NORTHWEST & ALASKA FISHERIES CENTER PROCESSED REPORT

MINIMUM SUSTAINABLE BIOMASSES OF MARINE ECOLOGICAL GROUPS OFF CENTRAL AND NORTHERN CALIFORNIA, OREGON, WASHINGTON AND VANCOUVER ISLAND COASTS

(A numerical evaluation of living marine resources off the west coast of the United States)

by

T. Laevastu and F. Favorite

Resource Ecology Task
Resource Ecology and Fisheries Management Division

MAY, 1977

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest and Alaska Fisheries Center
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ABSTRACT

A two-dimensional marine ecosystem model which emphasizes marine trophodynamics is used for quantitative evaluation of minimum sustainable biomasses of various marine ecological groups off the central west coast of North America. The biomasses of potential fishery resources and their annual turnover rates (as determined by ecosystem internal consumption--i.e., grazing) are presented.

The marine ecosystems are relatively unstable. The distribution of biomass of any fish with age depends on the growth rate change with the age of the species and on the changes of intensity of exploitation (fishery).

The ecosystem internal consumption (grazing) is a function of the size and age of the fish (i.e., the smaller, younger species are more suitable prey). The annual turnover rates and quantitative relations between biomasses of various ecological groups vary within relatively narrow limits from region to region. The U.S. commercial catch is quite insignificant compared to ecosystem internal consumption.

The minimum sustainable biomass on the central and northern California continental shelf is ca 65 tons/km^2 in upwelling areas. On the Oregon, Washington, and Vancouver Island continental shelves this biomass is ca 30 tons/km^2.

The consumption of finfish by toothed whales, dolphins, porpoises, and pinnipeds is considerably larger than the total (U.S. and foreign) commercial catch.

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Note: Resources south of Point Conception are excluded. B-minimum sustainable biomass in 10^3 tons; C-ecosystem internal consumption in 10^3 tons/year; T-mean annual turnover rate.

MINIMUM SUSTAINABLE BIOMASSES OF MARINE ECOLOGICAL GROUPS OFF CENTRAL AND NORTHERN CALIFORNIA, OREGON, WASHINGTON AND VANCOUVER ISLAND COASTS

I. OBJECTIVES OF THE STUDY

The numerical ecosystem models, recently devised at the Northwest and Alaska Fisheries Center (NWAFC), are logically valid and are reproducing well the conditions and processes within the marine ecosystems and are being used for evaluation of standing stocks of marine living resources. Consequently it was decided to enlarge these models to the limits of size and complexity set by available computer facilities (CDC 6400).

A Bulk Biomass Model (BBM), a trophodynamic model specially adapted for evaluation of standing stocks via trophic relations, was formulated:

—To determine the minimum sustainable biomasses (standing stocks) of various marine ecological groups (with emphasis on fisheries resources), along and off the central and northern California, Oregon, Washington, and Vancouver Island coasts. Minimum sustainable biomass is defined here as the biomass of a species (and/or ecological groups) which, with a given growth rate and estimated ecosystem internal consumption, neither declines nor increases within a year in a defined region. The ecosystem internal consumption is determined quantitatively within the model.

—To assess turnover rates, quantitative relations between biomasses of different ecological groups within the ecosystem, and the distribution of biomass with age in different species and/or ecological groups.

—To evaluate the marine ecosystem instability and seek a physical definition of optimum catch.

II. THE MODEL

As the marine living resources are dispersed and difficult to sample quantitatively, indirect methods must be used for their quantitative evaluation.

A. Assumptions

One of the basic methods for evaluation of the minimum sustainable biomass of any fish species or ecological groups of species is shown schematically in Figure 1. The following assumptions are made in this method:

1) The biomass is in quasi-equilibrium (i.e., no increase or decrease throughout the year).

2) No advection in and out of the region under consideration.

3) The growth of the biomass equals its removal, i.e., growth = grazing + fishery + mortality (grazing-is meant to present ecosystem internal consumption; fishery-is the loss due to fishing activity; and, mortality-includes only losses from old age and diseases).

$$\frac{dB}{dt} = \frac{\partial B}{\partial t} - \frac{\partial G}{\partial t} - \frac{\partial F}{\partial t} - \frac{\partial M}{\partial t} \qquad (1)$$

time change = growth - grazing - fishery - mortality of biomass

Growth rate can be computed from available data (e.g., as % of biomass per unit time--month, year). Removal by the fishery can be obtained from catch statistics. The true mortality of old age and diseases is usually very small in exploited populations (can be estimated to be 1 to 2% per month); in unexploited populations it can be of the order of 3% depending on species and ecological characteristics. The largest component of biomass removal is grazing (this component, together with mortality, has been summed in earlier population dynamics works as natural mortality) and can be computed in a relatively complete ecosystem model if the composition of food and food requirements (for maintenance and growth) are known and introduced into the

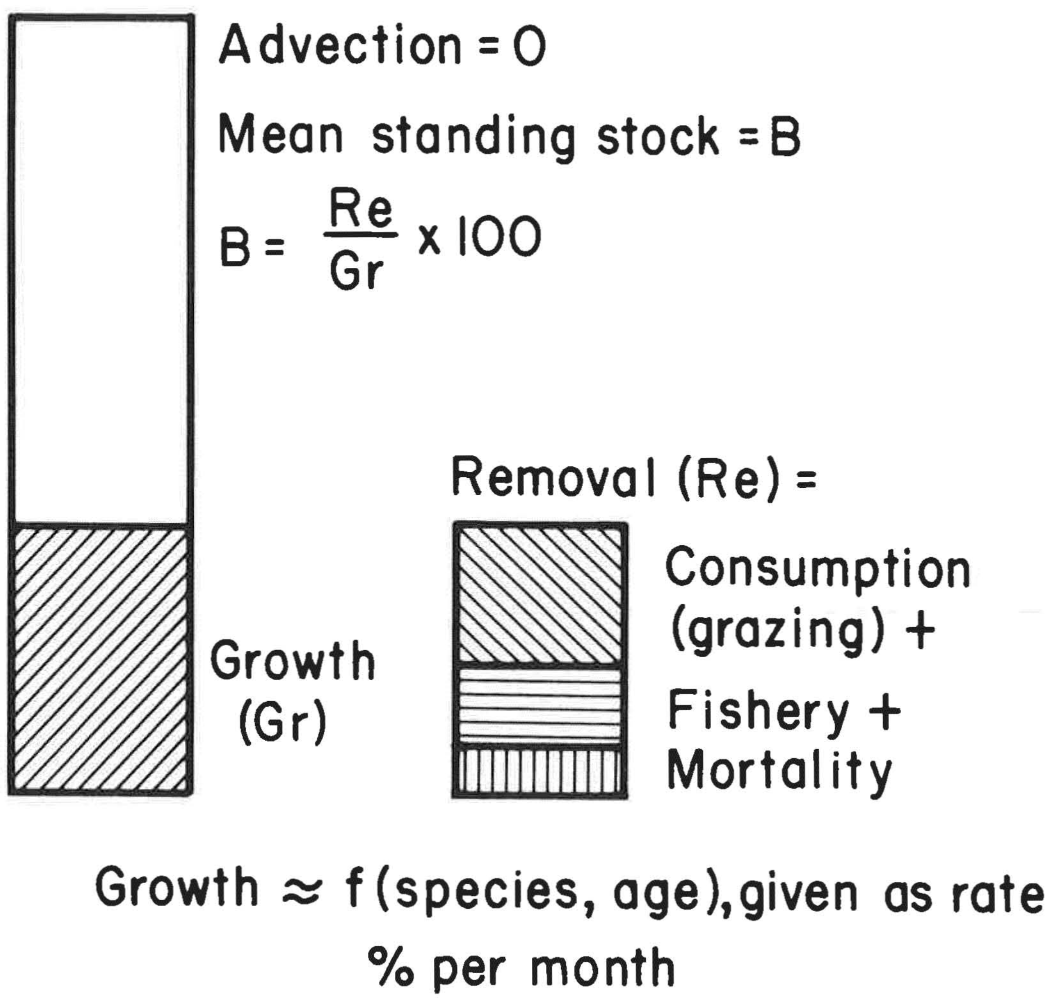

Figure 1.--Schematic presentation of quasi-equilibrium state of a standing stock as basic for computation of minimum sustainable biomass (B).

model. Thus, (1) can be expressed in empirical form as:

$$B = \frac{Re \times 100}{Gr} \qquad (2)$$

Where B is the minimum sustainable biomass of a given species or ecological group; Re is the sum of grazing (computed in the BBM model), removal by the fishery (catches) and natural mortality in weight per month; and Gr is the growth rate of the species in % of biomass per month. Growth rate is a characteristic of species (Figure 2) and declines rapidly with age; thus, in order to estimate a mean growth rate for a population, its mean age and/or distribution of biomass in different year classes must be known. The distribution of biomass with age can be computed if the growth rate and its change with age, and the quantitative distribution of grazing on different size of fish of a given species is known, and a steady state condition is assumed within a year.

The consumption of the biomass of a given species varies with the size (age) of the species. Only indirect information on this subject can be obtained from stomach analyses and from the consideration of the main predators of a given species. Furthermore, smaller fish (e.g., herring) and slow-growing fish (e.g., flounder) are vulnerable to predation (consumption) for a longer time than faster growing fish. Estimated monthly consumption of various year classes of three different species is presented (Figure 3) as a portion of the mean total biomass (mean standing stock) consumed (grazed) per month. Average turnover rates of the species (i.e., mean biomass divided by annual consumption, the latter obtained as a result of the model computations), average life length, and the size of these species at a given age (see Figure 2), are used as supporting information to derive the distribution of biomass predation with age (Figure 3).

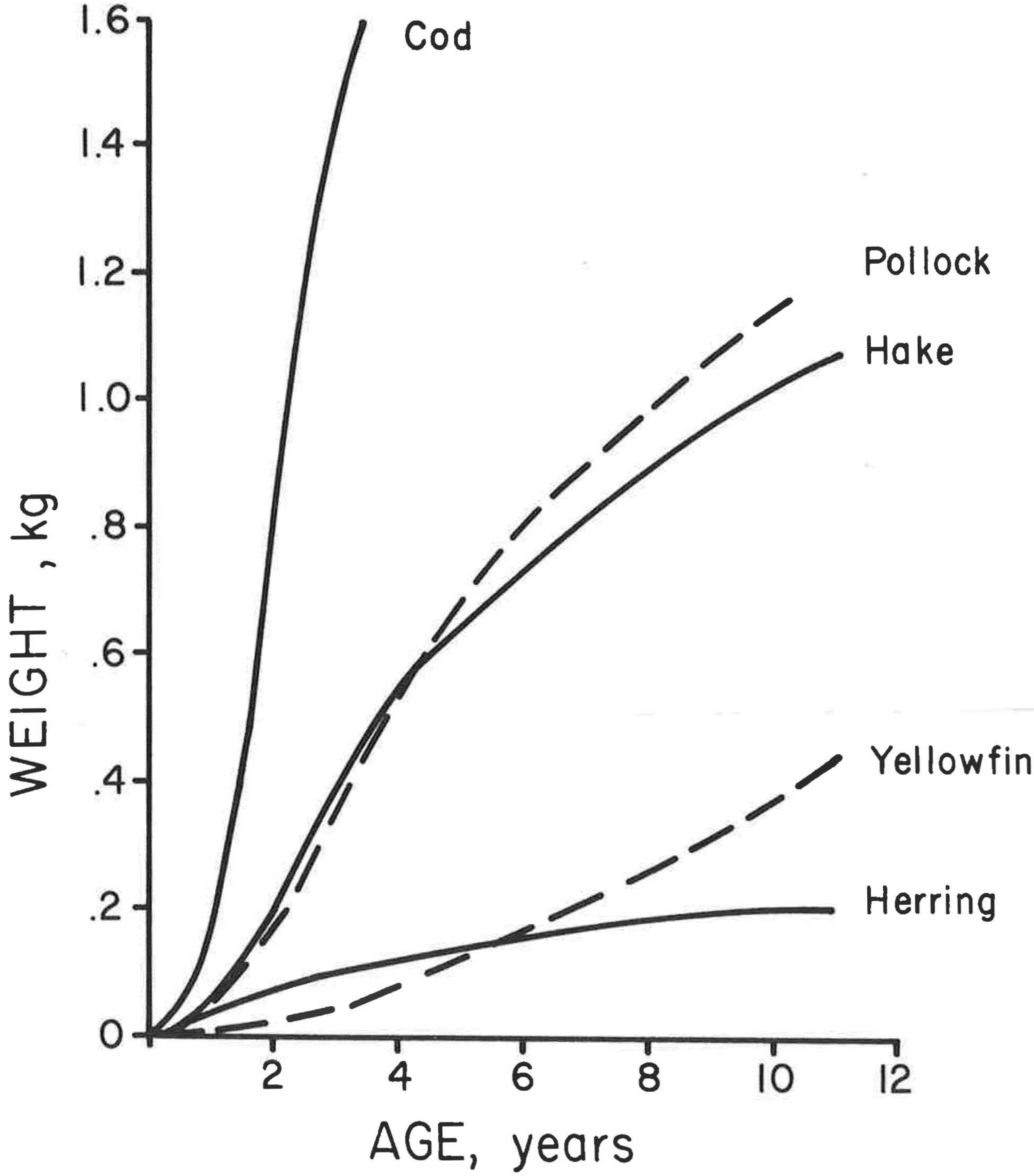

Figure 2.--Example of age-weight relations in some fish species.

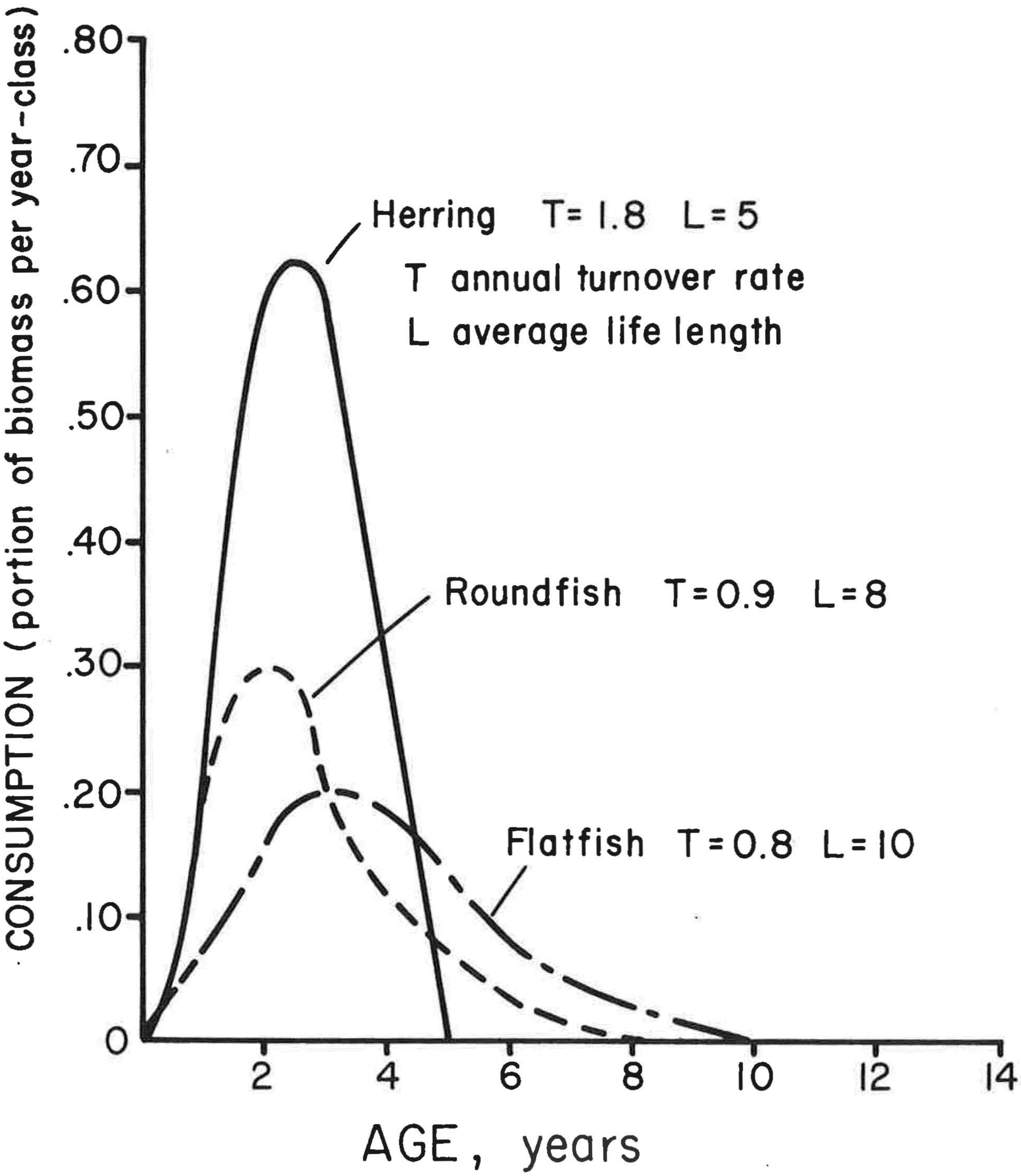

Figure 3.--Loss of biomass through grazing in three different fish, expressed as portion of minimum sustainable biomass per year class.

If, in addition to a steady state condition (i.e., consumption of a given year class equals its growth (Figure 4)), one assumes that there is a transfer of biomass into next year class equal to the grazing of the older biomass, plus further transfer to the older year class, the distribution of biomass in various year classes can be computed as % of total biomass (Figure 5) and as cumulative percentage of biomass (Figure 6).

The fishery is also selective in respect to size and, in some instances, year classes. Thus, the biomass distribution of an unexploited population must be different than an exploited population (Figure 7). The unexploited population accumulates some additional biomass in older generations which must be in equilibrium with higher mortality from old age, diseases, and specially from starvation. However, this excess is removed relatively rapidly when the species comes under exploitation. In exploited populations, the biomass distribution shifts with intensity of exploitation towards younger year classes. The distribution of the total predation, fishery, and mortality, within different year classes is different in small (usually slow growing) species than in large (usually faster growing) species (Figure 8).

The above models of biomass distribution and its changes do not allow the definition of maximum sustainable yield (MSY) nor optimum yield and raise serious doubts that either exists.

B. Formulation

The food flow diagram (Figure 9) of the Bulk Biomass Model (BBM) and the following basic formulas, although modified as required for computation of different ecological groups, form the basis of the model:

Monthly biomass balance formula:

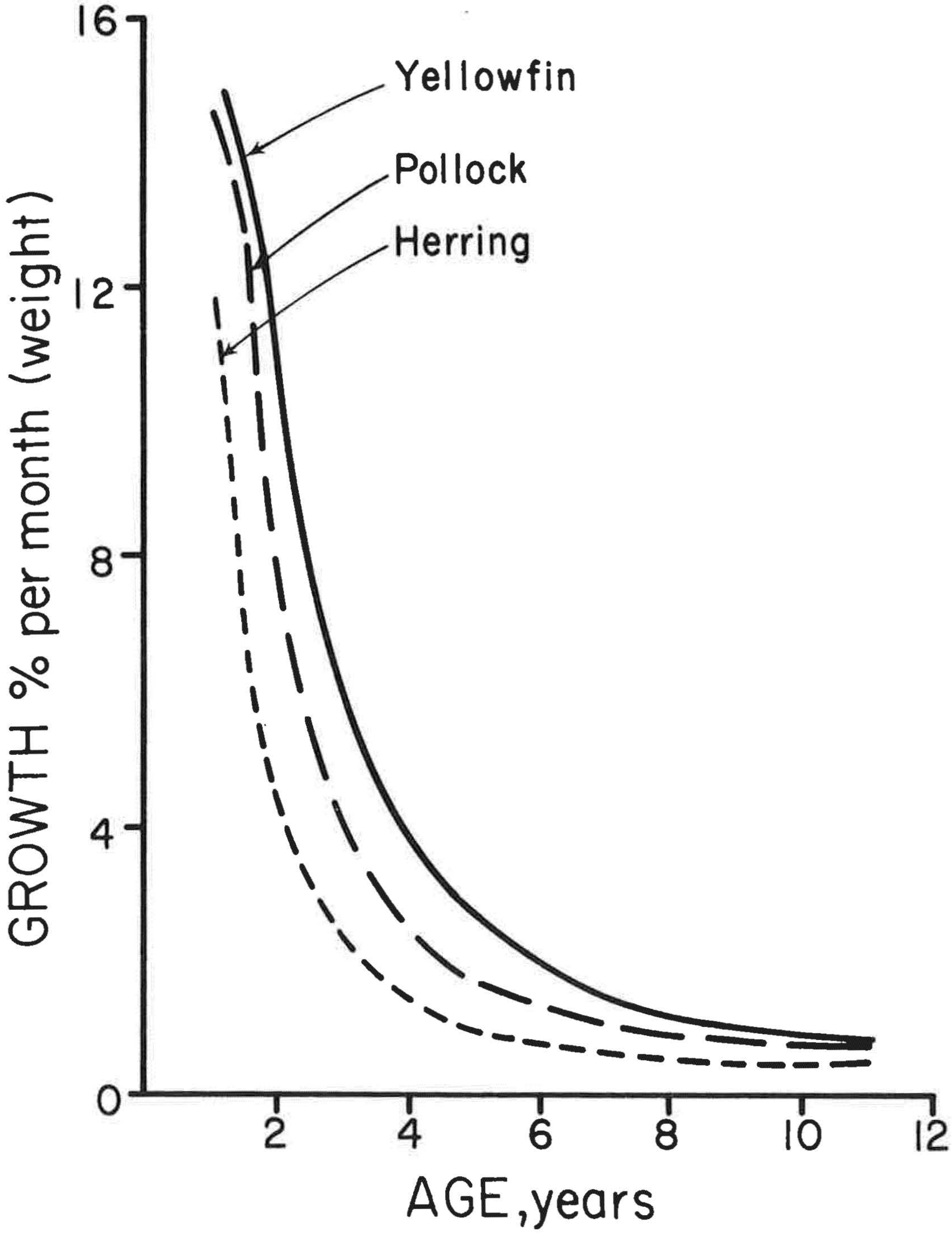

Figure 4.--Changes of monthly mean growth rate (% per month) with age in three different species.

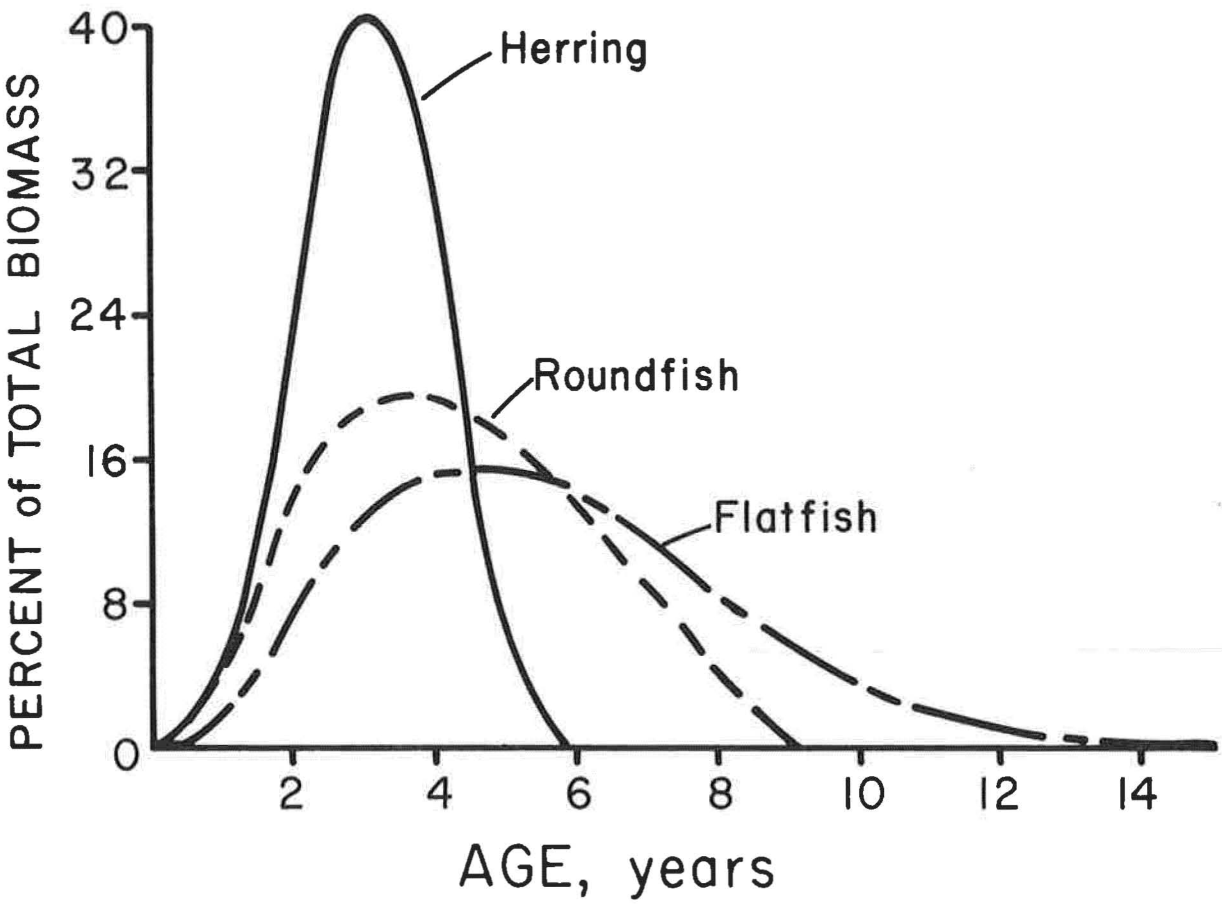

Figure 5.--Distribution of biomass in different year classes in three species, as dictated by ecosystem internal consumption.

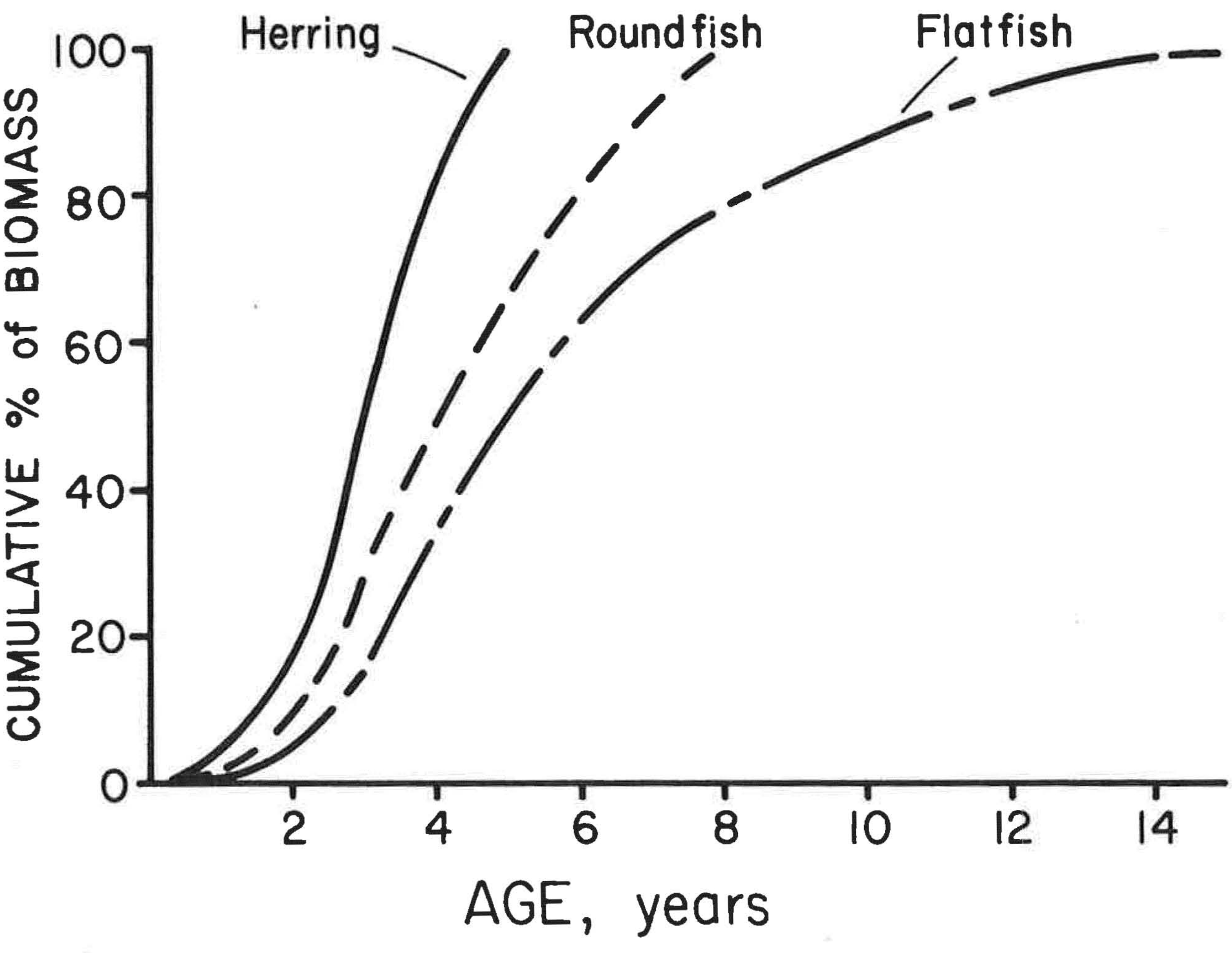

Figure 6.--Same as Figure 5, expressed as cumulative biomass.

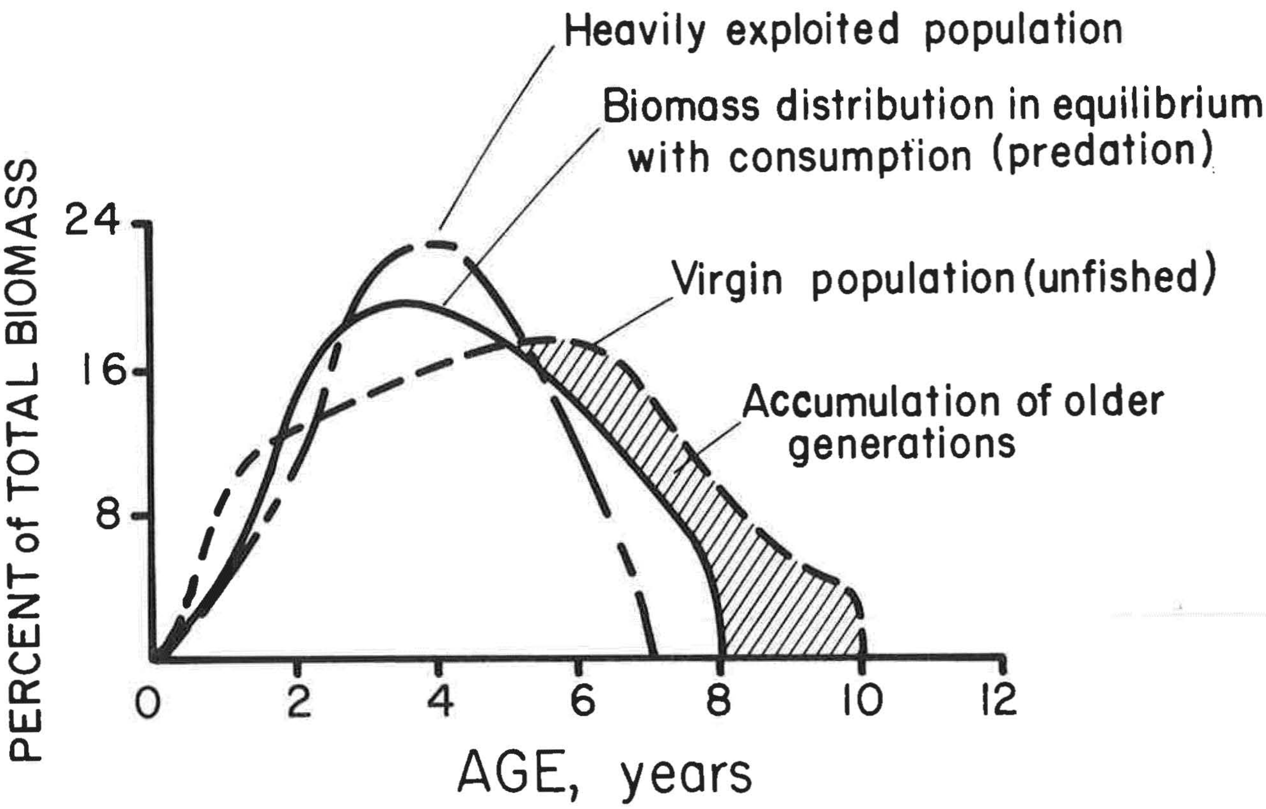

Figure 7.--Distribution of biomass in different year classes in minimum sustainable (equilibrium) population, in virgin (unexploited) population and in heavily exploited population.

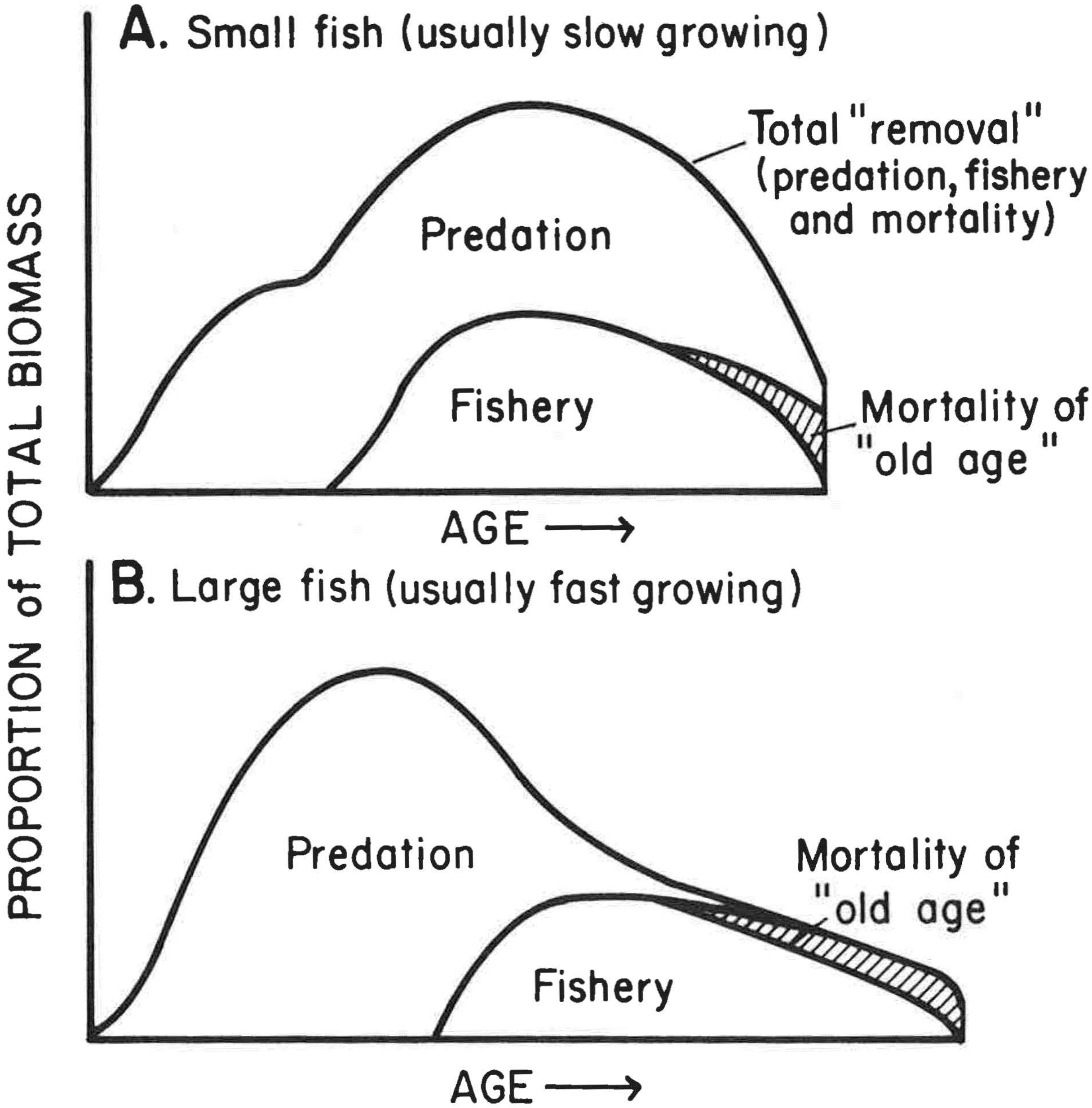

Figure 8.--The removal (loss) of biomass at different age in two different species (A) small fish (usually slow growing) and (B) large fish (usually fast growing).

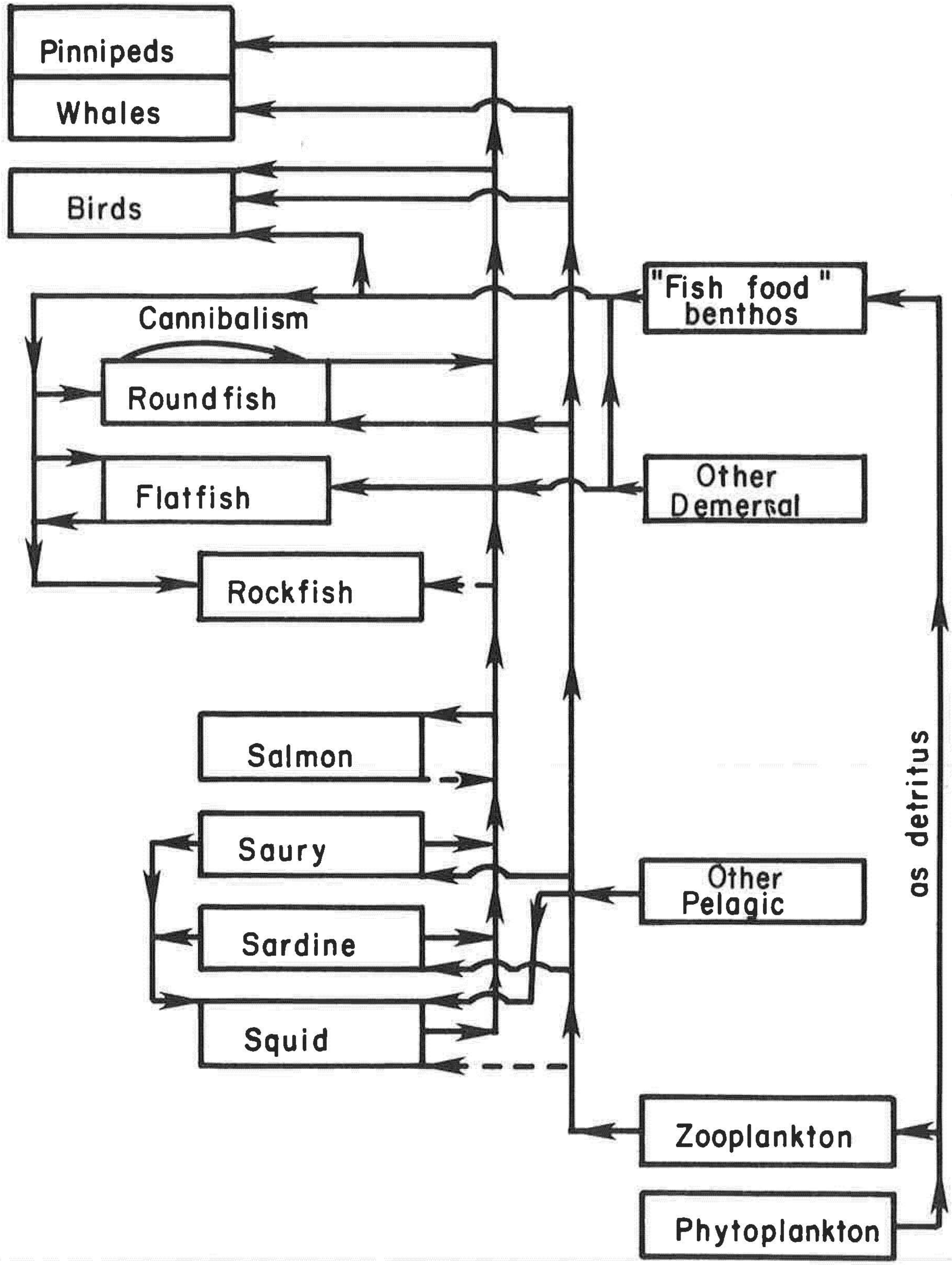

Figure 9. Schematic food flow diagram for BBM model.——major contribution; ---minor contribution.

$$B_{i,t} = B_{i,t-1} \left(2-e^{-g_{i,t}}\right) e^{-n-C_{i,t-1}} \tag{3}$$

$$\text{where: } g_{i,t} = g_{i,o} + g_{i,a} \cos\left(\alpha t - \mathcal{H}_{i,a}\right) \tag{4}$$

Food requirements and food proportioning formulas:

$$F_{i,t} = B_{i,t-1} \left(2-e^{-g_t}\right) K_{i,g} + B_{i,t} K_{i,m} \tag{5}$$

$$C_{i,j,t} = F_{i,t}\, \rho_{i,j}$$

$$C_{i,k,t} = F_{i,t}\, \rho_{i,k} \text{ -- etc.} \tag{6}$$

$$C_{i,t} = C_{u,i,t} + C_{k,i,t} + \ldots C_{n,i,t} \tag{7}$$

The symbols in the above equations are:

$B_{i,t}$ - minimum sustainable biomass (either total for the region or as kg/km^2) of ecological group i in month t

$g_{i,t}$ - monthly bulk growth coefficient (approximately growth in % per month) (g_o is mean growth coefficient and g_a is the annual range of its change; $\mathcal{H}$ is phase lag and α phase speed = 30^o per month).

$F_{i,t}$ - food requirement for growth and maintenance.

n - fishing mortality coefficient (approximate % per month)

K_g - food coefficient for growth (e.g., 1:3, 3 kg of food biomass gives 1 kg of growth).

K_m - food coefficient for maintenance (in terms of body (biomass) weight per time step)

$C_{i,t}$ - total amount of ecological group i consumed by other groups in unit time (month)

$\rho_{i,j}$ - proportion of ecological group j in the food of group i

The ecosystem internal consumption (grazing) ($C_{i,t}$) is computed in monthly time steps. However, total monthly $C_{i,t}$ is required for computation of biomass ($B_{i,t}$); therefore, previous month value of C ($C_{i,t-1}$) must be used.

The BBM model consists of a number of linear equations (and/or equations which can easily be linearized) with many unknowns. To make the solution possible and reliable (i.e., to narrow the error limits), it is necessary to prescribe as many quantities as possible. Thus, first the monthly amounts of mammals present in all computation areas (see description of the inputs in the next chapter) are prescribed. First-guess values of other biomasses are also introduced and these are changed in following iterative computations. However, it is advantageous to obtain more reliable estimates of one, or preferably two, major fish species or groups of species (the "base species"). The estimates of these "base species" are kept unchanged in the first few iterations, but are changed in the final iteration loops. Roundfish and flatfish have been selected in our present model as the base species. Roundfish biomass was taken from Alverson (1968) as a guide for estimation of the "base biomasses" of this group of species in the subareas of the model, assuming that 50% of the biomass is in prefishery juveniles. The estimate for flatfish biomass was obtained from Alverson, Pruter, and Ronholt (1964) with the same assumptions. In the future, other basic information, created by the BBM model, such as mean biomass per unit area (e.g., tons/km^2), turnover rate, etc., can be used for obtaining first guesses of biomasses of various ecological groups.

For the first month computation the values of ecosystem internal consumption ($C_{i,t-1}$) for previous month are required. These estimates are provided on the basis of experience and knowledge of turnover rates and vary from species to species (ca 3 to 9% for monthly mean biomass per month).

Relaxation methods with linear algebraic simultaneous equations can be used to solve the ecosystem model equation complex (Shaw 1953), however, a similar numerical iterative "successive corrections" method was used to solve the system of equations. This method consists of computing all biomasses and consumptions for a full year. Thereafter a "correction" for initial biomass estimates is computed:

$$B_{i,corr} = B_{i,1} + (B_{i,1} - B_{i,12}) /12 \qquad (8)$$

where $B_{i,corr}$ is the corrected biomass of i - species, $B_{i,1}$ is the initial guess for January and $B_{i,12}$ is the computed biomass for December. In most cases 4 to 6 initial iterations (base species kept unchanged) and about 20 final iterations are required for the convergence of solution.

The same model (BBM) can also be used in dynamic mode (i.e., migrations are allowed between computational subareas after initially computing the minimum sustainable biomass).

C. Input Data

The BBM model was applied to the central part of the eastern north Pacific coastal region from Point Conception to the northern tip of Vancouver Island and from the coast to 200 nautical miles offshore (Figure 10). This region was divided into four areas:

1) the Inland Waters (Puget Sound, including the Straits of Juan de Fuca and the Straits of Georgia);

2) off Vancouver Island;

3) off Washington/Oregon coast;

4) off northern and central California coast.

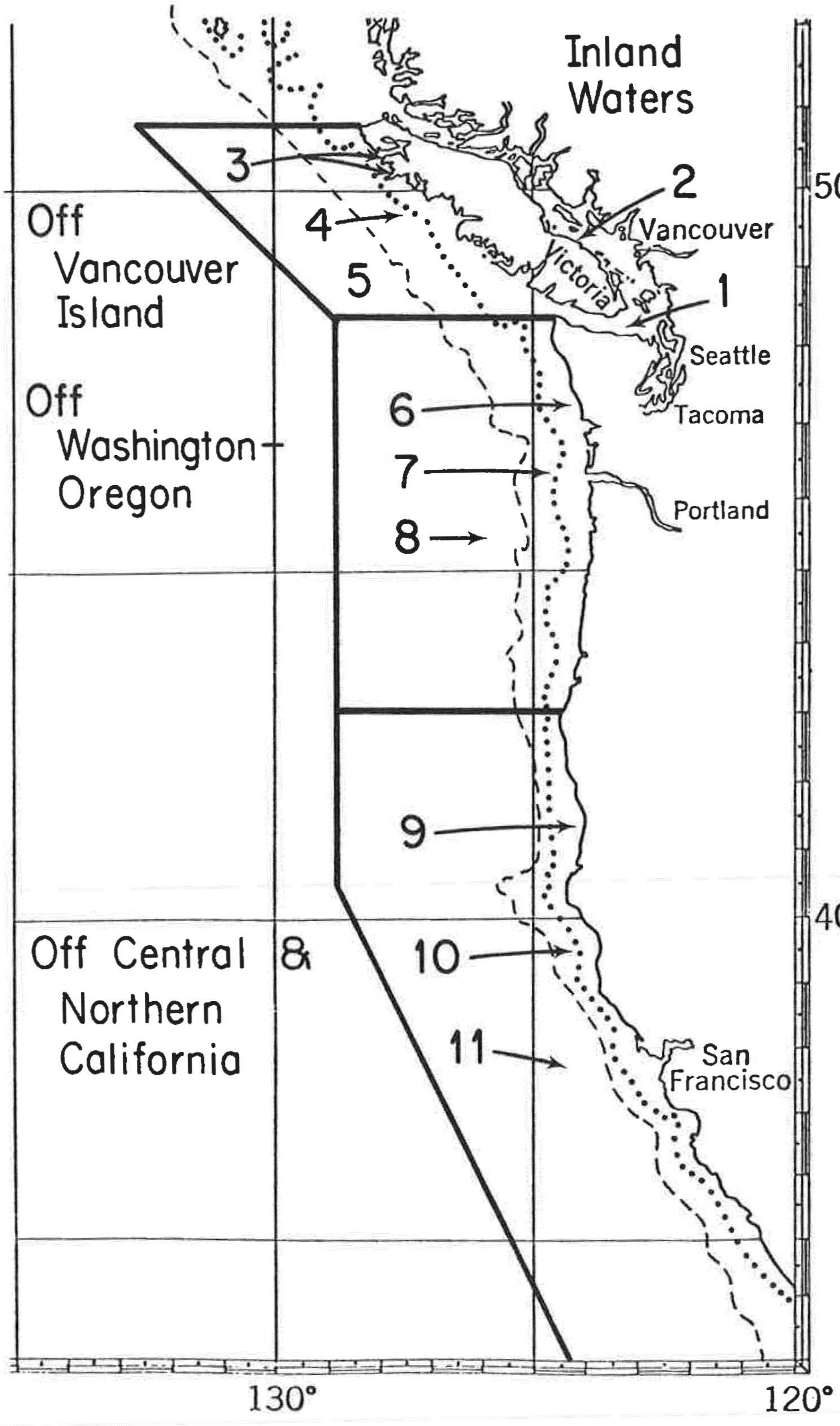

Figure 10.--The region covered by the model and the computational subareas.

Each of the areas off the coast was divided into three computational subareas: from the coast to 200 m depth; from 200 to 1,000 m depth; and from 1,000 m depth to 200 nautical miles offshore (Table 1).

The ecological groups and their major species composition and synonyms used in the model are given in Table 2. Usually in an area only one species in an ecological group is quantitatively dominant (e.g., hake in roundfish group and ocean perch in rockfish group), but there are also relatively heterogenous groups in which one species dominates in the northern part of the area (e.g., salmon) and another in the southern part (e.g., tuna).

The monthly numbers of fur seals and sea lions in various computation subareas (Tables 3 and 4) and the mean weights of mammals for converting numbers to weights (Table 5) are based on information obtained from the Marine Mammals Division of the Northwest and Alaska Fisheries Center, and Johnson (1975), McAlister and Perez (1976), and Fiscus and Barnes (1966). The monthly number of baleeen whales and toothed whales in different subareas (Tables 6 to 9) are based on information obtained from the Marine Mammals Division and the following references: Pike (1965); Doi, Nemoto, and Ohsumi (1967); Rice (1971); and Tillman (1975). Although sperm whales and porpoises and dolphins are listed separately, they are used in computations as a single group (toothed whales).

The average monthly number of marine birds per square kilometer in different subareas (Table 10) is based on previous estimates by Straty and Haight (1976), and Wiens and Scott (1975). In estimating the mean weight, the distribution of the heavier birds such as the shearwater and murre, which can be in excess of 700 g) and small birds (such as storm-petrel, ca 60 g) was considered.

Table 1

Computation Areas

Area No.	Geographical Limits	Depth Range		Area Square Mi.	Area Square Km.
1	Strait of Juan de Fuca	-		1,151	2,981
2	Strait of Georgia	-		4,174	10,813
3	North of Vancouver	0-200 m.		6,904	17,881
4	Island to Cape	200-1000 m.		4,349	11,263
5	Flattery	1000 m-200 n. mil.		22,097	57,230
			TOTAL	33,350	86,376
6	Cape Flattery to	0-200 m.		9,792	25,361
7	Cape Blanco	200-1000 m.		14,007	36,277
8		1000m - 200 n. mil.		53,251	137,919
			TOTAL	77,050	199,558
9	Cape Blanco to	0-200 m.		7,688	19,911
10	Point Conception	200-1000 m.		18,847	48,813
11		1000 m -200 n. mil.		87,873	227,590
			TOTAL	114,408	296,315

Table 2

Ecological groups, their synonyms, and species composition as used in the model

cx	Pinnipeds - fur seals, sea lions
cx	Baleen whales - blue whales, fin whales, grey whales, mink whales
cx	Toothed whales - sei whales, humpback whales, Bryde's whales, sperm whales, bottlenose whales
c	Phytoplankton - (simulation of approximate standing crop and computation of consumption)
c	Zooplankton - copepods and euphausids (emphasis on computation of consumption)
b	Squids - (all Cephalopods); pelagic
b	Sardines - sardines, anchovies, herring, smelts; pelagic
b	Saury - saury, mackerel, lanternfishes, (pomfret); pelagic
b	Salmon - salmons, tunas, bonitos; pelagic (salmon in northern, tuna in southern part of the region)
c	(Other pelagic fish) - pelagic phases (mainly 0 group) of roundfishes and rockfishes; other pelagic fish not listed above; only consumption computed
bxx	Roundfishes - hake and other gadids, sablefish; semipelagic
b	Rockfishes - mainly Scorpaenidae such as Pacific Ocean perch, etc.; demersal
bxx	Flatfishes - mainly flounders (Pleuronectidae and Bothidae); demersal
c	(Other demersal fish) - sculpins (Cottidae), Elasmobranchs, etc; only consumption computed
c	Benthos - "fish food" benthos only; consumption computed

x Monthly biomass prescribed in the model

xx Initial biomass estimation of these ecological groups weighed more than other estimates

b Ecological groups where minimum sustainable biomass was computed

c Ecological groups where only ecosystem internal consumption (grazing) was computed

Table 3

Number of fur seals (in thousands) in computation subareas

Month	Subareas 1	2	3	4	5	6	7	8	9	10	11
1 Jan	15	15	105	40	20	160	30	10	320	95	10
2 Feb	15	15	90	29	10	175	20	5	300	30	5
3 Mar	25	25	115	30	5	160	30	10	220	65	5
4 Apr	25	25	130	30	17	150	40	10	200	40	5
5 May	20	20	115	25	20	120	35	14	185	30	5
6 Jun	10	10	90	20	15	80	45	20	100	43	2
7 Jul	1	1	5	3	1	5	2	1	3	2	1
8 Aug	0.5	0.5	2	1	1	1.5	1	1	3	1	1
9 Sep	0.2	0.2	2	0.5	0.5	1.5	1	1	3	1	1
10 Oct	0.5	0.5	2	1	1	2.0	2	1	4	2	1
11 Nov	5	5	80	40	20	65	15	5	40	5	5
12 Dec	10	10	120	40	20	110	45	10	220	60	10

Table 4

Number of sea lions (in thousands) in computation subareas

Subareas

Month		1	2	3	4	5	6	7	8	9	10	11
1	Jan	0.5	0.3	3.8	0.2	0.1	6.0	1.0	0.1	25.0	3.0	2.0
2	Feb	0.6	0.4	4.0	0.2	0.1	6.5	1.5	0.1	25.0	3.0	2.5
3	Mar	0.5	0.4	4.0	0.2	0.1	6.0	1.0	0.1	25.0	3.0	2.0
4	Apr	0.6	0.4	3.5	0.3	0.1	5.5	2.0	0.1	18.0	2.0	1.5
5	May	0.3	0.3	3.0	0.2	0.05	5.0	2.5	0.05	9.0	1.5	1.0
6	Jun	0.2	0.3	2.0	0.2	0.05	4.5	1.0	0.05	6.0	1.0	0.2
7	Jul	0.1	0.2	1.5	0.1	0.05	3.0	0.5	0.05	1.5	0.5	0.1
8	Aug	0.1	0.2	1.5	0.1	0.05	1.5	0.5	0.05	1.5	0.5	0.1
9	Sep	0.1	0.2	1.5	0.1	0.05	2.0	1.0	0.05	1.5	0.5	0.1
10	Oct	0.3	0.3	2.0	0.3	0.1	2.5	2.0	0.1	5.0	1.0	1.0
11	Nov	0.4	0.4	2.5	0.2	0.1	6.5	1.5	0.1	12.0	1.5	1.5
12	Dec	0.5	0.3	2.9	0.2	0.1	6.0	1.0	0.1	20.0	2.5	2.0

Table 5

Mean Weights of Mammals and Birds

Fur seals	55 kg
Sea lions	250 kg
Baleen whales	40,000 kg
*Toothed whales	10,000 kg
Marine birds	0.4 kg
Porpoises, dolphins	100 kg

*Except sperm = 30,000 (accounted separately)

Table 6

Numbers of baleen whales in computation subareas

Subareas

Month	1	2	3	4	5	6	7	8	9	10	11
1 Jan	0	0	0	0	0	0	0	0	400	800	1000
2 Feb	0	0	0	0	0	0	0	0	400	800	1400
3 Mar	0	0	0	0	0	0	0	0	300	800	1300
4 Apr	0	0	0	0	0	40	80	150	100	400	1000
5 May	5	5	20	90	200	80	200	650	75	325	710
6 Jun	5	5	80	310	740	100	150	300	10	100	200
7 Jul	3	3	75	300	720	80	120	250	10	100	200
8 Aug	2	2	60	180	400	80	200	450	10	100	200
9 Sep	5	5	80	400	800	50	150	350	10	100	200
10 Oct	1	1	35	100	200	50	120	280	50	250	700
11 Nov	0	0	0	0	0	0	0	0	150	500	900
12 Dec	0	0	0	0	0	0	0	0	250	650	1200

Table 7

Numbers of toothed whales in computation subareas

Month	Subareas 1	2	3	4	5	6	7	8	9	10	11
1 Jan	50	50	150	500	1600	300	400	1500	2000	3000	4000
2 Feb	50	50	150	500	1500	300	400	1500	2000	3000	4000
3 Mar	35	35	160	560	1600	300	400	1500	2000	3000	4000
4 Apr	30	30	160	560	1600	300	450	1500	1500	2500	3500
5 May	20	20	160	560	1600	300	450	1500	1000	1500	1500
6 Jun	25	25	160	560	1600	300	450	1500	1000	1500	1500
7 Jul	40	40	220	650	1700	350	500	1600	1000	1500	1500
8 Aug	40	40	300	700	1700	350	500	1600	1000	1500	1500
9 Sep	30	30	200	600	1600	350	500	1600	1300	1800	1500
10 Oct	35	35	160	500	1500	300	450	1500	1500	1800	2500
11 Nov	40	40	160	500	1500	300	400	1500	1800	2000	3000
12 Dec	40	40	150	500	1500	300	400	1500	1800	2500	3500

Table 8

Number of sperm whales (toothed) in computation subareas

Subareas

Month	1	2	3	4	5	6	7	8	9	10	11
1 Jan	2	2	200	200	1000	300	500	1200	400	1200	5000
2 Feb	2	2	180	200	1000	300	500	1200	400	1200	5000
3 Mar	2	2	150	220	1200	300	500	1200	400	1200	5000
4 Apr	2	2	300	750	2200	380	600	1800	700	1800	6500
5 May	2	2	400	850	2600	450	650	2600	800	2000	7000
6 Jun	2	2	200	450	1200	380	600	2000	800	2000	7000
7 Jul	2	2	200	450	1200	380	620	2000	800	2000	7000
8 Aug	2	2	400	850	2600	450	650	2600	800	2000	7000
9 Sep	2	2	400	850	2600	450	640	2500	800	2000	7000
10 Oct	2	2	400	850	2600	420	630	2400	800	1800	6500
11 Nov	2	2	400	850	2600	400	620	2300	750	1500	6000
12 Dec	2	2	200	200	1000	380	600	1800	600	1400	5500

Table 9

Estimated number of porpoises and dolphins in computation subareas

(no estimates on monthly variation available)

Area	Number	Area	Number
1	50	7	3,000
2	50	8	6.000
3	300	9	4,000
4	500	10	5,000
5	1,200	11	16,000
6	3,000		

Table 10

Number of marine birds, per km^2 in computation subareas

Month		Subareas 1	2	3	4	5	6	7	8	9	10	11
1	Jan	10	10	15	2	0.2	15	1	0.2	15	2	0.2
2	Feb	15	15	10	2	0.2	15	1	0.2	15	2	0.2
3	Mar	15	15	15	3	0.2	15	1	0.2	15	3	0.2
4	Apr	20	20	20	5	0.3	20	2	0.3	15	4	1.0
5	May	30	30	30	5	0.3	30	5	0.3	15	4	1.0
6	Jun	20	20	20	3	0.3	30	2	0.3	10	4	0.1
7	Jul	15	15	20	3	0.3	25	1	0.3	10	5	0.1
8	Aug	15	15	20	5	0.3	20	1	0.3	10	5	0.2
9	Sep	20	20	20	6	0.3	20	1	0.3	15	5	0.5
10	Oct	20	20	25	5	0.2	15	3	0.2	15	4	1.0
11	Nov	15	15	15	4	0.2	15	2	0.2	15	3	0.5
12	Dec	15	15	15	2	0.2	15	1	0.2	15	2	0.2

The growth and mortality coefficients, used in the model, are given in Table 11. The growth coefficient was made a harmonic function of time:

$$G = G_o + G_v \cos(\alpha t - \mathcal{H}) \qquad (9)$$

where G_o is the annual mean growth coefficient, G_v is the total annual change of the growth coefficient, α is 30^o in monthly computation, t is time in month, and $\mathcal{H}$ is phase lag in degrees.

The food requirements (Table 12) are summarized from a variety of sources; the food requirements for finfish are taken notably from a recent excellent work by Tyler and Dunn (1976), but also from Alton and Nelson (1970), Shevtsov (1972), and Fields (1967). The lowest possible food requirements are used, as we are interested in computing minimum sustainable biomasses. The food requirements for mammals are based on the works of Sergeant (1969), McAlister and Perez (1976), Tarasevich (1968), and others. Although the marine birds' food requirement is usually estimated at 20% of body weight daily (Wiens and Scott 1975), a lower value of 12% was used in our model.

The composition of food of most species of fish is variable in space and time within certain limits which are usually dependent on the food availability. There are numerous, mainly qualitative, notes on food composition in the literature. In order to derive reasonable estimates of mean composition of food of any ecological group in a relatively large region, one has to scan voluminous literature in search of food composition data. The food composition by weight percentage of various ecological groups in the model (Tables 13 and 14) represents a synthesis of available information, which is admittedly meager and should be improved with future field work because the composition of food of any ecological group determines largely the interactions between different ecological groups and the model computation results.

Table 11

Growth and Mortality Coefficients

	Growth*	Total Mortality**	Natural Mortalities**	Fishing Mortalities**
Squids	0.138 to 0.258	0.045	(0.045)	
"Sardines"	0.128 to 0.228	0.020	0.01	0.01
"Saury"	0.120 to 0.220	0.035	(0.035)	
"Salmon"	0.04 to 0.08	0.036	0.006	0.03
Other pelagic fish	0.128 to 0.288	0.035	0.02	0.015
Roundfish	0.075 to 0.120	0.0215	0.01	0.015
Rockfish	0.065 to 0.115	0.0215	0.01	0.015
Flatfish	0.065 to 0.105	0.0215	0.01	0.015
Other demersal fish	0.06 to 0.12	0.02	0.015	0.005
Benthos ("fish food" benthos)	0.10	0.0215	(0.0215)	

*Growth and mortality coefficients are in % of biomass per month. Growth coefficient was made a harmonic function of time: minimum and maximum values are given in this table.

**Total mortality is a sum of fishing mortality and natural mortality (of old age and diseases); it was used in most computations. However, in some computations the natural and fishing mortalities were computed separately.

Table 12

Food Consumption (and/or requirements)

A. Fish, plankton and benthos

Squids	1:4 for growth only
"Salmon"	1:2.2 for growth + 1.35% body weight daily for maintenance
"Sardines") "Saury") Others, pelagic)	1:2 for growth + 1% body weight daily for maintenance
Roundfish	1.3% body weight daily
Rockfish	1% body weight daily
Flatfish	1% body weight daily
Other demersal fish	1.3% body weight daily
Benthos	1% body weight daily (phytoplankton).
Zooplankton	1.5% body weight daily

B. Mammals and birds

Fur seals) Sea lions)	5% body weight daily
Baleen whales, toothed whales, porpoises, dolphins	4% body weight daily
Marine birds	12% body weight daily

Table 13

<u>Composition of Food of Mammals and Birds</u>

<u>Fur seals</u>
58% roundfish
18% rockfish
4% saury, mackerel, pomfret
5% sardines, anchovies
11% squids
1% salmon, tuna
3% others

<u>Sea lions</u>
60% roundfish
20% rockfish
10% saury, mackerel, pomfret
4% salmon, tuna
6% others

<u>Baleen whales</u>
70% euphausids
14% copepods
9% squids
7% sardines, anchovies

<u>Toothed whales, porpoises, dolphins</u>
20% squids
20% sardines, anchovies
20% other pelagic fish
6% salmon, tuna
20% roundfish
14% saury, mackerel, pomfret

<u>Marine birds</u>
40% sardines, anchovies
5% flatfish
5% roundfish
5% rockfish
10% others
20% euphausids
10% squids
5% benthos

Table 14

Composition of Food of Plankton and Fish

Zooplankton
100% phytoplankton

Squids
20% copepods
30% euphausids
25% sardines
10% saury
15% other pelagic fish

Saury, mackerel
66% copepods
16% euphausids
10% phytoplankton
8% other pelagic fish

Roundfish
6%"sardines"
4%"saury"
0.5%"salmon"
10% squids
1% other pelagic fish
50% euphausids
3% flatfish
6.5% rockfish
14% benthos
3% roundfish
2% other demersal fish

Flatfish
58% benthos
18% other demersal fish
4% flatfish
4% rockfish
4% roundfish
9% euphausids
1.5% "sardines"
1.5% "saury"

Sardines, anchovies, smelt
71% copepods
12% euphausids
15% phytoplankton
2% other pelagic fish

Salmon, tuna
25% "sardines"
25% "saury"
10% other pelagic fish
15% squids
15% euphausids
10% roundfish

Rockfish
2.5% "sardines"
2.5% "saury"
2% other pelagic fish
15% euphausids
9% squids
40% benthos
20% other demersal fish
3% rockfish
3% flatfish
3% roundfish

III. DISTRIBUTION OF MINIMUM SUSTAINABLE BIOMASS OF MARINE ECOLOGICAL GROUPS

The distribution of minimum sustainable biomasses of marine ecological groups as defined in this model on the basis of mean composition of food, their ecosystem internal consumptions (grazing), and annual turnover rates, as computed with the BBM model are given (Tables 15 to 18) and summarized (Figures 11 to 17). With respect to productivity, the biomass in terms of weight per unit area (tons per km^2) is more meaningful (Table 19). The highest biomass of squids is found off California, where the bulk of the biomass of sardines and anchovies is also located--the smelts and herrings occurring further north, off Oregon and Washington coasts. Of the large pelagic fish, the salmon occur in the northern part of the areas and tuna in the south with considerable overlap of the two species groups off the Oregon coast. Unfortunately the highly variable past estimates of the standing stocks of pelagic species, prevents any meaningful comparison between these past estimates and our present result. However, the past estimates of the standing stocks of semidemersal and demersal fish, based on exploratory fishing results, are much more reliable than those of pelagic fish, where the sampling methods are difficult to quantify. If we assume that about 60% of the biomass of the demersal and semidemersal species are under exploitation or exploitable, we can convert values presented by Alverson (1968) to total biomass. The resulting comparison is favorable with respect to flatfish and roundfish off the U.S. west coast (flatfish-495 x 10^3 tons versus model value of 438.8 x 10^3 tons; roundfish-1290 x 10^3 tons versus model value of 1631 x 10^3 tons). These groups of species were, however, used as "base species" and the agreement between reported and computed values is expected. With

Table 15

"Minimum sustainable" biomass and ecosystem internal consumption of marine ecological groups along west coast of USA, 10^3 tons

Inland Waters

Ecological Groups	1. Puget Sound-Strait of Juan de Fuca			2. Strait of Georgia		
	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate
Squids	(12.9)	(20.1)	(1.56)	(14.5)	(22.7)	(1.57)
Sardines, anchovies, herrings	29.9	53.3	1.78	34.6	61.5	1.78
Saury, mackerel, pomfret	(15.5)	(24.0)	(1.55)	(17.7)	(27.2)	(1.54)
Salmon, tuna	3.2	1.0	0.31	3.7	1.0	0.27
Roundfish	21.4	15.4	0.72	23.3	16.7	0.72
Rockfish	13.5	9.9	0.73	15.6	11.1	0.71
Flatfish	7.9	5.7	0.72	10.3	6.8	0.66
"Fish food" benthos	-	51.8	-	-	63.1	-

Table 16

"Minimum sustainable" biomass and ecosystem internal consumption of marine ecological groups along west coast of USA, 10^3 tons

Off Vancouver Island

Ecological group	3. Coast to 200 m.			4. 200 to 1000 m.			5. 1000 m to 200 n. miles offshore		
	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate
Squids	69.7	111.8	1.60	66.6	107.9	1.62	121.1	199.9	1.65
Sardines, anchovies, herrings	159.9	288.9	1.81	152.2	277.0	1.82	269.8	496.5	1.84
Saury, mackerel, pomfret	83.6	131.7	1.58	87.5	137.7	1.57	169.6	269.2	1.59
Salmon, tuna	18.2	6.2	0.34	22.5	8.6	0.38	51.2	21.5	0.42
Roundfish	117.9	90.7	0.77	85.6	68.0	0.79	133.9	124.2	0.93
Rockfish	68.9	55.6	0.81	44.1	34.8	0.80	(42.9)*	(44.0)	(0.93)
Flatfish	37.3	28.9	0.77	29.3	21.3	0.73	(26.6)	(25.1)	(0.94)
"Fish food" benthos	-	255.6	-	-	187.4	-	-	(187.6)	-

*Values in parenthesis are less certain and represent mainly pelagic juveniles

Table 17

"Minimum sustainable" biomass and ecosystem internal consumption of marine ecological groups along west coast of USA, 10^3 tons

Washington/Oregon Coast

Ecological group	6. Coast to 200 m.			7. 200 to 1000 m.			8. 1000 m. to 200 n. miles offshore		
	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate
Squid	98.4	158.8	1.61	72.9	117.0	1.60	108.0	178.9	1.66
Sardines, anchovies, herring	226.9	412.9	1.82	170.8	308.1	1.80	241.1	443.5	1.84
Saury, mackerel, pomfret	120.5	190.7	1.58	95.4	148.8	1.56	146.7	235.2	1.60
Salmon, tuna	27.3	9.1	0.33	23.1	8.2	0.35	39.8	20.8	0.52
Roundfish	166.5	127.0	0.76	98.5	74.4	0.76	121.9	111.4	0.91
Rockfish	96.9	76.4	0.79	59.3	42.6	0.72	(42.8)*	(40.2)	(0.94)
Flatfish	54.8	40.9	0.75	41.8	27.5	0.66	(26.8)	(24.0)	(0.90)
"Fish food" benthos	-	364.8	-	-	255.2	-	-	(186.0)	-

*Values in parenthesis are less certain, representing mainly pelagic juveniles.

Table 18

"Minimum sustainable" biomass and ecosystem internal consumption of marine ecological groups along west coast of USA, 10^3 tons

Central and Northern California Coast

Ecological group	9. Coast to 200 m.			10. 200 to 1000 m.			11. 1000 m. to 200 n. miles offshore		
	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate	Mean biomass	Annual consumption	Annual turnover rate
Squid	207.8	337.6	1.62	209.3	333.5	1.59	252.5	405.9	1.61
Sardines, anchovies, herring	468.9	854.8	1.82	475.1	847.3	1.78	560.8	998.9	1.78
Saury, mackerel, pomfret	261.7	417.5	1.60	281.4	437.4	1.55	333.4	523.8	1.57
Salmon, tuna	65.4	25.6	0.39	78.0	29.3	0.38	89.1	45.5	0.51
Roundfish	337.5	258.7	0.77	253.6	200.8	0.79	271.0	237.8	0.88
Rockfish	166.7	142.6	0.86	109.3	93.3	0.85	(87.0)*	(86.1)	(0.99)
Flatfish	82.8	72.2	0.87	70.6	56.5	0.80	(50.6)	(50.5)	(1.00)
"Fish food" benthos	-	603.6	-	-	468.5	-	-	(374.9)	-

*Values in parenthesis are less reliable, representing mainly juveniles and pelagic stages.

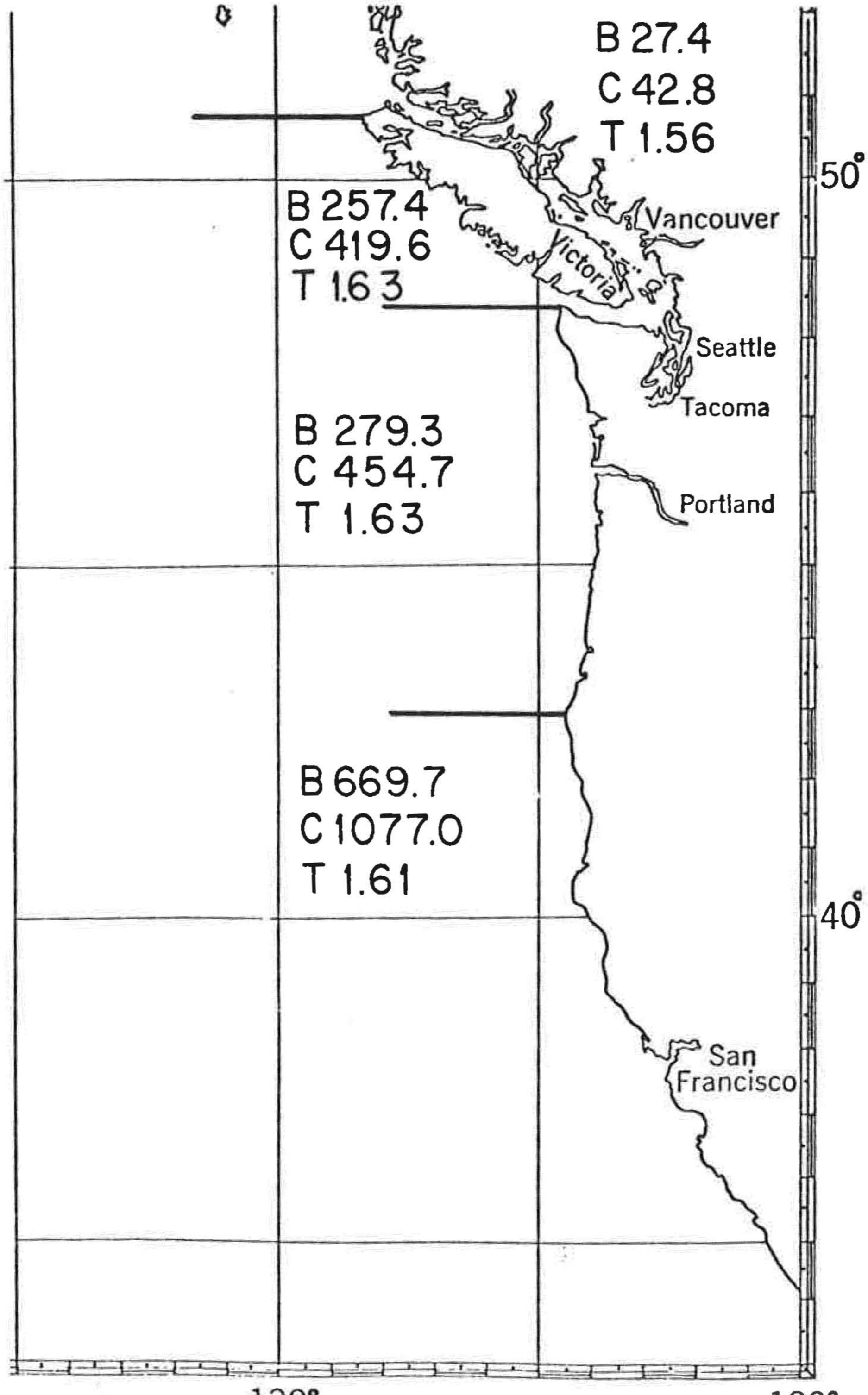

Figure 11.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of squids.

Note: Resources south of Point Conception are excluded. B-minimum sustainable biomass in 10^3 tons; C-ecosystem internal consumption in 10^3 tons/year; T-mean annual turnover rate.

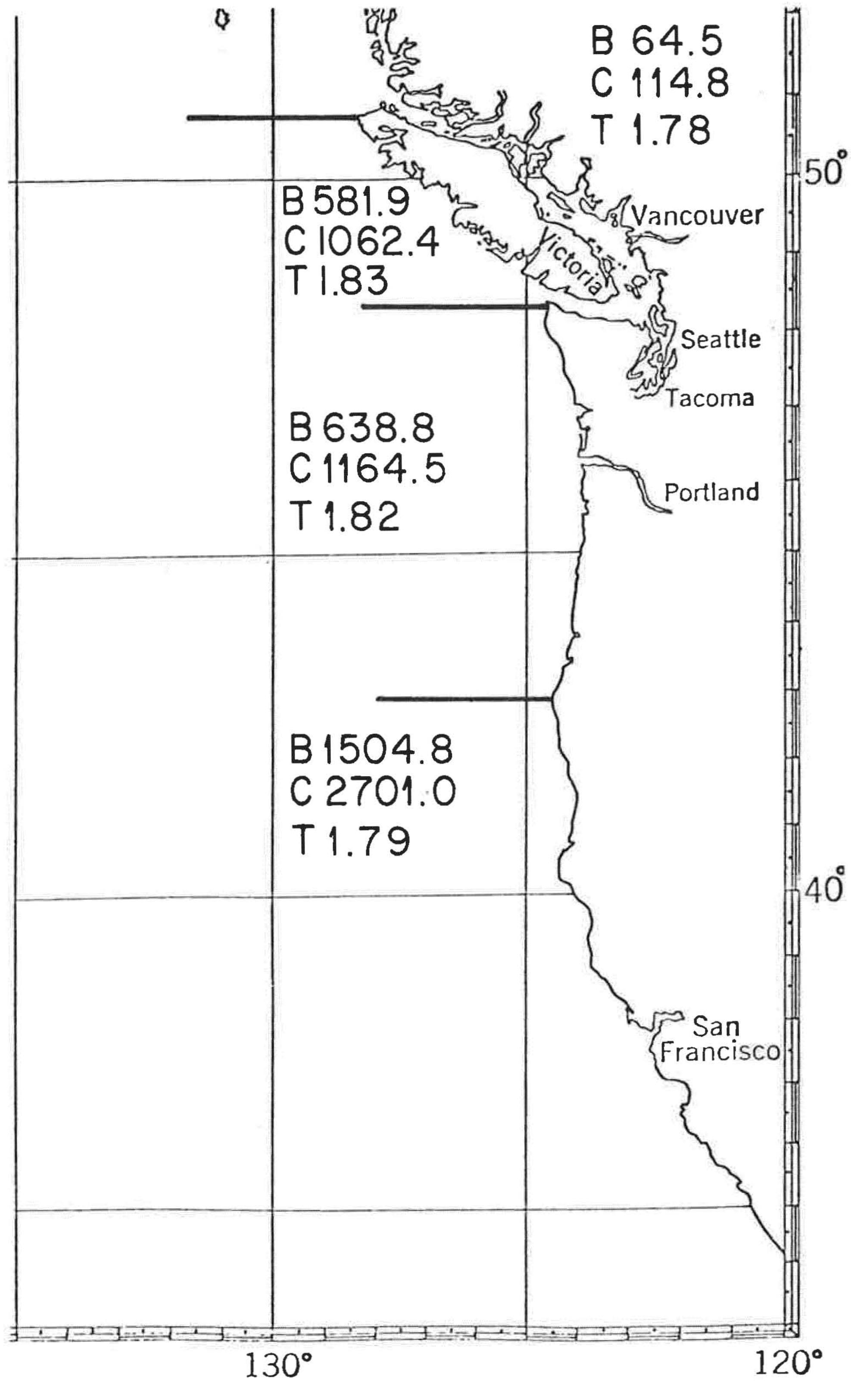

Figure 12.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of sardine, anchovy, smelt, and herring.

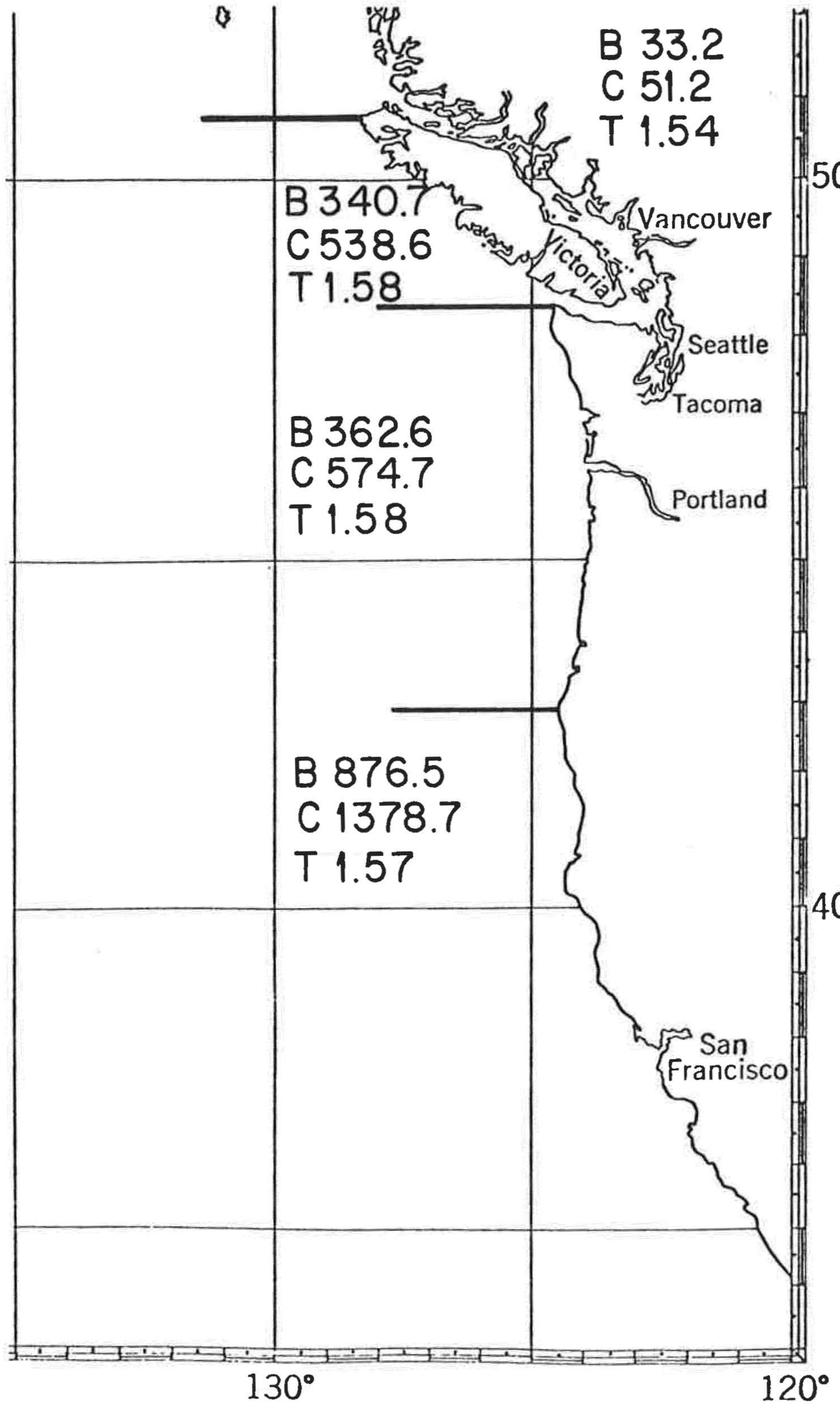

Figure 13.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of saury, mackerel, lanternfishes, and pomfret.

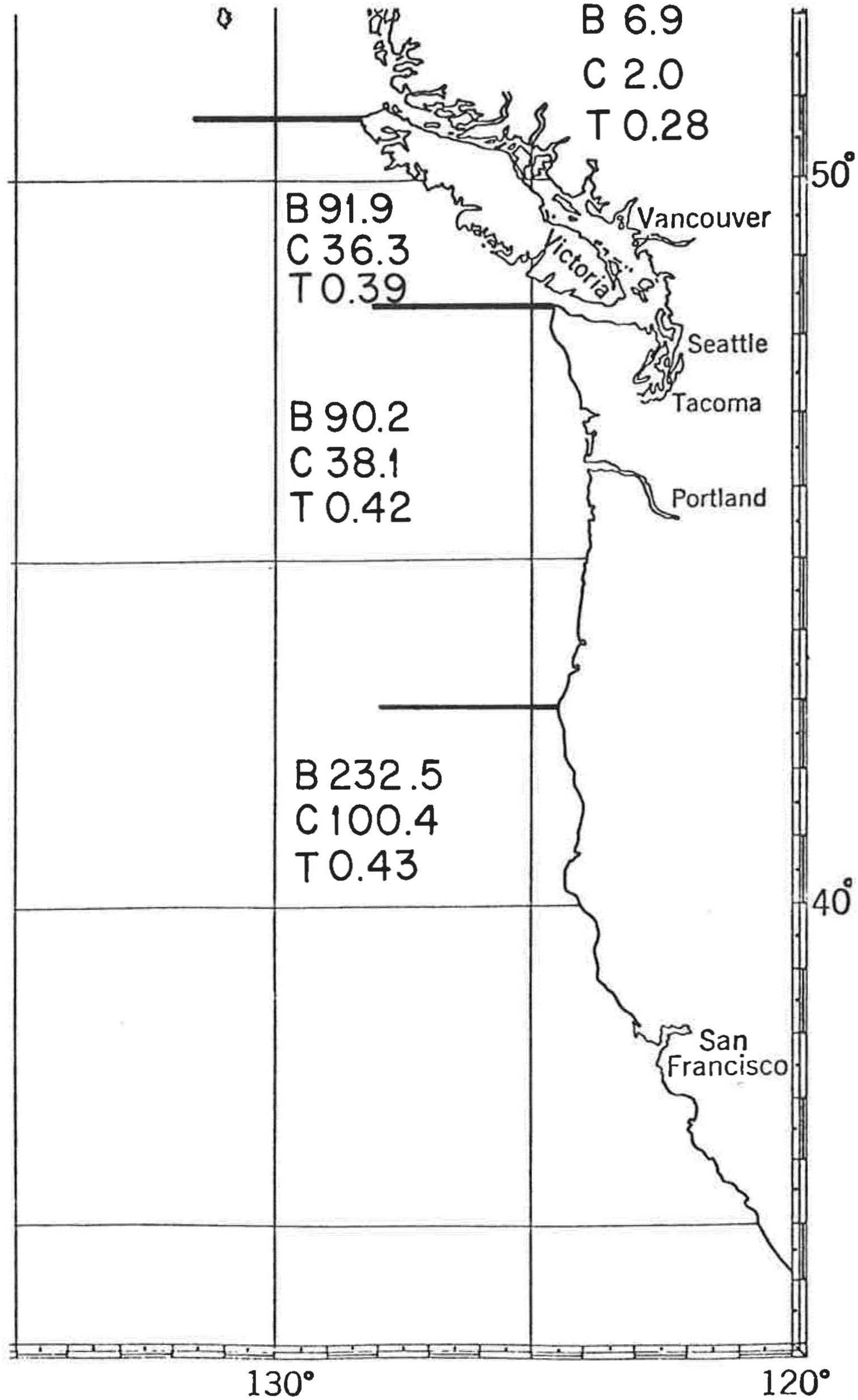

Figure 14.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of salmon, tuna, bonito.

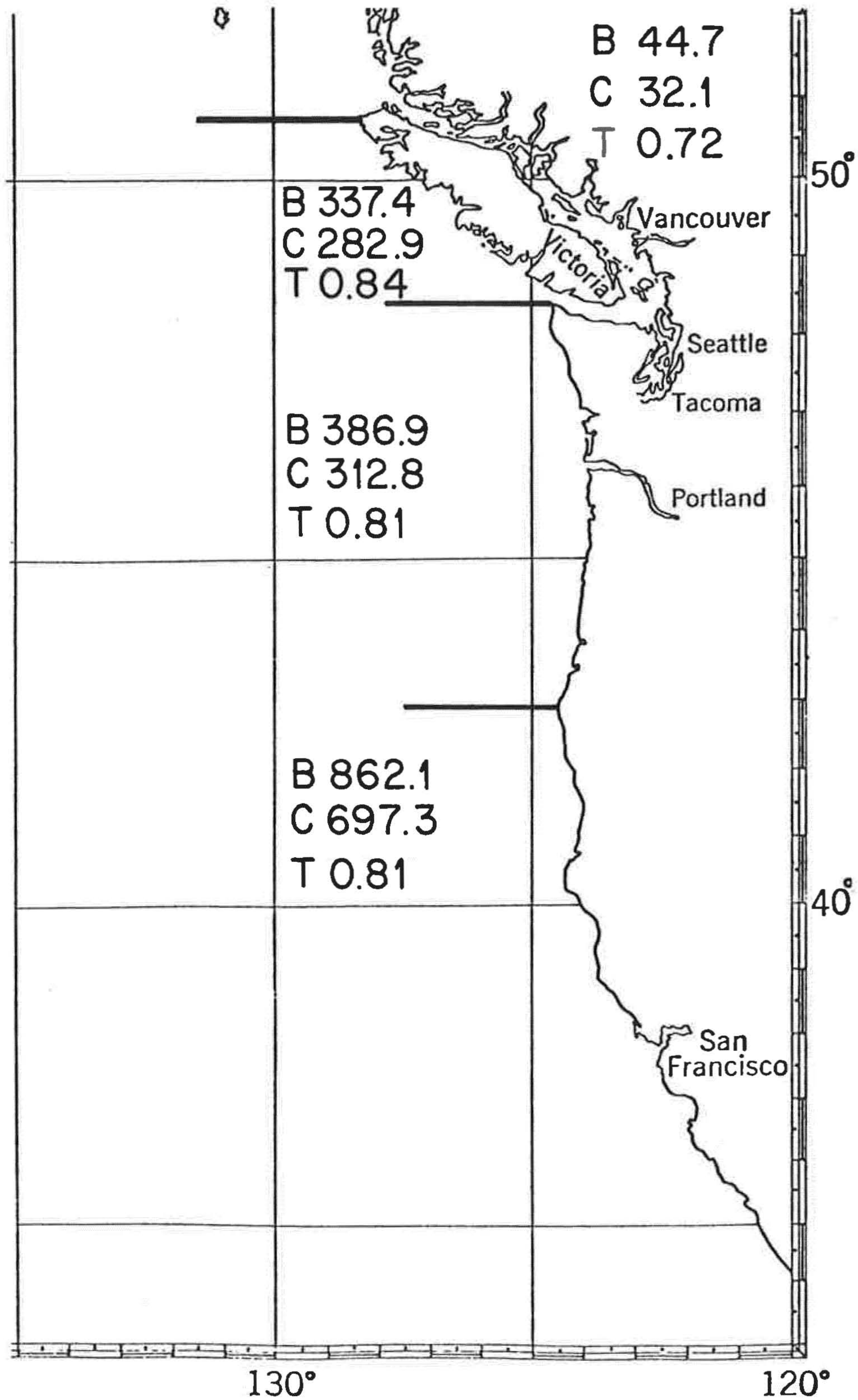

Figure 15.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of roundfish.

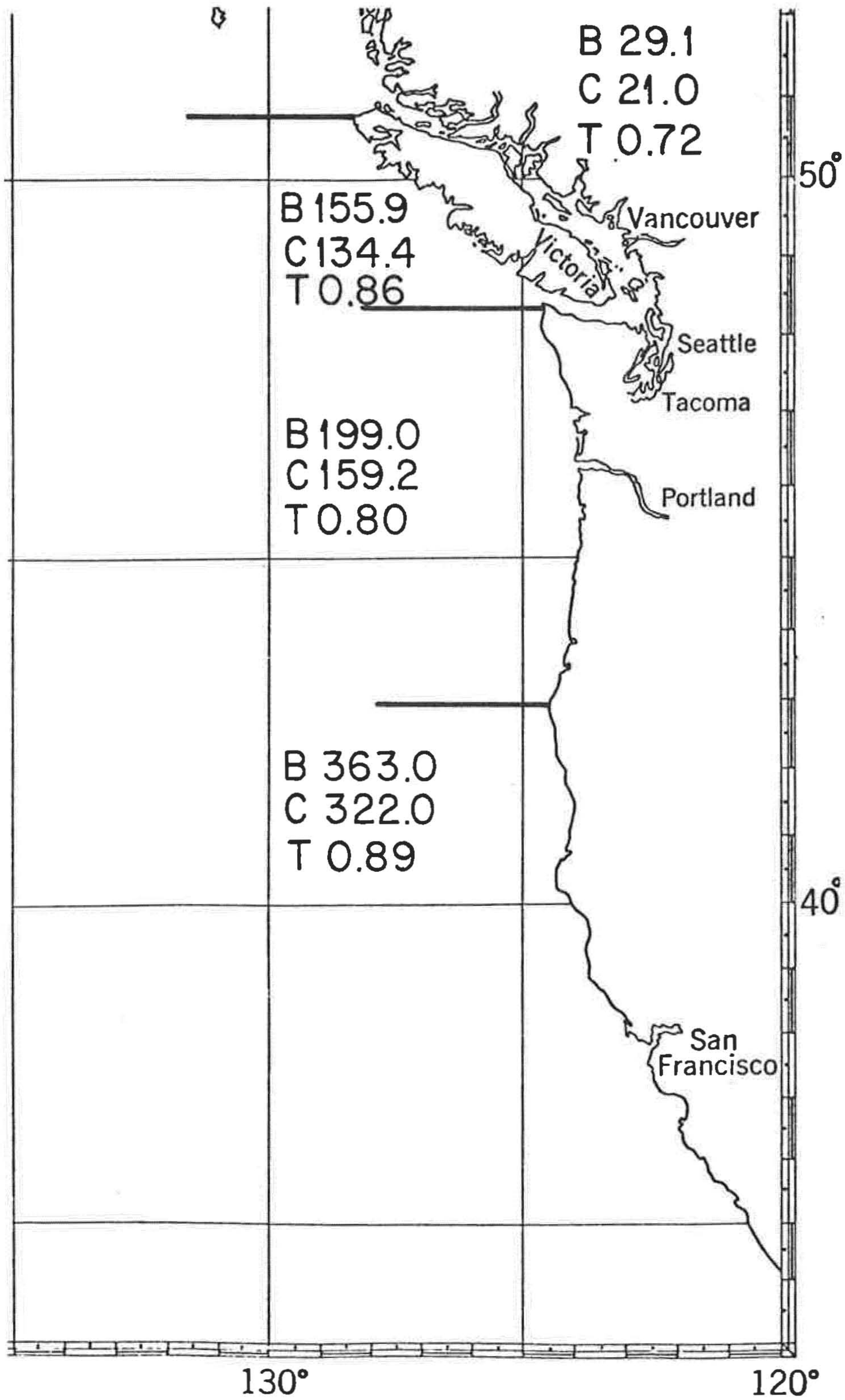

Figure 16.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of rockfish.

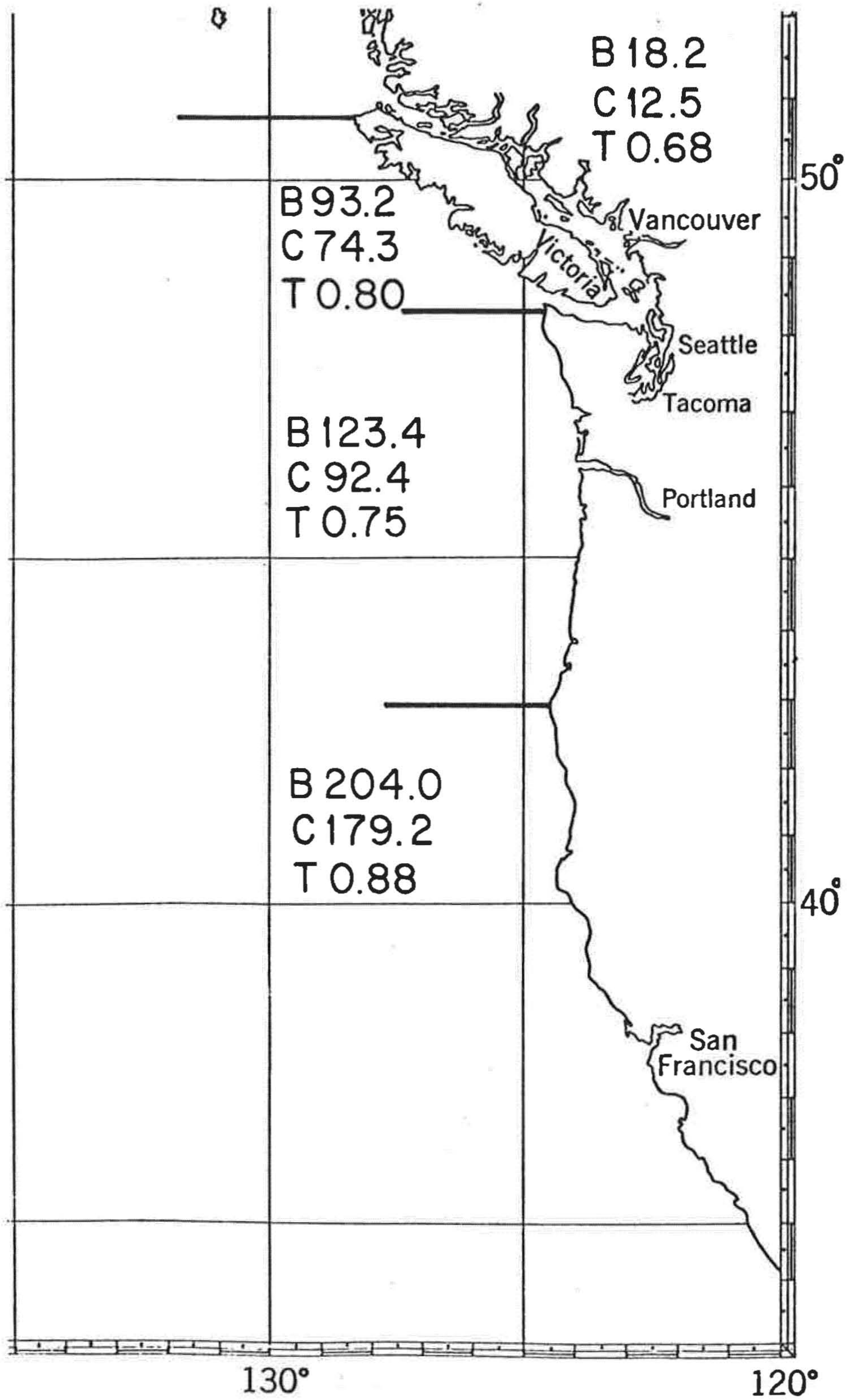

Figure 17.--Minimum sustainable biomass, ecosystem internal consumption, and annual turnover of flatfish.

respect to rockfish our computation result is only little more than half of Alverson's estimate (747 x 10^3 versus 1300 x 10^3 tons). Our computed result is, however, a minimum sustainable biomass.

Considering Table 19, we find that the highest biomass of finfish is found off California (ca 70 tons/km^2). This high biomass is probably due to the higher productivity there caused by upwelling, and corresponds well to latest estimates of biomass in upwelling areas, based on sonar surveys (e.g., Thorne et al 1977). The standing biomass per unit area in open ocean areas is considerably lower than on the continental shelf and slope, due to the marked reduction of one important ecological component-benthos. The present model was programmed to estimate the minimum biomasses; therefore, the total computed minimum biomass per unit area off Oregon, Washington, and Vancouver coasts might be lower than in nature.

It should be noted that the commercial catches of the U.S. (Table 20) are very low, actually nearly insignificant, in relation to the ecosystem internal consumption (Tables 15 to 18). An exception to this is salmon, where the adult biomass is accessible to intensive fishery, when the fish returns to spawn.

IV. CONSUMPTION BY MARINE BIRDS AND MAMMALS

The main ecological group consumed by baleen whales is krill (Table 21); the other ecological groups, such as sardines, are consumed as incidentals. On the other hand, the main food for toothed whales (including porpoises and dolphins), is finfish; their consumption by toothed whales as computed by the model (Table 22) indicates that the finfish consumption by toothed whales is more than five-fold the total U.S. catch off California, Oregon, and Washington coasts. This consumption is also considerably higher (nearly two-fold)

Table 19

"Minimum sustainable" biomass in tons/km^2

	Inland Waters	Off Vancouver Island			Washington/Oregon Coast			C & N California Coast		
		3	4	5	6	7	8	9	10	11
Squids	(2.0)	3.9	5.9	0.2	3.9	2.0	0.8	10.4	4.3	1.1
Sardines	4.7	8.9	13.5	4.7	8.9	4.7	1.7	23.5	9.7	2.5
Saury	2.4	4.7	7.8	3.0	4.8	2.6	1.1	13.1	5.8	1.5
Salmon	0.5	1.0	2.0	0.9	1.1	0.6	0.3	3.3	1.6	0.4
Roundfish	3.2	6.6	7.6	2.3	6.6	2.7	0.9	17.0	5.2	1.2
Rockfish	2.1	3.9	3.9	0.7	3.8	1.6	(0.3)	8.4	2.2	0.4
Flatfish	1.3	2.1	2.6	0.5	2.2	1.2	(0.2)	4.2	1.4	0.2
Fish food benthos	17.3	24.0	23.0	4.4	23.5	13.8	2.6	34.9	13.4	2.7
Total finfish	14.2	27.2	37.4	12.1	27.4	13.4	4.5	69.5	25.9	6.2

Table 20

Catches, thousand tons
(1973 statistics)

Species group	Washington	Oregon	California
Flatfishes (flounders)	3.9	5.7	15.9
Rockfishes (perch, other rockfishes)	8.6	2.5	10.6
Roundfishes (cod, hake, ling cod, sablefish)	6.0	2.0	6.7
Sardines (anchovies, herring, smelt)	4.3	0.5	128.1
Jack mackerel (+ Pacific mackerel)	-	-	9.5
Salmon, tuna (+ bonito)	33.5	19.1	151.4
Total, fish	57.8	29.6	321.9
Total shellfish, et al.	7.5	12.3	10.3

Table 21

Consumption by baleen whales
in 10^3 metric tons/year

Ecological group consumed	Inland Waters			Off Vancouver Island				Washington/Oregon Coast				C. & N. California Coast			
	1	2	Total	3	4	5	Total	6	7	8	Total	9	10	11	Total
Euphausids	0.7	0.7	1.4	11.8	46.4	102.8	161.0	16.1	34.3	81.7	132.1	59.3	165.5	302.7	527.5
Copepods	0.1	0.1	0.2	2.4	9.3	20.6	32.3	3.2	6.9	16.3	26.4	11.7	33.1	60.6	105.4
Squids	0.1	0.1	0.2	1.5	6.0	13.2	20.7	2.1	4.4	10.5	17.0	7.6	21.3	38.9	67.8
Sardines	0.1	0.1	0.2	1.2	4.6	10.3	16.1	1.6	3.4	8.2	13.2	5.9	16.6	30.3	52.8
TOTAL	1.0	1.0	2.0	16.9	66.3	146.9	230.1	23.0	49.0	116.7	188.7	84.5	236.5	432.5	753.5

Table 22

Consumption by toothed whales (including porpoises and dolphins) in 10^3 metric tons/year

Ecological group consumed	Inland Waters			Off Vancouver Island				Washington/Oregon Coast				C. & N. California Coast			
	1	2	Total	3	4	5	Total	6	7	8	Total	9	10	11	Total
Squids	1.1	1.1	2.2	7.6	20.9	61.3	89.8	12.4	17.9	59.8	90.1	48.9	76.1	130.9	255.9
Sardines	1.1	1.1	2.2	7.6	20.9	61.3	89.8	12.4	17.9	59.8	90.1	48.9	76.1	130.9	255.9
Saury	0.8	0.8	1.6	5.3	15.6	42.9	63.8	8.7	12.6	41.9	63.2	34.2	53.2	91.6	179.0
Other pelagic fish	1.1	1.1	2.2	7.6	20.9	61.3	89.8	12.4	17.9	59.8	90.1	48.9	76.1	130.9	255.9
Salmon/tuna	0.4	0.4	0.8	2.3	6.3	18.4	27.0	3.7	5.4	17.9	27.0	14.7	22.8	39.3	76.3
Roundfish	1.1	1.1	2.2	7.6	20.9	61.3	89.8	12.4	17.9	59.8	90.1	48.9	76.1	130.9	255.9
TOTAL	5.6	5.6	11.2	38.0	105.5	306.5	450.0	62.0	89.6	299.0	450.6	244.5	380.5	654.5	1,278.9

than the total commercial catch (i.e., U.S and foreign catch) in the region. Thus, an optimum fisheries management would require a significant reduction of marine mammals. This would be an unpopular decision.

The finfish consumption by pinnipeds (Table 23) is also higher than the U.S. commercial catch. On the other hand, the consumption of finfish by marine birds (Table 24) is relatively small, being highest off the Oregon coast where it reaches about one-third of the U.S. commercial catch.

V. SOME QUANTITATIVE TROPHIC RELATIONS IN THE MARINE ECOSYSTEM

There are several quantitative trophic relations in the marine ecosystem which have been brought to light as a result of our model computations. First, it is obvious from Tables 15 to 18 that the internal consumption in a marine ecosystem is very high indeed, specially in the pelagic components, where the annual turnover rate can exceed 1.8; whereas, in demersal and semidemersal components, this turnover rate is in general 0.6 to 0.8. Furthermore, the turnover rates of a given ecological group of species varies little from one region to another. The main reason for this relative constancy is that the turnover rate in a minimum sustainable biomass is greatly influenced by the mean growth rate of the biomass of this ecological group. If we compare the fishery catches (Table 20) with the ecosystem internal consumption, we find that the catches are insignificantly small.

The consumption of phytoplankton and the assumptions made in its computation are presented in Table 25. Various estimates of primary production off the west coast of North America are presented usually as between ca 70 and 175 gC/m^2 per year. Although relatively low estimates of primary production

Table 23

Consumption by pinnipeds
(fur seals and sea lions) in 10^3 metric tons/year

Ecological group consumed	Inland Waters			Off Vancouver Island				Washington/Oregon Coast				C. & N. California Coast			
	1	2	Total	3	4	5	Total	6	7	8	Total	9	10	11	Total
Roundfish	7.0	6.9	13.9	48.2	12.9	6.5	67.6	61.7	16.2	4.4	82.3	110.0	22.4	5.6	138.0
Rockfish	2.2	2.2	4.4	15.1	4.0	2.0	21.1	19.4	5.1	1.4	25.9	34.9	7.1	1.8	43.8
Salmon/tuna	0.2	0.2	0.4	1.2	0.3	0.1	1.6	1.7	0.5	0.1	2.3	3.6	0.6	0.3	4.5
Sardine/anchovy	0.5	0.5	1.0	3.5	1.0	0.5	5.0	4.3	1.1	0.3	5.7	6.6	1.5	0.2	8.3
Squids	1.2	1.2	2.4	7.8	2.3	1.2	11.3	9.4	2.4	0.8	12.6	14.5	3.4	0.4	18.3
Other pelagic fish	0.6	0.6	1.2	4.0	0.9	0.5	5.4	5.5	1.5	0.4	7.4	10.9	2.0	0.7	13.6
"Others"	0.4	0.4	0.8	2.8	0.7	0.3	3.8	3.8	1.0	0.2	5.0	7.2	1.4	0.4	9.0
TOTAL	12.1	12.0	24.1	82.6	22.1	11.2	115.9	105.8	27.8	7.6	141.2	187.7	38.4	9.4	235.5

Table 24

Consumption by marine birds
in 10^3 metric tons/year

Ecological group consumed	Inland Waters			Off Vancouver Island				Washington/Oregon Coast				C. & N. California Coast			
	1	2	Total	3	4	5	Total	6	7	8	Total	9	10	11	Total
Sardines	0.5	1.3	1.8	2.3	0.3	0.1	2.7	3.4	0.4	0.2	4.0	1.9	1.2	0.7	3.8
Flatfish	0.1	0.2	0.3	0.3	-	-	0.3	0.5	0.1	-	0.6	0.2	0.2	0.1	0.5
Roundfish	0.1	0.2	0.3	0.3	-	-	0.3	0.5	0.1	-	0.6	0.2	0.2	0.1	0.5
Rockfish	0.1	0.2	0.3	0.3	-	-	0.3	0.5	0.1	-	0.6	0.2	0.2	0.1	0.5
Euphausids	0.2	0.7	0.9	1.2	0.2	-	1.4	1.7	0.2	0.1	2.0	1.0	0.6	0.3	1.9
"Others"	0.1	0.3	0.4	0.6	0.1	-	0.7	0.8	0.2	0.1	1.1	0.5	0.3	0.2	1.0
Squids	0.1	0.3	0.4	0.6	0.1	-	0.7	0.9	0.1	0.1	1.1	0.5	0.3	0.2	1.0
Benthos	0.1	0.2	0.3	0.3	-	-	0.3	0.5	0.1	-	0.6	0.2	0.2	0.1	0.5
TOTAL	1.3	3.4	4.7	5.9	0.7	0.1	6.7	8.8	1.3	0.5	10.6	4.7	3.2	1.8	9.7

Table 25

Phytoplankton Consumption

	Inland Waters		Off Vancouver Island			Washington/Oregon Coast			C & N California Coast		
	1	2	3	4	5	6	7	8	9	10	11
Phytoplankton consumption by fish 10^3 tons	47	55	249	248	442	359	278	390	744	764	878
Phytoplankton consumption by zooplankton, 10^3 tons*	496	1,584	2,644	1,020	7,256	4,260	7,500	19,392	1,824	7,805	39,096
Phytoplankton consumption by fish food benthos, 10^3 tons	302	611	1,448	848	810	2,001	1,745	1,570	2,152	2,140	2,028
Total phytoplankton consumption, 10^3tons	845	2,250	4,341	2,116	8,508	6,620	9,523	21,352	4,720	10,709	42,002
Total phytoplankton consumption t/km^2	284	208	243	188	149	261	263	155	237	219	184
Annual mean phytoplankton standing crop mg/m^3	2,500	2,500	2,400	2,200	2,000	2,400	2,000	1,800	2,700	2,900	2,200
Annual phytoplankton consumption turnover rate**	0.4	0.6	0.5	0.6	0.7	0.5	0.4	0.6	0.6	0.7	0.6
Approximate percentage of annual production consumed ***	23	17	19	15	19	21	21	19	19	18	23

*Assuming zooplankton consumes 2% body weight daily (zooplankton standing crop see Table)

**This turnover rate refers to mean standing crop turnover assuming phytoplankton is distributed in upper 50 m of the sea. However, standing crop of phytoplankton reproduces itself many times during a year.

***Assuming that phytoplankton production is 125 g C/m^2 per year in areas 1,2,3,4,6,7,9,10 and 80 g C/m^2 in areas 5, 8 and 11.

have been used in our computations, only about 20% of the primary production is consumed and the phytoplankton annual consumption turnover rate is only 0.4 to 0.7. The relatively low utilization of phytoplankton further demonstrates that valid trophodynamic ecosystem models cannot be computed if one starts with primary production (or even with nutrients) and reflects why numerous earlier assessments with such "ecosystem models" have produced neither scientifically correct nor practically useful results.

The annual turnover rates of zooplankton are relatively high (Table 26). It is thought that the main reason for this can be found in inaccurate quantitative determination of zooplankton standing crop, specially the more mobile euphausids are difficult to catch quantitatively (Laevastu, Favorite, Dunn 1976).

VI. CONCLUSIONS

1. The numerical model computations with conservative model inputs (e.g. low food requirements) show very high ecosystem internal consumption and high turnover rate, specially in pelagic components of the marine ecosystem. The ecosystem internal consumption is considerably higher than the fishery (catch).

2. The high turnover rate indicates, among others, that grazing can be considered to be a more important factor in determining year class strength than the size of spawning stock and that partial starvation might be rather common in the sea.

3. The consumption by marine mammals, specially by toothed whales and pinnipeds, is considerably higher than the commercial catch by man. This suggests the necessity of controlling marine mammal populations to achieve maximum utilization of marine resources by man through wise management of the fishery resources.

Table 26

Zooplankton Consumption

	Inland Waters		Off Vancouver Island			Washington/Oregon Coast			C & N California Coast		
	1	2	3	4	5	6	7	8	9	10	11
Areas km^2	2,981	10,813	17,881	11,263	57,230	25,361	36,277	137,919	19,911	48,813	227,590
Consumption of zooplankton, 1000 tons	297	342	1,600	1,541	2,678	2,282	1.718	2,383	4,699	4,704	5,519
Consumption of zooplankton, mg/m^3 *	997	316	895	1,368	468	900	474	173	2,360	964	242
Annual mean standing crop mg/m^3 **	420	420	480	360	290	490	430	250	420	515	415
Annual consumption turnover rate	2.4	0.8	1.9	3.8	1.6	1.8	1.1	0.7	5.6	1.9	0.6

* Assuming zooplankton evenly distributed in upper 100 m.

** Very tentative estimates

$mg/m3 = tons/km^2 \times 10$

4. The computed minimum sustainable biomass in the California region is comparable to that found with sonar surveys in upwelling regions in general (60 to 70 $tons/km^2$). Off the Oregon and Washington coasts the minimum sustainable biomass is lower (<30 $tons/km^2$) than off California and it is lowest in offshore (open ocean) areas.

5. The utilization of phytoplankton (primary organic production) is low (ca 20%) and the corresponding utilization of zooplankton high (turnover rates up to ca 6) in the marine ecosystem.

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