u>Gadus macrocephalus</u>), Atka mackerel (<u>Pleurogrammus monopterygius</u>), sablefish (<u>Anoplopoma fimbria</u>), and Pacific ocean perch (<u>Sebastes alutus</u>).

The stocks of pollock in the eastern Bering Sea are heavily fished, and are consequently affected by fishery management and regulatory decisions.

1.3. Objective of the Study

The objective of this study was to determine the possible population dynamics of an exploited cannibalistic fish population as exemplified by an age-structured energetics and population model, POL. The model was developed to simulate the eastern Bering Sea pollock population, fishery, and surrounding ecosystem. By varying the parameters, initial conditions or equations used for POL, it is possible to explore the predicted consequences of different management or regulatory decisions or of alternative hypotheses incorporated into the model. The model was derived and extended from basic ideas set forth in Bledsoe (1979).

The results of the study will be reported in three parts:

1) Model description

2) Model fitting, validation, and initial experiments

3) Results of further model experiments

1.4.   Short Model Description

The model, POL, consists of equations describing a walleye pollock population with up to 20 age classes (cohorts), as well as a euphausiid population, a copepod population, and a phytoplankton population. The equations describing the euphausiids and copepods are pooled age models. The large ocean region described in the model is assumed to be homogeneous in space, so it is represented by a single point. The model is driven by an assumed carbon (phytoplankton) primary production rate, which varies according to the season of the year, but otherwise does not vary from year to year. The phytoplankton standing stock is eaten by the copepods. The euphausiids may eat either the phytoplankton or the copepods, and the pollock may eat phytoplankton, copepods, euphausiids, or cannibalize other pollock. The model is intended to apply to walleye pollock populations (such as in the eastern Bering Sea) where sources of food other than phytoplankton, copepods, euphausiids, and walleye pollock

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can be disregarded. It might be possible to model similar animal populations which have comparable food chains with little modification, but the model would have to be modified before populations which have other important sources of food could be simulated. Besides cannibalism, sources of pollock mortality in the model are other predators (not explicitly represented), fishing, and starvation. The dynamics of the various populations in the model are determined by a set of simultaneous, first-order, nonlinear, ordinary differential equations, which are solved by a variable time step Runge-Kutta Merson method of numerical integration (modified from a computer algorithm given in Christiansen 1970). The model is programmed in the FORTRAN IV computer language. A diagram of simulated populations and possible energy flows in the model is shown in Figure 3. Energy is either measured in grams of carbon (phytoplankton, copepods, euphausiids), or in grams of tissue wet weight (copepods, euphausiids, pollock).

The model is intended to provide insight into long term dynamic behavior (taking place over a time span of a year or more), which may result from comparatively short term behavior (taking place over a time span of a week or a month or more). Shorter term dynamic behavior, such as diel variation in feeding rates, is not modeled, but is
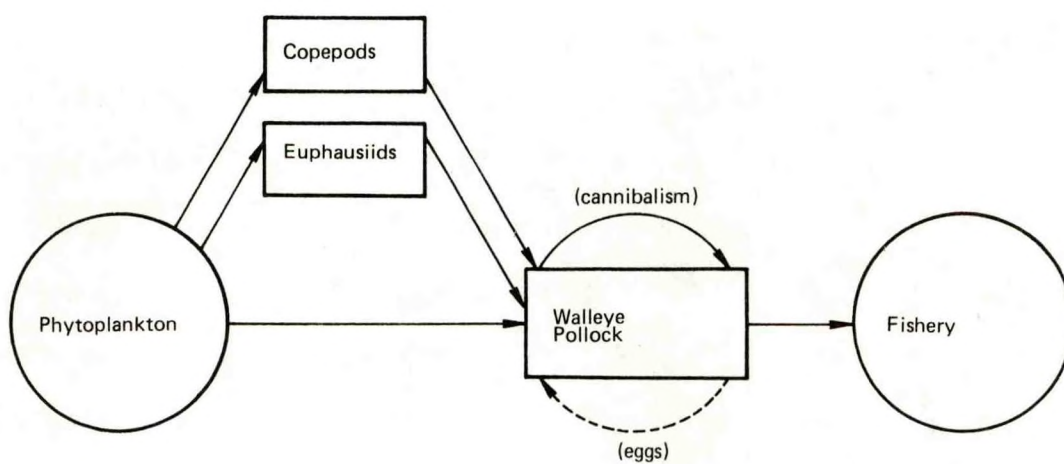
Figure 3. Simulated populations and possible energy flows in the model.

instead represented by average values for the relevant parameters. Nevertheless, for the present parameter set, the numerical integration subroutine may use a variable time step as short as 1/2048 of a year (about 4.3 hours) in order to achieve the desired numerical accuracy.

II.   LITERATURE REVIEW

(See also the references given in the section on parameter values and origins).

2.1.   Mathematical Simulation in Ecology

Many previous studies show the usefulness of mathematical simulation in ecological modeling.

Oster and Takahashi (1974) described the generalized partial differential equations which underlie many age-structured predator-prey models; they also described how long-term population fluctuations could occur in predator and prey populations due to differential effects on different age classes of short term fluctuations in forcing functions (i.e. driving functions).

May and Oster (1976) found that three different modes of nontransient dynamic behavior (stable equilibrium, periodic oscillations, or seemingly random and chaotic fluctuations) could occur in a hypothetical population described by a very simple deterministic stock-recruitment relationship.

Parrish (1975) constructed a dynamic simulation model which could be easily modified to model trophic webs of any size or form. He used it to study effects of age class structure, reproductive time lag, and population

regulation by starvation and fecundity control in trophic webs of two, three, and four levels.

Chang (1974) calculated yield per recruit isopleths for walleye pollock in the Bering Sea using a single species Ricker (1958) model with various values of natural and fishing mortality. However, the weight of fish at a given age was not a function of the amounts of food eaten, and he did not explore possible effects of cannibalism.

Andersen and Ursin (1977) constructed a multispecies model of the North Sea ecosystem using a numerically integrated set of simultaneous differential equations. Their results seemed to correspond to real population changes which could not be described using a single species Beverton and Holt (1957) model.

Laevastu and Favorite (1976b) used a numerical model of the eastern Bering Sea ecosystem with eight populations consisting of fur seals, sea lions, walleye pollock, Pacific herring (and similar fish), copepods, euphausiids, and two species of seabirds. The pollock population was subdivided into three length classes (<25 cm, 25-45 cm, >45 cm FL). The diets of the walleye pollock were determined using fixed food composition ratios independent of prey abundances. Their model also included a spatial grid, so that spatial or advection effects, such as geographic variability and migration, could also be

studied. Various transfer coefficients, with a time step of 1 week for advection functions and 1 month for trophodynamic subroutines, were used in order to predict changes in the populations over time. They obtained tentative results that the interaction of different age-specific growth rates and cannibalism in walleye pollock can cause long-term fluctuations in the eastern Bering Sea walleye pollock population with a period of about 12 years, and that these fluctuations are affected by the fishery. They also obtained the tentative result that the level of fishing intensity on walleye pollock which existed at the time their paper was written (which they considered would produce a yearly harvest of around 1.25 million t of walleye pollock) would result in higher average yearly catches of walleye pollock, and in larger standing stocks of walleye pollock and herring, than would result from fishing intensities reduced by 20% or 50%. The fishing intensity coefficients used were varied as a function of time and space in their model, but they did not give the values used. Laevastu and Favorite did not at that time, however, attempt to evaluate consequences of further increases in fishing intensities, such as whether sustainable increases in the average yearly catches of walleye pollock would result.

2.2.   Cannibalism

Many examples from the ecological literature also
indicate the possible importance of cannibalism in
influencing walleye pollock population dynamics.

Fox (1975) surveyed a wide variety of literature and
concluded cannibalism is not aberrant behavior, but is a
normal response in many animals to a variety of
environmental factors; in addition, it is an age-specific
process which can cause rapid changes in age distribution
and population size. He listed 48 herbivores and 89
predators (including 8 species of marine predators) as
being cannibalistic.

Dahlberg (1979) surveyed literature and listed a
number of marine fish species with high larval mortality
due to predation and cannibalism.

Eickwort (1973) found that only very small increases
in individual fitness were needed to give selective
advantage to larvae of the cannibalistic chrysomelid
beetle, Labidomera clivicollis. She suggested that
cannibalism most probably resulted in selective advantage
at points in the life cycle where other sources of
mortality were high, or nutritional benefits were great.

Takahashi and Yamaguchi (1972) found that in July and
August 1970, in the eastern Bering Sea, more than 40% of

the weight of the stomach contents of walleye pollock > 50 cm FL consisted of other walleye pollock.

Mito (1974) found that early juvenile and one year old walleye pollock were major food items of walleye pollock on the fishing ground in the southeastern Bering Sea in October and November 1972. He suggested that cannibalism was a larger source of mortality in walleye pollock than predation by other fish species.

Wespestad (1978) found an average of 51% of the volume of stomach contents of walleye pollock were other walleye pollock in February and March 1978, in the central Bering Sea.

Walleye pollock may be cannibalistic in other regions besides the Bering Sea. For example, Rogers et al. (1980) studied the seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island in the Gulf of Alaska. In their study they caught significant amounts of pollock only in the summer months and November 1978, in deep troughs of 70-100 m. In summer 1978, they found no evidence of predation by walleye pollock upon either walleye pollock or any other fish. At least 90% by weight of the diet consisted of shrimp. In contrast, in November 1978, they found that at least 39% by weight of the diet of walleye pollock consisted of other walleye pollock.

2.3.   References for Further Information on Pollock

Information on the biology of walleye pollock, their distribution and environment, and walleye pollock fisheries may be found in Pruter (1973), Chang (1974), Low (1974), Pereyra et al. (1976), Pruter (1976), Bakkala and Smith (1978), Low and Akada (1978), Bakkala et al. (1979), and Smith (1981).

III.   MODEL MECHANISMS AND POPULATIONS

Detailed tables defining the parameters and variables
used in the explanations of the model compartments and
mechanisms are given in Appendices A and B.   Tables
listing the values and sources of the reference set of
initial conditions and adjusted parameters are given in a
section on parameter values and origins.

3.1.   Classification, Nomenclature, and Units
                    of Model Variables

Model variables may be classified as exogenous and
endogenous variables.   In order to model a system, one
must have a theory (or set of hypotheses) about how the
system works.   The values of an exogenous model variable
are independent of the state of the system being modeled,
according to that theory.   In contrast, the values of
endogenous variables are at least in part determined by
the state of the system being modeled, according to that
theory.

Time is often an important exogenous model variable,
as was the case in POL. Other exogenous variables include
those determined by driving functions, which are (usually)
dynamic functions of time.   In POL, the gross primary
production of organic carbon by phytoplankton was a

driving function. In other ecological models, air temperature or frequency of storms might often be represented as driving functions.

Another important class of exogenous model variables are the parameters (constants, coefficients) of the system. These are not dynamic in character. Some examples in POL were spatial dimensions, the maximum possible feeding rate of euphausiids on copepods (P_{49}), and the wet weight of an average copepod (ZW_2). Indices, which can take on only integer values, are frequently important exogenous model variables.

Endogenous model variables may be classified as principal system variables (PSV's) and intermediate system variables (ISV's) (Bledsoe 1976: 35).

The PSV's include those variables in which the investigator is principally interested. The PSV's also include those variables which, together with the exogenous model variables, determine (describe) the state of the system at any point in time. However, a PSV is not necessarily a state variable, which in engineering terminology is a dependent variable in a differential equation. A PSV may be determined by some other means, although in POL most PSV's were defined by differential equations.

The PSV's in the model included the numbers (N_i) of individuals in each pollock cohort i, the average wet weight (W_i) and fork length (L_i) of individuals in each pollock cohort i, and the fractions of each pollock cohort i consisting of mature females (FCF_i) and males (FCM_i). Additional PSV's were total weight of phytoplankton organic carbon (PHY), total copepod biomass wet weight (COPE), total euphausiid biomass wet weight (EUPH), total number of surviving pollock eggs (E), and pollock fishery yield wet weight (YLD). All these PSV's may be necessary to completely describe the state of the system, though all might not be necessary at certain times or for certain parameter values. Most of these PSV's were calculated using differential equations. Exceptions were: 1) E (which was calculated algebraically but could have been equivalently calculated using a differential equation); and 2) each FCM_i and FCW_i, which were calculated algebraically from the corresponding L_i at the beginning of a breeding season.

For convenience certain variables may be defined as intermediate steps in the determination of PSV's. These variables are classified as intermediate system variables (ISV's). Some examples from POL are the mortality rate of phytoplankton due to copepod consumption (ZM_1), and the average instantaneous feeding rate of an individual

pollock in cohort i (RC_i). The distinction between a PSV and an ISV actually may be merely a matter of convention, since a variable that may be of great interest to one investigator might not be interesting to another. A possible example of this in POL was the biomass of each pollock cohort i (B_i).

Dummy or temporary variables are variables defined for convenience in writing equations or computer programming statements. They are usually temporary in a specific mathematical development, and may be repeated elsewhere with a different meaning. In the present study, the letters A through E, X, and variable names beginning with J or U were sometimes used as temporary variables, although B, D, and E were also used to refer to certain permanent variables. However, it is clear from the context when a temporary variable is intended.

It would have been convenient to use entirely single letter variable names in this study; however, the large number of variables used in POL precluded that possibility. Consequently, variable names generally consisted of one or more capitalized letters or numbers (for example, E, PHY, Q2), which may have been indexed with a subscript (for example, L_i). A variable with a subscript usually corresponded to an indexed array if it appeared in the FORTRAN computer program implementation of

the model [for example, P_{84}, L_i, and $D_{j+3,i}$ corresponded to P(84), L(I), and D(J+3,I) in the FORTRAN computer program]. Indices were capitalized in the computer program. Variables other than indices, which included one or more lower case letters, were not used in the computer program (for example, $\underline{Avail}_j$ and $\underline{tpm}_i$ did not appear in the computer program). Some variables, though not underlined in equations, were underlined in the text in order to avoid any possibility of confusion between a variable name and a word of text (for example, the variable $\underline{a}$ in the text was not underlined when it appeared in an equation). Derivatives of a given variable with respect to time were indicated by a superscripted prime (for example, PHY' and W_i' were the time derivatives of PHY and W_i).

Standard mathematical functions were given their standard names. Any special functions were given a name consisting of one or more capital letters or numbers; for example, FLTTOP, FOOD, PULSE, RCON1, RLNGTH, SEL, STEPR1, SUM, and WVB were special functions.

Time was measured in years in the model, unless noted otherwise. The variable TT was the simulated "present" time in the model (it also appeared as the dummy variable T). It was measured in years with respect to a time zero, which was assumed to occur at 0000 hours on Jan. 1 of some

year. The variable YT was the time of year expressed as a fraction of a year, so YT = TT modulo 1.

Weights and lengths were measured in grams (g) and centimeters (cm) in the model. In calculations involving density (biomass per unit volume), the region modeled was assumed to have an effective volume of 5 km^3 (see the section on assumptions about the environment and migrations).

3.2. Assumptions About the Environment and Migrations

No seasonal temperature variations were explicitly built into the model.

The region modeled was assumed to consist of 100 km^2 of ocean. In calculations involving density, the region was assumed to have an effective depth of 50 m (similar to Favorite et al. 1977: 216), which implies a volume of 5 km^3 of water. Since pollock seem to be migratory to some extent (Okada 1979; see also a review of the subject by Pereyra et al. 1976: 370-374), in order to simplify the model, it was assumed that migrations into and out of the area modeled were in equilibrium for each pollock cohort, and that the environment (including vulnerability of pollock to fishing) was homogeneous both inside and outside of the area modeled. Since actual fishing effort is not homogeneously distributed, it was also assumed that

all pollock within a given cohort were equally likely to migrate into or out of an area where they would be vulnerable to the fishery. These assumptions were mathematically equivalent to no migration. However, by setting parameters, the migration of cohort 1 pollock into the model area could be simulated. This is described in the section on pollock numbers (mortalities).

3.3.   Discrete Time Events

The model could be considered a hybrid between discrete time and continuous time models (Bledsoe 1976), in that certain events occurred periodically (cyclically) at certain fixed discrete instants of time in the model, but time was considered to be "continuous" in between the discrete time events. For a fuller discussion of the distinction between discrete (fixed time increment) and continuous (variable time increment) models, see Naylor et al. (1966: 126-136).

A list and further explanation of the possible discrete time events which could occur in the model is given in Appendix B.

3.4.   Phytoplankton

The gross primary production of carbon in the model over one simulated year's time is constant from year to year. It is equal to the constant

$$P_{27} + P_{28} + P_{29} + P_{30} + P_{31} \times [1 - P_{26} + P_{21}] \tag{1}$$

where P_{27} through P_{30} are parameters determining gross production at different time periods of the year, P_{31} is a constant underlying production rate, and P_{26} and P_{21} are the times of the year that winter begins and ends.

This gross primary production is the integral (over one year's time) of the gross carbon primary production rate, which is the underlying driving (forcing) function in the model. This rate at a given time of the year is graphed in Figure 4. It is described by the function

$$
\begin{aligned}
&\text{PULSE}(YT, P_{88}, P_{21}, P_{32}) \\
&+\text{PULSE}(YT, P_{36}, P_{23}, P_{33}) \\
&+\text{FLTTOP}(YT, P_{37}, P_{24}, P_{25}, P_{33}, P_{35}) \\
&+\text{PULSE}(YT, P_{38}, P_{25}, P_{35}) \\
&+P_{31}
\end{aligned}
\tag{2}
$$
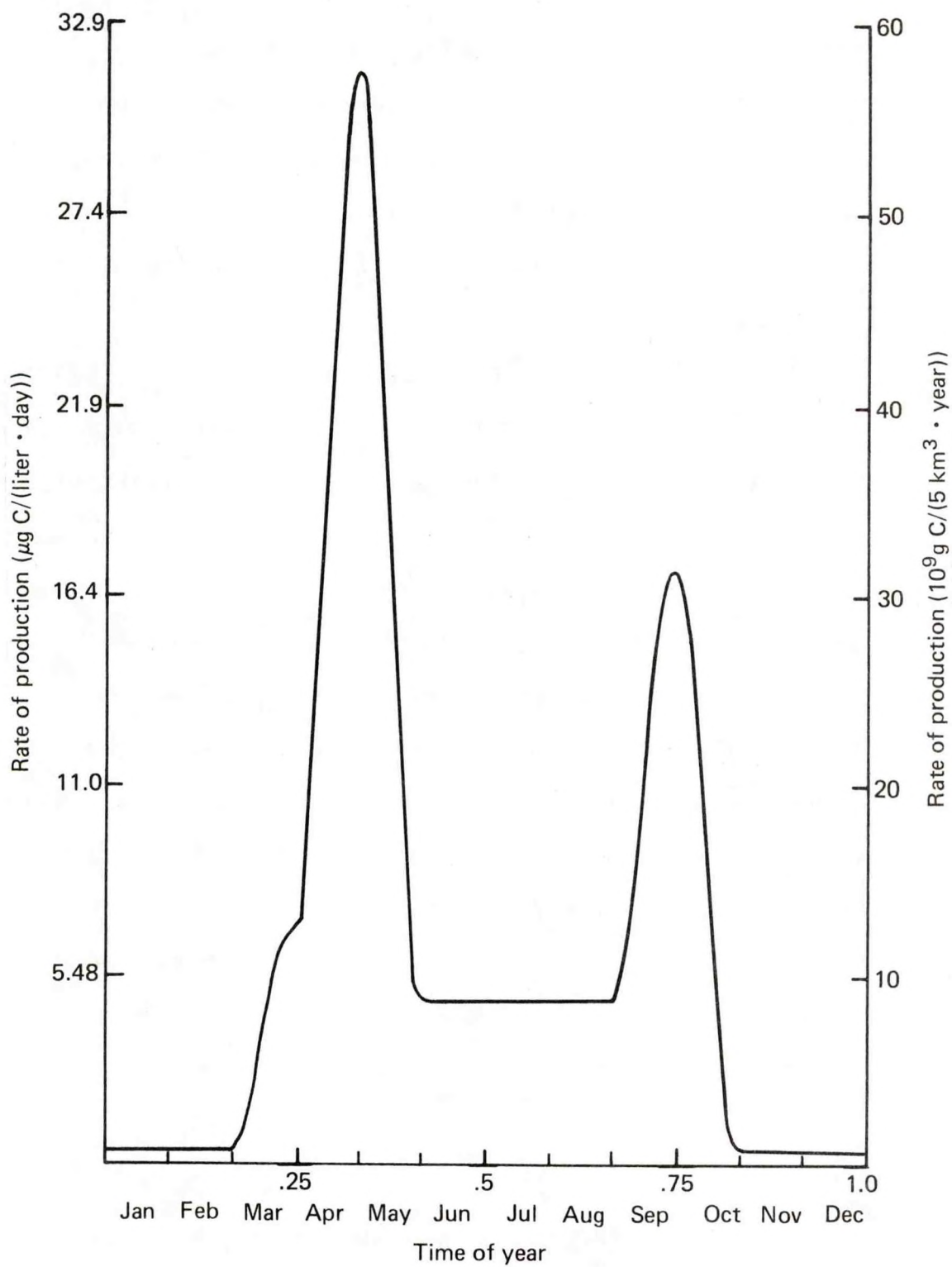
Figure 4. The instantaneous gross production rate of carbon
in the model at different times of a simulated year.

where YT is the time of the year; PULSE is a function generating a pulse (defined in Appendix D); FLTTOP generates a pulse with a flat top (defined in Appendix D); P_{88} and P_{36} to P_{38} determine the total gross productions generated by PULSE or FLTTOP; and the remaining parameters of PULSE and FLTTOP give the time boundaries of the two functions.

The parameters of the functions PULSE and FLTTOP are used to control the amount of primary production in the model during any given time period. The amounts of gross production which will result can be calculated without running the model by using the analytic expressions for the integrals of PULSE and FLTTOP given in Appendix D.

As an approximation of the actual gross primary product of carbon, the relevant parameters of the present parameter set were calculated so the gross primary production of carbon during a given season of the year in the model was equal to the values given in McRoy and Goering (1975: table 5) for the total Bering Sea primary production (excluding production attributed to rivers and lagoons), assuming that production was evenly distributed throughout the area of the total sea, that the total sea has an area of 2.281×10^6 km^2 (ibid., table 1, citing Lisitsyn 1966), and that the volume modeled in POL (5 km^3) corresponded to a surface area of 100 km^2.

The differential equation describing the dynamics of the phytoplankton is

$$V_1' = PHY' \qquad (3)$$

$$= PULSE(YT, P_{88}, P_{21}, P_{32})$$
$$+ PULSE(YT, P_{36}, P_{23}, P_{33})$$
$$+ FLTTOP(YT, P_{37}, P_{24}, P_{25}, P_{33}, P_{35})$$
$$+ PULSE(YT, P_{38}, P_{25}, P_{35})$$
$$+ P_{31}$$
$$- P_{39} \times PHY - ZM_1 - ZM_2 - ZM_3$$

where PHY is the standing stock of phytoplankton $(gC/5km^3)$, P_{39} is a respiration and other loss rate, and ZM_1 to ZM_3 are mortality rates due to consumption by copepods, euphausiids, and pollock, respectively.

At the end of each time step in the numerical integration subroutine, PHY is tested, and if PHY<NMIN, PHY is set to 0, where NMIN is a minumum allowed population value.

3.5.   Zooplankton

There are two size classes of zooplankton in the model. One size class is intended to imitate copepods, the other size class is intended to imitate euphausiids. Only phytoplankton, copepods, euphausiids, and pollock

were included in the model as a first approximation to the actual ecosystem, because copepods, euphausiids, and pollock are the major food items of pollock in the southeastern Bering Sea.

3.5.1. Copepods

The total copepod biomass, COPE, is modeled. Every individual copepod is assumed to have the same length, $ZLNG_2$, and wet weight, ZW_2.

It was assumed in the model that if copepods are feeding, they feed continuously. Their feeding is represented by an Ivlev feeding function which is offset from the origin, so the copepods will stop feeding when their food supply reaches a low level, which is equivalent to a prey refuge. This feeding curve is described by an Ivlev feeding function

$$ZM_1 = \begin{cases} 0., \text{ if } PHY \times P_{42} \leq P_{41} \\ \\ P_{43} \times COPEC \times [1-e^{P_{44} \times (P_{41}-PHY \times P_{42})}], \\ \text{ if } PHY \times P_{42} > P_{41} \end{cases} \tag{4}$$

where COPEC is the weight of organic carbon contained in the total copepod biomass, and P_{41} through P_{44} are parameters.

The dynamics of the copepod biomass are described by the differential equation

$$V_2' = COPE' \tag{5}$$
$$= P_{46}/P_{45} \times ZM_1 - P_{47} \times COPE - ZM_4/P_{45} - ZM_5$$

where COPE is the wet weight of the copepod biomass; ZM_4 and ZM_5 are copepod mortality rates due to consumption by euphausiids and pollock, respectively; P_{45} and P_{46} are parameters; and P_{47} is a respiration and other loss rate.

At the end of each time step in the numerical integration subroutine, COPE is tested, and if COPE<NMIN, COPE is set to 0.

3.5.2. Euphausiids

The total euphausiid biomass, EUPH, is modeled, but all individual euphausiids are assumed to have the same length, $ZLNG_3$, and wet weight ZW_3.

The euphausiids may eat either phytoplankton or copepods. The euphausiids are considered to practice prey switching; they never eat phytoplankton and copepods simultaneously, but instead eat only that prey which is

most available to them. Many euphausiid species perform daily vertical migrations (Sameoto 1976: 2575; and Parsons et al. 1967: 11), which may cause their feeding rate to vary within the day. Nonetheless, as a simplification, it was assumed in the model that if euphausiids are feeding, they feed continuously with any diel periodicity being "averaged out." If diel periodicity of feeding rates were included in the model, the times steps used in numerical integration would often have to be much shorter than those presently used, which would greatly increase the computer resources needed for a given simulation run. Euphausiid feeding rates are calculated separately in the model for feeding on phytoplankton and for feeding on copepods. Both feeding curves are calculated using a rectilinear function named FOOD.

The feeding rates are described by the following expressions.

Phytoplankton:

$$ZM_2 = \begin{cases} 0 \text{ if } P_{54} \times PHY \leq P_{53} \\ \\ EUPHC \times FOOD(P_{54} \times PHY, P_{51}, P_{52}, P_{53}) \\ \quad \text{if } P_{54} \times PHY > P_{53} \end{cases} \tag{6}$$

where EUPHC is the weight of organic carbon contained in the total euphausiid biomass, FOOD is a rectilinear feeding function (defined in Appendix D), and P_{51} to P_{54} are parameters.

Copepods:

$$ZM_4 = \begin{cases} 0., & \text{if } P_{55}\times COPEC \leq P_{69} \\ \\ EUPHC\times FOOD(P_{55}\times COPEC, P_{49}, P_{50}, P_{69}) \\ \quad \text{if } P_{55}\times COPEC > P_{69} \end{cases} \qquad (7)$$

where P_{49}, P_{50}, P_{55}, and P_{69} are parameters.

To represent prey switching, if $ZM_2 > ZM_4$, then ZM_4 is set to zero, so no copepods are eaten by the euphausiids. Otherwise, ZM_2 is set to zero, in which case no phytoplankton is eaten by the euphausiids.

The dynamics of the euphausiid biomass are described by the differential equation

$$V_3' = EUPH' \qquad (8)$$
$$= P_{56}\times[ZM_2 + ZM_4]/P_{48} - P_{57}\times EUPH - ZM_6,$$

where either ZM_2 or ZM_4 equals 0, and where EUPH is the wet weight of the euphausiid biomass; P_{48} and P_{56} are parameters; P_{57} is a respiration and other loss rate; and ZM_6 is a euphausiid mortality rate due to consumption by pollock. At the end of each time step in the numerical integration subroutine, EUPH is tested, and if EUPH<NMIN, EUPH is set to 0.

3.6.   Pollock

Pollock are the most complex and detailed component of the model. Numbers, weights and lengths for up to 20 age classes (cohorts) of pollock are calculated by integrating differential equations describing these quantities. Other quantities affecting or describing the simulated pollock population are calculated by other means.

3.6.1. Pollock Cohorts

For the purposes of this study, a pollock cohort was defined to be all the pollock of a given age. In addition to the pollock eggs, up to COMAX cohorts can exist in the model at a given time. To simplify the model, the pollock cohorts were assumed to be equally spaced in time, with the difference in age between any two consecutive pollock

cohorts being equal to the parameter DTAU, which for the present parameter set equals one year.

Cohorts are updated by setting N_1 equal to E, setting E equal to 0, moving the former cohort 1 into cohort 2, moving the former cohort 2 into cohort 3, and so forth for each cohort. If COMAX cohorts exist when the cohorts are to be updated, the last cohort ceases to exist the instant the cohorts are updated. For the present parameter set, the cohort update occurs on May 13 (discrete event identifier 4).

3.6.2. Pollock Numbers (Mortalities)

The population size in numbers of individuals, N_i, in pollock cohort i is determined by integrating the differential equation

$$N_i' = -[M_i+MT_i+SM_i+UFISH_i+UPRED_i] \times N_i \qquad (9)$$

where N_i is the number of pollock in cohort i, and M_i, MT_i, SM_i, $UFISH_i$, and $UPRED_i$ are "other", cannibalism, condition dependent, fishing, and weight dependent mortality terms, respectively, which are further explained in subsequent sections. If the logical variable PLENTY is

false, N_1' is set to 0, which may be used to prevent the complete extinction of pollock in the model as follows.

At the end of each time step in the numerical integration subroutine, each N_i is tested, and if $N_i < NMIN$, N_i is set to equal 0, except N_1 is set to P_{74}. If N_1 is set to P_{74}, the logical variable PLENTY is set to false. If P_{74} is large enough, this makes it impossible for pollock to become extinct in the model, because N_1' is subsequently set to 0 and W_1 is not allowed to decrease below a certain limit (see the section on unconstrained pollock weights). These actions continue until the next cohort update, when PLENTY is reset to true. To prevent pollock extinction, P_{74} must be larger than NMIN; how much larger is a function of the pollock mortality rates in the model. The use of P_{74} can be considered analogous to the immigration of cohort 1 pollock into the area modeled after their extinction within that area.

3.6.2.1. Other Mortality--M_i is a constant instantaneous mortality term, representing mortality not described by other terms of the differential equation for N_i'. For example, M_i can be used to represent deaths due to disease or senility.

3.6.2.2. Cannibalism Mortality--MT_i is the instantaneous mortality rate on cohort i due to being cannibalized. How

it is calculated is more fully described in the section on pollock feeding.

3.6.2.3.   Condition Dependent Mortality--SM represents condition dependent instantaneous mortality. It is due to poor pollock condition, which may result in the model due to lack of food (starvation) or due to loss of weight while breeding.

SM is calculated using the following formulas.

For cohort 1:

$$
SM_i = \begin{cases} 0. & \text{if } CN_i \geq P_{83} \\ \\ P_{82} \times [P_{83} - CN_i]^{P_{81}} \\ \quad \text{if } CN_i < P_{83} \end{cases} \tag{10}
$$

where CN_i is a condition index of cohort i, and P_{81} to P_{83} are parameters.

For cohort 2 and over:

$$
SM_i = \begin{cases} 0. & \text{if } CN_i \geq P_{73} \qquad\qquad (11) \\[2em] P_{72} \times [P_{73} - CN_i]^{P_{71}} \\ \quad \text{if } CN_i < P_{73} \end{cases}
$$

where P_{71} to P_{73} are parameters.

These formulas for SM use the hazard function derived from the Weibull probability distribution. The Weibull distribution is often used in reliability engineering to model the probability of failure of materials under a given amount of stress (Bury 1975: sections 16.6,16.12). Using graphical analysis, it was found that the functional form of the Weibull distribution also seemed to fit the mortality data collected by Ivlev (1961: tables 79-80) for the freshwater fish tench (Tinca tinca), pike (Esox lucius), and sheatfish (Silurus glanis). Ivlev thought that predatory fish appeared to be the most resistant to starvation (ibid., page 265). Because pollock are predatory, the data for the species tench, pike, and sheatfish were used, because those species were the most resistant to starvation among those tested by Ivlev. Before fitting the Weibull distribution to the data,

mortalities were censored which occurred before what Ivlev thought was the onset of starvation. The fraction of the weight lost from the original weight was used as the measure of stress for fitting the Weibull function. However, in the model the stress on pollock was measured by using an average condition index, CN, defined by the equation

$$CN_i = W_i / WL_i \tag{12}$$

where W_i is the actual average individual wet weight of pollock in cohort i, and WL_i is the expected (or "normal") weight for a pollock in cohort i.

WL_i is calculated using a length-weight relationship, with

$$WL_i = \begin{cases} P_{80} \times L_i^{P_{63}} & , \text{ if } L_i \leq P_4 \\ \\ P_{70} \times L_i^{3} & , \text{ if } L_i \geq P_4 \end{cases} \tag{13}$$

where L_i is the average fork length of a pollock in cohort i; P_{63}, P_{70}, and P_{80} are parameters; and P_4 is the length at which the two different length-weight relationships

give the same expected weight; that is,

$$P_4 = [P_{80}/P_{70}]^{1/(3-P_{63})}. \tag{14}$$

Consequently, the resulting relationship determining WL_i is a continuous function of L_i.

3.6.2.4. <u>Fishing Mortality</u>--$UFISH_i$ is the instantaneous mortality rate due to fishing. $UFISH_i$ is more fully described in the section on yield of the pollock fishery.

3.6.2.5. <u>Weight Dependent Mortality</u>--$UPRED_i$ is a weight dependent instantaneous mortality term intended to represent the increased risk associated with being a small pollock. It can be attributed to the increased predation and other hazards presumably encountered by a small pollock. A simple representation for UPRED was decided upon, using the equation

$$UPRED_i = P_{97}/[W_i + P_{98}] \tag{15}$$

where P_{97} and P_{98} are parameters.

3.6.3. Optional Constrained Pollock Growth

Pollock growth in length and weight may optionally be constrained to follow certain equations closely related to von Bertalanffy and allometric growth equations. For the equations determining unconstrained growth in length and weight, see the sections on unconstrained pollock lengths and weights.

In order to simplify the model, both males and females of a given age class were assumed to have the same length, despite indications that females tend to reach maximum lengths about 5% to 13% longer than males (Pereyra et al. 1976: 237; Bakkala and Smith 1978: 90). For any pollock cohort i such that $i \leq NVON$, where NVON is an integer parameter, the length and weight of individuals in the cohort are determined by the differential equations

$$L_i' = \begin{cases} D9, & \text{if } L_i < P_{77} \\ \\ KAYx[D7-L_i], & \text{if } L_i \geq P_{77} \end{cases} \qquad (16)$$

$$W_i' = \begin{cases} D6, & \text{if } L_i < P_{77} \\ \\ L_i' x W_i / L_i x D2, & \text{if } L_i \geq P_{77} \end{cases} \qquad (17)$$

where D2, D6, D7, D9, KAY, and P_{77} are parameters.

These are also differential equations for the algebraically determined functions RLNGTH and WVB, which are described in Appendix D. If the length $[L_i]$ of an individual in cohort i is less than P_{77}, then its length and weight will implicitly be exact linear functions of its age. If, however, $L_i \geq P_{77}$, then its length will implicitly be a function of its age as given by the von Bertalanffy growth equation (Ricker 1975: section 9.6.2.):

$$L_i = D7 x [1 - e^{KAY x [D4 - age_i]}] \qquad (18)$$

where D4 is a parameter.

Its weight also will implicitly be a function of its age as a result of the implied length-weight relationship

$$W_i = D8 \times [L_i]^{D2} \tag{19}$$

where D8 is a parameter.

Under these constraints, the simulated weight and length of individual pollock are completely independent of their food supply. These constraints are optional, however, because when starting the simulation the parameter NVON can be set to any integer, and if NVON≤0, no cohort will be constrained to grow according to the above equations.

3.6.4. Unconstrained Pollock Lengths

As was also the case for constrained pollock growth, in order to simplify the model, both males and females of a given age class were assumed to have the same length, despite indications that females tend to reach maximum lengths about 5% to 13% longer than males.

For any pollock cohort i for which i>NVON, the average length, L_i, of an individual pollock in the cohort is determined by integrating a differential equation. It is assumed that a pollock never shrinks in length, so that the length derivative, L_i', is always greater than or equal to 0.

During the time period that cohort 1 pollock cannot eat (they do not eat for a certain amount of time after hatching), the differential equation for their length is given by

$$L_1' = P_{91} \tag{20}$$

where P_{91} is a parameter.

If the cohort 1 pollock may eat (that is, if the relative maximum feeding rate $EATER_1 > 0$), then

$$L_1' = P_{92} \times MAX(0 \ , \ MIN[1 \ , \ [CN_1 - RCON1(YT)]/P_{93}]) \tag{21}$$

where RCON1 is a piecewise linear function of the time of year (defined in Appendix D), and P_{92} and P_{93} are parameters.

This equation indicates that cohort 1 pollock do not grow in length if their condition index [CN_1] falls below a required condition determined by a function of the time of year, RCON1(YT), which is described in Appendix D. If their condition index is greater than this critical value, their growth rate is a linearly increasing function of their condition index, unless their growth rate reaches a maximum value [P_{92}].

The function RCON1(YT) is an expression of the hypothesis that cohort 1 pollock will place a different emphasis at different times of the year on growth in length versus storing energy for later use. Possible mechanisms for this might be a sensitivity to temperature changes at the onset of fall, or alternatively, a biological clock. In effect, it is possible to use RCON1 to express the hypothesis that the cohort 1 pollock store energy in the fall in order to survive through the winter.

For cohort 2 and older pollock, the differential equation determining the growth in length (FL) of an individual pollock is

$$
L_i' = \begin{cases}
P_{99} \times \text{MAX}(0 \ , \ \text{MIN}[1 \ , \ [CN_i - P_{90}]/P_{100}]), & (22) \\
\quad \text{if } L_i \le P_{68} \\
\\
P_{99} \times \text{MAX}(0 \ , \ \text{MIN}(1 \ , \ W_i/[P_{104} \times L_i^{P_{105}}] - P_{106})), \\
\quad \text{if } L_i > P_{68}
\end{cases}
$$

where P_{68} is the length at which the two different above branches give the same value for L_i'; and P_{90}, P_{99}, P_{100}, and P_{104} to P_{106} are parameters.

This equation is an expression of the hypothesis that a pollock does not grow in length if its condition index is below a certain critical value, but that if the condition index is greater than the critical value, the growth rate $[L_i']$ is a linearly increasing function of the condition index until the growth rate reaches a certain maximum value $[P_{99}]$.

For pollock less than P_{68} in length, the condition index used is the usual condition index, CN, used elsewhere in the model. For pollock greater than P_{68} in length, a special condition index used nowhere else in the model is calculated, given by

$$
W_i/[P_{104} \times L_i^{P_{105}}] - P_{106}. \tag{23}
$$

This special condition index makes it possible to express the hypothesis that the longer pollock, compared to the shorter pollock, put a lessened emphasis on growth in length and a greater emphasis on storing up energy for such possible purposes as greater fecundity and improved survival while laying eggs.

3.6.5. Unconstrained Pollock Weights

For a discussion of constrained growth in weight, see the section on optional constrained pollock growth.

For any pollock cohort i for which i>NVON, the average weight, W_i, of an individual pollock in the cohort is calculated by integrating the differential equation

$$W_i' = MIN[P_3, P_{117} \times W_i^{P_{118}}] \times [RC_i - P_1 \times W_i^{P_2}] \tag{24}$$

where RC_i is the average instantaneous feeding rate of individual pollock in cohort i, and P_1, P_2, P_3, P_{117}, and P_{118} are parameters.

If the logical variable PLENTY is false, if $CN_1 < P_{75}$, and if $W_1' < 0$, then W_1' is set to 0. This may be used to prevent the complete extinction of the first cohort of pollock in the model, because it prevents their weights from going below a certain lower limit.

The term $MIN[P_3, P_{117} x W_i^{P_{118}}]$ is used to generate an upper limit, P_3, to pollock food conversion efficiencies. Other than this upper limit, the equation for W_i' is based on the findings of Jones and Hislop (1978) concerning the growth of North Sea cod (Gadus morhua), haddock (Melanogrammus aeglefinus), saithe (Pollachius virens), and whiting (Merlangius merlangus). Jones and Hislop calculated conversion efficiencies using data from fish of 5-900 g. Their conversion efficiency formula for fish in this weight range cannot be extrapolated without modification to larval stages. If this formula is used for larval pollock, which start out weighing approximately 0.1 mg formalin wet weight (Haryu 1980), the formula indicates that these small fish would have a food conversion efficiency greater than 1.

3.6.6. Pollock Feeding

The actual feeding rate of an individual pollock at a given instant in time in the model is calculated as a complicated function of actual prey density (biomass per volume), prey availability or vulnerability, size selectivity (certain sizes of prey may be more preferred by the pollock), the density of different categories of

food as perceived by the pollock, pollock prey switching, the total density of all food items as perceived by the pollock, and the consumption rates of the pollock as a function of perceived food densities and the search rate of the pollock.

3.6.6.1.   Pollock Food Item Categories--The different possible food items (or food item categories) for pollock in the model are phytoplankton, copepods, euphausiids, and the various cohorts of pollock.   This represents a simplification of the actual variety of foods of pollock, but it seems reasonable from the following studies.

Takahashi and Yamaguchi (1972) in July and August 1970, in the eastern Bering Sea, found that copepods, euphausiids, and pollock accounted for more than 87% of the stomach contents (by weight) of all size classes of pollock from 20.1 to 55.0 cm FL, and more than 61% of the stomach contents (by weight) of all size classes of pollock from 55.1 to 80.0 cm FL.

Mito (1974) in October and November 1972, in the southeastern Bering Sea, found that the euphausiid, Thysanoessa inermis, and juvenile pollock were the most important food items for pollock greater than 19 cm FL.

Clarke (1978: table 1) in April-June 1977, in the southeastern Bering Sea, found that 97% (by count) of the

food items in the stomachs of larval pollock (0.48 - 1.77 cm standard length) were copepods or euphausiids.

3.6.6.2. <u>Perceived</u> <u>Food</u> <u>Densities</u>--A generalized formula for the food density of food item category j as perceived by pollock cohort i (before allowing for prey switching) is given by the formula

$$D_{j,i} = SEL(WL_i, Weight_j, L_i) \times Avail_j \times Biomass_j \qquad (25)$$

where $D_{j,i}$ is the perceived food density ($D_{j,i}$ is further modified by prey switching, as described in the section on pollock prey switching); SEL is a food size selection function (more fully described in Appendix D); and the variable $\underline{Avail}_j$ refers to the relative availability or vulnerability of food item category j to the pollock.

A constant Q2 is used to express the assumption that a pollock will not eat any prey item which is longer than Q2 of its own length. Q2 is not used for cohort 1 (the reasons for this are discussed in Appendix D in the section describing the food size selection function SEL), but it is used for the other cohorts. For these other cohorts, if $Length_j > Q2xL_i$, where $Length_j$ is the length of an individual in food item category j, the perceived food density of food item category j is set to 0.

Some examples of the actual use of this generalized formula are given for

Phytoplankton:

$$D_{1,i} = SEL(WL_i, ZW_1, L_i) \times P_{60} \times PHY \qquad (26)$$

where P_{60} functions both as a constant indicating the availability of phytoplankton to pollock, and also as a conversion factor for converting PHY (measured in grams carbon) to grams wet weight, and ZW_1 is the wet weight of individual phytoplankton.

Copepods:

$$D_{2,i} = SEL(WL_i, ZW_2, L_i) \times 1 \times COPE \qquad (27)$$

where the relative availability of the copepods to pollock is implicitly assumed to be 1, and ZW_2 is the wet weight of individual copepods.

Euphausiids:

$$D_{3,i} = SEL(WL_i, ZW_3, L_i) \times 1 \times EUPH \tag{28}$$

where the relative availability of the euphausiids to pollock is implicitly assumed to be 1, and ZW_3 is the wet weight of individual euphausiids.

A cannibalized pollock cohort (cohort j):

$$D_{j+3,i} = \begin{cases} 0, \text{ if } L_j > Q2 \times L_i, \text{ or } L_j \leq P_{65}, \text{ or } B_j \leq 0 \tag{29} \\ \\ SEL(WL_i, W_j, L_i) \times MIN[P_5, (L_j - P_{65}) \times P_{66}] \times B_j, \\ \quad otherwise; \end{cases}$$

where B_j is the wet weight of the total biomass of pollock cohort j, and Q2, P_5, P_{65}, and P_{66} are parameters.

The reasons for the use of the term

$$MIN[P_5, (L_j - P_{65}) \times P_{66}] \tag{30}$$

are more fully described in the section on vulnerability to being cannibalized.

3.6.6.3.   Vulnerability to Being Cannibalized--The function $MIN[P_5,(L_j-P_{65})xP_{66}]$ is used in calculating the perceived density of the cannibalized pollock cohorts (see the section on perceived food densities for further details).   It represents vulnerability to being cannibalized as a rectilinear increasing function of length, with a final maximum vulnerability. It is one way of expressing the fact that when pollock are still short in length, they apparently stay closer to the sea surface, but as they grow longer, they tend to live at deeper depths (Pereyra et al. 1976: 372). So, as long as they stay close to the surface, they are presumably not vulnerable to cannibalization by older pollock living at deeper depths, but as they grow older and move deeper, they presumably become more vulnerable to cannibalization. For the present parameter set, the smaller pollock are fully available as a food source of older pollock by the time the smaller pollock reach 3.5 cm total length. [see P_{66}].

3.6.6.4. Pollock Prey Switching--No prey switching occurs if each prey item category consists of more than a certain critical fraction of the total food perceived by cohort i, but if a prey item category falls below that level, prey switching occurs. Pollock prey switching is performed for a given cohort i as follows:

After the perceived food densities [the $D_{j,i}$] for cohort i initially have been calculated, the summation over j of $D_{j,i}$ is calculated and stored in the temporary variable UFF. Then each $D_{j,i}$ is tested, and may be changed as follows:

$$D_{j,i} = \begin{cases} D_{j,i}, \text{ if } D_{j,i} \geq P_{76} \text{ x UFF}^* & (31) \\ \\ 0, \text{ if } D_{j,i} \leq P_{67} \text{ x UFF} \\ \\ D_{j,i} \text{ x } [D_{j,i} - P_{67} \text{ x UFF}]/[P_{76} \text{ x UFF} - P_{67} \text{ x UFF}] \\ \text{ if } P_{67} \text{ x UFF} < D_{j,i} < P_{76} \text{ x UFF} \end{cases}$$

where P_{67} and P_{76} are parameters. These prey switching calculations are not iterative; they are only done once for each pollock cohort each time derivatives are calculated.

3.6.6.5. Pollock Feeding Rates--After being modified by prey switching, the perceived food densities [the $D_{j,i}$] for a given cohort i are again summed over j and the sum is stored in FD_i, which is the total density of food perceived by cohort i to be available. Then the average instantaneous feeding rate [RC_i] of an individual pollock

---

* Note $D_{j,i}$ does not change in value in this case.

in cohort i is calculated using the following general
formula:

$$RC_i = FOOD(FD_i, FDU_i, cmax, cmin) \times EATER_i \times L_i^{P_{119}} \qquad (32)$$

where P_{119} is a parameter, $EATER_i$ is a relative maximum
average feeding rate (described below and in the section
on pollock breeding behavior), and

$$FDU_i = \begin{cases} P_7 & \text{for cohort 1} \qquad (33) \\ P_{17} & \text{for cohort 2 and over, if } L_i < P_{111} \\ P_{114} & \text{for cohort 2 and over, if } L_i \geq P_{111} \end{cases}$$

where the array FDU is set when a simulation run is begun,
and at each cohort update time thereafter.

Also,

$$cmax = \begin{cases} P_8 \times W_i^{P_{101}} & \text{for cohort 1} \qquad (34) \\ \\ P_{18} \times W_i^{P_{102}} & \text{for cohort 2 and over} \end{cases}$$

and

$$
cmin = \begin{cases} P_9 x W_i{}^{P_{101}} & \text{for cohort 1} \\ \\ P_{19} x W_i{}^{P_{102}} & \text{for cohort 2 and over} \end{cases} \tag{35}
$$

The quantities cmax and cmin are the upper and lower critical points, respectively, of the rectilinear function named FOOD. The quantities cmax and cmin have been made into functions of weight in order to model the hypothesis that critical points (which determine food densities at which food consumption rates are reduced due to food scarcity) are lower for larger fish than for smaller fish, all other factors (such as prey differences due to size selectivity) being equal. This might result from the fact that as fish grow larger, they seem to be capable of higher sustained swimming speeds [for an example of this in the case of North Sea cod (Gadus morhua), see Jones (1978); for the case of rainbow trout (Salmo gairdneri), see Fry and Cox (1970)]. As a result, large fish may be capable of searching a larger volume of water in a given amount of time than smaller fish--and thus find more food than the smaller fish, all other factors being equal.

Pollock larvae are known to not eat for a certain period of time after hatching while their mouth, anus, and other organs develop, and their yolk sac is absorbed

(Hamai et al. 1971, 1974). During this time period, $EATER_1$ equals 0. When they begin eating in the model, $EATER_1$ is set to P_{61}. The calculation of $EATER_i$ for $i \geq 2$ or for cohorts which may breed is more fully described in the section on pollock breeding behavior.

3.6.6.6. Resulting Prey Mortalities--The mortality rate on prey item j resulting from the feeding of pollock cohort i is calculated using the general formula

$$preym_{i,j} = [\text{total food consumption rate of the entire pollock cohort i}] \times [\text{fraction of total food perceived by cohort i to consist of item j}]. \tag{36}$$

Then for a given prey item j, the total mortality rate [tpm_j] resulting from pollock predation is simply the sum over i of the $preym_{i,j}$. A more formal equation for $preym_{i,j}$ is

$$preym_{i,j} = [RC_i \times N_i] \times [D_{j,i}/FD_i]. \tag{37}$$

In the computer program a mathematically equivalent method of calculating the total prey mortalities [tpm_j] is used for optimization purposes. The quantities tpm_j [which are represented by other variables in the program]

are each preset to 0. Then for each pollock cohort i the temporary variable

$$UB = RC_i x N_i / FD_i \qquad (38)$$

is calculated and the calculation

$$tpm_j = tpm_j + UBxD_{j,i} \qquad (39)$$

is performed for each food item, j, consumed. Slight modifications to this calculation are used for some food items in order to calculate $\underline{tpm_j}$ in the proper units.

Some examples are:

Phytoplankton:

$$ZM_3 = ZM_3 + UBxD_{1,i}/P_{40}. \qquad (40)$$

Division by P_{40} is necessary to give ZM_3 the units of gC per unit of volume per unit of time.

Copepods:

$$ZM_5 = ZM_5 + UBxD_{2,i}. \qquad (41)$$

Euphausiids:

$$ZM_6 = ZM_6 + UBxD_{3,i}. \tag{42}$$

A cannibalized pollock cohort:

$$MT_j = MT_j + UBxD_{j+3,i}/B_j, \text{ for } D_{j+3,i} > 0. \tag{43}$$

Division by B_j is necessary to give MT_j the units of year^{-1}.

3.6.7 Pollock Breeding and Fecundities

3.6.7.1. <u>Sex Ratios</u>--P_{20} is the fraction of the total numbers of pollock which are females, and $P_{120}=1-P_{20}$ is the fraction of the total numbers of pollock which are males. It is assumed that these sex ratios apply to the individual pollock cohorts (including the eggs laid) at all times; that is, the ratio of females in any cohort to the total number in that cohort equals P_{20}, and similarly the ratio of males in any cohort to the total number in that cohort equals P_{120}. Implicit in this is the assumption that differing mortality rates between male and female pollock do not exist at any point in their life

history. This is a reasonable assumption since Pereyra et al. (1976: 230) found that differences in relative age composition between male and female pollock did not appear significant.

3.6.7.2. Proportions of Pollock Mature--Bakkala and Smith (1978: 93-94) found that the proportion of pollock mature enough to lay eggs or produce milt was fairly well described by a sigmoidal function of length. Their results were used in the model as follows.

For females, for each cohort i calculate

$$UF = e^{[P_{109} \times e^{P_{110} \times L_i}]} \tag{44}$$

where UF is a temporary variable, and P_{109} and P_{110} are parameters. Then

$$FCF_i = \begin{cases} 0, & \text{if } UF < P_{86} \\ P_{20} \times UF, & \text{if } P_{86} \leq UF \leq P_{87} \\ P_{20}, & \text{if } UF > P_{87}, \end{cases} \tag{45}$$

where FCF_i is the fraction of cohort i mature enough to lay eggs, and P_{86} and P_{87} are parameters.

For males, for each cohort i calculate

$$UM = e^{[P_{107} \times e^{P_{108} \times L_i}]} \tag{46}$$

where UM is a temporary variable, and P_{107} and P_{108} are parameters.

Then

$$FCM_i = \begin{cases} 0, \text{ if } UM < P_{86} \\ P_{120} \times UM, \text{ if } P_{86} \leq UM \leq P_{87} \\ P_{120}, \text{ if } UM > P_{87}, \end{cases} \tag{47}$$

where FCM_i is the fraction of cohort i mature enough to produce milt.

3.6.7.3. Breeding Behavior--Chang (1974: 118-119,168-169) presented data from Maeda (1972) and Kaganovskaya (1950) indicating that breeding pollock feed little or not at all during their spawning period in the eastern Bering Sea and in the Gulf of Korea.

To express this reduced feeding, the feeding rates of cohorts in the model may be reduced during the breeding period by multiplication by $EATER_i$. Pollock feeding rates

are more fully described in the section on pollock feeding. At the beginning of the breeding period, $EATER_i$ is calculated for the cohorts which might possibly breed, by using the equation

$$EATER_i = P_{61} - P_{62} \times [FCM_i + FCF_i] \tag{48}$$

where P_{61} and P_{62} are parameters.

This makes the reduction in the feeding rate of cohort i proportional to the total fraction of cohort i mature enough to breed. At the end of the breeding period, each $EATER_i$ which might have been changed is reset to P_{61}.

3.6.7.4. Fecundities--Data reported by Shew (1978) for large oocytes (diameters 0.594-1.5 mm) of pollock from the southeastern Bering Sea measuring 40-66 cm FL (511-3395 gm in weight) were reanalyzed, and it was found that the equation

$$Fecundity = Constant \times Weight \tag{49}$$

adequately described the data.

Shew had divided the pollock oocytes into two size categories: large (diameters 0.594-1.5 mm) and small (diameters 0.059-0.535 mm). It was assumed in the

computer model, POL, that only the large oocytes were released in a given spawning season, and that all ova laid by pollock at that time were the same size and weight. The fecundities of pollock were calculated in the computer simulation model using the equation

$$UC = W_i \times P_6 \tag{50}$$

where UC is a temporary variable recalculated for each pollock cohort and P_6 is a parameter.

3.6.7.5. Reduction in Weight due to Spawning--The energy and resources used by an individual pollock in order to reproduce was represented in the model by a loss of weight at the instant gametes were released. It was assumed in the model that male and female pollock of the same weight had an equal loss in weight at that time. This weight loss is given by the formula

$$UV = W_i \times P_6 \times P_{10} \tag{51}$$

where UV is a temporary variable recalculated for each pollock cohort and P_{10} is a parameter.

The number of ova laid by pollock cohort i in a given breeding period is equal to

$$W_i \times P_6 \times N_i \times FCF_i. \tag{52}$$

The total number of ova [ETT] laid by all the pollock cohorts in a given breeding period, is simply the sum of the total number of ova laid by each individual cohort. However, if the logical parameter DOBEV is true, ETT is always set to P_{64} instead.

After the ova are laid, the average new weight of individuals in cohort I is given by

$$\text{new weight} = W_i - W_i \times P_6 \times P_{10} \times [FCF_i + FCM_i]. \tag{53}$$

However, if the weight and length of that particular cohort are being constrained to grow according to a particular growth curve (see the section on optional constrained growth), the above reduction in weight is not made, so the new weight is equal to the old weight immediately before the ova were laid.

3.6.7.6.   Egg Survival--The egg mortality rate is given by a constant, EF, so that the number of eggs which survive to hatch is given by

$$E = ETT \times e^{-EF \times EGGDUR}. \tag{54}$$

If E<NMIN, then E is set to P_{74}. EGGDUR is the length of time (in years) from the time the ova are laid (a discrete, instantaneous event in the model), to the time the eggs hatch (another discrete, instantaneous event),

Since EF is a constant, it is implied that the egg mortality rate is independent of all the other state variables in the model. This assumption could be relaxed (for instance, in order to model euphausiid predation on pollock eggs), if the variable E was instead determined by integrating a differential equation. However, this was not done in this model.

3.7.   Yield of the Pollock Fishery

The yield or total catch of the pollock fishery [YLD] is measured in the model in units of weight per volume; specifically, in $g/(5 \text{ km}^3)$, since that is the volume of the portion of the ocean being modeled.

YLD is set to 0 each time fishing starts in the model. Then until the end of the fishing season, YLD is calculated by integrating the differential equation

$$V_4'=YLD'=\text{Sum over all pollock cohorts i of} \qquad (55)$$
$$B_i \times UFISH_i$$

where P_{84} and P_{85} are parameters, and

$$UFISH_i = F_i/[1 + e^{(P_{84}-L_i) \times P_{85}}].$$ (56)

$UFISH_i$ is calculated using a logistic function intended to represent a recruitment curve to the fishery, with vulnerability to the fishery increasing with increasing length. Such a function was used by Kimura (1978) to describe the selectivity ogive of certain fish nets on English sole (Papophrys vetulus) or haddock (Gadus aeglefinus). This function is a simplification of the complexities which exist in the actual recruitment curve to the fishery due to different kinds of gear, geographical and seasonal variability, and different emphases placed on catching pollock (i.e. whether pollock are the primary target, or whether pollock are just incidentally caught). For a discussion of these complexities, see Chang (1974: 42-52,63-77).

3.8.   Some Model Statistics

Various statistics are calculated by the model to aid in describing model behavior.

3.8.1. Zooplankton Statistics

3.8.1.1. <u>Cumulative</u> <u>Biomasses</u> <u>Over</u> <u>Time</u>--$VCUM_1$ is the integral of the copepod biomass, COPE, over time, and $VCUM_2$ is the integral of the euphausiid biomass, EUPH, over time. They are useful for calculating the average zooplankton biomass during a given time period, though they are not otherwise used in the model. They are not calculated in the model except when they potentially may be printed in the model output. $VCUM_1$ and $VCUM_2$ are set to zero each time newly hatched pollock begin eating (discrete time event 6). The differential equations which are integrated to calculate $VCUM_1$ and $VCUM_2$ are

$$V_6' = VCUM_1' = COPE, \qquad (57)$$

and

$$V_7' = VCUM_2' = EUPH. \qquad (58)$$

3.8.1.2. <u>Minimum</u> <u>Zooplankton</u> <u>Biomass</u> <u>Attained</u>--The minimum value [ZBS] which the total zooplankton biomass attains in the model, during the time span starting with the instant newly hatched pollock begin eating and ending with the instant the next cohort of newly hatched pollock begin eating, is calculated at the same time derivatives

are calculated for numerical integration. The equation used is

$$ZBS = MIN(COPE+EUPH,ZBS). \tag{59}$$

New calculations for ZBS are started each time the newly hatched pollock may begin eating in the model (discrete time event 6).

3.8.2. Pollock Statistics

3.8.2.1. Average Pollock Generation Time--For the purposes of this model, the generation time for any ovum is defined to be the age of its mother at the instant it was laid. The average generation time calculated is weighted by the number of ova laid.

In order to calculate the average generation time, the quantity

$$\tag{60}$$

egw_i=(total ova cohort i)x(age cohort i when ova laid)

is calculated for each pollock cohort. The sum of all the egw_i, divided by the total number [ETT] of ova laid by all pollock cohorts, gives the average generation time for the ova.

Equivalently, this average generation time is equal to

UG/ETT - EGGDUR (61)

where UG is the sum over i of

$W_i \times P_6 \times N_i \times FCF_i \times DTAU \times i$ (62)

and where DTAU is a constant equal to the difference in age between any two consecutive pollock cohorts.

For a more complete explanation of the meaning of FCF, ETT, DTAU, and EGGDUR, see the section on pollock breeding and fecundities.

3.8.2.2. Pollock Biomass, Ages 2 through 12--The biomass of the age 2 through age 12 pollock [B313] is the sum of the biomasses of cohorts 3 through 13.

3.8.2.3. Total Pollock Biomass--The total pollock biomass, BTT, is the sum over i of the biomasses of the individual pollock cohorts, B_i.

3.8.2.4. Total Pollock Numbers--The total pollock numbers, NTT, is the sum over i of the numbers of individual pollock [N_i] in each cohort.

IV.   PARAMETER VALUES AND ORIGINS

Definitions of variables used as parameters are given
in Appendix A.

As much as possible, parameters are for areas near
the Pribilof Islands, at around 56° N and 169° W.

When calculating parameters dependent on temperature,
a temperature of $2-4^{o}$ C was assumed, which is reasonable
for that area (Robinson 1976). Serobaba (1970) found that
$2-4^{o}$ C was the most frequently observed temperature range
for major walleye pollock populations (those forming
commercial concentrations), though concentrations could be
found from -1° to 4° C. For pollock, length refers to
fork length, unless noted otherwise (total length was used
for larval pollock before they had a forked tail).

Although it was necessary to adjust many parameters,
an attempt was made to stay within the range of
"reasonable" values given in the literature, when such a
range (such as confidence intervals) was given or could be
calculated or approximated from the published data using
statistical methods. Unfortunately, it was not always
possible to determine such a range from the data given in
the literature, so in those cases a subjective judgment
was made as to what departures from the literature values
were reasonable.

Tables giving the values and sources for the reference set of initial conditions and parameters are given below. (The definitions of the variables used are given in Appendix A).

4.1.   Initial Conditions

Initial conditions at time .6650390625 [Sept. 1] of various state variables (those which could be described by differential equations) are given in Table 1.

Initial values for PHY, COPE, EUPH, W_1, L_1, N_1, and N_2 were chosen while a preliminary set of parameters was still being used. Values were chosen which appeared would be close to the nontransient values which would result in the model using the final reference set of parameters, and which also appeared to be reasonable from available data.

The value of PHY = 2.36×10^8 gC/5 km^3 = .944g/m^3 is reasonable from Meshcheryakova (1970: fig. 4), who found the phytoplankton biomass (wet weight) ranged from less than 0.1 to more than 6 g/m^3 in September 1964, in the 0-25 m water layer of the eastern Bering Sea.

The value of COPE+EUPH = 8.32×10^8 g/5 km^3 = 8.32 g/m^2 (assuming an effective depth of 50 m) is reasonable (though perhaps somewhat low) from ibid. (fig. 8), who found that the total zooplankton biomass ranged from 1 to 100 g/m^2 in the second half of August 1964, in the 0-100 m

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Table 1.--Initial starting conditions* (Conversions to various units of
        measure are also shown).

PHY[#] = .236x10^9 gC/5 km^3, .472x10^{-1} gC/m^3, .472x10^2 micrograms C/liter,

        .472x10^{10} g/5 km^3, .944 g/m^3, .472x10^2 g/m^2 [@]

COPE = .232x10^9 g/5 km^3, .464x10^{-1} g/m^3, .232x10^1 g/m^2

EUPH = .600x10^9 g/5 km^3, .120 g/m^3, .600x10^1 g/m^2

  E = 0 per 5 km^3

YLD = 0 g/5 km^3

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* The simulated time of start is 1 September.

Phytoplankton was assumed to contain 1 gC per 20 g wet weight [see P$_{40}$].

@ An effective depth of 50 m was assumed for volume to area conversions.

Table 1.--Initial starting conditions (continued).

Pollock cohort i	Length L_i cm	Weight W_i g	Numbers N_i per 5 km^3	Biomass B_i ** g/5 km^3	Numbers N_i per km^2	Biomass B_i kg/km^2
1	5.833	.88459	$.30000 \times 10^9$	$.265 \times 10^9$	$.300 \times 10^7$	$.265 \times 10^4$
2	20.159	$.57342 \times 10^2$	$.21300 \times 10^7$	$.122 \times 10^9$	$.213 \times 10^5$	$.122 \times 10^4$
3	32.481	$.23723 \times 10^3$	$.76302 \times 10^6$	$.181 \times 10^9$	$.763 \times 10^4$	$.181 \times 10^4$
4	40.990	$.47429 \times 10^3$	$.40748 \times 10^6$	$.193 \times 10^9$	$.407 \times 10^4$	$.193 \times 10^4$
5	46.870	$.70683 \times 10^3$	$.21794 \times 10^6$	$.154 \times 10^9$	$.218 \times 10^4$	$.154 \times 10^4$
6	50.930	$.90519 \times 10^3$	$.11638 \times 10^6$	$.105 \times 10^9$	$.116 \times 10^4$	$.105 \times 10^4$
7	53.740	$.10618 \times 10^4$	$.34797 \times 10^5$	$.369 \times 10^8$	$.348 \times 10^3$	$.369 \times 10^3$
8	55.670	$.11799 \times 10^4$	$.14308 \times 10^5$	$.169 \times 10^8$	$.143 \times 10^3$	$.169 \times 10^3$
9	57.010	$.12663 \times 10^4$	$.59806 \times 10^4$	$.757 \times 10^7$	$.598 \times 10^2$	$.757 \times 10^2$
10	57.940	$.13285 \times 10^4$	$.22535 \times 10^4$	$.299 \times 10^7$	$.225 \times 10^2$	$.299 \times 10^2$
11	58.570	$.13725 \times 10^4$	$.89706 \times 10^3$	$.123 \times 10^7$	$.897 \times 10^1$	$.123 \times 10^2$
12	59.020	$.14035 \times 10^4$	$.35813 \times 10^3$	$.503 \times 10^6$	$.358 \times 10^1$	$.503 \times 10^1$
13	59.320	$.14252 \times 10^4$	$.14236 \times 10^3$	$.203 \times 10^6$	$.142 \times 10^1$	$.203 \times 10^1$
14	59.530	$.14403 \times 10^4$	$.56883 \times 10^2$	$.819 \times 10^5$	.569	.819
15	59.680	$.14508 \times 10^4$	$.22676 \times 10^2$	$.329 \times 10^5$	.227	.329
16	59.780	$.14581 \times 10^4$	$.90190 \times 10^1$	$.132 \times 10^5$	$.902 \times 10^{-1}$	.132
17	59.850	$.14631 \times 10^4$	$.36121 \times 10^1$	$.528 \times 10^4$	$.361 \times 10^{-1}$	$.528 \times 10^{-1}$
18	59.890	$.14666 \times 10^4$	$.14346 \times 10^1$	$.210 \times 10^4$	$.143 \times 10^{-1}$	$.210 \times 10^{-1}$

** $B_i = W_i \times N_i$

Table 1.--Initial starting conditions (continued).

Pollock cohort i	Numbers N_i per 0.6×10^6 km^2	Biomass B_i t/0.6×10^6 km^2##	Numbers N_i per 0.8×10^6 km^2	Biomass B_i t/0.8×10^6 km^2
1	$.180 \times 10^{13}$	$.159 \times 10^7$	$.240 \times 10^{13}$	$.212 \times 10^7$
2	$.128 \times 10^{11}$	$.733 \times 10^6$	$.170 \times 10^{11}$	$.977 \times 10^6$
3	$.458 \times 10^{10}$	$.109 \times 10^7$	$.610 \times 10^{10}$	$.145 \times 10^7$
4	$.244 \times 10^{10}$	$.116 \times 10^7$	$.326 \times 10^{10}$	$.155 \times 10^7$
5	$.131 \times 10^{10}$	$.924 \times 10^6$	$.174 \times 10^{10}$	$.123 \times 10^7$
6	$.698 \times 10^9$	$.632 \times 10^6$	$.931 \times 10^9$	$.843 \times 10^6$
7	$.209 \times 10^9$	$.222 \times 10^6$	$.278 \times 10^9$	$.296 \times 10^6$
8	$.858 \times 10^8$	$.101 \times 10^6$	$.114 \times 10^9$	$.135 \times 10^6$
9	$.359 \times 10^8$	$.454 \times 10^5$	$.478 \times 10^8$	$.606 \times 10^5$
10	$.135 \times 10^8$	$.180 \times 10^5$	$.180 \times 10^8$	$.240 \times 10^5$
11	$.538 \times 10^7$	$.739 \times 10^4$	$.718 \times 10^7$	$.985 \times 10^4$
12	$.215 \times 10^7$	$.302 \times 10^4$	$.287 \times 10^7$	$.402 \times 10^4$
13	$.854 \times 10^6$	$.122 \times 10^4$	$.114 \times 10^7$	$.162 \times 10^4$
14	$.341 \times 10^6$	$.492 \times 10^3$	$.455 \times 10^6$	$.655 \times 10^3$
15	$.136 \times 10^6$	$.197 \times 10^3$	$.181 \times 10^6$	$.263 \times 10^3$
16	$.541 \times 10^5$	$.789 \times 10^2$	$.722 \times 10^5$	$.105 \times 10^3$
17	$.217 \times 10^5$	$.317 \times 10^2$	$.289 \times 10^5$	$.423 \times 10^2$
18	$.861 \times 10^4$	$.126 \times 10^2$	$.115 \times 10^5$	$.168 \times 10^2$

t = metric tons

Table 1.--Initial starting conditions (continued).

Pollock cohort i	Numbers N_i per 1.0×10^6 km^2	Biomass B_i t/1.0×10^6 km^2	Numbers N_i per 1.2×10^6 km^2	Biomass B_i t/1.2×10^6 km^2
1	$.300 \times 10^{13}$	$.265 \times 10^7$	$.360 \times 10^{13}$	$.318 \times 10^7$
2	$.213 \times 10^{11}$	$.122 \times 10^7$	$.256 \times 10^{11}$	$.147 \times 10^7$
3	$.763 \times 10^{10}$	$.181 \times 10^7$	$.916 \times 10^{10}$	$.217 \times 10^7$
4	$.407 \times 10^{10}$	$.193 \times 10^7$	$.489 \times 10^{10}$	$.232 \times 10^7$
5	$.218 \times 10^{10}$	$.154 \times 10^7$	$.262 \times 10^{10}$	$.185 \times 10^7$
6	$.116 \times 10^{10}$	$.105 \times 10^7$	$.140 \times 10^{10}$	$.126 \times 10^7$
7	$.348 \times 10^9$	$.369 \times 10^6$	$.418 \times 10^9$	$.443 \times 10^6$
8	$.143 \times 10^9$	$.169 \times 10^6$	$.172 \times 10^9$	$.203 \times 10^6$
9	$.598 \times 10^8$	$.757 \times 10^5$	$.718 \times 10^8$	$.909 \times 10^5$
10	$.225 \times 10^8$	$.299 \times 10^5$	$.270 \times 10^8$	$.359 \times 10^5$
11	$.897 \times 10^7$	$.123 \times 10^5$	$.108 \times 10^8$	$.148 \times 10^5$
12	$.358 \times 10^7$	$.503 \times 10^4$	$.430 \times 10^7$	$.603 \times 10^4$
13	$.142 \times 10^7$	$.203 \times 10^4$	$.171 \times 10^7$	$.243 \times 10^4$
14	$.569 \times 10^6$	$.819 \times 10^3$	$.683 \times 10^6$	$.983 \times 10^3$
15	$.227 \times 10^6$	$.329 \times 10^3$	$.272 \times 10^6$	$.395 \times 10^3$
16	$.902 \times 10^5$	$.132 \times 10^3$	$.108 \times 10^6$	$.158 \times 10^3$
17	$.361 \times 10^5$	$.528 \times 10^2$	$.433 \times 10^5$	$.634 \times 10^2$
18	$.143 \times 10^5$	$.210 \times 10^2$	$.172 \times 10^5$	$.252 \times 10^2$

(or else, surface to bottom) water layer of the eastern Bering Sea, and that over a considerable part of the shallows in this region it ranged from 10 to 50 g/m^2 (ibid., p.101).

L_1=5.833 cm is reasonable (through perhaps somewhat low) from Cooney et al. (1979: fig. 19), and W_1=.8846 g is close (within 5%) of the normal weight of 0.9256 g estimated using the length-weight relationship

$$W_1 = P_{80} \times L_1^{P_{63}}.$$

$N_1 = 3 \times 10^8$ and $N_2 = 2.13 \times 10^6$ are basically educated guesses. The ratio N_1/N_2 implies a total instantaneous mortality rate of 4.95 $year^{-1}$, and the ratio N_2/N_3 implies a total instantaneous mortality rate of 1.03 $year^{-1}$, which seem to be possible rates [compare with Low (1979: 4)].

While initial values for N_1 through N_{18} were being decided for the model, it was assumed that the pollock population, measured by Low (1979: table 7) using virtual population analysis, occupied a total effective area of 1×10^6 km^2, though this total effective area is uncertain. Laevastu and Favorite (1976a: 17), used an estimate of 0.8×10^6 km^2 for the total area of the eastern Bering Sea. Alton and Fredin (1974: fig.1) described statistical areas totaling 0.5623×10^6 km^2 along the eastern Bering Sea shelf edge where Japanese trawlers fished for pollock, and catch statistics from these areas were used by Low (1979:

table 1) in his virtual population analysis. Okada (1979) described results of echosounder surveys that had been conducted from 29 June-7 August 1977, and 17 June-16 July 1978, over much of the Aleutian Basin. Substantial populations of pollock were found within the depth range (primarily 0-200 m) surveyed and verified by midwater trawling. No pollock were caught less than 40 cm FL [i.e. less than about 5 years old]. In contrast, during the same time periods commercial fishing operations over the continental shelf caught substantial numbers of pollock down to about 20 cm FL (ibid., fig. 3), which must have been about 2 years old. Since no small pollock were found over the Aleutian Basin, it seems reasonable to hypothesize that the pollock found there at least in part came from populations near the eastern Bering Sea shelf edge, where they had been exploited by trawl fisheries. Serobaba (1974: 546) stated that the spawning grounds of pollock in the Bering Sea are bounded by the ice edge and by the continental slope. He also stated that during the spawning period pollock eggs are noted where depths are between 50 and 300 m, though eggs are sometimes taken (singly) farther out at sea, where depths exceed 1000 m. Thus it seems that many of the pollock over the Aleutian Basin must migrate to spawning sites in shallower water, and a reasonable hypothesis is that at least part of these

migrate to spawning sites known to exist near the eastern Bering Sea shelf edge (Pereyra et al. 1976:   fig. X-4), where they are exploited by trawl fisheries.   Smith (1981: 534) also found some evidence (particularly for 1975-76) which could be explained by migrations of pollock out of, and into, a survey area located in the central eastern Bering Sea continental shelf region [this area was mostly included within the statistical areas of Alton and Fredin (1974)].   Thus it appears that the effective area occupied by the pollock population exploited by commercial fisheries near the eastern Bering Sea shelf edge could range from 0.5623×10^6 km^2 to more than 1.2×10^6 km^2 (combining the areas of Okada 1979, and Alton and Fredin 1974), depending on the extent of migrations.

It was assumed that the effective depth in the area occupied by the exploited pollock population is the same as the effective depth of 50 m used in the model, so that the model variables N_i and B_i may be taken to refer either to a volume of 5 km^3, or to an area of 100 km^2.

N_3 through N_{13} seem reasonable compared to the population estimates in Low (1979:   table 7), assuming that the area effectively occupied by the populations estimated is 1×10^6 km^2. N_3 through N_{13} have been adjusted [with W_3 through W_{13} being held constant] to give a total biomass for age 2 through 12 pollock equal to

7×10^8 g/5 km^3 = 7×10^8 g/100 km^2 = 7×10^6 mt/1×10^6 km^2, which is reasonable from ibid. N_{14} through N_{18} can be calculated from N_{13} by assuming an instantaneous total mortality rate of 0.92 year^{-1}, which is the same as the instantaneous total mortality rates implied by the values for N_{11} through N_{13}.

L_2 through L_{18} and W_2 through W_{18} are within 3% of the values which would be calculated for those variables using the functions RLNGTH and WVB (which are described in Appendix D).

E is zero because all the eggs have hatched in the model (discrete time event 4).

It does not really matter what the initial value of YLD is, because the values YLD takes on do not affect the model dynamics, and YLD is reset to 0 whenever fishing is restarted (discrete time event 7). Consequently, the only values of YLD which are affected by its initial value are those calculated before the first occurrence of discrete time event 7.

4.2. Discrete Time Events and Various Other Parameters

Table 2 gives the schedule of occurrence of discrete time events in a given simulated year. Various print times may also occur in addition to the discrete time events listed in Table 2.

Table 3 lists other input parameters for the model.

Tables defining the various parameters and discrete time events are given in Appendices A and B.

Table 2. Time of Occurrence of Discrete Time Events

Discrete Event Identifier (IEV)	Event Time (years)	Event Date	Source
2	.24609375	Apr. 1	Pollock prepare to breed. Reasonable from Chang (1974: fig. 19).
3	.3095703125	Apr. 23	Pollock breed. Reasonable from Waldron and Vinter (1978). (See EGGDUR, EF).
4	.3642578125*	May 13	Cohort update; pollock eggs hatch. Reasonable from Hamai et al. (1971), assuming a temperature of $3.5^{\circ}C$ (see Robinson 1976). (See EGGDUR, EF).
5	.328125	May 1	Pollock breeding period ends. Reasonable from Chang (1974: fig. 19).
6	.3896484375	May 22	Pollock larvae may begin feeding. Reasonable from Hamai et al. (1974), assuming a temperature of $3.5^{\circ}C$ (see Robinson 1976).
7	.3642578125*	May 13	Fishing season begins (same as discrete time event 4).

Table 2. Time of Occurrence of Discrete Time Events
          (continued).

8   .3642578125*   May 13   Fishing   season
                                          ends.   (same   as
                                          discrete   time
                                          event 4).

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*   For the reference set of parameters, discrete events
    4, 7, and 8 are arranged so that they actually are
    performed in the order 8, 7, 4, which implies fishing
    is continuous.

Table 3. Parameter Values

Parameter	Value	Source or Explanation
ACCRCY	.005	[2 significant digits desired]
COMAX	20	Reasonable from Pereyra et al. (1976: 381) for DTAU=1.
DOBEV	.FALSE.	
DTAU	1 year	
D2	2.977	Pereyra et al. (1976: 234).
D4	.18 years	Reasonable from Pereyra et al. (1976: table IX-21).
D7	60. cm	Same source as D4.
D8	.0075 g/cm^{D2}	Pereyra et al. (1976: 234).
EF	38. year^{-1}	For EGGDUR = .0547 years (see discrete time events 3 and 4), this causes 12.5% of the eggs to survive to hatch, which is reasonable for the eggs of the Baltic cod [apparently _Gadus morhua_] (Grauman 1973).
F_1 to F_{20}	= .3 year^{-1}.	Adjusted to fit known pollock characteristics and population dynamics. When combined with other sources of mortality, the resulting total mortality rates appear reasonable compared to those calculated from Smith (1981: table 33-3). The resulting equilibrium fishery yield appears reasonable from Low (1979: 6).

Table 3.   Parameter Values (continued)

FISHIN   .TRUE.

FSTART   .3642578125 years   [May 13] Same as discrete
           time event 7.

ICANE   3   ICANE = 3 is reasonable for
           beginning the simulation after a cohort update
           but before the next time the pollock are
           simulated to prepare to breed, so long as the
           first cohort to possibly participate in breeding
           is cohort 2. This is reasonable from Bakkala
           and Smith (1978: table 26).

KAY   .37 year^{-1} Same source as D4.

M_1 to M_4 = .2 year^{-1}.   Adjusted   to   fit   known
           pollock characteristics and population dynamics.
           The lowest value for the instantaneous natural
           mortality rate used by Low (1979: 4) for an age
           class (age 2) of pollock.

M_5 .3 year^{-1}.   Adjusted   to   fit   known
           pollock   characteristics   and   population
           dynamics. When combined with other sources of
           mortality, the resulting total mortality rates
           appear reasonable compared to those calculated
           from Smith (1981: table 33-3) and the natural
           mortality rates in Low (1979: 4).

M_6 to M_{11} = .4 year^{-1}.   Adjusted   to   fit   known
           pollock characteristics and population dynamics.
           Same source as M_5.

M_{12} .7 year^{-1}.   Adjusted   to   fit   known
           pollock characteristics and population dynamics.
           Reasonable   compared   to   mortality   rates
           calculated from Smith (1981: table 33-3).

Table 3. Parameter Values (continued)

M_{13} 1.0 year^{-1}. Same source as M_{12}.

M_{14} to M_{20} = 1.3 year^{-1}. Same source as M_{12}.

NC 18 Same source as COMAX.

NMIN 1. Arbitrarily picked. (See also P_{74}).

NVON 0

P_1 $4.0\ g^{1-P_2}/year$ [$.011\ g^{0.2}/day$]. Calculated using data for North Sea cod (Gadus morhua), haddock (Melanogrammus aeglefinus), saithe (Pollachius virens), and whiting (Merlangius merlangus) reported in Jones and Hislop (1978: 248). P_1 was calculated assuming 1 g wet weight of either fish food or fish flesh contains 1 kcal (ibid., p. 245), and that the mean body temperature of pollock is 4° C.

P_2 .8 Same source as P_1.

P_3 .84 A reasonable extrapolation from data in Jones and Hislop (1978: table 2). Compare with P_{56}.

P_5 1. Arbitrarily picked.

P_6 230.2 ova/g Calculated from data used by Shew (1978). E (the number of large pollock ova laid) can be modeled as a function of W (the wet weight of a breeding pollock) using the ordinary (least squares) linear regression model E=a+bW. However, the parameter a was not

Table 3.   Parameter Values (continued)

significantly different from zero at the 95%
level (df=71, significance=73%).   Furthermore,
an examination of a plot of the values for E
versus W showed that though the relationship
between E and W appeared to be linear (df=71,
correlation=.70, significance>99.9%), the
variance of E about the regression line did not
appear to be constant, but rather approximately
proportional to W.   Under such circumstances,
the best linear unbiased estimator for P_6 in the
model $E=P_6 \times W$ is the ratio estimator:

$$P_6 = (\text{mean of E})/(\text{mean of W}) \tag{63}$$

(Cochran 1977:   158-160), so this ratio
estimator was used to determine P_6.   (See P_{10}).

P_7 $.107[\text{g/year}]/\text{cm}^{P_{119}}$ $[.000293 \text{ [g/day]}/\text{cm}^{2.95}]$.
Adjusted to fit known pollock characteristics
and population dynamics.   A multiple linear
least squares regression (including some dummy
variables) was performed using 43 data points
(transformed using logarithms) from Jones (1974:
appendix tables VI-VII).   The data points were
measured for Atlantic cod (Gadus morhua),
haddock, and whiting, which were 136-1174 g in
weight and 23-53 cm in length.   Joint 95%
confidence intervals were calculated using
Bonferroni's inequality (Bickel and Doksum 1977:
162) for the seven different parameters
estimated from this data.   Then P_7, P_{17}, P_{114},
and P_{119} were calculated by combining values
taken from within the 95% confidence intervals
of the appropriate parameters.   It was assumed
that pollock food is digested at the same rate
as the saithe used as food in some of Jones'
(1974) experiments, that pollock live at a
temperature of 4° C, and that the equilibrium
weight (g) of food in the stomach of a pollock
of length L (cm), which has been feeding at its
maximum rate over a long period of time, is
given by $4 \times 10^{-4} \times L^3$ [the maximum (though perhaps
non-equilibrium) weight of food found for North

Table 3.   Parameter Values (continued)

Sea cod (<u>Gadus</u> <u>morhua</u>) by Daan (1973:   table XII)].

P_8 $5 \times 10^8 \text{ g}^{1-P_{101}}/5 \text{ km}^3$ [$.1 \text{ g}^{1.15}/m^3$].   Adjusted to fit known pollock characteristics and population dynamics.

P_9 $6 \times 10^7 \text{ g}^{1-P_{101}}/5 \text{ km}^3$ [$.012 \text{ g}^{1.15}/m^3$].   Adjusted to fit known pollock characteristics and population dynamics.

P_{10} .00087 g/ovum.   [.87 mg/ovum] P_{10} was chosen so that $P_{10} \times P_6 = .20$, which implies that 20% of the total body weight of a spawning pollock is lost the instant gametes are released (discrete time event 3).   This is equivalent to a loss of 25% of the somatic weight, which is a reasonable value for the total somatic energy lost in spawning for certain Atlantic gadoids (Jones and Johnston 1977:   42).

P_{11} 1.   Arbitrarily picked.

P_{12} .25 years   Arbitrarily picked.

P_{13} .0003136 g   [.3136 mg] Adjusted to fit known pollock characteristics and population dynamics.   For this value of P_{13}, a newly hatched pollock has a weight of .00020 g (.2 mg) when it begins eating (its length at that time is .522 cm or 5.22 mm).   This weight is reasonable from Haryu (1980:   fig. 5), assuming a 20% loss of weight in formalin and a 4.4% loss in length in formalin, which are reasonable losses (ibid., p. 127, citing various authors).

Table 3. Parameter Values (continued)

P_{14} .466 cm   [4.66 mm]   Reasonable from Hamai (1971: 16-17).

P_{15} 1.0 years   Arbitrarily picked.

P_{16} .01 cm^{-1} Adjusted to fit known pollock characteristics and population dynamics.

P_{17} Same as P_7.

P_{18} $5 \times 10^8 \text{ g}^{1-P_{102}}/5 \text{ km}^3$ [$.1 \text{ g}^{1.15}/\text{m}^3$]   Same source as P_8.

P_{19} $6 \times 10^7 \text{ g}^{1-P_{102}}/5 \text{ km}^3$ [$.012 \text{ g}^{1.15}/\text{m}^3$]   Same source as P_9.

P_{20} .5   [1 female per male] Reasonable from Pereyra et al. (1976: table IX-19).

P_{21} 59 days   [Mar. 1] Reasonable from McRoy and Goering (1975). Converted to years by division by 365 before use.

P_{22} 120 days   [May 1] Same source as P_{21}. Converted to years by division by 365 before use.

P_{23} 90 days   [Apr. 1] Same source as P_{21}. Converted to years by division by 365 before use.

Table 3. Parameter Values (continued)

P_{24} 151 days   [Jun. 1]   Same   source   as P_{21}.   Converted to years by division by 365 before use.

P_{25} 243 days   [Sep. 1]   Same   source   as P_{21}.   Converted to years by division by 365 before use.

P_{26} 304 days   [Nov. 1]   Same   source   as P_{21}.   Converted to years by division by 365 before use.

P_{27} 1.052×10^9 gC/5 km^3 [172 [mgC/m^2]/day average, 3.45 [mgC/m^3]/day average, 2.4×10^7 metric tons C for the total sea area] P_{27} through P_{31} were calculated from McRoy and Goering (1975: table 5) using values for the total Bering Sea primary production of carbon (excluding production attributed to rivers and lagoons), assuming that production is evenly distributed throughout the area of the total sea, that the total sea has an area of 2.281×10^6 km^2 (ibid., table 1, citing Lisitsyn 1966), and that the volume modeled in POL_2 (5 km^3) corresponds to a surface area of 100 km^2.

P_{28} 5.217×10^9 gC/5 km^3 [855   [mgC/m^2]/day average, 17.1 [mgC/m^3]/day average, 11.9×10^7 metric tons C for the total sea area]   Same source as P_{27}.

P_{29} 2.192×10^9 gC/5 km^3 [238   [mgC/m^2]/day average, 4.77 [mgC/m^3]/day average, 5.0×10^7 metric tons C for the total sea area]   Same source as P_{27}.

P_{30} 3.025×10^9 gC/5 km^3 [496   [mgC/m^2]/day average, 9.92 [mgC/m^3]/day average, 6.9×10^7

Table 3.   Parameter Values (continued)

metric tons C for the total sea area]   Same source as P_{27}.

P_{31} 0.8001×10^9 [gC/5 km^3]/year [21.9   [mgC/m^2]/day average, .438 [mgC/m^3]/day average, 0.6×10^7 metric tons C for the total sea area over the entire winter]. The total sea production over the entire winter was divided by the length of the winter to calculate P_{31}. [See P_{27}].

P_{39} 36.82 year^{-1} [.10 day^{-1},   .0042 hour^{-1}] From Anderson et al. (1977:   530).   In addition, it is assumed that other sources of loss or mortality, besides zooplankton grazing, are insignificant (ibid., pp. 532,546).

P_{40} 20. g/gC   An approximation which is reasonable from Strathmann (1967: fig. 2) assuming an individual phytoplankton cell has a volume of 2.6×10^4 cubic microns (the volume of Cosinodiscus angstii, Frost 1972: table 1) and a specific gravity of 1.02 g/ml (Alexander 1977: 368).

P_{41} 2.85×10^8 gC/5 km^3 [.057 gC/m^3, 57 mgC/m^3, 57 micrograms C/l]   A value for Calanus plumchrus, stage V, used by McAllister (1970: fig. 11), which was derived from Parsons and LeBrasseur (pers. commun. to McAllister).

P_{42} 1.   Arbitrarily picked.

P_{43} 160 year^{-1} [.44 day^{-1}, 44% of the copepod's body weight per day, .018 hour^{-1}] Adjusted to fit known pollock characteristics and population dynamics. Same source as P_{41}. P_{43} is intermediate between values for stages IV and V of Calanus plumchrus (continuous feeding is assumed).

Table 3. Parameter Values (continued)

P_{44} 7.3×10^{-10} 5 km^3/gC [3.65 m^3/gC, 3.65 1/mgC, .00365 1/microgram C] Adjusted to fit known pollock characteristics and population dynamics. Same source as P_{43}.

P_{45} .052 gC/g Calculated by combining values from Mullin (1969: 295).

P_{46} .8 McAllister (1970: 430).

P_{47} 5.32 year^{-1} [.0146 day^{-1}] Adjusted to fit known pollock characteristics and population dynamics. P_{47} was calculated using dry weights and percentage carbon figures given in Ikeda (1974: table 11) for Calanus plumchrus, copepodite stage V, starved for 0 or 14 days at 13.8-16.0° C.

P_{48} .072 gC/g Calculated from data for Euphausia pacifica in Lasker (1966: table I).

P_{49} 60. year^{-1} [.164 day^{-1}, or 16.4% of the euphausiid's body weight per day] Adjusted to fit known pollock characteristics and population dynamics. Reasonable from data given in Ross (1979: table 14). for Euphausia pacifica somewhere between 8 to 12° C.

P_{50} 1.375×10^8 gC/5 km^3 [.0275 gC/m^3, 27.5 mgC/m^3, 27.5 micrograms C/1, 1 Artemia salina nauplius per 20 ml] Reasonable from Lasker (1966: fig. 11) assuming one Artemia salina nauplius contains 5.5×10^{-4} mg C (ibid., p. 1310).

P_{51} 54.5 year^{-1} [.15 day^{-1}, 15% of the euphausiid's body weight per day] From Parsons et al. (1967: table 1), assuming that the Euphausia pacifica experimented with consumed

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Table 3. Parameter Values (continued)

their entire daily (24 hour) ration within 8 hours (ibid., p. 11).

P_{52} 4.466×10^9 gC/5 km^3 [.8932 gC/m^3, 893.2 mgC/m^3, 893.2 micrograms C/l, 172×10^5 cubic microns of phytoplankton per ml] A least squares linear regression line was calculated using the four data points for Euphausia pacifica in Parsons et al. (1967: fig. 4B) measured between a phytoplankton concentration of 0 and 200×10^5 cubic microns of phytoplankton cells per ml of water, assuming that phytoplankton cell contains .052 mgC/mm^3 (ibid. p. 12). P_{52} was set equal to the intercept of this regression line with the maximum feeding rate for E. pacifica given in ibid. (table 1).

P_{53} 4.252×10^8 gC/5 km^3 [.08504 gC/m^3, 85.04 mgC/m^3, 85.04 micrograms C/l, 16.35×10^5 cubic microns of phytoplankton per ml] Same source as P_{52}. P_{53} was set equal to the intercept of the regression line with the X axis.

P_{54} 1.   Arbitrarily picked.

P_{55} 1.   Arbitrarily picked.

P_{56} .84   [84%]   A   value   for Euphausia pacifica feeding on Artemia salina nauplii (Lasker 1966: 1305,1314).

P_{57} 9.1 year^{-1} [.025 day^{-1}, .0010 hour^{-1}] Adjusted to fit known pollock characteristics and population dynamics. P_{57} was taken from within the confidence interval (8.96 , 14.4), which was calculated for a 1.5 cm Thysanoessa inermis at 4° C using the equation (Sameoto 1976: 2573):

Table 3. Parameter Values (continued)

(mg dry body weight)=

$$.000712 \times (\text{total length in mm})^{3.38} \qquad (64)$$

and

$$\text{LOG}_{10}(\text{microliters } O_2 \text{ used in respiration} \qquad (65)$$
$$\text{per day}) = 1.37 + 1.16 \times \text{LOG}_{10}(\text{mg dry body weight})$$

(calculated from 9 data points, standard error of estimate=.13; ibid.: table 1). The above confidence interval was an underestimate of a true 95% confidence interval for P_{57}. A true 95% confidence interval would be somewhat wider, but insufficient information was given in Sameoto's paper to calculate such an interval.

Sameoto apparently used a value of about .0048 calories per microliter of oxygen to convert from oxygen used in respiration to calories used in respiration (compare table 1 with column 4 of table 3 in ibid.). He also found that a T. inermis contained 4.91 kcal per g dry weight. (ibid., table 5). These constants were used to calculate P_{57}, assuming the respiration rate is the same whether it is measured in terms of calories, gC, or g dry weight. P_{57} includes losses due to molting which were calculated assuming that the dry molt weight is 5.7% of the dry body weight (ibid., p. 2571), that 17% of the dry weight of the molt is organic carbon (a value for Euphausia pacifica used by Lasker 1966: 1303, 1315), and using the equation (Sameoto 1976: 2570):

$$\text{mean days between molts} = \qquad (66)$$
$$15.3 - 0.91 \times (\text{temperature in degrees C})$$

P_{58} 6.4   Adjusted to fit known pollock characteristics and population dynamics. P_{58} was estimated as follows: Define R as the ratio of the wet weight of the aggregate of copepods found in the stomach of a pollock to the wet weight of the aggregate of euphausiids

Table 3. Parameter Values (continued)

found in its stomach. A number of values for R were calculated using data for each length class of pollock between 20.1 and 60.0 cm FL in Takahashi and Yamaguchi (1972: fig. 11) as reproduced in Laevastu and Favorite (1976b: fig. 2), and for each length class of pollock between 25 and 44.9 cm FL in Bailey and Dunn (1979: table 4). Pollock length classes were 5 cm in width. The weights of pollock in each length class were approximated by assuming that the length (cm) of every pollock in the class was equal to the midpoint of the length class, and that the weight, WPRED, of each pollock in the length class was given by the equation (Chang 1974: table 36, citing Yamaguchi and Takahashi 1972):

$$WPRED=.00867 \times Length^{2.940} \tag{67}$$

The values of R and WPRED calculated for each length class were then used to estimate the coefficients $\underline{a}$ and $\underline{b}$ in the least squares linear regression model:

$$LN(R)=a + b \times LN(WPRED) \tag{68}$$

This model fitted the data fairly well (12 data points were used, r=-.87, significance of r>99.9%).

Define WC and WE as the respective average wet weights of the copepods and euphausiids before they were eaten, and define BC and BE as the respective biomass densities of copepods and euphausiids available to the feeding pollock. Assume that for a prey weight WPREY (WPREY may equal either WC or WE), the size selectivity of the pollock is given by the equation:

$$g(WPRED,WPREY) = e^{(P_{59} \times [LN(WPRED/WPREY)-P_{58}]^2)} \tag{69}$$

The above equation is a reparameterization of equation (16) used by Andersen and Ursin (1977: section 2.3.6.1.) to model the prey size

Table 3. Parameter Values (continued)

selection of various marine species.   Also assume that

$$R=(BC/BE) \times [g(WPRED,WC)/g(WPRED,WE)] \times U \qquad (70)$$

where U is a lognormally distributed random variable such that LN(U) has a mean of 0. Among other things, modeling R with this equation implies that the rates at which copepods and euphausiids are digested by pollock are equal, and that the effect of pollock prey switching is negligible. Taking logarithms of both sides of this equation, it is found after some algebraic manipulation that:

$$P_{58}=[LN(BC/BE)-a]/b - 0.5 \times LN(WE \times WC) \qquad (71)$$

and

$$P_{59}=b/[2 \times LN(WE/WC)] \qquad (72)$$

From these equations, the values for P_{58} and P_{59} were calculated. The values used for the parameters were b=-0.91773 (the best estimate for b from the linear regression described above), WC=.0025 g (a value for Calanus plumchrus in LeBrasseur et al. 1969: table 1), WE=.04 g (compare to the value for ZW_3 used in this simulation), and BC/BE=17 (reasonable for Saanich Inlet, British Columbia, in June and July 1966 - see Parsons et al. 1967: 11-12). In addition, the 50% individual confidence interval for parameter a of (3.22091, 4.60847) was used from the linear regression described above. The corresponding 50% individual confidence interval for parameter b was (-1.03492, -0.80054). Because the length classes for pollock probably contained unequal numbers of pollock, and because the values for WPRED, WC, WE, and BC/BE were not measured at the time and place the stomach content studies on pollock were performed, these are not true 50% confidence intervals for parameters a and b, but they still give some idea of the possible ranges of a and b. Using the confidence interval for a, and the value b=-0.91773, it is

Table 3.   Parameter Values (continued)

calculated that $P_{59}=-0.166$, with P_{58} being in the interval (5.03 , 6.54). [If the best estimate from the linear regression of $\underline{a}=3.91469$ were used, one would get $P_{58}=5.78$]. This range for P_{58} and the value for P_{59} seem comparable to the values for the equivalent parameters used by Andersen and Ursin (1977: table 10) for various species of fish. Their $\underline{eta}$ is equivalent to P_{58}, and their $\underline{sigma}$ is equivalent to $1/SQRT[-2xP_{59}]$.

P_{59} -.166 $[1/SQRT[-2 \times P_{59}] = 1.74]$
Same source as P_{58}.

P_{60} 0.0 g/gC   Clarke (1978) found that phytoplankton was not an important food item for any larval pollock (from 0.48 to 1.77 cm standard length) in April to June, 1977 in the southeastern Bering Sea, which indicates $P_{60}=0.0$ is reasonable. In contrast, Gorbunova (1954) found that phytoplankton predominated in the diets of pollock from 0.7 to 1.0 cm total length.   However, she mainly studied pollock along the Asian coast of the Pacific Ocean from Anadyr' Bay [northwestern Bering Sea] to Korea Bay [northeastern Yellow Sea] in March through December, with the basic data being collected in 1949-1951.

P_{61} 1.   Arbitrarily picked.

P_{62} 1.   Arbitrarily picked.

P_{63} 3.579   Assume that a 0.52 cm (5.2 mm) pollock loses about 4.423% of its length (the slight difference between standard and total length for this size pollock was neglected) and about 20% of its weight in formalin (reasonable from sources cited in Haryu 1980: 127), and use the formula (ibid.) for the weight of 5-8 mm pollock in formalin:

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Table 3. Parameter Values (continued)

LOG_{10}(mg weight)=   (73)
          6.3694xLOG_{10}(mm length) - 5.3227

Then it is calculated that the true wet weight
of a 0.52 cm (5.2 mm) pollock must be around
.000162 g (.162 mg). Assume that the wet weight
of a 12 cm pollock is given by the formula
(Pereyra et. al. 1976: 234):

$$W = .0075 \times L^{2.977}$$ (74)

Then it is found that the weight of a 12 cm
pollock is about 12.2 g. The normal length-
weight relationship for pollock from 0.52 to 12
cm in length was therefore approximated by a
curve of the form
$W = P_{80} \times L^{P_{63}}$ which passes through the weights
.00162 g and 12.2 g. Solving for P_{63} and P_{80}, it
is found that P_{63}=3.579 and P_{80}=.00168.

P_{64} 1×10^{10} ova/5 km^3 [2 ova/m^3, 100 ova/m^2,
1000 ova/10 m^2] P_{64} is used only if logical
variable DOBEV is true. P_{64} is reasonably close
to the maximum egg densities found by Waldron
and Vinter (1978: tables 6 and 8). However,
P_{64} may be low when it is considered that it
represents all the eggs laid in an entire
breeding season, including those later lost to
predators or other sources. In contrast, the
values measured by Waldron and Vinter were
average values over a time span of about 4 to 13
days (not the entire breeding season), which
were measured in the sea after some consumption
by predators and other losses had presumably
already occurred.

P_{65} .57   [.57 is converted in the
computer program to 2.0 cm (20. mm)] Gorbunova
(1954: table 24) found that post-larval pollock
from 20 to 35 mm total length were passing from
a pelagic form of life to life near the bottom.
See the section on recruitment to being
cannibalized.

Table 3. Parameter Values (continued)

P_{66} 3.5 cm   [35 mm] Same source as P_{65}.
          P_{66} is modified after input (see the definition
          of P_{66} in Appendix table A-1).

P_{67} .01   Arbitrarily picked.

P_{68} 44.1686 cm   See   the   definitions   of
             P_{68} and P_{70}.

P_{69} 3.93×10^7 gC/5 km^3 [.00786 gC/m^3, 7.86 mg/Cm^3,
          7.86 micrograms C/l, 1 <u>Artemia</u> <u>salina</u> nauplius
          per 70 ml]   A reasonable extrapolation from
          Lasker (1966: fig. 11) - see also the value
          for P_{50}.

P_{70} .0075 g/cm$^{3.0}$ Pereyra et al. (1976:   234)
          found a pollock length-weight relationship
          of
          $W = .0075 \times L^{2.977}$, so in various places in the
          model the relationship $W = P_{70} \times L^3$ is used.

P_{71} 2.   One   parameterization   of
          the Weibull hazard function is given by the form
          $(b/a^b) \times (c-X)^{(b-1)}$, where $P_{71} = b-1$, $P_{72} = b/a^b$,
          and $P_{73} = c$. As described in the section on
          condition dependent mortality for pollock, rough
          estimates were made of a=.0797, b=3.055, c=.752
          (tench); a=.0590, b=1.5856, c=.758 (pike); and
          a=.0658, b=4.762, c=.747 (sheatfish).   Thus
          a=.069336,   b=3.0,   and   c=.75   seem   to   be
          reasonable guesses for pollock, which gives
          $P_{71} = 2.$, $P_{72} = 9000.$, and $P_{73} = .75$. (See P_{81}, P_{82},
          P_{83}).

P_{72} 9000 year^{-1} Same source as P_{71}.

Table 3.   Parameter Values (continued)

P_{73} .75   Same source as P_{71}.

P_{74} 0. numbers/5 km^3 Arbitrarily   picked. P_{74}
                 should either equal 0 or else be greater than
                 NMIN.   See the section on pollock numbers
                 (mortalities).

P_{75} .6   Arbitrarily   picked. P_{75}
                 should be less than or equal to MIN(P_{89},P_{96}).

P_{76} .06   Arbitrarily picked.

P_{78} 6.4   Adjusted   to   fit   known
                 pollock characteristics and population dynamics.
                 Same source as P_{58}.

P_{79} -.02   Adjusted   to   fit   known
                 pollock characteristics and population dynamics.
                 Contrast with the value for P_{59}.

P_{80} .00168 g/cm$^{P_{63}}$ Same source as P_{63}.

P_{81} 2.   Same source as P_{71}.

P_{82} 9000 year^{-1} Same source as P_{71}.

P_{83} .75   Same source as P_{71}.

Table 3. Parameter Values (continued)

P_{84} 40. cm Reasonable from Takahashi and Yamaguchi (1972: table 2) using the age-length relationship given in Chang (1974: table 36, but with length in cm):

$$L = 77.6 \times [1 - e^{-.14x(age + 0.4)}] \qquad (75)$$

P_{85} .463 cm^{-1} [$1/P_{85}$ = 2.16 cm] $1/P_{85}$ is equivalent to the <u>sigma</u> (logistic standard deviation) of 2.16 cm estimated by Kimura (1978) for the selectivity ogive of a trawl net, using data for haddock (<u>Gadus aeglefinus</u>) given in Beverton and Holt (1957: table 14:12).

P_{86} .01 Arbitrarily picked.

P_{87} .99 Arbitrarily picked.

P_{89} .75 Adjusted to fit known pollock characteristics and population dynamics. [Compare with P_{75}].

P_{90} 1.05 Adjusted to fit known pollock characteristics and population dynamics. (See P_{106}).

P_{91} 2.1915 cm/year [.06 mm/day] Reasonable for larval pollock at 2 and 5° C. (estimated from Hamai et al. 1971, 1974).

P_{92} 35. cm/year [.96 mm/day] Adjusted to fit known pollock characteristics and population dynamics. A high value for post-larval pollock, though it still seems to be reasonable from Cooney et al. (1979: fig. 19).

Table 3. Parameter Values (continued)

P$_{93}$ .3   Arbitrarily picked.

P$_{94}$ .7470703125 years   [Oct. 1] Adjusted to fit
          known pollock characteristics and population
          dynamics.

P$_{95}$ .83203125 years   [Nov. 1] Adjusted to fit
          known pollock characteristics and population
          dynamics.

P$_{96}$ 1.   Adjusted to fit known
          pollock characteristics and population dynamics.

P$_{97}$ .04914 g/year   [49.14 mg/year] Once P$_{98}$
          was chosen P$_{97}$ was calculated by assuming that
          if W$_1$=.00020 g (compare to the value for P$_{13}$),
          then UPRED+M$_1$=EF.   Then P$_{97}$ was solved for in
          the expression UPRED=P$_{97}$/[W$_1$+P$_{98}$].

P$_{98}$ .0011 g   [1.1 mg] Adjusted to fit
          known pollock characteristics and population
          dynamics. (See P$_{97}$).

P$_{99}$ 35. cm/year   [.96 mm/day] Adjusted to
          fit known pollock characteristics and population
          dynamics. Same source as P$_{92}$.

P$_{100}$ .1   Arbitrarily   picked.
          (See P$_{104}$, P$_{106}$).

P$_{101}$ -.15   Adjusted to fit known
          pollock characteristics and population dynamics.
          Fry and Cox (1970) presented data of their own
          and also cited data from various other authors,
          indicating that the swimming speeds of various
          fish species (pollock were not discussed) are
          approximately proportional to W^a, where
          parameter a ranged from 0.13 to 0.33.   This

Table 3.   Parameter Values (continued)

would indicate a possible range for P_{101} of -0.13 to -0.33.   Fry and Cox (ibid.) presented or cited data for rainbow trout (Salmo gairdneri), herring (Clupea harengus), sockeye salmon (Oncorhynchus nerka), brown trout (Salmo trutta), yellow perch (Perca flavescens), walleye (Stizostedion vitreum), dace (Leuciscus leuciscus), and three species of minnow (scientific names not given).

P_{102} -.15   Adjusted   to   fit   known pollock characteristics and population dynamics. Same source as P_{101}.

P_{104} 5.98×10^{-5} g/cm$^{P_{105}}$ Adjusted   to   fit   known pollock characteristics and population dynamics. Using least squares linear regression, pollock used by Shew (1978) were found to have the length-weight relationship:

$$LN(W) = -7.42132 + 3.66765 \times LN(L) \qquad (76)$$

[N=73, r=.95, significance of r>99.9%], which implies the length-weight relationship

$$W = 5.98 \times 10^{-4} \times L^{3.66765} \qquad (77)$$

So, P_{104} was set equal to $5.98 \times 10^{-4} \times P_{100}$.   See also P_6, P_{106}.

P_{105} 3.66765   Adjusted   to   fit   known pollock characteristics and population dynamics. Same source as P_{104}.

P_{106} 10.5 P_{106} equals P_{90}/P_{100}.

P_{107} -725.947   Bakkala   and   Smith (1978: 94).

Table 3. Parameter Values (continued)

P_{108} $-.224$ cm^{-1} Same source as P_{107}.

P_{109} -867.088 Same source as P_{107}.

P_{110} $-.209$ cm^{-1} Same source as P_{107}.

P_{111} 47.5 cm   Reasonable from Takahashi and Yamaguchi(1972: fig. 11). However, it doesn't matter what P_{111} is, so long as P_{17} equals P_{114}.

P_{112} 25 cm   Reasonable from Takahasi and Yamaguchi (1972: fig. 11). However, it doesn't matter what P_{112} and P_{113} are, so long as P_{58} equals P_{78}.

P_{113} 55 cm   Same source as P_{112}.

P_{114} Same as P_{17}.

P_{115} 1.   Arbitrarily picked.

P_{116} 1.   Arbitrarily picked.

P_{117} $.79$ g$^{-P_{118}}$ A value used by Jones and Hislop (1978) for North Sea cod (Gadus morhua), haddock (Melanogrammus aeglefinus), saithe (Pollachius virens), and whiting (Merlangius merlangus). See the section on unconstrained pollock weights.

P_{118} $-.15$ Same source as P_{117}.

Table 3. Parameter Values (continued)

P_{119} 2.95   Adjusted   to   fit   known
             pollock characteristics and population dynamics.
             Same source as P_7.

PLENTY   .TRUE.

Q2   .46   Mito(1974: 56).

RDWGHT   .TRUE.

TD   .03125 years   [1/32 years; about 11 days]
          The initial value for TD may be varied from
          TDMIN to TDMAX by the numerical integration
          subroutine.

TDMAX   .5 years

TDMIN   .00048828125 years   [1/2048 years; about 4.3
          hours]

TF   .6650390625 years   [Sept. 1]

TL   55.6650390625 years   [Sept. 1]

$ZLNG_1$ .0035 cm   [35 microns]   The   mean
           cell diameter of _Coscinodiscus angstii_ (Frost
           1975: table 1).

$ZLNG_2$ .46 cm   [4.6 mm] Calculated for a
           copepod weighing 2.5 mg using Fulton (1968:
           figures 6 and 7).

$ZLNG_3$ 1.5 cm   Reasonable from Mauchline
           and Fisher (1969) for the genus _Thysanoessa_

Table 3. Parameter Values (continued)

(species <u>spinifera</u>, <u>longpipes</u>, <u>inermis</u>, and <u>raschii</u>).

ZW_1 2.65×10^{-8} g   [.0265 micrograms, 26.5 nanograms]   Calculated assuming a volume of 2.6×10^4 cubic microns (the volume of <u>Coscinodiscus angstii</u>, Frost 1972: table 1), and a specific gravity of 1.02 g/ml (specific gravity of phytoplankton, Alexander 1977: 368).

ZW_2 .0025 g   [2.5 mg] Weight of a <u>Calanus plumchrus</u> (Le Brasseur et al. 1969: table 1).

ZW_3 .047 g   [47 mg] Weight of an euphausiid assuming a length of 1.5 cm (Fulton 1968: fig. 9).

V.   REFERENCES

Alexander, V.

   1977. Phytoplankton   studies   in   the   Bering   Sea.
   In Environmental assessment of the Alaskan continental

   shelf, Annual Reports 11:357-423.   U.S. Dep. Commer.,

   Natl. Oceanic Atmos. Admin., Environ. Res. Lab.,

   Boulder, Colo.

Alton, M. S., and R. A. Fredin.

   1974. Status of Alaska pollock in the eastern Bering

   Sea.   Unpubl. manuscr., 21 p.   Northwest and Alaska

   Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725

   Montlake Blvd. E., Seattle, WA 98112.

Andersen, K. P., and E. Ursin.

   1977. A multispecies extension to the Beverton and Holt

   theory of fishing, with accounts of phosphorus

   circulation and primary production. Medd. Dan. Fisk.

   Havunders. 7:319-435.

Anderson, G. C., R. K. Lam, B. C. Booth, and J. M. Glass.

    1977. A description and numerical analysis of the factors affecting the processes of production in the Gulf of Alaska, final report. In Environmental assessment of the Alaskan continental shelf. Annual Reports 7:477-798. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Environ. Res. Lab., Boulder, Colo.

Bailey, K., and J. Dunn.

    1979. Spring and summer foods of walleye pollock, Theragra chalcogramma, in the eastern Bering Sea. Fish. Bull., U.S. 77(1):304-308.

Bakkala, R., W. Hirschberger, and K. King.

    1979. The groundfish resources of the eastern Bering Sea and Aleutian Islands Regions. Mar. Fish. Rev. 41(11):1-24.

Bakkala, R., and G. B. Smith.

    1978. Demersal fish resources of the eastern Bering Sea: spring 1976. Processed Rep., 234 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Bakkala, R., V. Wespestad, L. Low, and J. Traynor.

    1980. Condition of groundfish resources of the eastern
Bering Sea and Aleutian Islands region in 1980.
Unpubl. rep., 97 p., Northwest and Alaska Fish. Cent.,
Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E.,
Seattle, WA 98112. (Document submitted to the Annual
Meeting of the International North Pacific Fisheries
Commission, Anchorage, Alaska, October 1980.)

Beverton, R. J. H., and S. J. Holt.

    1957. On the dynamics of exploited fish populations.
U. K. Minist. Agric. Fish. Food, Fish. Invest., Ser.
2, Vol. 19:533 p.

Bickel, P. J., and K. A. Doksum.

    1977. Mathematical statistics. Holden Day, Inc.,
San Francisco, Calif., 493 p.

Bledsoe, L. J.

    1976. Simulation of a grassland ecosystem. Ph.D.
Thesis, Colorado State Univ., Fort Collins, Colo.,
346 p.

Bledsoe, L. J.

[1979.] Mechanisms of population-energetics linkages in age-structured food web models. _In_ S. J. Lipovsky and C. A. Simenstad (editors), Gutshop '78, p. 200-214. Univ. Wash., Seattle, Div. Mar. Resour., Wash. Sea Grant, WSG-WO-79-1.

Burroughs Corporation.

1978 [including changes dated through Nov., 1979]. B 7000/B 6000 series FORTRAN reference manual. Burroughs Corp., El Monte, Calif.

Bury, K. V.

1975. Statistical models in applied science. John Wiley & Sons, New York, 625 p.

Chang, S.

1974. An evaluation of the eastern Bering Sea fishery for Alaska pollock (_Theragra chalcogramma_, Pallas): population dynamics. Ph.D. Thesis, Univ. Washington, Seattle, Wash., 281 p.

Christiansen, J.

1970. Numerical solution of ordinary simultaneous differential equations of the 1st order using a method for automatic step change. Numer. Math. 14:317-324.

Clarke, M. E.

   1978. Some aspects of the feeding biology of larval
      walleye pollock, Theragra chalcogramma (Pallas), in
      the southeastern Bering Sea. In Progress report
      PROBES phase I, 1977-78, p. 314-364. Univ. Alaska,
      Inst. Mar. Sci., P.O. Box 95102, Fairbanks, AK 99701.

Cochran, W. G.

   1977. Sampling techniques. 3rd ed. John Wiley & Sons,
      New York, 428 p.

Cooney, R. T., T. S. English, and T. Nishiyama.

   [1979]. Upper trophic level ecology with emphasis on
      juvenile Alaska pollock in the southeast Bering Sea.
      In Progress report PROBES phase I, 1977-78, p. 241-
      403. Univ. Alaska, Inst. Mar. Sci., P.O. Box 95102,
      Fairbanks, AK 99701.

Daan, N.

   1973. A quantitative analysis of the food intake of
      North Sea cod, Gadus morhua. Neth. J. Sea Res.
      6(4):479-517.

Dahlberg, M. D.

   1979. A review of survival rates of fish eggs and
      larvae in relation to impact assessments. Mar. Fish.
      Rev. 41(3):1-12.

Eickwort, K. R.

   1973. Cannibalism and kin selection in Labidomera
   clivicollis (Coleoptera: Chrysomelidae). Am. Nat.
   107(955):452-453.

Favorite, F., and T. Laevastu.

   1981. Finfish and the environment. In D. W. Hood and
   J. A. Calder (editors), The eastern Bering Sea shelf:
   oceanography and resources, Volume 1, p. 597-610.
   U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Off.
   Mar. Pollut. Assess., U.S. Gov. Print. Off.,
   Washington, D.C.

Favorite, F., T. Laevastu, and R. R. Straty.

   1977. Oceanography of the northeastern Pacific Ocean and
   eastern Bering Sea, and relations to various living
   marine resources. Processed Rep., 280 p. Northwest
   and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA,
   2725 Montlake Blvd. E., Seattle, WA 98112.

Fox, L. R.

   1975. Cannibalism in natural populations. Annu. Rev.
   Ecol. Syst. 6:87-106.

Frost, B. W.

1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod Calanus pacificus. Limnol. Oceanogr. 17(6):805-815.

Frost, B. W.

1975. A threshhold feeding behavior in Calanus pacificus. Limnol. Oceanogr. 20(2):263-266.

Fry, F. E. J., and E. T. Cox.

1970. A relation of size to swimming speed in rainbow trout. J. Fish. Res. Board Can. 27(5):976-978.

Fulton, J.

1968. A laboratory manual for the identification of British Columbia marine zooplankton. Fish. Res. Board Can. Tech. Rep. 55, 141 pp.

Gorbunova, N. N.

 1954. Razmnozhenie   i   razvitie   mintaya   Theragra
      chalcogramma   (Pallas)   (The   reproduction   and
      development of walleye pollock (Theragra chalcogramma
      (Pallas))).   Tr. Inst. Okeanol.   Akad. Nauk SSSR
      11:132-195.   In Russian.   (Transl. by S. Pearson,
      1972, 106 p., Northwest and Alaska Fish. Cent., Natl.
      Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E.,
      Seattle, WA 98112.

Grauman, G. B.

 1973. Investigations of factors influencing fluctuations
      in abundance of Baltic cod. Rapp. P. -V. Reun. Cons.
      Int. Explor. Mer 164:73-76.

Hamai, I., K. Kyushin, and T. Kinoshita.

 1971. Effect of temperature on the body form and
      mortality in the developmental and early larval stages
      of the Alaska pollock, Theragra chalcogramma (Pallas).
      Bull. Fac. Fish. Hokkaido Univ. 22(1):11-29.

Hamai, I., K. Kyushin, and T. Kinoshita.

 1974. On the early larval growth, survival and variation
      of body form in the walleye pollock, Theragra
      chalcogramma (Pallas), in rearing experiment feeding
      the different diets. Bull. Fac. Fish. Hokkaido Univ.
      25(1):20-35.

Haryu, T.

   1980. Larval distribution of walleye pollock,
   Theragra chalcogramma (Pallas), in the Bering Sea,
   with special reference to morphological changes.
   Bull. Fac. Fish. Hokkaido Univ. 31(2):121-136.

Ikeda, T.

   1974. Nutritional ecology of marine zooplankton. Mem.
   Fac. Fish. Hokkaido Univ. 22(1):1-97.

Ivlev, V. S.

   1961. Experimental ecology of the feeding of fishes.
   (Translated from Russian by D. Scott.) Yale Univ.
   Press, New Haven, Conn., 302 p.

Jones, R.

   1974. The rate of elimination of food from the stomachs
   of haddock Melanogrammus aeglefinus, cod Gadus morhua
   and whiting Merlangius merlangus. J. Cons. Int.
   Explor. Mer 35(3):225-243.

Jones, R.

   1978. Estimates of the food consumption of haddock
   (Melanogrammus aeglefinus) and cod (Gadus morhua). J.
   Cons. Int. Explor. Mer 38(1):18-27.

Jones, R., and J. R. G. Hislop.

    1978. Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. Int. Explor. Mer 38(2):244-251.

Jones, R., and C. Johnston.

    1977. Growth, reproduction and mortality in gadoid fish species. In J. H. Steele (editor), Fisheries mathematics, p. 37-62. Academic Press, New York.

Kaganovskaya, S. M.

    1950. Materialy k poznaniyu mintaya (Data for a biological study of Alaska pollock). Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 32:103-119. In Russian. (Transl. by Fish. Lab., Lowestoft, England).

Kimura, D. K.

    1978. Logistic model for estimating selection ogives from catches of codends whose ogives overlap. J. Cons. Int. Explor. Mer 38(1):116-119.

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Laevastu, T., and F. Favorite.

  1976a. Evaluation of standing stocks of marine resources
    in the eastern Bering Sea (using a static-trophic
    numerical bulk biomass model BBM). Processed Rep., 35
    p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish.
    Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA
    98112.

Laevastu, T., and F. Favorite.

  1976b. Dynamics of pollock and herring biomasses in the
    eastern Bering Sea (An introductory study of
    fluctuations of pollock and herring stocks using
    preliminary 8-component Dynamic Numerical Marine
    Ecosystem Model). Processed Rep., 50 p. Northwest
    and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA,
    2725 Montlake Blvd. E., Seattle, WA 98112.

Lasker, R.

  1966. Feeding, growth, respiration, and carbon
    utilization of a euphausiid crustacean. J. Fish. Res.
    Board Can. 23(9):1291-1317.

LeBrasseur, R. J.,   W. E. Barraclough,   O. D. Kennedy, and T. R. Parsons.

   1969. Production studies in the   Strait of   Georgia.
   Part III.   Observations on the food of larval and
   juvenile fish in the Fraser River plume, February to
   May, 1967. J. Exp. Mar. Biol. Ecol. 3(1):51-61.

Lisitsyn, A. P.

   1966.   Protsessy   sovremennogo   osadkoobrazovaniya   v
   Beringovom more (Recent sedimentation in the Bering
   Sea).   Izd. Nauka, Moscow.   In Russian. (Transl. by
   Isr. Program Sci. Transl., 1969, 614 p., avail. U.S.
   Dep. Commer., Natl. Tech. Inf. Serv., Springfield,
   Va., as TT 68-50315).

Low, L. L.

   1974. A study of four major groundfish fisheries of the
   Bering Sea. Ph. D. Thesis, Univ. Washington, Seattle,
   Wash., 241 p.

Low, L. L.

   1979. Status of the pollock resource in the eastern
      Bering Sea. In R. Bakkala, L. Low, and V. Wespestad,
      Condition of groundfish resources in the Bering Sea
      and Aleutian area, p. 1-16. Northwest and Alaska
      Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725
      Montlake Blvd. E., Seattle, WA 98112. (Document
      submitted to the Annual Meeting of the International
      North Pacific Fisheries Commission, Tokyo, Japan,
      October 1979.)

Low, L. L., and J. Akada.

   1978. Atlas of groundfish catch in the northeastern
      Pacific Ocean, 1964-1976. Processed Rep., 546 p.
      Northwest and Alaska Fish. Cent., Natl. Mar. Fish.
      Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA
      98112.

Maeda, T.

   1972. Fishing grounds of the Alaska pollack. Bull. Jpn.
      Soc. Sci. Fish. 38(4):362-371, 415. In Japanese,
      figure captions and summary in English.

Mauchline, J., and L. R. Fisher.

   1969. The biology of marine euphausiids. Adv. Mar.
      Biol., Vol. 7. Academic Press, New York, 454 p.

May, R. M., and G. F. Oster.

   1976. Bifurcations and dynamic complexity in simple
   ecological models. Am. Nat. 110(974):573-599.

McAllister, C. D.

   1970. Zooplankton rations, phytoplankton mortality and
   the estimation of marine production. In J. H. Steele
   (editor), Marine food chains, P. 419-457. Oliver and
   Boyd, Edinburgh, Scotland.

McRoy, C. P., and J. J. Goering.

   1974. The influence of ice on the primary productivity
   of the Bering Sea. In D. W. Hood and E. J. Kelley
   (editors), Oceanography of the Bering Sea with
   emphasis on renewable resources, p. 403-421. Univ.
   Alaska, Fairbanks, Inst. Mar. Sci., Occas. Publ. No.
   2.

McRoy, C. P., and J. J. Goering.

   [1975.] Primary production budget for the Bering Sea.
   In D. W. Hood and Y. Takenouti (editors), Bering Sea
   oceanography: an update 1972-1974, p. 97-107. Univ.
   Alaska, Fairbanks, Inst. Mar. Sci., Rep. 75-2.

Meshcheryakova, I. M.

  1970. Plankton vostochnoi chasti Beringova morya v
     vesennii i osennii gidrologicheskie sezony (Plankton
     of the eastern Bering Sea in spring and autumn). Tr.
     Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz.
     Okeanogr. 70 (Izv. Tikhookean. Nauchno-issled. Inst.
     Rybn. Khoz. Okeanogr. 72):98-114. In Russian.
     (Transl. by Isr. Program Sci. Transl., 1972, p. 92-108
     in P. A. Moiseev (editor), Soviet fisheries
     investigations in the northeastern Pacific, Part 5,
     avail. U.S. Dep. Commer., Natl. Tech. Inf. Serv.,
     Springfield, Va., as TT 71-50127.

Mito, K.

  1974. Food relationships among benthic fish populations
     in the Bering Sea on the Theragra chalcogramma fishing
     grounds in October and November of 1972. M.S. Thesis,
     Hokkaido Univ., Hokodate, Japan. (Transl. by Lang.
     Serv. Div. U.S. Dep. Commer., Natl. Oceanic Atmos.
     Admin., Natl. Mar. Fish. Serv., NOAA, Washington,
     D.C., 1977, 235 p.)

Motoda, S., and T. Minoda.

 1974. Plankton of the Bering Sea. In D. W. Hood and
   E. J. Kelley (editors), Oceanography of the Bering Sea
   with emphasis on renewable resources, p. 207-241.
   Univ. Alaska, Fairbanks, Inst. Mar. Sci., Occas. Publ.
   No. 2.

Mullin, M. M.

 1969. Production of zooplankton in the ocean: the
   present status and problems. Oceanogr. Mar. Biol.
   Annu. Rev. 7:293-314.

Naylor, T. H., J. L. Balintfy, D. S. Burdick, and K. Chu.
 1966. Computer simulation techniques. John Wiley
   & Sons, New York, 352 p.

Okada, K.

 1979. Biological characteristics and distribution of
   pelagic pollock stocks on the Aleutian Basin. Unpubl.
   manuscr, 26 p. Fishery Agency of Japan, 2-1
   Kasumigaseki, Chiyoda-ku, Tokyo, Japan.

Oster, G., and Y. Takahashi.

 1974. Models for age-specific interactions in a periodic
   environment. Ecol. Monogr. 44(4):483-501.

Parrish, J. D.

  1975. Marine trophic interactions by dynamic simulation of fish species. Fish. Bull., U.S. 73(4):695-716.

Parsons, T. R., R. J. LeBrasseur, and J. D. Fulton.

  1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. Oceanogr. Soc. Jpn. 23(1):10-17.

Pereyra, W. T., J. E. Reeves, and R. G. Bakkala.

  1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Processed Rep., 619 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Pileggi, J., and B. G. Thompson.

  1980. Fisheries of the United States, 1979. U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Curr. Fish. Stat. No. 8000, 131 p.

Pruter, A. T.

  1973. Development and present status of bottomfish resources in the Bering Sea. J. Fish. Res. Board Can. 30(12), Part 2:2373-2385.

Pruter, A. T.

   1976. Soviet fisheries for bottomfish and herring off
   the Pacific and Bering Sea coasts of the United
   States.   Mar. Fish. Rev. 38(12):1-14.

Ricker, W. E.

   1958. Handbook of computations for biological statistics
   of fish populations. Bull. Fish. Res. Board Can. 119:
   300 p.

Ricker, W. E.

   1975. Computation and interpretation of   biological
   statistics of fish populations.   Bull. Fish. Res.
   Board Can. 191:   382 p.

Robinson, M. K.

   1976. Atlas of the north Pacific Ocean monthly mean
   temperatures and mean salinities of the surface layer,
   U.S. Dep. Navy, Naval Oceanogr. Off. Ref. Publ. 2, 173
   p.

Rogers, D. E., B. J. Rogers, and M. E. Wangerin.

   1980. Seasonal composition and food web relationships of
   marine organisms in the nearshore zone of Kodiak
   Island - including ichthyoplankton, zooplankton, and
   fish. A report on the fish component of the study.
   Unpubl. manuscr., 109 p. Fish. Res. Inst., Univ.
   Wash., WH-10, Seattle, WA 98195.

Ross, R. M.

   1979. Carbon and nitrogen budgets over the life of
   Euphausia pacifica. Ph.D. Thesis, Univ. Washington,
   Seattle, Wash., 260 p.

Sameoto, D. D.

   1976. Respiration rates, energy budgets, and molting
   frequencies of three species of euphausiids found in
   the Gulf of St. Lawrence. J. Fish. Res. Board Can.
   33(11):2568-2576.

Serobaba, I. I.

    1970. Raspredelenie mintaya Theragra chalcogramma (Pallas) v vostochnoi chasti Beringova morya i vozmozhnosti ego promysla (Distribution of walleye pollock Theragra chalcogramma (Pallas) in the eastern Bering Sea and prospects of its fishery). Tr. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 70 (Izv. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. 72):433-442. In Russian. (Transl. by Isr. Program Sci. Transl., 1972, p. 442-451 in P. A. Moiseev (editor), Soviet fisheries investigations in the northeastern Pacific, Part 5, avail. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 71-50127.)

Serobaba, I. I.

    1974. Spawning ecology of the walleye pollock (Theragra chalcogramma) in the Bering Sea. Vopr. Ikhtiol. 14(4):635-644. In Russian. (Transl. in J. Ichthyol., 1972, 14(4):544-552.)

Shew, D. M.

    1978. Pollock fecundity study; preliminary report. Unpubl. manuscr., 42 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Smith, G. B.

   1981. The biology of walleye pollock. In D. W. Hood and
      J. A. Calder (editors), The eastern Bering Sea shelf:
      oceanography and resources, Volume 1, p. 527-551.
      U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Off.
      Mar. Pollut. Assess., U.S. Gov. Print. Off.,
      Washington, D.C.

Strathmann, R. R.

   1967. Estimating the organic carbon content of
      phytoplankton from cell volume or plasma volume.
      Limnol. Oceanogr. 12(3):411-418.

Takahashi, Y., and H. Yamaguchi.

   1972. Stock of the Alaska pollack in the eastern Bering
      Sea. Bull. Jpn. Soc. Sci. Fish. 38(4):389-399, 418-
      419. In Japanese, figure captions and summary in
      English.

Waldron, K. D., and B. M. Vinter.

   1978. Ichthyoplankton of the eastern Bering Sea.
      Processed Rep., 88 p. Northwest and Alaska Fish.
      Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake
      Blvd. E., Seattle, WA 98112.

Wespestad, V.

    1978. Winter food habits of pollock in the eastern Bering Sea. Unpubl. manuscr., 13 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

Yamaguchi, H., and Y. Takahashi.

    1972. Growth and age estimation of the Pacific pollock, in the eastern Bering Sea. Bull. Far Seas Fish. Res. Lab. 7:49-69. In Japanese. (Transl. by Transl. Bur., Multilingual Serv. Div., Dep. Secr. Can., 1974, 39 p.)

APPENDIX A.

Definitions of Variables Used

Short definitions of the most important variables used in the text and computer program are listed in Table A-1 (variables listed as not being an input are calculated from other quantities input). For tables listing values for the input variables, see the section on parameter values and origins.

Table A-1.   Variable Definitions

Variable
Name   Units and Short Definition

AC   An array containing the values of various
              state variables from a given time. They are
              used to check whether a stationary population
              structure has occured.

ACCRCY   (unitless) An input variable determining the
              number of significant digits desired when
              numerically integrating the differential
              equations of the model.
                         (-N)
              ACCRCY=.5x[10   ] usually gives a solution
              locally accurate to at least N digits. If
              ACCRCY$\geq$1, no accuracy check is made, and no step
              size changes are made during numerical
              integration. See U5.

AOFF   (years; not an input) An age offset used to
              calculate the age of pollock at a given time of
              year. The age of a pollock in cohort i is equal
              to (i-1)xDTAU+MOD(TT+AOFF,DTAU).

ASTOP   A logical variable. If ASTOP=.TRUE., the
              simulation run will soon be stopped because the
              criterion for a stationary population structure
              was met at least once.

$Avail_j$ (unitless) The availability or vulnerability of
              food item category j to pollock. See the
              section on the perceived food densities of
              pollock.

B   (g/5 km^3) An array containing the wet weights
              of the biomasses of the individual pollock

Table A-1. Variable Definitions (continued)

cohorts. However, in subroutines AGESTA and SHOW, B is used to represent all the variables in common block STATE.

BTT   (g/5 km^3) The total biomass of all pollock in the model.

B313   (g/5 km^3) The biomass of pollock cohorts 3 through 13 (ages 2 through 12).

CN   (unitless) An array. CN_i contains the average condition index for fish in pollock cohort i.

COMAX   The maximum number of pollock cohorts allowed to exist at any given time in a simulation run. COMAX should be less than or equal to KD.

COPE   (g/5 km^3) The total wet weight of the copepod biomass.

COPE'   ([g/5 km^3]/year) The derivative of COPE.

COPEC   (gC/5 km^3) The total organic carbon contained in the copepod biomass. COPEC=P_{45}xCOPE.

CT   (years) The simulated elapsed time between the present time as simulated in the model and what would have been last beginning of a cycle of discrete time events. CT=MOD(TT+CYCLE-CYOFF,CYCLE). CT is only calculated when

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Table A-1. Variable Definitions (continued)

preparing to start a simulation run. It is used
to determine which discrete time event will next
be performed.

CYCLE   (years) The simulated elapsed time in the model
          between the occurrence of the first event in the
          cycle of discrete time events and the next
          occurrence of the first event in the cycle.
          CYCLE is the period of the cycle of discrete
          events in the model (see CT above). CYCLE must
          be an integral multiple of DTAU.

CYOFF   (years; not an input) The simulated elapsed time
          in the model between time zero (0000 hours on a
          certain Jan. 1) and the first subsequent
          occurrence of the last discrete event in the
          cycle of discrete time events (see CT).

D   (g/5 km^3) D is a two dimensional array.
          $D_{j,i}$ contains the density of food item
          category j as perceived by pollock cohort i.   D
          is also used to contain intermediate steps in
          the calculation of the perceived food densities.

DBUG   A logical variable. If DBUG=.TRUE., extensive
          and voluminous printouts are made of various
          variables and quantities as an aid to checking
          calculations and detecting errors.

DD   A logical variable. If DD=.TRUE., certain
          variables are periodically written onto a data
          file in machine readable format for later
          analysis.

Table A-1. Variable Definitions (continued)

DOBEV   A logical variable. If DOBEV=.TRUE., certain growth and fecundity equations are used and certain parameters are set so that the model (POL) behaves like a single species Beverton and Holt (1957) model or a Ricker (1958) model.

DOGRPH   A logical variable. If DOGRPH = .TRUE., line printer graphs of certain quantities are made.

DTAU   (years) The simulated elapsed time between two consecutive cohort updates in the model. This also means that DTAU is the difference in age between any two consecutive pollock cohorts. CYCLE must be an integral multiple of DTAU.

D2   (unitless) The power used to calculate the weight from the length for pollock over age P_{12} under conditions of constrained growth. Under such conditions,

$$W_i = D8 \times L_i^{D2} .$$

D4   (years) The hypothetical age that a pollock growing according to the constrained (von Bertalanffy) growth in length equation would have been 0 centimeters in length.

D6   (g/year; not an input) The rate that a pollock grows in weight if it is growing according to the constrained growth equations and if it is less than P_{12} in age (linear growth). $D6 = [WVB(P_{12}) - P_{13}]/P_{12}$.

Table A-1. Variable Definitions (continued)

D7   (cm) The length that a pollock would attain if
            it lived to an infinite age and if it was
            growing according to the constrained (von
            Bertalanffy) growth in length equation.

D8   (g/cm^{D2}) The coefficient used to calculate the
            weight from the length for pollock over age P_{12}
            under conditions of constrained growth.   (see
            D2).

D9   (cm/year; not an input) The rate that a pollock
            grows in length if it is growing according to
            the constrained growth equations and if it is
            less than P_{12} in age (linear growth).
            $D9=[P_{77}-P_{14}]/P_{12}$.

E   (eggs/5 km^3) The   total number   of surviving
            pollock eggs at a given time.

EATER   (unitless) An array. $EATER_i$ contains a relative
            maximum possible average feeding rate for
            pollock in cohort i.

EF   (year^{-1}) The instantaneous mortality   rate of
            pollock eggs.

EGGDUR   (years; not an input) The simulated elapsed time
            in the model from the instant pollock eggs are
            laid until the instant they hatch.

Table A-1. Variable Definitions (continued)

ETT   (ova/5 km^3) The total number of pollock ova laid
           at a given time.

EUPH   (g/5 km^3) The total wet weight of the
           euphausiid biomass.

EUPH'   ([g/5 km^3]/year) The derivative of EUPH.

EUPHC   (gC/5 km^3) The total organic carbon contained
           in the euphausiid biomass. EUPHC=EUPHxP_{48}.

F   (year^{-1}) An array containing the instantaneous
           fishing mortality rates for the individual
           pollock cohorts. F may be set once when
           preparing for a computer run, or it may
           optionally be reset (discrete time event 7)
           using the formula F_i=XETOF x XEFFRT, for
           $1 \leq i \leq$ COMAX.

FCF   (unitless) An array containing the fractions
           of the individual pollock cohorts which consist
           of mature females.

FCM   (unitless) An array containing the fractions of
           the individual pollock cohorts which consist of
           mature males.

FD   (g/5 km^3) An array containing the total
           perceived food densities for the individual
           pollock cohorts.

Table A-1. Variable Definitions (continued)

FDU   ([g/year]/cm$^{P_{119}}$) An array containing
             coefficients used to calculate the maximum
             feeding rates for the individual pollock
             cohorts.

FISHIN   A logical variable. FISHIN=.TRUE., indicates
             that fishing is presently occurring in the
             simulation run.

FSTART   (years) The simulated most recent time that
             fishing started in the model.

GCN   (unitless) An array containing the maximums
             attained by the condition indexes [CN's] of the
             individual pollock cohorts since the last cohort
             update. (For cohort 1, since either the last
             cohort update or since they began eating after
             being newly hatched - whichever occurred most
             recently).

HLCAND   (cm) An overestimate of the maximum length
             of pollock which may be cannibalized during a
             given time period.

HOMAX   (cm/year; not an input) The maximum rate which
             any pollock may ever grow in length in the
             model. HOMAX=MAX[P_{91},P_{92},P_{99}]

IAKE   The number of state variables last checked to
             see whether a stationary population structure
             had occurred. (See AC).

Table A-1. Variable Definitions (continued)

ICANAQ   The first pollock cohort which may be
          cannibalized is the ICANAQ'th cohort of the NZ
          cohorts which "actually" exist (See NZ).

ICAND   Cohort ICAND is the last pollock cohort which
          might be cannibalized.

ICANDQ   The last pollock cohort which may be
          cannibalized is the ICANDQ'th cohort of the NZ
          cohorts which "actually" exist (see NZ).

ICANE   Cohort ICANE is the first pollock cohort which
          might participate in breeding. After the cohort
          update (but before the next time to prepare to
          breed), it is the first cohort which might have
          participated in breeding.

ICANF   Cohort ICANF is the first pollock cohort which
          might cannibalize. $ICANF = P_{15}/DTAU + 1$

ICANFQ   The first pollock cohort which might cannibalize
          is the ICANFQ'th cohort of the NZ cohorts which
          "actually" exist (See NZ).

ID   An array containing a title for the printout.

IDOF   The first pollock cohort which might cannibalize
          is the IDOF'th cohort of the NZ cohorts which
          "actually" exist (See NZ). (IDOF is a
          refinement of ICANFQ).

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Table A-1. Variable Definitions (continued)

IER   IER is the total number of variables for which
           the accuracy criterion was not always met during
           numerical integration over a given time period.
           It is set to 0 at the beginning of each time
           period.

IERTOT   The sum of all the values of IER for an entire
           simulation run.

IEV   An array containing the event identifiers
           of the discrete time events.

IEXIST   The first pollock cohort which actually exists
           in the model and which may be cannibalized is
           the IEXIST'th cohort of the NZ cohorts recently
           counted as existing in the model (See NZ).

IFILE   An array containing numbers identifying the
           files on which graphs are to be made.

IGL   An array containing the present line number on
           the page of files on which graphs are being made
           in the model.

IGR   An array containing the locations in common
           block STATE of various quantities to be graphed.
           If IGR_j equals 0, then the j'th quantity is not
           in common block STATE.

IHD   An array containing the values used to calculate
           scales for labeling the graphs being printed.

Table A-1. Variable Definitions (continued)

IHDEC   An array containing decrements used to calculate
            scales for labeling the graphs being printed.

IPAIR   A   variable   (used   in   subroutine   PARMOD)
            indicating whether discrete time events are
            properly paired or not.

ISEQ   A   variable indicating   the   sequence   number of
            the discrete time event being performed or about
            to be performed.

ITRAN   An array containing identifiers indicating which
            transformation is to be performed for quantities
            to be graphed on a given file.

IXX2   The   time (hour,   minute,   second, sixtieth of a
            second) a given computer run of the model was
            started.

JAQ   The same as ICANAQ.

JB   The last pollock cohort which cannot cannibalize
            is the JB'th cohort of the NZ cohorts which
            "actually" exist (See NZ).

JCOH   In   subroutine ISV,   the first cohort for which
            food has not been calculated is the JCOH'th
            cohort of the NZ cohorts which "actually" exist
            (See NZ).

Table A-1. Variable Definitions (continued)

JD   The same as KD.

JDQ   The same as ICANDQ.

JEV   The same as NEV.

JEXIST   The same as IEXIST.

JVON   The same as NVON.

KAY   (year^{-1}) The Brody growth coefficient (as
            defined by Ricker 1975: section 9.6.1). It is
            used to determine the growth rate for pollock
            older than P_{12} which are growing according to
            the constrained (von Bertalanffy) growth in
            length equation.

KD   The dimension of various arrays in the computer
            program which describe pollock cohorts. Some
            examples of these arrays are B, CN, EATER, F,
            FCF, FCM, FD, FDU, GCN, L, M, MT, N, RC, SM, W,
            and WL. COMAX should be less than or equal to
            KD.

KE   The number of distinct quantities being
            calculated by numerical integration at a given
            time in the model.

Table A-1. Variable Definitions (continued)

L   (cm) An   array   containing the   average   fork
            lengths of pollock in the individual pollock
            cohorts.

L'   (cm/year) An array containing the derivatives
            of pollock lengths (L).

LAYING   A   logical   variable.   During   the   time   period
            when the feeding rate of possibly breeding
            pollock may be reduced due to their breeding
            habits, LAYING=.TRUE. Otherwise, LAYING=.FALSE.

LC   An array containing scaled quantities calculated
            from quantities to be graphed.

LIER   A   variable   containing   a   ":"   if   the   accuracy
            criterion was met during numerical integration.
            If the accuracy criterion was not always met
            since the last print-out of graphs, LIER
            contains a "=".

LPRED   (cm) The length of the predator.

LTRAN   An array containing the names of transformations
            which can be used to transform quantities before
            graphing them.

M   (year^{-1}) An   array   containing   instantaneous
            pollock mortality rates not otherwise accounted
            for.

Table A-1. Variable Definitions (continued)

MT   (year^{-1}) An array containing instantaneous
            mortality rates for the individual pollock
            cohorts due to deaths from being cannibalized.

N   (numbers/5 km^3) An array containing the numbers
            of pollock in the individual pollock cohorts.

N'   ([numbers/5 km^3]/year) An array containing
            the derivatives of the pollock population
            numbers (N).

NC   Pollock cohort NC is the last existing pollock
            cohort. NC is not reset during numerical
            integration, but it may be reset afterwards (See
            NZ).

NEV   The number of discrete time events in a cycle.

NFILE   The number of files being used to make graphs.

NGR   The total number of quantities to be graphed.

NMIN   (The same units as the population being tested)
            A minimum population value allowed. If the
            population becomes less than NMIN, that
            population is set to 0. PHY, COPE, EUPH, E, and
            the individual pollock cohorts [N_i] are examples
            of populations for which this is done.

Table A-1. Variable Definitions (continued)

NOCOH   A logical variable. NOCOH=.TRUE. means that all the pollock cohorts have ceased to exist in the model (that is, each N_i became less than NMIN). However, some pollock eggs may still exist in the model (that is, E may still be greater than or equal to NMIN).

NOCUM   A logical variable. While NOCUM = .TRUE., certain quantities (See VCUM) are not numerically integrated, because they are not being printed out or otherwise used.

NOUPDA   A logical variable. NOUPDA=.TRUE. indicates a time for the eggs to hatch was not input, so no cohort update can occur.

NQ   An array of indices of quantities to be numerically integrated (See NZ).

NTT   (numbers/5 km^3) The total number of all pollock in the model.

NVON   Pollock cohort i grows according to the constrained growth equations if and only if i$\leq$NVON.

NXTEV   (years) An array containing the times (time points) that the discrete time events are to be performed.

NZ   The number of "existing" pollock cohorts. (Note: NZ and NQ are set each time subroutine CALC is

<u>Table A-1. Variable Definitions (continued)</u>

called. As numerical integration continues, the population of a given cohort may fall to 0, but since NZ and NQ are not immediately reset, numerical integration continues for that cohort; that is, the numerical integration subroutine considers that the cohort still exists. IEXIST is immediately reset, however).

P   An array containing various parameters. (The definitions of the various elements of P follow below).

P_1 (g$^{[1-P_2]}$/year) Coefficient in the respiration term of the unconstrained (physiological) differential equation for pollock weights.

P_2 (unitless) Exponent in the respiration term of the unconstrained (physiological) differential equation for pollock weights.

P_3 (unitless) Maximum possible food conversion efficiency of pollock in the unconstrained (physiological) differential equation for pollock weights.

P_4 (cm; not an input) Critical length for changing from the length-weight relationship for small fish to the length-weight relationship for large fish. See the section on pollock condition dependent mortality.

P_5 (unitless) Maximum relative availabilty (vulnerability) of pollock to cannibalizers.

Table A-1. Variable Definitions (continued)

P_6 (ova/g) "Regression"   coefficient   of   pollock
         fecundity on weight.

P_7 ([g/year]/[cm$^{P_{119}}$]) Coefficient   used   to
         calculate the maximum possible sustained feeding
         rate for pollock in cohort 1 (See P_{17}, P_{114}).

P_8 (g$^{[1-P_{101}]}$/5 km^3) Coefficient   used   in
         calculating   the   critical   value   for   the   total
         food density perceived by pollock in cohort 1 at
         which they begin their maximum feeding rate.
         (See P_{18}).

P_9 (g$^{[1-P_{101}]}$/5 km^3) Coefficient   used   in
         calculating   the   critical   value   for   the   total
         food density perceived by pollock in cohort 1,
         at which their feeding ceases. (See P_{19}).

P_{10} (g/ovum) The grams wet weight of pollock tissue
         "used" to produce one ovum. Note that $P_6 \times P_{10}$ is
         the fraction of its original weight which a
         pollock loses at the instant breeding occurs in
         the model. See also P_{13}.

P_{11} (unitless) A factor used   to adjust P_{27} through
         P_{31} simultaneously.

Table A-1. Variable Definitions (continued)

P_{12} (years) The age at which pollock start growing according to the von Bertalanffy growth curve, if they are growing according to the constrained growth in length equation. (See P_{77}).

P_{13} (g) The wet weight of a newly hatched pollock (which should presumably be less than P_{10}).

P_{14} (cm) The length of a newly hatched pollock.

P_{15} (years) The age at which pollock may begin cannibalizing.

P_{16} (cm^{-1}) A parameter used to interpolate between P_{59} and P_{79}

P_{17} ([g/year]/[$cm^{P_{119}}$]) Coefficient used to calculate the maximum possible sustained feeding rate for those pollock in cohorts 2 and over which are less than P_{111} in length at cohort update time or when a simulation run is started (See P_7, P_{111}, P_{114}).

P_{18} ($g^{[1-P_{102}]}$/5 km^3) Coefficient used in calculating the critical value for the total food density perceived by pollock in cohorts 2 and over, at which they begin their maximum feeding rate. (See P_8).

Table A-1. Variable Definitions (continued)

P_{19} $(g^{[1-P_{102}]}/5\ km^3)$ Coefficient used in calculating the critical value for the total food density perceived by pollock in cohorts 2 and over, at which their feeding ceases. (See P_9).

P_{20} (unitless) Proportion of female pollock in the total pollock population (See P_{120}).

P_{21} (input in units of days, but then converted to years) The time of year that winter ends and the algal bloom in sea ice begins. Legal input values are $P_{21} \le P_{23} \le P_{22}$. See P_{88}.

P_{22} (input in units of days, but then converted to years) The time of year that the algal bloom in sea ice ends. See P_{21}.

P_{23} (input in units of days, but then converted to years) The time of year that spring begins. See P_{21}.

P_{24} (input in units of days, but then converted to years) The time of year that spring ends and summer begins.

P_{25} (input in units of days, but then converted to years) The time of year that summer ends and fall begins.

Table A-1. Variable Definitions (continued)

P_{26} (input in units of days, but then converted to years) The time of year that fall ends and winter begins.

P_{27} (gC/5 km^3) The total gross primary production of carbon during the time period of algal bloom in sea ice (excluding primary production accounted for by P_{28}).

P_{28} (gC/5 km^3) The total gross primary production of carbon during spring (excluding primary production accounted for by P_{27}).

P_{29} (gC/5 km^3) The total gross primary production of carbon during summer.

P_{30} (gC/5 km^3) The total gross primary production of carbon during fall.

P_{31} ([gC/5 km^3]/year) An underlying gross primary production rate which is constant throughout the year.   From time P_{26} to time P_{21} [that is, during winter], it is the only primary production which occurs in the model.

P_{32} (years; not an input) The duration of algal bloom in sea ice. $P_{32} = P_{22} - P_{21}$.

P_{33} (years; not an input) The length of spring. $P_{33} = P_{24} - P_{23}$.

Table A-1.   Variable Definitions (continued)

P_{34} (years; not an input)   The length of summer. $P_{34}=P_{25}-P_{24}$.

P_{35} (years; not an input)   The length of fall. $P_{35}=P_{26}-P_{25}$.

P_{36} (gC/5 km^3) The total gross primary production of carbon attributed exclusively to the spring pulse.   After P_{37} is calculated, P_{36} is set equal to $P_{28}-0.5 \times P_{33} \times P_{37}/P_{34}-P_{31} \times P_{33}$. See the section on phytoplankton.

P_{37} (gC/5 km^3) The total gross primary production of carbon attributed exclusively to summer constant production (excluding also production accounted for using P_{31}). $P_{37}=P_{29}-P_{31} \times P_{34}$.

P_{38} (gC/5 km^3) The total gross primary production of carbon attributed exclusively to the fall pulse. $P_{38}=P_{30}-0.5 \times P_{35} \times P_{37}/P_{34}-P_{31} \times P_{35}$.

P_{39} (year^{-1}) The instantaneous respiration rate for phytoplankton plus phytoplankton mortality not otherwise accounted for.

P_{40} (g/gC) A conversion factor for calculating the wet weight of phytoplankton from the weight of organic carbon contained in the phytoplankton. Compare with P_{60}.

Table A-1. Variable Definitions (continued)

P_{41} (gC/5 km^3) The critical point of the concentration of phytoplankton [PHY] at which the copepods cease eating.

P_{42} (unitless) The availability (vulnerability) of phytoplankton to copepods.

P_{43} (year^{-1}) The maximum rate at which copepods can graze on phytoplankton.

P_{44} (5 km^3/gC) A constant used to determine the steepness of the feeding curve for copepods feeding on phytoplankton.

P_{45} (gC/g) A conversion factor used to calculate the amount of organic carbon in copepods from their wet weight.

P_{46} (unitless) The assimilation efficiency of copepods eating phytoplankton.

P_{47} (year^{-1}) The instantaneous respiration and molting rate for copepods plus copepod mortality not otherwise accounted for.

P_{48} (gC/g) A conversion factor used to calculate the amount of organic carbon in euphausiids from their wet weight.

Table A-1. Variable Definitions (continued)

P_{49} (year^{-1}) The maximum rate of euphausiid consumption of copepods.

P_{50} (gC/5 km^3) The copepod density at which euphausiids feeding on copepods begin their maximum feeding rate.

P_{51} (year^{-1}) The maximum rate of euphausiid consumption of phytoplankton.

P_{52} (gC/5 km^3) The phytoplankton density at which euphausiids feeding on phytoplankton begin their maximum feeding rate.

P_{53} (gC/5 km^3) The phytoplankton density at which euphausiids feeding on phytoplankton cease feeding.

P_{54} (unitless) The availability (vulnerability) of phytoplankton to euphausiids.

P_{55} (unitless) The availability (vulnerability) of copepods to euphausiids.

P_{56} (unitless) The assimilation efficiency of euphausiids feeding on copepods (assumed to also hold true for euphausiids feeding on phytoplankton).

Table A-1. Variable Definitions (continued)

P_{57} (year^{-1}) The instantaneous respiration and molting rate for euphausiids plus euphausiid mortality not otherwise accounted for.

P_{58} (unitless) After pollock reach a length equal to P_{113}in the model, P_{58} is the natural logarithm of the ratio of an individual pollock's "weight" to its most preferred prey weight. The function STEPR1 is used to "interpolate" between P_{58} and P_{78}. See the explanation of SEL in Appendix D.

P_{59} (unitless) After pollock reach a length equal to $(P_{79} - P_{59})/P_{16}$ in the model, P_{59} determines how selective an individual pollock is regarding its food size. Prior to that time, its selectivity is determined by linear interpolation between P_{79} and P_{59}. $P_{59} \leq P_{79} \leq 0$. See explanation of SEL in Appendix D.

P_{60} (g/gC) The product of the availability (vulnerability) of phytoplankton to pollock times a factor for converting PHY (with units of gC/5 km^3) to g wet weight/5 km^3. See P_{40}.

P_{61} (unitless) The initial value for the elements of EATER during the time periods when the pollock are eating normally. P_{61} should not be less than P_{62}. See the section on pollock breeding behavior.

P_{62} (unitless) A coefficient used in calculating EATER from FECUND. P_{61} should not be less than P_{62}.

Table A-1. Variable Definitions (continued)

P_{63} (unitless) An exponent used to calculate the "normal" weight of pollock. For pollock with length $L_i \leq P_4$, $WL_i = P_{80} x L_i^{P_{63}}$.

P_{64} (ova/5 km^3) The total number of pollock ova laid if DOBEV=.TRUE.

P_{65} (unitless, then cm) On input, P_{65} is a factor used to multiply P_{66} to calculate the length at which recruitment to being cannibalized begins. P_{65} is then set to that length, so $P_{65} = P_{66} x P_{65}$.

P_{66} (cm or years, then cm^{-1}) On input, P_{66} is either the length or the negative of the age at which pollock are first fully recruited to being cannibalized. If $P_{66} \leq 0$, it is converted from the negative of the age to length by setting P_{66} equal to RLNGTH($-P_{66}$). In any case, after P_{65} is calculated, P_{66} is set equal to $P_5/[P_{66}-P_{65}]$.

P_{67} (unitless) The critical fraction of the total diet of pollock at which a food item category is totally excluded from the diet of the pollock due to prey switching.

P_{68} (cm) The pollock length at which the condition indices calculated using WL and $P_{104} x L_i^{P_{105}}$ are equal. See P_{70}. See also the section on unconstrained pollock lengths.

P_{69} (gC/5 km^3) The copepod density at which euphausiids feeding on copepods cease feeding.

Table A-1. Variable Definitions (continued)

P_{70} (g/cm^3) A coefficient used to calculate the "normal" weight [WL] of pollock. If $L_i \geq P_4$, $WL_i = P_{70} \times L_i^3$. See P_{68}, P_{80}. See also the section on pollock condition dependent mortality.

P_{71} (unitless) An exponent used in calculating the condition dependent instantaneous mortality rates for pollock cohorts 2 and over.

P_{72} (year^{-1}) A coefficient used to calculate the condition dependent instantaneous mortality rates for pollock cohorts 2 and over.

P_{73} (unitless) The critical condition at which condition dependent mortality begins for pollock cohorts 2 and over.

P_{74} (numbers/5 km^3) If either N_1 or E become less than NMIN, N_1 or E is set to P_{74}. P_{74} should either be greater than NMIN or exactly equal to 0. If P_{74} is large enough, the pollock cannot become extinct. See also P_{89} and PLENTY.

P_{75} (unitless) If logical variable PLENTY is false, P_{75} is a lower bound for the condition index [CN_1] of cohort 1 pollock. This is because if PLENTY is false, and also $CN_1 < P_{75}$ and $W_1' < 0$, then W_1' is set to zero, so the weight [W_1] of an individual pollock in cohort 1 decreases no further. P_{75} should be less than or equal to $MIN(P_{89}, P_{96})$.

Table A-1. Variable Definitions (continued)

P_{76} (unitless) The critical fraction of the total diet of pollock at which a food item category begins to be excluded from the diet of the pollock due to prey switching.

P_{77} (cm; not an input) The length of pollock growing according to the constrained growth equations when a switch to von Bertalanffy growth occurs. $P_{77}=RLNGTH(P_{12})$.

P_{78} (unitless) Same as P_{58}, but used for pollock of length $\leq P_{112}$. See P_{58}.

P_{79} (unitless) Same as P_{59}, but used for pollock shorter in length. See P_{59}.

P_{80} $(g/cm^{P_{63}})$ A coefficient used to calculate the "normal" weight of pollock. If $L_i \leq P_4$, $WL_i=P_{80}xL_i^{P_{63}}$. See P_{70}.

P_{81} Same as P_{71}, but for pollock cohort 1 only.

P_{82} Same as P_{72}, but for pollock cohort 1 only.

P_{83} Same as P_{73}, but for pollock cohort 1 only.

P_{84} (cm) The length at which pollock are 50% recruited to the fishery; that is, if all values

Table A-1. Variable Definitions (continued)

in array F are equal, then P_{84} is the length at which the vulnerability of pollock to the fishery reaches 50% of its maximum level (see the section on the yield of the pollock fishery). The actual median length of fish in the catch will usually be different from P_{84}, depending on factors such as the actual population sizes of pollock cohorts and the actual values of F and P_{85}.

P_{85} (cm^{-1}) A coefficient determining the steepness of the curve for recruitment of pollock to the fishery.

P_{86} (unitless) Values for the fractions of mature pollock less than P_{86} are set to 0. See the section on proportions of pollock mature.

P_{87} (unitless) Values for the fractions of mature pollock greater than P_{87} are set to P_{20} or P_{120}. Compare with P_{86}.

P_{88} $(gC/5\ km^3$; not an input) The total gross primary production of carbon attributed exclusively to the algal bloom in sea ice. $P_{88}=P_{27}-P_{31}\times[P_{23}-P_{21}]$. See the section on phytoplankton.

P_{89} (unitless) For cohort 1 pollock shortly after hatching, the critical condition below which no growth in length occurs. RCON1 is used to "interpolate" between P_{89} and P_{96}. P_{89} may also be used together with P_{74} to keep cohort 1 pollock from becoming extinct. Compare with P_{75}.

Table A-1. Variable Definitions (continued)

P_{90} (unitless) For cohort 2 and older pollock, the critical condition below which no growth in length occurs.

P_{91} (cm/year) The rate of growth in length of newly hatched (cohort 1) pollock before they are capable of eating.

P_{92} (cm/year) The maximum rate of growth in length of pollock in cohort 1 after they are capable of eating.

P_{93} (unitless) The difference in condition of a cohort 1 pollock which is capable of eating and which has just begun growing in length at the maximum rate [P_{92}], and one which has just ceased growing in length.

P_{94} (years) A critical point in the piecewise linear function RCON1. Legal input values are $P_{103} \leq P_{94} \leq P_{95} \leq 1$.

P_{95} (years) A critical point in the piecewise linear function RCON1. See P_{94}.

P_{96} (unitless) For older cohort 1 pollock, the critical condition below which no growth in length occurs. RCON1 is used to "interpolate" between P_{89} and P_{96}.

Table A-1. Variable Definitions (continued)

P_{97} (g/year) A coefficient used in calculating the instantaneous weight dependent mortality rate for pollock. $\text{UPRED}=P_{97}/[W_i+P_{98}]$.

P_{98} (g) A constant used in calculating the instantaneous weight dependent mortality rate for pollock. $\text{UPRED}=P_{97}/[W_i+P_{98}]$.

P_{99} (cm/year) The same as P_{92}, but for cohort 2 and older pollock.

P_{100} (unitless) The same as P_{93}, but for cohort 2 and older pollock.

P_{101} (unitless) For cohort 1 pollock, an exponent used to calculate the improved ability of larger (heavier) pollock to feed at lower food densities. See P_8, P_9, and the section on pollock feeding rates.

P_{102} (unitless) The same as P_{101}, but for cohort 2 and older pollock. See P_{18}, P_{19}.

P_{103} (years; not an input) A critical point in the piecewise linear function RCON1. When preparing for a simulation run, P_{103} is set equal (in subroutine PARMOD) to the time of year of the last cohort update in a cycle of discrete time events. See P_{94}.

Table A-1. Variable Definitions (continued)

P_{104} $(g/cm^{P_{105}})$ A coefficient used to calculate the condition of a pollock greater than P_{68} in length for the purposes of determining whether it is in good enough condition to grow in length.   See P_{70}, and the section on unconstrained pollock lengths.

P_{105} (unitless) An exponent used in the same calculations as P_{104}.

P_{106} (unitless) A constant used in determining the required condition before a pollock greater than P_{68} in length may grow in length.   See P_{104}, P_{105}.

P_{107} (unitless) A parameter used in calculating the maturity of male pollock as a function of length.   See the section on proportions of pollock mature.

P_{108} (cm^{-1}) Another parameter used in calculating the maturity of male pollock as a function of length.   See P_{107}.

P_{109} (unitless) The same as P_{107}, but for female pollock.

P_{110} (cm^{-1}) The same as P_{108}, but for female pollock.

P_{111} (cm) The length at which pollock switch from one maximum feeding rate [P_{17}] to another [P_{114}]

Table A-1. Variable Definitions (continued)

at cohort update time (or at the time a simulation run is started).

P_{112} (cm) A pollock of length P_{112} or less has a most preferred prey size preference parameter equal to P_{78} in the size selection function SEL.

P_{113} (cm) A pollock of length P_{113} or greater has a most preferred prey size preference parameter equal to P_{58}. See P_{112}.

P_{114} The same as P_{17}, but for pollock with lengths greater than or equal to P_{111} at cohort update time (or when a simulation run is started).

P_{115} (unitless) A factor used to multiply the initial number of pollock eggs and the initial numbers of pollock in the individual pollock cohorts in order to modify the initial starting conditions when preparing for a simulation run.

P_{116} (unitless) The same as P_{115}, but used to multiply PHY, COPE, and EUPH.

P_{117} ($g^{[-P_{118}]}$) A coefficient used to calculate the food conversion efficiency of pollock. See P_3.

P_{118} (unitless) An exponent used to calculate the food conversion efficiency of pollock. See P_3, P_{117}.

Table A-1. Variable Definitions (continued)

P_{119} (unitless) An exponent used to calculate the maximum possible sustained feeding rate (or digestive rate) of pollock as a function of length. See P_7, P_{17}, P_{114}.

P_{120} (unitless; not an input) The proportion of male pollock in the total pollock population. $P_{120}=1-P_{20}$.

PCHEND   A logical variable. If PCHEND = .TRUE., variables describing the state of the system being modeled are "punched" at the end of the simulation run using a machine readable format onto computer cards, a disk file, or magnetic tape. These variables enable the simulation run to be restarted and run still further.

PHY   (gC/ 5 km^3) The weight of the total organic carbon contained in the phytoplankton biomass.

PHY'   ([g/5 km^3]/year) The derivative of PHY.

PLENTY   A logical variable. If N_1 becomes less than NMIN, PLENTY is set to .FALSE., and N_1 is set to P_{74}. In subsequent derivative calculations, N_1' is forced to equal 0, and whenever $CN_1 < P_{75}$, W_1' is not allowed to become less than 0. Thus W_1 is not allowed to decrease so long as $CN_1 < P_{75}$. These actions continue until the next cohort update, when PLENTY is reset to .TRUE. See P_{74}, P_{75}. See also the section on pollock numbers (mortalities).

Table A-1. Variable Definitions (continued)

PREDUR   (years; not an input) The simulated elapsed time
              in the model from the instant the pollock
              prepare to breed until the instant they actually
              breed. (However, PREDUR is presently not used
              in the model).

$preym_{i,j}$ The instantaneous mortality rate resulting on
              prey item category j as a result of
              feeding by pollock cohort i.

P7   (units may vary) The maximum feeding "rate"
              (used in the rectilinear function FOOD).

P8   (units may vary) The critical value for
              beginning the maximum feeding rate (used in the
              rectilinear function FOOD).

P9   (units may vary) The critical value at which
              feeding ceases (used in the rectilinear function
              FOOD).

Q2   (unitless) A factor used to calculate an upper
              limit to prey size for pollock. For those
              pollock for which this limit is calculated, a
              pollock of length LPRED will not eat prey of
              length greater than Q2xLPRED.

RC   (g/year) An array containing the actual
              average instantaneous individual feeding rate of
              pollock in each pollock cohort.

Table A-1. Variable Definitions (continued)

RDWGHT   A logical variable. RDWGHT = .TRUE. indicates that the initial weights and lengths for individual pollock cohorts are to be input while preparing for a simulation run, instead of being calculated using functions WVB and RLNGTH.

RIPEN   A logical variable. RIPEN=.TRUE. indicates that pollock eggs have been laid and have not yet hatched.

RQMAX   If the accuracy criterion for numerical integration was not met at anytime during a simulation run, then RQMAX is the maximum estimated relative integration error calculated for any variable during that run. Otherwise, RQMAX equals 0.

SCALC   An array containing scaling constants for use in making graphs.

SCALM   An array containg scaling multipliers for use in making graphs.

SHER   If the accuracy criterion is not met during numerical integration, various diagnostic quantities are stored in the two dimensional array, SHER, as an aid to determining why the accuracy criterion was not met.

SHOWB   A logical variable. If SHOWB = .TRUE., various quantities (B, B313, BTT) are calculated and printed out.

Table A-1. Variable Definitions (continued)

SHOWD   A   logical   variable.   If SHOWD = .TRUE.,
             various quantities (food fractions, RC, GCN, CN,
             FD, SM, MT, and ZM) are printed out.

SM   (year^{-1}) An   array   containing   condition
             dependent instantaneous mortality rates for the
             individual pollock cohorts (mortalities due to
             low CN_i's).

STPNCH   (years) Once the simulated time in the model is
             greater   than   or   equal   to STPNCH, various
             variables describing the state of the system
             being modeled are "punched" using a machine
             readable format onto computer cards, a disk
             file, or magnetic tape whenever the subroutine
             PRINTR is called.

STPRNT   (years) Once the simulated time in the model is
             greater than or equal to STPRNT, printouts of
             various   quantities   are   made using calls to
             subroutine PRINTR.

T   (years) The same as TT.

TCUM   (years) The   simulated   time   in   the   model
             that calculations were last started for VCUM and
             ZBS.

TD   (years) The   time   step   to   be   used   for
             numerical integration.   After being input, it
             may be varied in range from TDMIN to TDMAX by
             the numerical integration subroutine.

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Table A-1. Variable Definitions (continued)

TDIMIN   (years) The minimum value for TD used since
            the last printout (that is, since the last call
            to subroutine PRINTR).

TDL   (years) The last time step used for
            numerical integration (compare to TD).

TDMAX   (years) The maximum step size ever allowed to
            be used for numerical integration.

TDMIN   (years) The minimum step size ever allowed to be
            used for numerical integration.

TEV   (years) An array. On input, TEV contains the
            times that the discrete time events are to
            occur, measured in years after time 0, with
            $0 \leq TEV_i < CYCLE$ for each element TEV_i. TEV is then
            sorted into ascending order (IEV^i is rearranged
            the same way TEV is rearranged), and transformed
            so TEV_i contains the amount of time simulated to
            occur between the event I-1 and event I, except
            TEV_1 contains the amount of time between event
            NEV (which is the last event) and event 1.

TF   (years) The time in the model (relative to time
            zero) at which a simulation run is supposed to
            start. If TF>TL, TF and TL are interchanged.

time zero   Time zero is always assumed to occur in the
            model at 0000 hours on a certain January 1 (that
            is, at the instant a certain year hypothetically
            started).

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Table A-1. Variable Definitions (continued)

TL   (years) The time in the model (relative to time
            zero) at which a simulation run is supposed to
            end. If TF>TL, TF and TL are interchanged.

TP   (years) The simulated interval in the model
            between regularly scheduled print times. See
            the definitions of discrete time events in
            Appendix Table B-1.

tpm_j The instantaneous mortality rate on prey item
            category j due to feeding by all pollock.
            Compare with $\underline{preym}_{i,j}$.

TPOFF   (years) The time in the first simulated year
            that the first regularly scheduled print time is
            to occur (see TP). If TPOFF is less than 0 when
            it is input, TPOFF is set to equal TF.

TPT   (years) A time decrement (calculated from TP and
            TPOFF) used to calculate when regularly
            scheduled print times are to occur.

TSTP   The number of times the time points (NXTEV) have
            been set up for a cycle of discrete events.

TT   (years) The simulated "present time" in the
            model, with respect to some time zero which
            occurred at 0000 hours on a certain Jan. 1.

UDYLD   ($[g/5\ km^3]$/year) A temporary variable in the
            computer program used in calculating YLD'.

Table A-1. Variable Definitions (continued)

UFISH$_i$ (year^{-1}) The instantaneous fishing mortality rate of pollock cohort i after taking into consideration how recruited (vulnerable) that cohort is to the fishery. It is represented by the temporary variable UFISH in the computer program.

UG   (units vary) A temporary variable in the computer program used to calculate the average generation time for pollock.

UMIN   The same as NMIN.

UPRED$_i$ (year^{-1}) The instantaneous weight dependent mortality rate for pollock cohort i. See P_{97}, P_{98}. It is represented by the temporary variable UPRED in the computer program.

U5   (unitless; not an input) A tolerance level for judging whether a stationary population structure has occurred. U5=ACCRCY+ACCRCY.

V   (units vary) An array containing various quantities being numerically integrated. For example, it may contain PHY, COPE, EUPH, and YLD.

V'   (units vary) An array containing derivatives of various quantities being numerically integrated. For example, V' may contain arrays N', W', and L'.

Table A-1. Variable Definitions (continued)

VCUM   ([g]x[years]/5 km^3) $VCUM_1$ and $VCUM_2$ contain the integrals over time of COPE and EUPH, respectively. Each element of VCUM is set to 0 at the instant newly hatched pollock start eating in a simulation run.

W   (g) An array containing the average wet weights of individual pollock in the individual pollock cohorts.

W'   (g/year) An array containing the derivatives of individual pollock weights (W).

WL   (g) An array containing the expected weights of individual pollock in the individual pollock cohorts as calculated from their lengths (L) using a length-weight relationship. See the section on condition dependent pollock mortality.

WOO   (g; not an input) The weight that a pollock would attain if it lived to an infinite age and if it was growing according to the constrained growth equations.

$$WOO = D8 \times D7^{D2} \; .$$

WPRED   (g) The weight of a predator (or the expected weight for a predator at a given length).

WPREY   (g) The weight of the prey.

Table A-1. Variable Definitions (continued)

XCATCH   (metric tons) The amount of pollock caught
          during a given time period. See XEFFRT.

XCPUE   (metric tons per 1000 pair trawl horsepower-
          hours trawled) The catch per unit effort during
          a given time period. See XEFFRT.

XEFFRT   (1000 pair trawl horsepower-hours trawled) The
          nominal fishing effort during a given time
          period. XEFFRT=XCATCH/XCPUE. See XETOF.

XETOF   (year^{-1}/[1000 pair trawl horsepower-hours
          trawled]) A factor (catchability coefficient)
          for converting nominal fishing effort [XEFFRT]
          into instantaneous fishing mortality rates
          [F].

XX1   The date (month, day, year) a given computer run
          of the model was started.

YLD   (g/5 km^3) The wet weight of the yield (catch)
          of the fishery for pollock.

YLD'   ([g/5 km^3]/year) The derivative of YLD.

YT   (years) The simulated present time of the year
          in the model. YT=MOD(TT,1).

Table A-1. Variable Definitions (continued)

ZBS
$(g/5\ km^3)$ The minimum value attained by the total zooplankton biomass (COPE+EUPH). New calculations for ZBS are started each time newly hatched pollock may first begin eating (discrete time event 6).

ZLNG
An array containing the assumed lengths of individual phytoplankton, copepods, and euphausiids, respectively.

ZM
An array containing various instantaneous mortality rates. The individual elements of ZM are defined below.

ZM_1
$([gC/5\ km^3]/year)$ The phytoplankton mortality rate due to consumption by copepods.

ZM_2
$([gC/5\ km^3]/year)$ The phytoplankton mortality rate due to consumption by euphausiids.

ZM_3
$([gC/5\ km^3]/year)$ The phytoplankton mortality rate due to consumption by pollock.

ZM_4
$([gC/5\ km^3]/year)$ The copepod mortality rate due to consumption by euphausiids.

ZM_5
$([g/5\ km^3]/year)$ The copepod mortality rate due to consumption by pollock.

Table A-1. Variable Definitions (continued)

ZM_6 ($[g/5\ km^3]$/year) The euphausiid mortality rate due to consumption by pollock.

ZW   (g) An array containing the assumed wet weight of individual phytoplankton, copepods, and euphausiids, respectively.

APPENDIX B

Definitions of Discrete Time Events

A table giving the times the various discrete time events occur is given in the chapter on parameter values and origins.

In the computer program, event identifiers are stored in array IEV, and times of the year that the discrete events are to be performed are stored in array TEV.

Some discrete events are optional in that they might never occur in a given simulation run. The events occur cyclically in the model, and all of them can occur one or more times in a given cycle. The difference in age between any two consecutive cohorts in the model is given by the parameter DTAU, and the period of a cycle of discrete events is given by the parameter CYCLE. CYCLE must be an integer multiple of DTAU, so that the egg hatch times (cohort updates) are equally spaced in time. [If they were not equally spaced in time, the present method of calculating the age of pollock in the model would have to be changed, as well as the usage of certain arrays, such as M and F].

If any discrete events coincide with a regularly scheduled print time (calculated using TPT, TP, or TL in subroutine SIM), the discrete events are performed first, before the scheduled printing is performed. This ensures

that any discrete events are performed before the simulation run is ended - even if the discrete events occur "simultaneously" with the end of the simulation run. Conversely, when a simulation run is being started, it is assumed that any discrete events which are supposed to occur "simultaneously" with the start of the simulation run have already occurred.

Table B-1. Definitions of discrete time events

Discrete event identifier (IEV)	Short definition of event
(none)	Regularly scheduled print times calculated using TPT, TP, or TL in subroutine SIM.
1	Print times (except the above regularly scheduled print times calculated using TPT, TP, or TL).
2	Pollock prepare to breed (each $EATER_i$ may be reduced).
3	Pollock gametes (ova and milt) are released (each W_i may be reduced).
4	Cohort update time: the pollock eggs hatch.
5	Pollock cease their breeding period (each $EATER_i$ may be set to P_{61}).
6	Newly hatched pollock may begin eating ($EATER_1$ is set to P_{61}).
7	Fishing starts (beginning of the fishing season). In addition, new values for certain variables may optionally be read in and array F reset.
8	Fishing ends (end of the fishing season).
9	[unused]

Table B-1. Definitions of discrete time events (continued)

10   [unused]

11   0000 hours on Jan. 1 (time zero is always
            exactly 0000 hours on Jan. 1 of some year).

_____

APPENDIX C

Summary Table of Differential Equations

I. Phytoplankton Biomass (Carbon)

$$V_1' = PHY'$$ (3)

$$= PULSE(YT, P_{88}, P_{21}, P_{32})$$

$$+ PULSE(YT, P_{36}, P_{23}, P_{33})$$

$$+ FLTTOP(YT, P_{37}, P_{24}, P_{25}, P_{33}, P_{35})$$

$$+ PULSE(YT, P_{38}, P_{25}, P_{35})$$

$$+ P_{31}$$

$$- P_{39} \times PHY - ZM_1 - ZM_2 - ZM_3.$$

II. Copepods

A. Copepod Biomass

$$V_2' = COPE'$$ (5)

$$= P_{46}/P_{45} \times ZM_1 - P_{47} \times COPE - ZM_4/P_{45} - ZM_5.$$

B. Copepod Cumulative Biomass

$$V_6' = VCUM_1' = COPE.$$ (57)

III. Euphausiids

A. Euphausiid Biomass

$$V_3' = EUPH'$$ (8)

$$= P_{56} \times [ZM_2 + ZM_4]/P_{48} - P_{57} \times EUPH - ZM_6,$$

where either ZM_2 or ZM_4 equals 0.

B. Euphausiid Cumulative Biomass

$$V_7' = VCUM_2' = EUPH.$$ (58)

IV. Pollock

A. Pollock Numbers

$$N_i' = -[M_i + MT_i + SM_i + UFISH_i + UPRED_i] \times N_i.$$ (9)

If logical variable PLENTY is false, N_1' is set to 0.

B. Pollock Lengths (constrained)

$$L_i' = \begin{cases} D9, \text{ if } L_i < P_{77} \\ \\ KAY \times [D7 - L_i], \text{ if } L_i \geq P_{77}. \end{cases} \quad (16)$$

C. Pollock Weights (constrained)

$$W_i' = \begin{cases} D6, \text{ if } L_i < P_{77} \\ \\ L_i' \times W_i / L_i \times D2, \text{ if } L_i \geq P_{77}. \end{cases} \quad (17)$$

D. Pollock Lengths (unconstrained)

1. Cohort 1 (unconstrained length)

$$L_1' = \begin{cases} P_{91}, \text{ if } EATER_1 \leq 0 \\ \\ P_{92} \times MAX(0 , MIN[1 , [CN_1 - RCON1(YT)]/P_{93}]), \\ \text{ if } EATER_1 > 0. \end{cases} \quad (20 \text{ and } 21)$$

2. Cohorts 2 and Older
(unconstrained lengths)

$$
L_i' = \begin{cases}
P_{99} \times MAX(0 \ , \ MIN[1 \ , \ [CN_i - P_{90}]/P_{100}]), & (22) \\
\quad \text{if } L_i \leq P_{68} \\
\\
P_{99} \times MAX(0 \ , \ MIN(1 \ , \ W_i/[P_{104} \times L_i^{P_{105}}] - P_{106})), \\
\quad \text{if } L_i > P_{68}.
\end{cases}
$$

E. Pollock Weights (unconstrained)

$$
W_i' = MIN[P_3, P_{117} \times W_i^{P_{118}}] \times [RC_i - P_1 \times W_i^{P_2}]. \tag{24}
$$

If logical variable PLENTY is false,
if $CN_1 < P_{75}$, and if $W_1' < 0$,
W_1' is set to 0.

V. Pollock Fishery Yield

$$
V_4' = YLD' = \text{Sum over all pollock cohorts i} \qquad \text{(55 and 56)}
$$
$$
\text{of } B_i \times F_i/[1 + e^{(P_{84} - L_i) \times P_{85}}].
$$

APPENDIX D

Mathematical Functions

Detailed tables defining the parameters and variables used in the explanations of the model functions are given in Appendix A. Tables listing the values and sources of the reference set of initial conditions and adjusted parameters are given in the section on parameter values and origins.

D.1. FLTTOP

The function FLTTOP is differentiable and analytically integrable. A graph of FLTTOP is shown in Figure D-1.

FLTTOP is defined by the equation

$$
\text{FLTTOP}(T,A,B,C,D,E) =
\begin{cases}
0.0 \text{ if } T \leq B-D & (78) \\[4pt]
0.5 \text{ x } A/(C-B) \text{x} [1-\text{COS}(\text{PI}/D \text{ x } (T-B+D))] \\ \quad \text{if } B-D<T<B \\[4pt]
A/(C-B), \text{ if } B \leq T \leq C \\[4pt]
0.5 \text{ x } A/(C-B) \text{x} [1-\text{COS}(\text{PI}/E \text{ x } (T-C-E))] \\ \quad \text{if } C<T<C+E \\[4pt]
0.0 \text{ if } T \geq C+E
\end{cases}
$$

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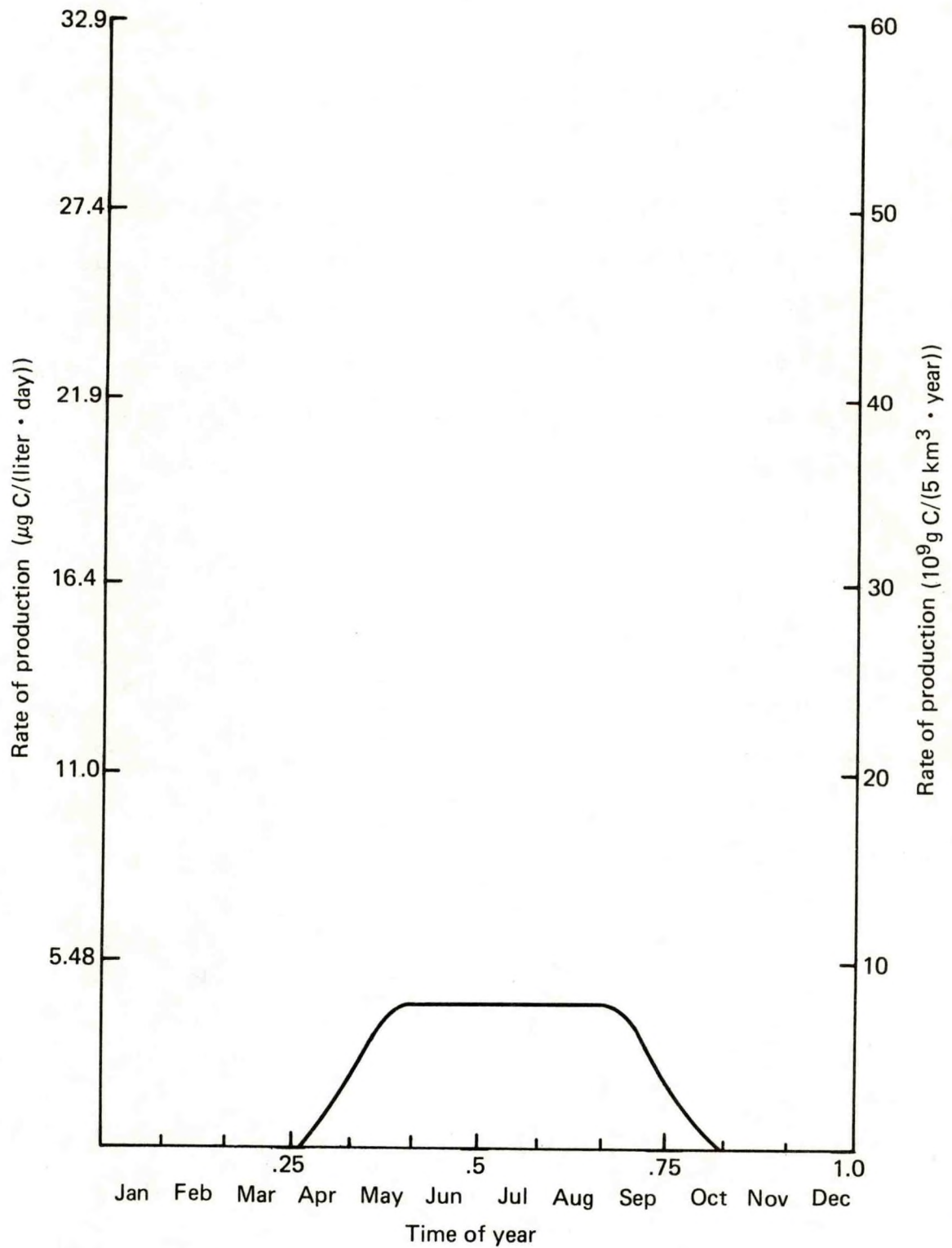
Figure D-1. The function FLTTOP.

where PI=3.1415926535898. T is the independent variable, and A, B, C, D, and E are parameters such that B and C are the values of T at the left and right endpoints of the line segment forming the "flat top" of FLTTOP [B $\leq$ C], and D and E are the widths of the strictly increasing and strictly decreasing portions of FLTTOP.

FLTTOP has the property that its integral, as T varies from negative infinity to positive infinity, is equal to its integral from B-D to C+E. Both of these integrals equal the analytic expression

$$0.5 \text{ x } D \text{ x } A/(C-B) + A + 0.5 \text{ x } E \text{ x } A/(C-B) \tag{79}$$

D.2. FORTRAN Intrinsic Functions and Operators

The correspondence between the name used in Burroughs B7000/B6000 series FORTRAN and the name used in the text is shown in Table D-1.

A short definition of the functions and operators used in the text is given in Table D-2.

Table D-1.   Correspondence Between FORTRAN and
             Text Functions

FORTRAN name	Text name
ABS	ABS
ALOG	LN
ALOG10	LOG_{10}
AMAX1	MAX
AMIN1	MIN
AMOD	MOD
COS	COS
EXP	e
MAX1	MAX
MIN0	MIN
MOD	MOD
SQRT	SQRT
+	+
-	-
*	x
/	/
**	(expressed with superscripts)

Table D-2. Definition of Functions and Operators Used
     in Text

Text Name	Definition* (with FORTRAN name(s) in parentheses)
ABS	absolute value (ABS)
COS	cosine (COS)
e	exponential function (EXP)
LN	natural logarithm [logarithm to the base e] (ALOG)
LOG_{10}	common logarithm [logarithm to the base 10] (ALOG10)
MAX	choose maximum value (AMAX1, MAX1)
MIN	choose minimum value (AMIN1, MINO)
MOD	remaindering (AMOD, MOD)
SQRT	square root (SQRT)
+	add (+)
-	subtract (-)
x	multiply (*)
/	divide (/)
(superscripts)	exponentiate [raise to a power] (**)

* The definitions in this table came from Burroughs Corporation (1978).

D.3. The Ivlev Feeding Function

An Ivlev feeding function, IV(U), may be described by the relation:

$$IV(U) = \begin{cases} 0, & \text{if } U \leq C \\ A \times [1 - e^{(B \times [C-U])}], & \text{if } U > C \end{cases} \tag{80}$$

where U is the independent variable, and A, B, and C, are nonnegative parameters. A graph of a typical Ivlev feeding function is shown in Figure D-2.

D.4. The Logistic Function

The logistic function may be written in the form

$$A / [1 + e^{(B \times [C-U])}] \tag{81}$$

where U is the independent variable and A, B, and C are parameters. A graph of a typical logistic function is shown in Figure D-3.
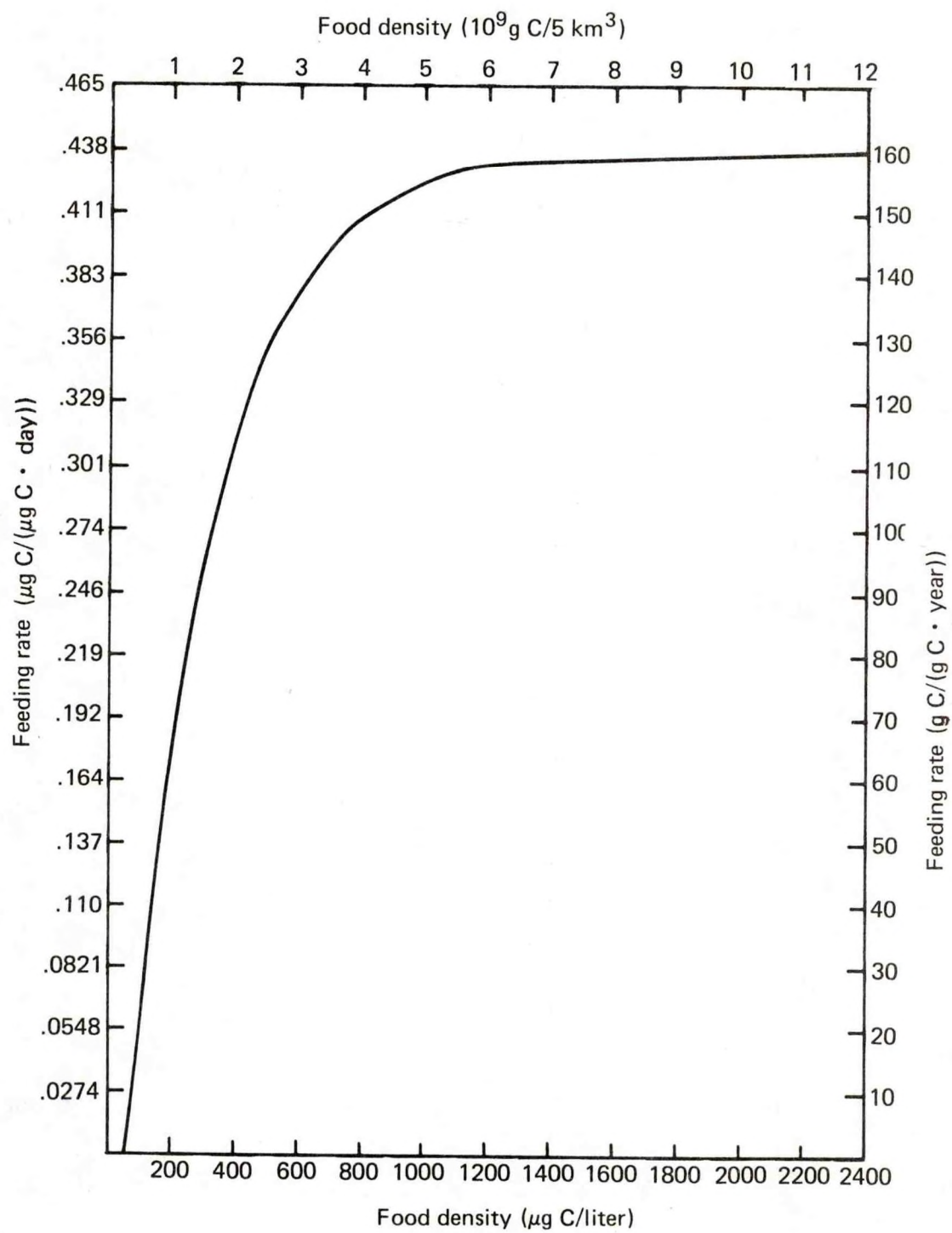
Figure D-2.   The Ivlev feeding function.
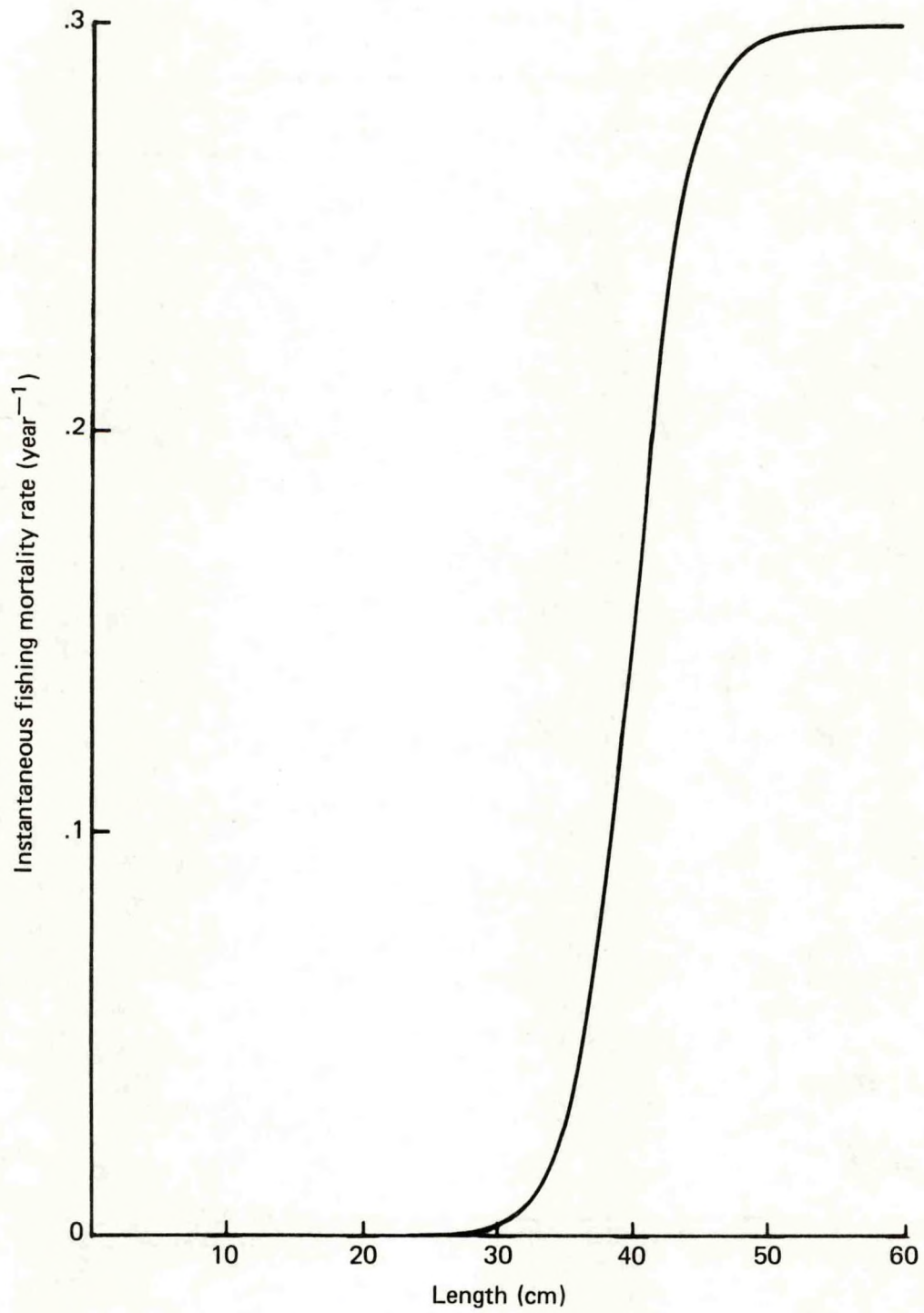
Figure D-3.   The logistic function.

D.5. PULSE

The function PULSE generates a pulse which is differentiable and analytically integrable. PULSE is defined by the relation

$$
PULSE(T,A,B,C) = \begin{cases} 0. \text{ for } T \leq B \text{ or } T \geq B+C & (82) \\ \\ A/C \times [1-COS(TWOPI/C \times [T-B])] \\ \quad \text{otherwise} \end{cases}
$$

where TWOPI = 2 x PI = 6.2831853071796, $\underline{A}$ is the area under PULSE, $\underline{B}$ is the left critical point of PULSE, and $\underline{C}$ is the width of PULSE at its base.

A graph of PULSE is shown in Figure D-4.

PULSE(T,A,B,C) has the useful property that its integral, as T varies from minus infinity to positive infinity, is equal to its integral from B to B+C. Both of these integrals equal A.

D.6. RCON1

RCON1 is used while calculating the derivative of the length of pollock in cohort 1. (See the section on unconstrained pollock lengths).

RCON1 is a piecewise linear function determined by the equations:
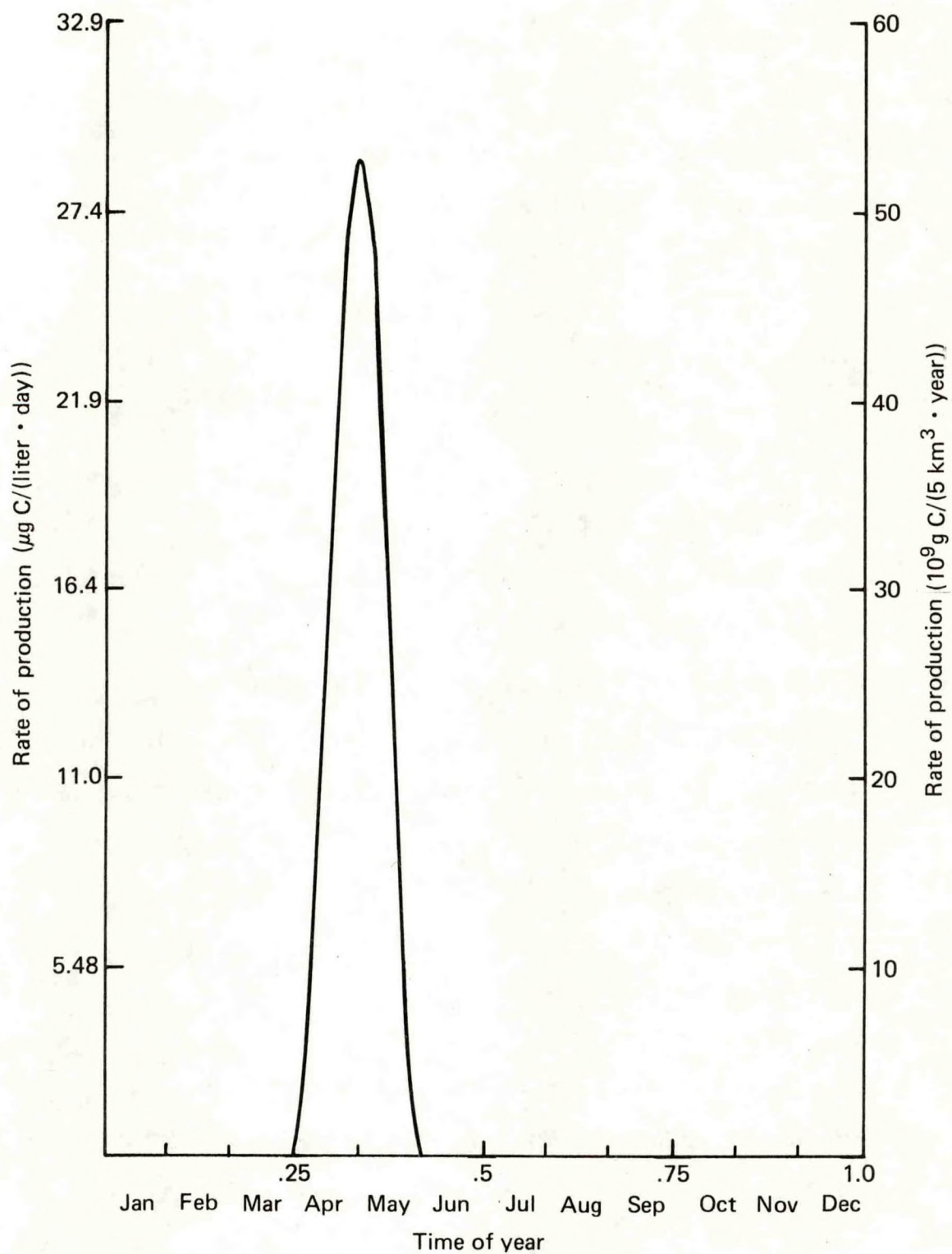
Figure D-4.   The function PULSE.

$$RCON1(YT) = \begin{cases} P_{89}, & \text{if } YT \geq P_{103} \text{ and } YT \leq P_{94} \qquad (83) \\ \\ P_{96}, & \text{if } YT \geq P_{95} \text{ or } YT < P_{103} \\ \\ [P_{96}-P_{89}] \times [YT-P_{94}]/[P_{95}-P_{94}]+P_{89}, \\ \quad \text{if } YT > P_{94} \text{ and } YT < P_{95} \end{cases}$$

where YT is the time of year, P_{89} and P_{96} are parameters, and P_{94}, P_{95}, and P_{103} are critical points (parameters) such that $P_{103} \leq P_{94} \leq P_{95} \leq 1$.

A graph of RCON1 is shown in Figure D-5.

D.7. Rectilinear Functions (e.g. FOOD, STEPR1)

A piece-wise linear function consisting of two parallel rays with a line segment connecting the endpoints of the two rays is defined to be a rectilinear function. A graph of a typical rectilinear function is shown in Figure D-6.

The main advantage of rectilinear functions is simplicity. One disadvantage is that they might cause sharp changes to unrealistically occur in the results if the underlying process represented by the rectilinear function is not truly rectilinear.

STEPR1 is a typical rectilinear function used in the model. The algorithm for STEPR1 can be expressed by
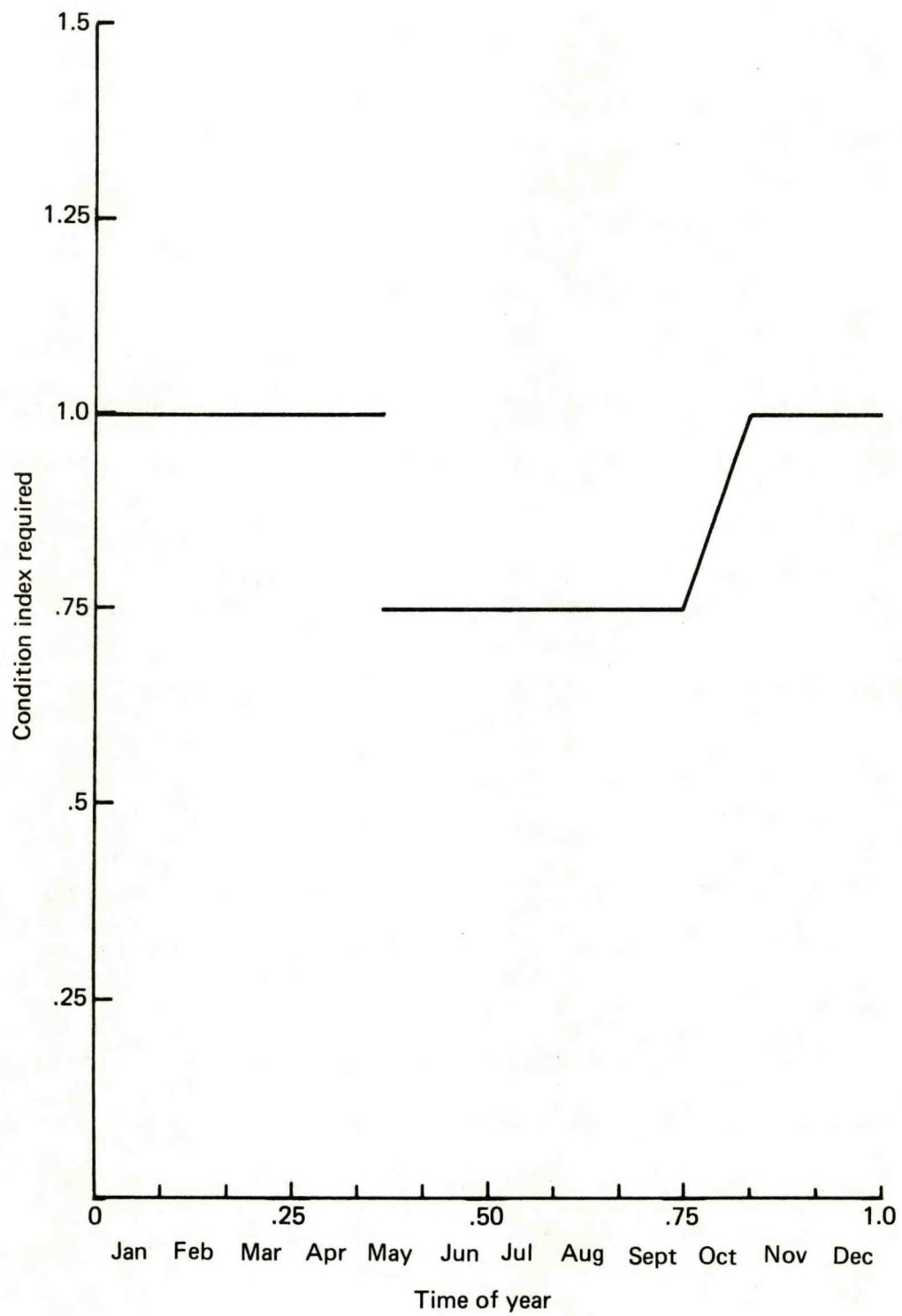
Figure D-5. The function RCON1.
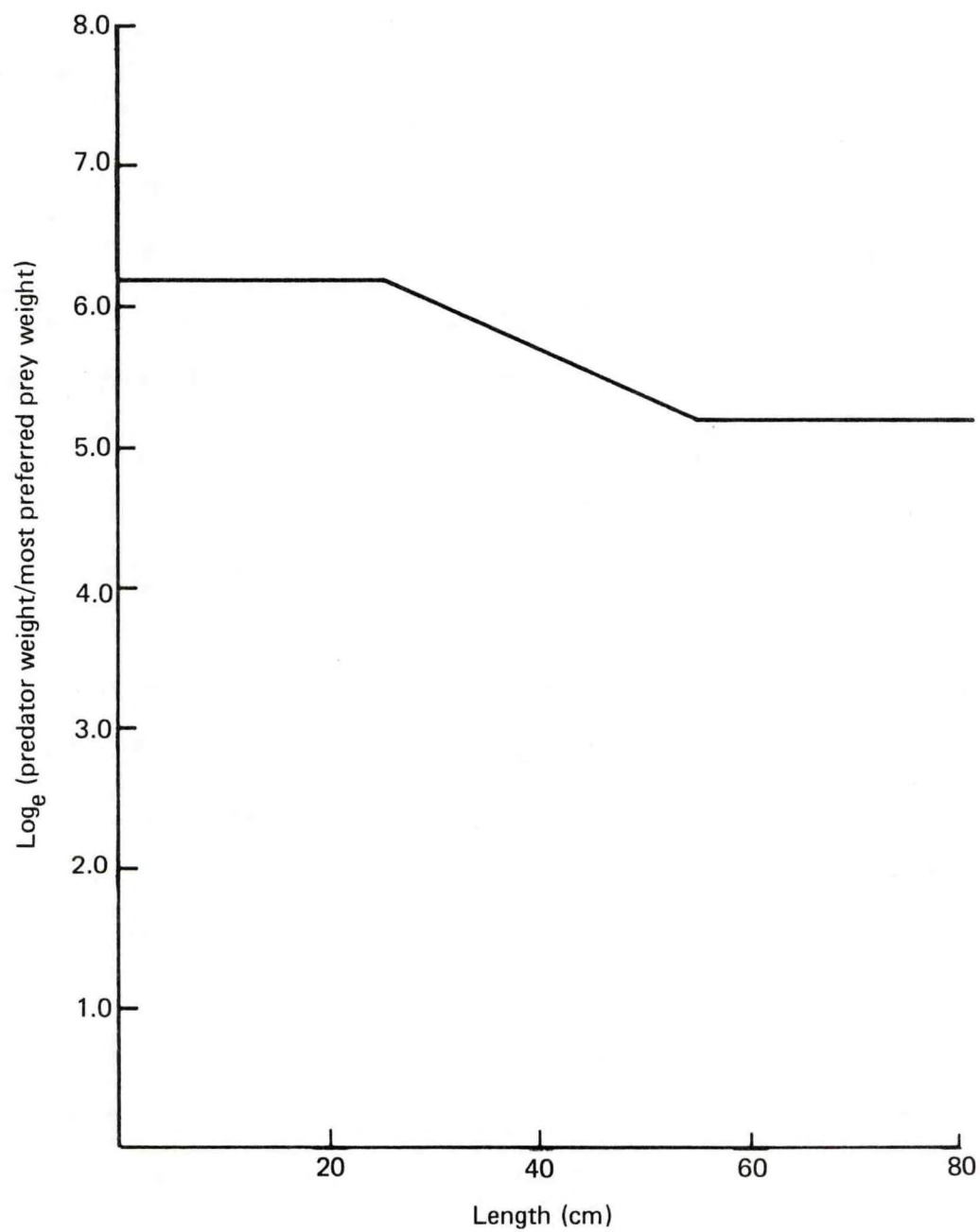
Figure D-6. A typical rectilinear function, STEPR1 (with P_{58} = 5.2, and P_{78} = 6.2).

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$$
\text{STEPR1}(H,CL,CR,UL,UR) = \begin{cases} UL, & \text{if } H\underline{<}CL & (84) \\ (UR-UL)\times(H-CL)/(CR-CL) + UL, & \text{if } CL<H<CR \\ UR, & \text{if } H\underline{>}CR \end{cases}
$$

where H is the independent variable, UL and UR are parameters, and CL and CR are critical points (parameters).

The actual order the different "if" statements are performed has been changed in the computer model in order to optimize the computer evaluation of STEPR1, but the changes make no difference in the results calculated.

For optimization purposes, the order of the evaluation of the "if" statements may be changed in any rectilinear function, if it is expected that the independent variable will usually be within a certain range.

For the function FOOD the above algorithm is also changed slightly to take advantage of the simplifications possible for special cases of the parameters (UL always equals zero in the cases where FOOD is used).

The algorithm for FOOD is given by

$$
\text{FOOD}(\text{UFD},\text{P7},\text{P8},\text{P9}) = \begin{cases} 0, & \text{if UFD} \leq \text{P9} \\ \text{P7}, & \text{if UFD} \geq \text{P8} \\ \text{P7} \times (\text{UFD}-\text{P9})/(\text{P8}-\text{P9}), & \text{if P9} < \text{UFD} < \text{P8} \end{cases} \tag{85}
$$

where UFD is the independent variable, P_7 is a parameter, and P_8 and P_9 are critical points (parameters).

A graph of FOOD is shown in Figure D-7.

D.8. RLNGTH

The function RLNGTH calculates the length of a pollock of age UA. If $\text{UA} < P_{12}$, growth in length is assumed to be a linear function of its age. If $\text{UA} \geq P_{12}$, growth in length is assumed to follow a von Bertalanffy growth curve as described in Ricker (1975: section 9.6.2). The algorithm for RLNGTH is given by

$$
\text{RLNGTH}(\text{UA}) = \begin{cases} \text{D9} \times \text{UA} + P_{14}, & \text{if UA} < P_{12} \\ \text{D7} \times (1- e^{[\text{KAY} \times (\text{D4}-\text{UA})]}), & \text{if UA} \geq P_{12} \end{cases} \tag{86}
$$

where UA is the age, and D4, D7, D9, KAY, P_{12} and P_{14} are parameters.
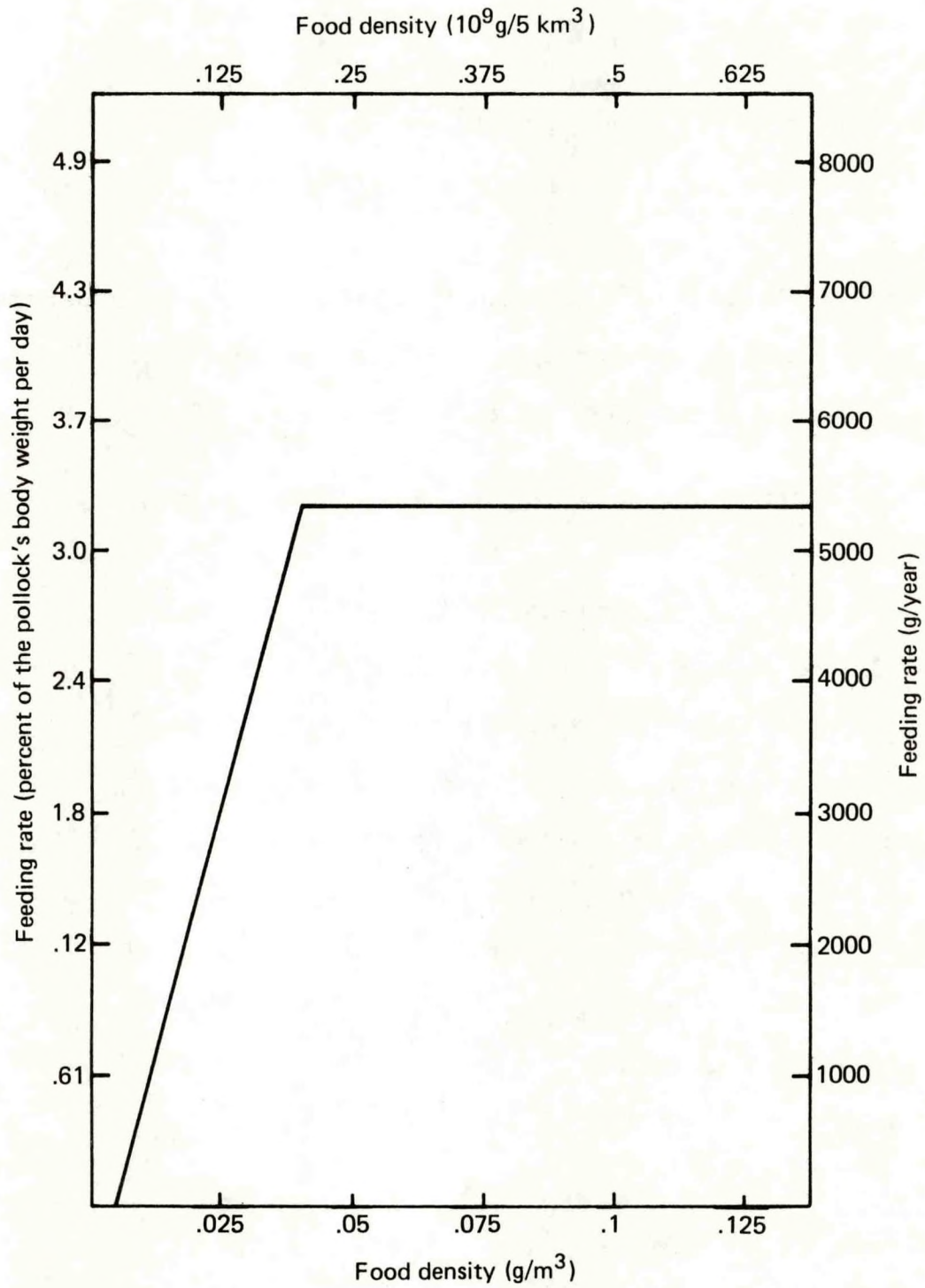
Figure D-7.   The rectilinear function FOOD, for a
              walleye pollock weighing 450 g.

The function RLNGTH is used to calculate initial lengths for pollock when setting up initial starting conditions for the model, if the lengths of the pollock were not input. A graph of RLNGTH is shown in Figure D-8.

D.9. The Food Size Selection Function, SEL

The size selection function SEL is used to model pollock prey size preferences. It is essentially a reparameterized version of the lognormal probability density function. A simpler, though related, reparameterization of the lognormal probability function was used by Andersen and Ursin (1977) to represent the size preferences of various species in the North Sea. Andersen and Ursin's function calculates size selectivity as a function of the ratio of the weight of the predator to the weight of the prey. SEL, for pollock of a given length, calculates size selectivity as a function of the ratio of the "normal" weight of the pollock (as calculated from the length using a length-weight relationship) to the weight of the prey. Both SEL and Andersen and Ursin's function are "log-symmetric" in the sense that the predator selects prey twice the preferred prey weight equally readily as prey half the preferred prey weight. Graphs of SEL are shown in Figures D-9 and D-10.
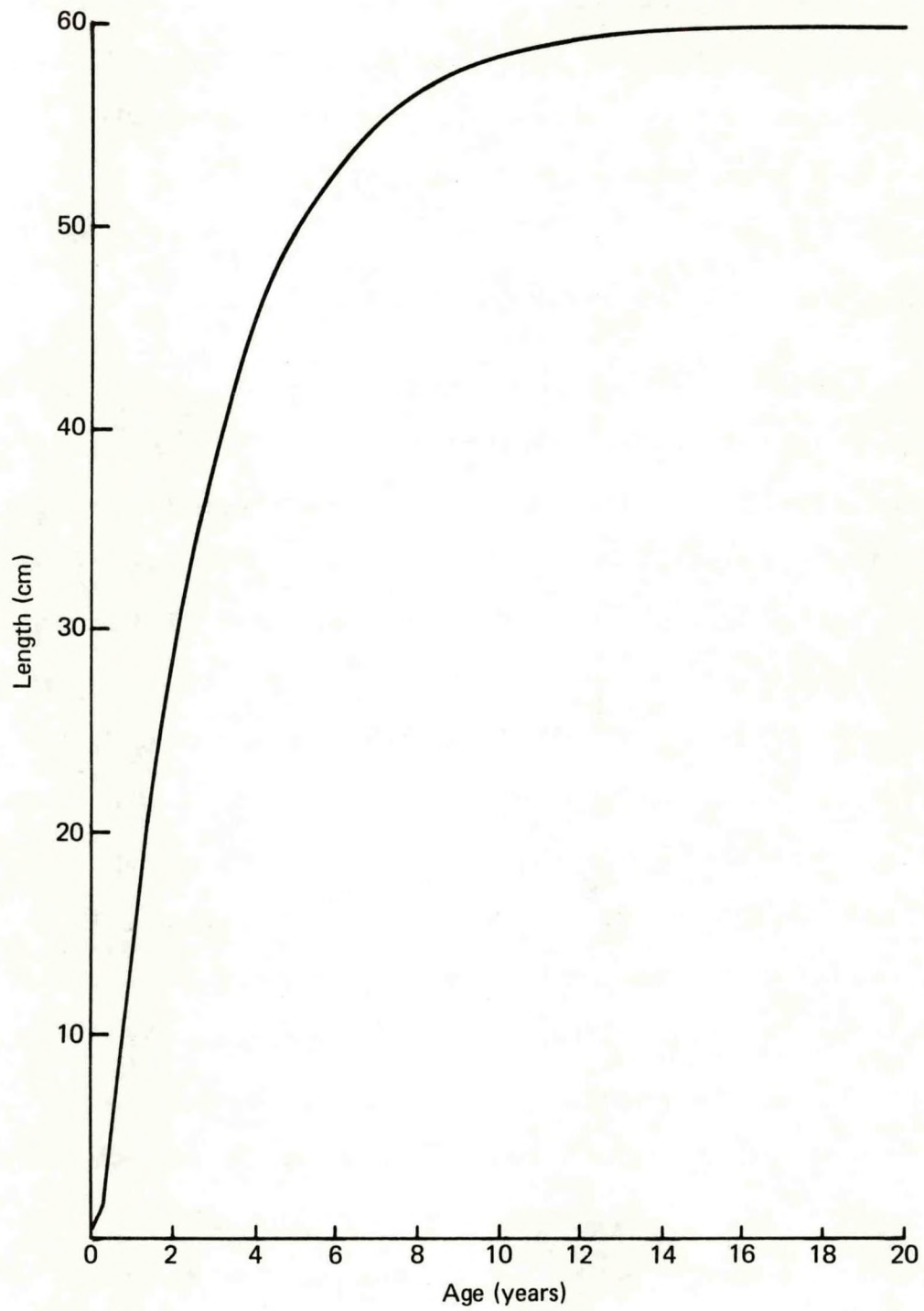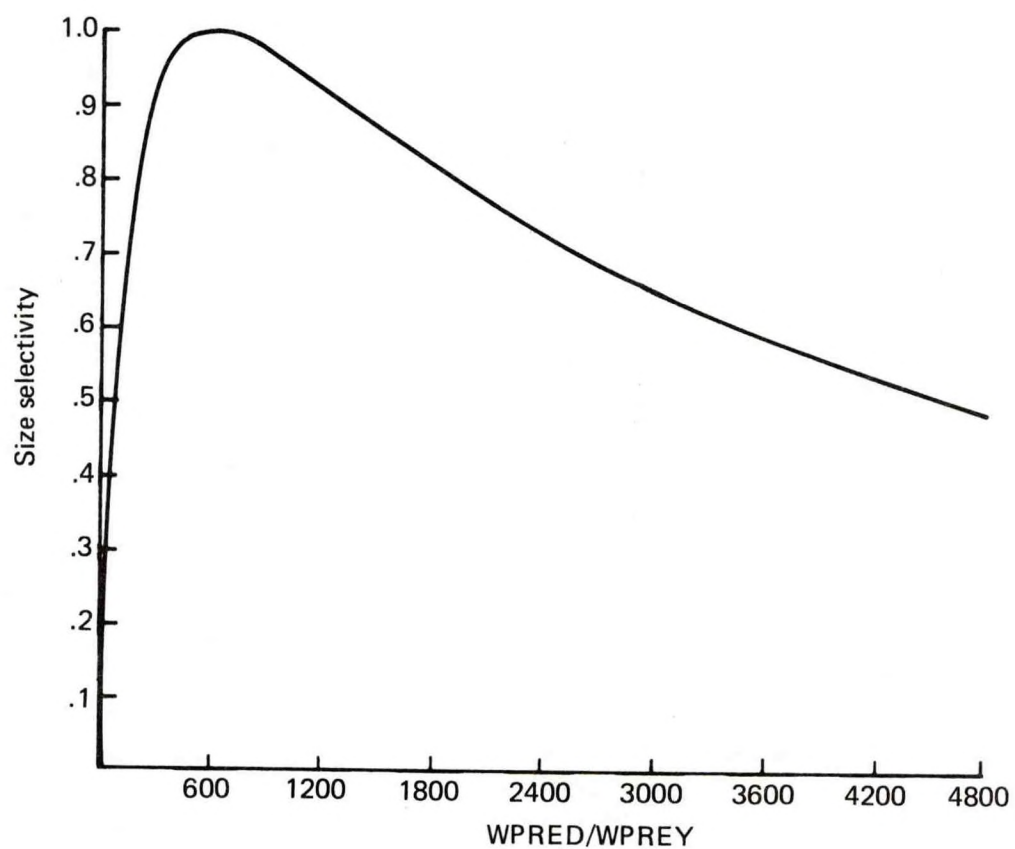
Figure D-8. The function RLNGTH.

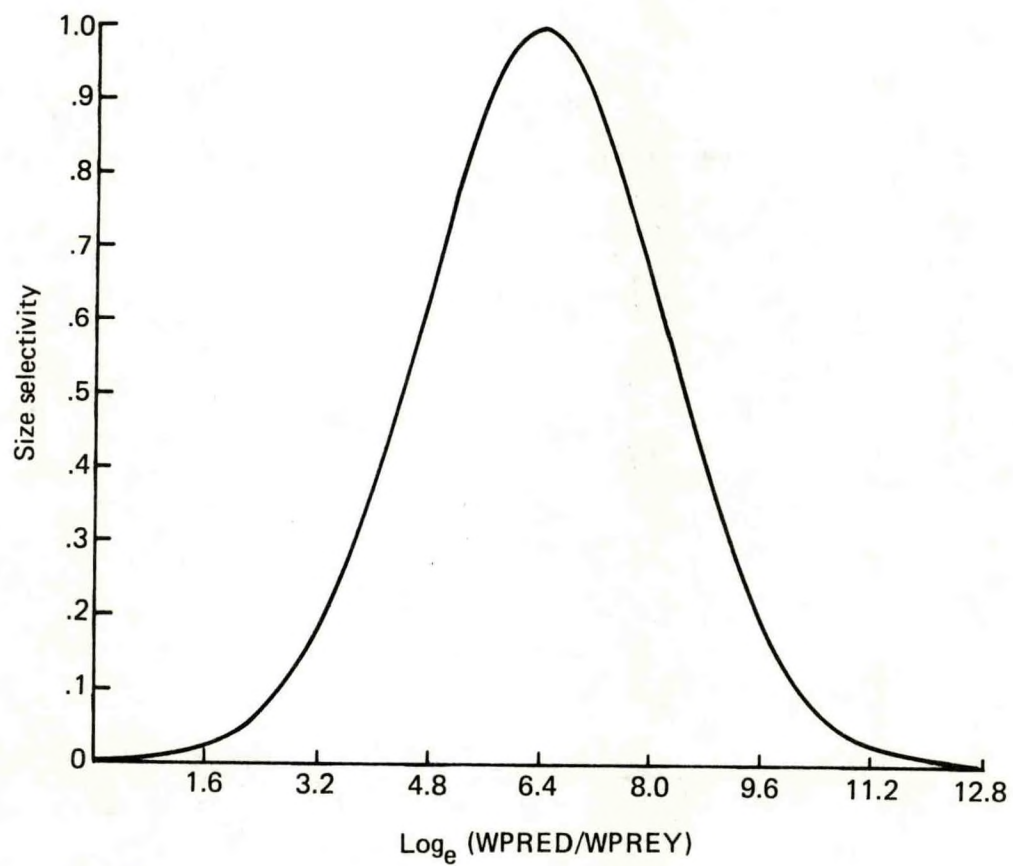Figure D-9. The function SEL (with LPRED = 30 cm).

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Figure D-10.   The function SEL (with LPRED = 30 cm).

The formula for SEL is

$$SEL(WPRED, WPREY, LPRED) = e^U, \text{ where} \tag{87}$$

$$U = [LN(WPRED/WPREY) - STEPR1(LPRED, P_{112}, P_{113}, P_{78}, P_{58})]^2$$

$$\times MAX[P_{79} - P_{16} \times LPRED, P_{59}],$$

and where WPRED is the "weight" of the predator, WPREY is the "weight" of the prey, LPRED is the length of the predator, and P_{16}, P_{58}, P_{59}, P_{78}, P_{112} and P_{113} are parameters.

The function $STEPR1(LPRED, P_{112}, P_{113}, P_{78}, P_{58})$ is used to calculate the natural logarithm of the ratio of the predator's "weight" to the predator's most preferred prey weight. It is a rectilinear function of the length, LPRED, of the predator. It is used to simulate the possibility that the preferred predator to prey weight ratio may change as the predator (pollock) grows in length.

The function $MAX[P_{79} - P_{16} \times LPRED, P_{59}]$ determines the "spread" of the size selectivity curve; that is, whether the predator is highly selective regarding the size of its prey, or relatively unselective regarding the size of its prey. If $P_{79} > P_{59}$, this "selectivity" increases as the predator grows in length, until it reaches a length where its selectivity is determined entirely by P_{59}, at which

point its selectivity changes no further. $MAX[P_{79}-P_{16} \times LPRED, P_{59}]$ is a piecewise linear function of length.

In the model the sizes of different prey items are rigidly determined in that all members of a given food item category or cohort are the same weight and length. In real life, however, there is much more variability, due to individual variation and differences between life history stages and species. This spread in sizes would have been difficult to simulate in the model, so instead the effects of this spread were approximated by increasing the spread (or decreasing the selectivity) of the size selection function. A similar solution was used by Andersen and Ursin (1977: 338-339). The effects of the spread in sizes of the food items seemed to be most important for larval pollock in the model, because newly hatched pollock are about the same size as certain adult copepods, which are presumably much too large for larval pollock to eat. Nonetheless, a newly hatched pollock still eats the earlier life stages of copepods and euphausiids (Clarke 1978). For this reason the factor Q2 is not used in the model to set a maximum size limit for food items for cohort 1 (Q2 is used for cohorts 2 and over). In addition, newly hatched pollock start out highly unselective regarding their prey size in the model,

but as the effect of lack of variability in the size of their prey items in the model decreases as the newly hatched pollock grow in length, the function $MAX[P_{79}-P_{16}xLPRED,P_{59}]$ is used to increase their selectivity to a more normal level.

D.10. The Sigmoidal Function

The sigmoidal function may be written in the form

$$e^{[A \times e^{(B \times U)}]} \tag{88}$$

where U is the independent variable, and A and B are parameters less than zero. A graph of a typical sigmoidal function is shown in Figure D-11.

D.11. SUM

The function SUM(B,JI,JJ) is a utility function used in the computer program to calculate the sum of the JI'th through the JJ'th elements, inclusive, of any one dimensional array B. If JI>JJ, the sum calculated is set equal to zero.
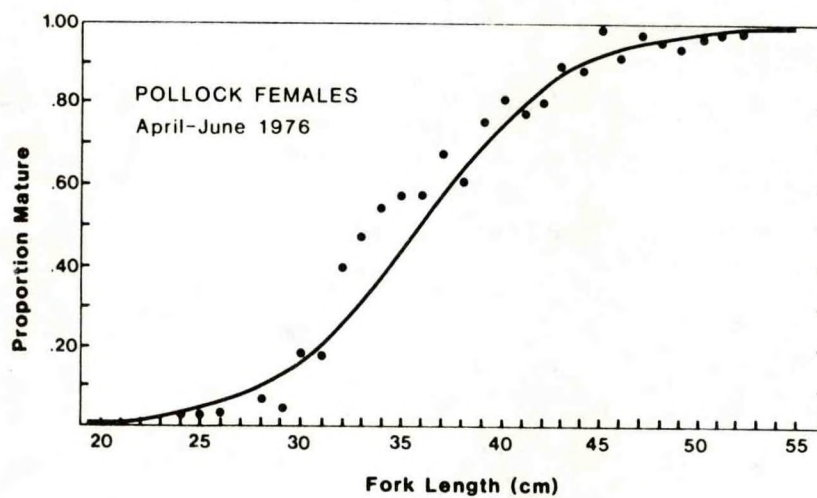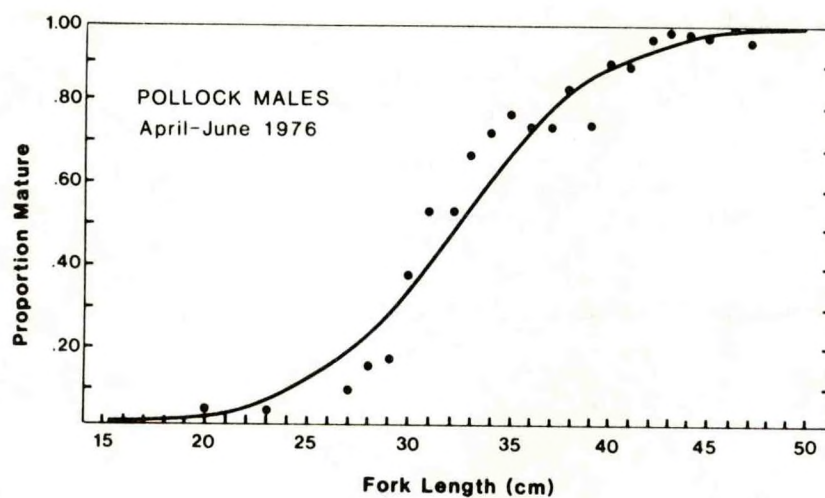
Figure D-11.   Examples of the sigmoidal function as
fitted to data (after Smith 1981).

D.12. WVB

The function WVB is used to calculate the weight of a pollock of age UA. If $UA<P_{12}$, the weight of the pollock is assumed to be a linear function of its age. If $UA \geq P_{12}$, its growth in weight is assumed to be allometric (as defined in Ricker 1975: 209); that is, its weight is assumed to be a power function of its length. Also, its length is assumed to be described by a von Bertalanffy growth curve, which is described in the section of the function RLNGTH.   WVB(UA) is calculated using the algorithm

$$WVB(UA) = \begin{cases} D6 \times UA + P_{13}, \text{ if } UA<P_{12} \\ \\ WOO \times UE^{D2}, \text{ if } UA \geq P_{12}, \end{cases} \quad (89)$$

where $UE = 1-e^{KAYx(D4 - UA)}$, UA is the age, and D2, D4, D6, KAY, P_{12}, P_{13} and WOO are parameters.

If $UA \geq P_{12}$, the above algorithm is equivalent to calculating

$$WVB(UA) = D8 \times [RLNGTH(UA)]^{D2} \qquad (90)$$

because $WOO = D8 \times D7^{D2}$.

When establishing initial conditions for the model, WVB is used to calculate initial weights of pollock, if their weights were not input. A graph of WVB is shown in Figure D-12.
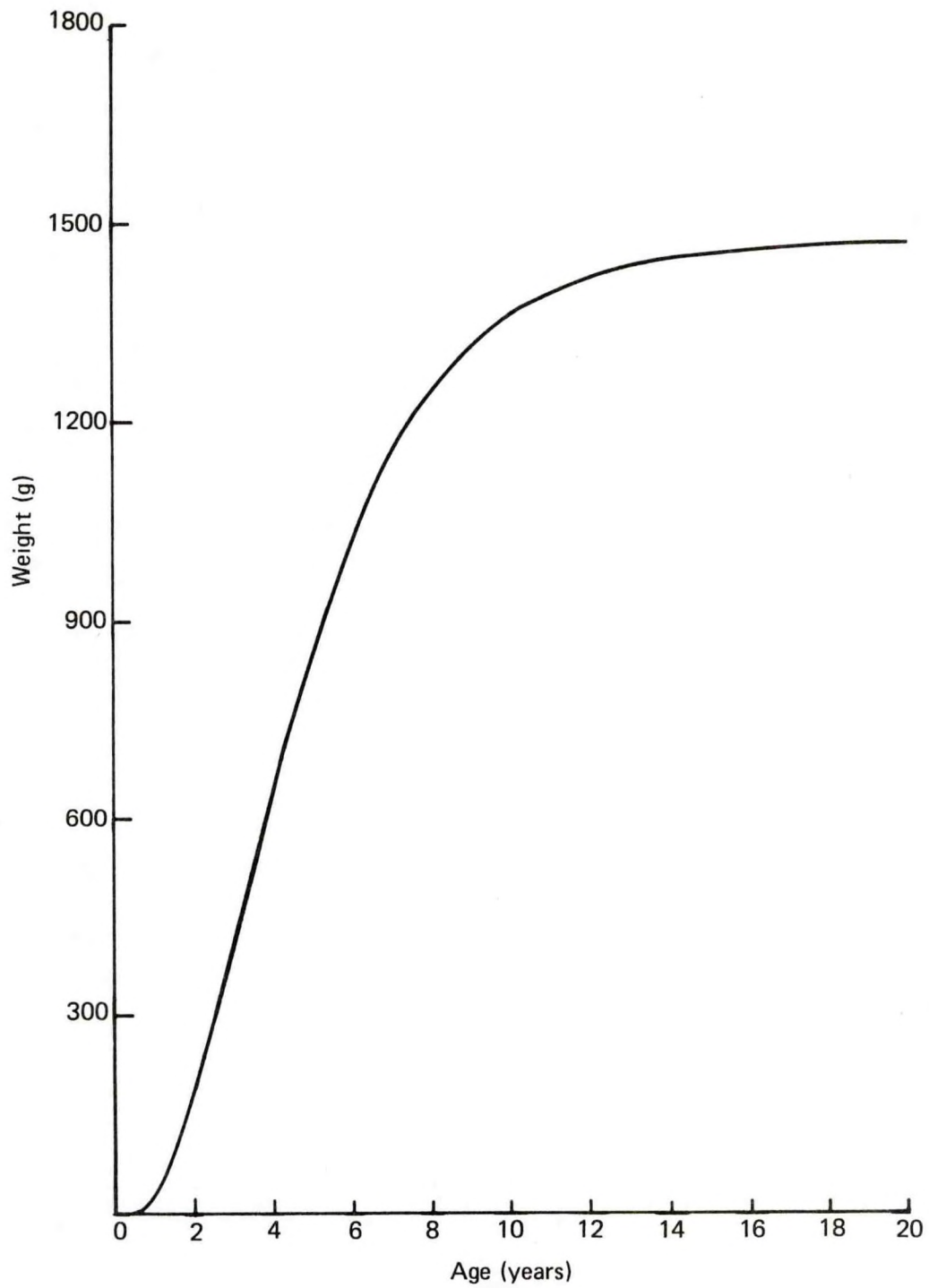
Figure D-12. The function WVB.

APPENDIX E

Simplified Program Flow Chart

Computer program subroutines particularly important to the flow of the program are flow charted in Figure E-1, accompanied by a short explanation of their principal purpose.
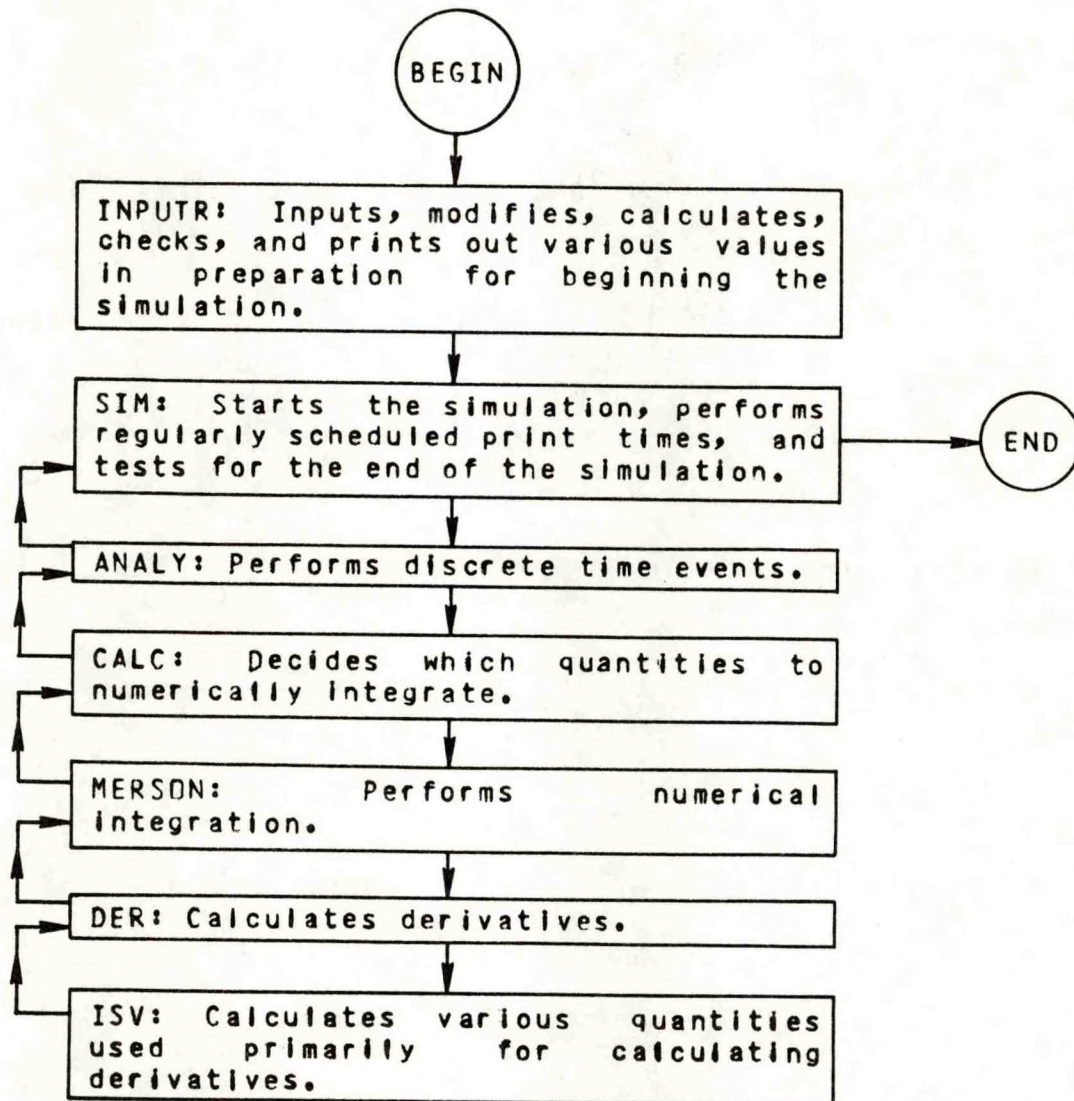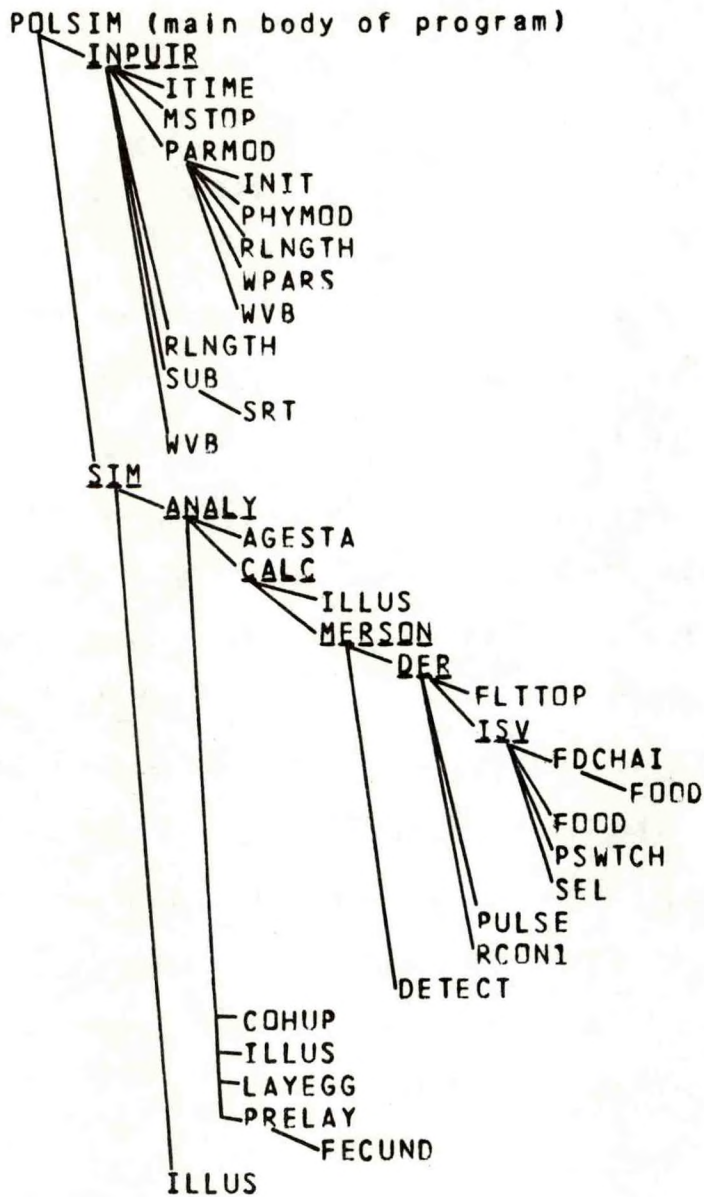
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Figure E-1.   Simplified flow chart of subroutines in the
computer program implementation of the model.

APPENDIX F

Calling Hierarchy in the Computer Program

The main body of the program and the various subroutines and functions make up the program units. Figure F-1 gives the partial calling hierarchy in the computer program; that is, it partially lists which program units may call certain other program units. Certain program units (for example, ILLUS, MSTOP, RLNGTH, STEPR1, SUM, and WVB) could conceivably be called almost anywhere in the program, so only part of their possible actual calls are listed. Program units may call program units below them in the next column to their right. The order the program units are listed does not indicate the order they may actually be called. However, the simplified program flowchart gives the order the underlined subroutines may be called.

```
POLSIM (main body of program)
      INPUIR
            ITIME
            MSTOP
            PARMOD
                  INIT
                  PHYMOD
                  RLNGTH
                  WPARS
                  WVB
            RLNGTH
            SUB
                  SRT
            WVB
      SIM
            ANALY
                  AGESTA
                  CALC
                        ILLUS
                        MERSON
                              DER
                                    FLTTOP
                                    ISV
                                          FDCHAI
                                                FOOD
                                          FOOD
                                          PSWTCH
                                          SEL
                                    PULSE
                                    RCON1
                              DETECT
                  COHUP
                  ILLUS
                  LAYEGG
                  PRELAY
                        FECUND
      ILLUS
```

The subroutine ILLUS is used to print out tables and graphs. Its calling hierarchy is given below:

```
ILLUS
      PRINTR
      SHOW
            GRAPHR
            LCSET
```
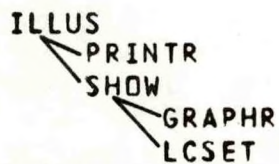
Figure F-1.   Partial calling hierarchy of computer program units.