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NUMERICAL EVALUATION OF MARINE ECOSYSTEMS PART I. DETERMINISTIC BULK BIOMASS MODEL (BBM)

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Resource Ecology Task
Resource Ecology and Fisheries Management Division

July 1978

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

The wise management of marine fishery resources requires the consideration of the total marine ecosystem in a given region, as the components are interacting and the fishery on one or more species will, in many instances affect the abundance and distribution of other species as well, i.e., the abundance of one species might be declining, the other increasing.

A deterministic method to estimate either the minimum sustainable and/or saturation biomasses of species and/or groups of ecologically similar species in a given region is described. This method can also be applied to unexploited or underexploited resources. Trophodynamic approaches are used that permit the quantitative determination of the major component of the natural mortality--the predation or grazing mortality. The error limits depend on the accuracy of some trophodynamic data. Migration is not considered because detailed migrations are an integral part of the large ecosystem model--DYNUMES, for which the present model serves as one of the initial input subroutines.

1. OBJECTIVES OF THE MODEL

Extensive amounts of various data and knowledge on fisheries resources, particularly on their abundance and distribution, are necessary for solving nationally the new fisheries management problems, created by extended marine resource jurisdiction boundaries. It has become clear that successful fisheries management requires the consideration of the total marine ecosystem; for example, because of intensive interspecies interactions the fishery on one species affects the abundance and distribution of other species. Furthermore, the fishery itself can shift rapidly from one species to another underexploited species.

One of the initial tasks in developing management strategies is the resource assessment--the determination of the abundances of species present (stock sizes) and their distributions, and their saturation biomasses which reflect the carrying capacity of the system.

The relatively simple past considerations of marine productivity, using basic organic production and zooplankton and benthos productions as the basis for evaluation of fish production in the ecosystem has not led to any fruitful results, mainly because of lack of consideration or accurate documentation of the interactions and energy sinks in the system.

The Virtual Population Analysis (VPA) has been a useful tool in the past for heavily exploited stocks, but is not applicable to little exploited or unexploited stocks (Ulltang, 1977). One of the great shortcomings in VPA and in other single species approaches has been the uncertainty in

estimating M--the "natural mortality". Predation is one of the major components in the natural mortality, and we have attempted to determine the predation mortality deterministically with the help of trophodynamics of the total ecosystem. New, advanced marine ecosystem models, emphasizing the fisheries aspects of the ecosystems have been developed recently (Andersen and Ursin 1977, Laevastu and Favorite 1977a) which seem to provide important research and management tools required in the near future. These models require considerable effort for compilation for a given region and are quite expensive to run even on the largest available computers.

The deterministic Bulk Biomass Model (BBM), described below, is perhaps the simplest possible form of a total ecosystem model and, in addition, serves as one of the initial input subroutines for large ecosystem model (Dynamical Numerical Marine Ecosystem Model--DYNUMES III) for the determination of initial biomass inputs. The BBM can, however, be used indepedently and provides, with modest effort, a considerable amount of initial quantitative information on ecosystem components in a specific region.

The objectives of the BBM model formulation are:

1) To determine either the minimum sustainable biomass or saturation biomass of a given species and/or ecological group in a given region.

2) To determine the ecosystem internal consumption of a given species (i.e., to determine the predation or grazing mortalities which are the main components of natural mortalities--M), and the biomass turnover rates.

3) To determine quantitatively the trophic couplings between different species or groups of species, and to evaluate the marine ecosystem stability.

It is possible to run the model also in predictive mode (after satisfaction of requirements in 1 and 2 above) and thus determine the fluctuations in stocks caused by the fishery as well as any other long-term fluctuation, the causes for which can be introduced into the model.

The minimum sustainable biomass is defined as the level of the biomass of a given species, or an ecological group of species, which with a given highest plausible growth rate and lowest plausible ecosystem internal consumption (i.e. lowest plausible food requirements) does neither decline nor increase within the course of a year (January to January). Saturation biomass is similarly defined (i.e., no increase or decrease of biomass from one January to the next January), except the lowest plausible growth rates and highest plausible food requirements are used in the computations. An equilibrium biomass (sometimes also defined as virgin biomass) is obtained from the model if the mean growth rates and mean food requirements are used and no fishery is computed.

Some of the advantages and disadvantages of the BBM, as compared to some other models (approaches) are listed below. (For an evaluation of common errors and shortcomings of VPA see Ulltang 1977).

Advantages of BBM (as compared to VPA)

1) Possible to determine the minimum sustainable, equilibrium and saturation biomasses in little exploited, unexploited (virgin), and extensively exploited stocks with a known or given fishing mortality.

2) The total ecosystem in a given region is considered, with large-scale quantitative interspecies interactions. (A given, larger region is also divided into smaller ecological subregions which can be treated with different conditions--i.e., input data.)

3. A detailed, direct computation of predation mortality (i.e., direct determination of largest component of natural mortality) is made.

4. It is possible to examine the effects of changing fishing intensity (i.e., variable fishing mortality--F, in different subregions and months) on target species as well as the indirect effects of such fisheries on species that are unfished or little fished, but are trophically related to target species (i.e., constituting the food source for the target species or sharing a common food source).

5. There is a time (season and age of species) variable growth computation (with a time variable growth coefficient), which allows the simulation of large-scale effects of environmental anomalies via effects on growth, mortality and trophodynamics.

6. The model is not wholly dependent on extensive biometric measurements of catch (i.e., age composition of stocks) as is VPA, but if these data are available, full use can be made of these data.

7) Large-scale migrations into the region and between the subregions can be included if some quantitative estimates of these migrations are possible in a given region.

Disadvantages of BBM

1) The model is heavily dependent on good, reliable estimates of the quantitative composition of food of species and/or ecological groups. Food composition is not variable in space and time according to its availability, as is the case in DYNUMES.

2) There is low spatial resolution, the growth rate is not variable in time except between subregions; thus, the spatial variability of source-sink areas cannot be resolved. Migrations (e.g., seasonal depth migrations in flatfish) cannot be specified in detail.

3) The BBM is suitable for determining the current state of heavily exploited stocks and making future prognoses on them. If the species under study is divided into year classes, the year class strength is prescribed from measurements, the predation of the species is made density (availability) dependent, and the fishing mortality is prescribed from the most recent catch data. Considering the additional labor involved and the additional information gained from DYNUMES, it is in most cases more advantageous to use the latter for sensitive detailed studies of heavily exploited stocks.

Several applications of the BBM model have been made in NWAFC, the results of which are available in technical reports (Laevastu and Favorite 1976, 1977b, Livingston; 1977, 1978). The basic model program documentation (Laevastu 1978) is also available on request from NWAFC.

2. PRINCIPLES AND FORMULAS

The time change of the biomass of a species can be presented in parametric form as:

$$\frac{dB}{dt} = B + G - C - F - M - \vec{V} \qquad (1)$$

If we assume that there is no migration or advection into a given region ($\vec{V}=0$), and further assume that there is no change of biomass from one year to another--i.e. equilibrium conditions prevail ($\frac{dB}{dt} = 0$) (although we allow seasonal changes within the year to occur), then the biomass growth (G) equals its removal or loss (C+F+M). The loss is thus a sum of predation (consumption) (C), fishing mortality (F), and mortality from "old age", diseases and "spawning mortality" (M).

The method of any biomass estimation is dependent on the availability of proper data. The growth rate of a biomass can be computed from empirical weight-age and age distribution of biomass data (Laevastu and Favorite 1978), the latter being required because the growth rate decreases with an increase of cohort size (age). Fishing mortality for an exploited population can be obtained from catch statistics and can be assumed to be constant under equilibrium conditions.

The ecosystem internal consumption (predation) is a major cause of mortality (Ware 1975). It depends on grazing by many species in the ecosystem, for which the given species is a food item. Thus, average composition of food for all species and/or ecological groups in a marine ecosystem in a given region is required for the computation of predation. Data on this subject is usually available, but quite widespread in the fisheries literature. In evaluating the food composition, size dependent feeding, with some species selectivity (Daan 1973, Ursin 1973) must be considered as a dominant feeding behavior in the marine ecosystem. Predation computations furthermore require that all major ecosystem components must be included in the numerical models. In addition, data on food requirement for growth, maintenance, and for sex products development are required and available to some extent in the literature (e.g., Jones 1978, Daan 1973, and others).

The mortalities from old age and diseases are relatively small in most species under exploitation, as compared to the sum of predation and fishing mortalities. The old age and disease mortalities, usually lumped together, can either be estimated by the subtraction of predation and fishing mortalities from total mortality, the latter being computed with another model (Laevastu and Favorite 1978), or estimated subjectively by considering the life span of the species, fishery, fecundity, growth rate, and general importance of the species as a forage species in a given ecosystem. The old age/disease mortality is usually a relatively small component of total mortality and consequently errors made in its estimation do not impair the results of biomass computations by any appreciable amount.

In the present task of equilibrium biomass computations the recruitment of larval stages is assumed to be proportional to the biomass present. This in turn is largely a function of growth rate and predation. Thus, in this model recruitment is largely regulated by variation in growth rate and predation pressure, which simulates the regulatory mechanisms which are considered to occur in unexploited natural populations (Ware 1975).

Given the availability of adequate data, apropos to Equation 1, iterative solutions to equilibrium biomasses in a given ecosystem for defined regions can be obtained. A computer program for this purpose was developed, tested, and applied at NWAFC (the formulas used in this model are described below). However, plausible "first guess" biomass estimates of species or ecological groups, together with the corresponding data on growth, mortality, and trophodynamics are required before an iterative solution with the following two basic criteria can be sought (symbols are defined in Section 4):

$$C_c = B_a \, (2 - \exp^{-g}) \exp^{-(f+o+d+s)} - B_a \tag{2}$$

and

$$B_{i(r,l_1)} = B_{i(r,l_2)} \tag{3}$$

Computations were carried out in monthly time steps. The monthly biomass equation is:

$$B_{i(r,t)} = B_{i(r,t-1)}(2 - \exp^{-g_{i(t)}}) \exp^{-f_{i(r,t)}} - C_{i(r,t-1)} - D_{i(r,t)} \tag{4}$$

The monthly growth coefficient is a harmonic function of time, which holds for medium and higher latitudes:

$$g_{i(t)} = \bar{g}_i + a_i \cos(\alpha t - \mathcal{H}_i) \tag{5}$$

A first guess of the monthly fishing mortality coefficient can be approximated from the catch data and estimated biomass; it must be recomputed for final runs, when better biomass data have been obtained from the preliminary runs with the model:

$$f_{i(r,t)} \approx \frac{P_{i(r,t)}}{B_{i(r,t)}} \tag{6}$$

Ecosystem internal consumption (predation) is the sum of consumption of the given species by other species/ecological groups in the system; thus, the previous time step consumption must be used in the computations, which does not, however, cause any appreciable error:

$$C_{i(r,t-1)} = \sum_{1}^{n} F_{i(r,t-1)} \tag{7}$$

The consumption by each species/ecological group is computed with a relatively commonly used trophodynamic formula:

$$F_{i,j(r,t)} = \left\{ \left[B_{j(r,t)} (1 - \exp^{-g_{j(t)}} \right] R_j + (B_{j(r,t)} K_i) \right\} q_{i,j} \tag{8}$$

The mortalities from old age, diseases and spawning mortalities can be lumped together:

$$D_{i(r,t)} = O_{i(r,t)} + I_{i(r,t)} + S_{i(r,t)} \tag{9}$$

These mortalities can be computed with mortality coefficients which are added to the fishing mortality coefficient (see Formula 2).

First guess biomasses of finfish species/groups of species are introduced into the program as inputs. Because of computer core limitations, it is not practical to introduce into the model all species separately. A grouping into ecologically and trophically similar groups has been found practical--e.g., semidemersal fish (cod, hake), demersal flatfish (e.g., turbot, halibut), small pelagic fish (e.g., capelin, sand lance), etc. However, some single, dominant, and commercially important species should be treated as single species (e.g., herring, pollock, etc.) and, if desired, divided into age groups. In consecutive computer runs, any species can be separated from a group (after proper reprogramming) and investigated separately if so desired.

Marine mammals and birds are prescribed in monthly time steps. Due to the relatively large errors in the estimation of these ecological groups, no growth and mortality computations are performed; however, the consumption of fish and other ecological groups by mammals and birds must be computed.

The first guess of the biomass of "fish food benthos" is usually estimated by considering factors affecting its abundance, such as depth in the subregion, type of bottom, latitude, and especially available quantitative data on benthos.

Monthly phytoplankton and zooplankton standing stocks, the latter after separation into copepods and euphausids, are simulated using harmonic formulas:

$$Z_r = Z_o + Z_m \cos(\alpha_1 T - \mathcal{H}_1) + Z_{ms} \cos(\alpha_2 T - \mathcal{H}_2) \tag{10}$$

The simulated plankton standing stocks are tuned to available plankton data. These simulations do not enter into other computations in the model. They are used to compare the plankton production with utilization, the latter being computed in detail in the model.

Relaxation methods (Shaw 1953) can be used to solve the ecosystem equation complex; however, a logical (for the particular problem adapted) iteration procedure for the adjustment of biomasses in each January that makes use of the two following criteria is employed:

$$B_{cg} = B_g - \left[(B_{1,1} - B_{2,1})/12\right] \tag{11}$$

$$B_{cf} = \left[(C_1 + B_g)/B_{gg}\right] B_g \tag{12}$$

where:

$$B_{gg} = B_g \ (2 - \exp^{-g}) \exp^{-m} \tag{13}$$

A mean of the above two, Formulas 11 and 12, is formed as the new adjusted biomass:

$$B_c = (B_{cg} + B_{cf})/2 \tag{14}$$

In most cases 50 to 200 years (in real time) computations are required for conversion, because the consumption (predation) adjustment is a complex process.

If the current biomass of one or more species has been empirically ascertained (e.g., by extensive surveys of spawning biomass, sonar surveys, extensive exploratory fishery, etc.), these "ascertained biomasses" can be kept constant (i.e., not passed through the iterative adjustment procedure). Consequently, the computed predation on these ascertained species might not be in proper balance with the biomass and an adjustment of their fraction in the food of other species must be made, using Formula 2 and Formula 15:

$$q_{cj} = \frac{C_c}{C_{i(r,t-1)}} q_{i,j} \tag{15}$$

After the conversion has been achieved in computations, the convergence criteria can be bypassed and the model run in a predictive mode for various investigations--e.g., long-term and cyclic changes in the ecosystem caused by the fishery and other factors; however, these must be introduced into the model. In the predictive mode, density (food availability) dependent feeding must be used, either by Formulas 2 and 15 above or with a more complex approach as found in DYNUMES model (Laevastu and Favorite 1978).

3. BASIC INPUT DATA AND THEIR ACCURACY

Up to fifteen subregions have been handled within one BBM model study at NWAFC. The selected number of subregions is usually determined by the faunal changes in the region under consideration and by the availability of input data. Examples of two BBM model subregions are given in

Figures 1 and 2. In both examples the depth of water has been one of the considerations for subdivision of the area (e.g., from coast to 200 meters depth--the coastal subregions; and, from 200 to 1,000 meters--the slope subregions). The areas of the subregions must be ascertained and are introduced into the model.

As the BBM model is deterministic, conventional sensitivity analyses are neither necessary nor possible. In deterministic models, sensitivity analyses become studies of specific responses of the systems to expected changes of parameters. The variations in results of deterministic models depend largely on accuracy and reliability of the input data, some of which are discussed below.

The availability, quality, and accuracy of basic input data for BBM models can vary considerably from one region to another and from one species/group of species to another. The monthly growth coefficients of the biomasses range generally between 3 and 12% per month. Available data usually allow the determination of this coefficient with an accuracy of a few percent of actual value. However, in some instances, particularly little investigated species, the estimated values of growth coefficients can vary up to, but not exceeding 20%. As any estimate can be above or below a plausible true value, the total error caused by inaccurate growth coefficient estimates in a system comprised of many species would not cause errors in the final biomass estimates in excess of 15%. If minimum sustainable biomasses are desired as the results of model computations, growth coefficients approaching the upper plausible limits should be used.

Mean monthly fishing mortality coefficients can be computed from catch statistics. The year to year variation in the fishery affects the validity of these computations. The true natural mortality from old age and diseases and possible spawning and "starvation" mortalities (fish older than 6 months considered) are usually small in exploited populations compared to fishing and predation mortalities, the latter being computed within the model. In unexploited and in short-lived species, such as squids, these mortality coefficients are larger but still considerably smaller than the predation mortality. The possible errors made in the estimates of fishing and true mortality coefficients do not normally cause errors in biomass estimates in excess of 10% in careful work (preliminary test results with model by changing coefficients in reasonable limits).

The BBM model interspecies interactions are based on average (fixed) food composition, whereas the DYNUMES model emphasizes interspecies interactions via competition for food according to its availability and distribution. Data for food requirements for growth, maintenance, and reproduction are deficient in most species, although for some species excellent information is available (e.g., Jones 1978, Daan 1973), which can be generalized to other species. If food requirement is computed as the growth/food intake ratio only (i.e., no additional maintenance ratio is specified) this ratio is about 1:3, with some variation between ecological groups. If, in addition to growth/food ratio, food requirement for maintenance (in terms of percent biomass per body weight daily) is specified, the growth/food ratio is about 1:1.5 and maintenance requirements vary normally between 0.5 and 1.2 percent body weight daily. If an overall food intake

coefficient is used (without separation of growth and maintenance requirements), the food coefficient is usually between 0.7% and 1.8% of body weight daily. The latter approach is preferable. The food coefficient has seasonal change in higher latitudes, which is approximated by a harmonic curve in the present model. If minimum sustainable biomasses are desired, the lowest plausible food coefficient should be used in the model.

Voluminous data in the literature show that the composition of food of a given species can vary considerably in space and time. This variability is introduced into large ecosystem models (e.g., DYNUMES) using food availability as a criterion. In the deterministic BBM, different food compositions can be specified for different subregions and different seasons if available data indicates such to be the case. Some inaccuracies in specification of food composition may be introduced in the grouping of species into ecological groups. However, the main criterion in ecological grouping of species in the BBM model is the similarity of composition of food and feeding habits.

The model is rather sensitive to changes in food coefficients. However, the uncertainties and errors introduced by trophic coefficients normally do not induce an error in excess of 30% in the final biomass computation according to preliminary experimental determination with the model.

Estimates of the numbers of marine mammals and birds present in given subregions are associated with some uncertainties; however, the amounts of mammals and birds in most ocean areas are not large. Model computations with plausible minimum mean and maximum numbers of mammals and birds, can be made to evaluate their possible effects on marine

ecosystem. As marine mammals and birds are consumers only, the errors introduced by inaccurate estimates affect the computation of the final biomasses only partially and this error would normally not exceed 15% of the final value of biomasses (determined by prescribing minimum and maximum estimates of mammals present).

The use of the BBM model is a prerequisite for the application of advanced deterministic dynamical numerical marine ecosystem simulations in any given region.

4. LIST OF SYMBOLS

a_i	-half of the magnitude of annual growth coefficient change
B_a	-prescribed "ascertained" biomass
B_c	-adjusted biomass in January
B_{cg}	-adjusted biomass due to biomass change within a year
B_{cf}	-adjusted biomass due to consumption (predation)
B_g	-adjusted biomass from previous year
B_{gg}	-resultant biomass from growth and mortality
$B_{i(r,1_1)}$	-biomass of species i in subregion r, first year January (1_1)
$B_{i(r,1_2)}$	-same biomass as above in second year January (1_2)
$B_{i(r,t)}$	-biomass of species i in subregion r at time step t
$B_{i(r,t-1)}$	-as above, but previous time step (t-1)
$B_{j(r,t)}$	-biomass of species j in subregion r at time step t
$B_{1,1}$	- biomass in January, previous year
$B_{2,1}$	- biomass in January, actual year
C_c	-"constant consumption" for prescribed "ascertained" biomasses

C_1 -predation (consumption)

$C_{i(r,t-1)}$ -predation (consumption of species i in subregion r in previous time step (t-1)

$D_{i(r,t)}$ -mortality from old age, diseases, and spawning mortality (species i, subregion r, time step t)

d -disease mortality coefficient

$f_{i(r,t)}$ -fishing mortality coefficient (species i, subregion r, time step t)

$F_{i,j(r,t)}$ -predation (consumption) of species i by species j in subregion r in time step t

$\bar{g}_i$ -annual mean monthly growth coefficient of species i

$g_{i,t}$ -growth coefficient of species i in time step t

$g_{j,t}$ -growth coefficient of species j

$I_{i(r,t)}$ -mortality from diseases (and starvation)

K_j -food coefficient for maintenance, species j

O,o -old age mortality coefficient

$O_{i(r,t)}$ -mortality from "old age"

$P_{i(r,t)}$ -catch of species i in subregion r in time step t

$q_{i,j}$ -fraction (decimal) of species i in food of species j

R_j -ratio of growth to food biomass consumed (species j)

$S_{i(r,t)}$ -spawning mortality

S,s -spawning mortality coefficient

T -time (in month)

Z_m -half of the magnitude of the change of main (spring) plankton biomass (first harmonic constant)

Z_{ms}	-half of the magnitude of the change of secondary (autumn) plankton biomass (second harmonic constant)
Z_o	-annual mean plankton standing stock
Z_r	-standing stock of plankton
α_1, α_2	-phase speed (usually 30° and 60°, respectively)
$\mathcal{H}_1, \mathcal{H}_2$	-phase lags of primary and secondary plankton maxima

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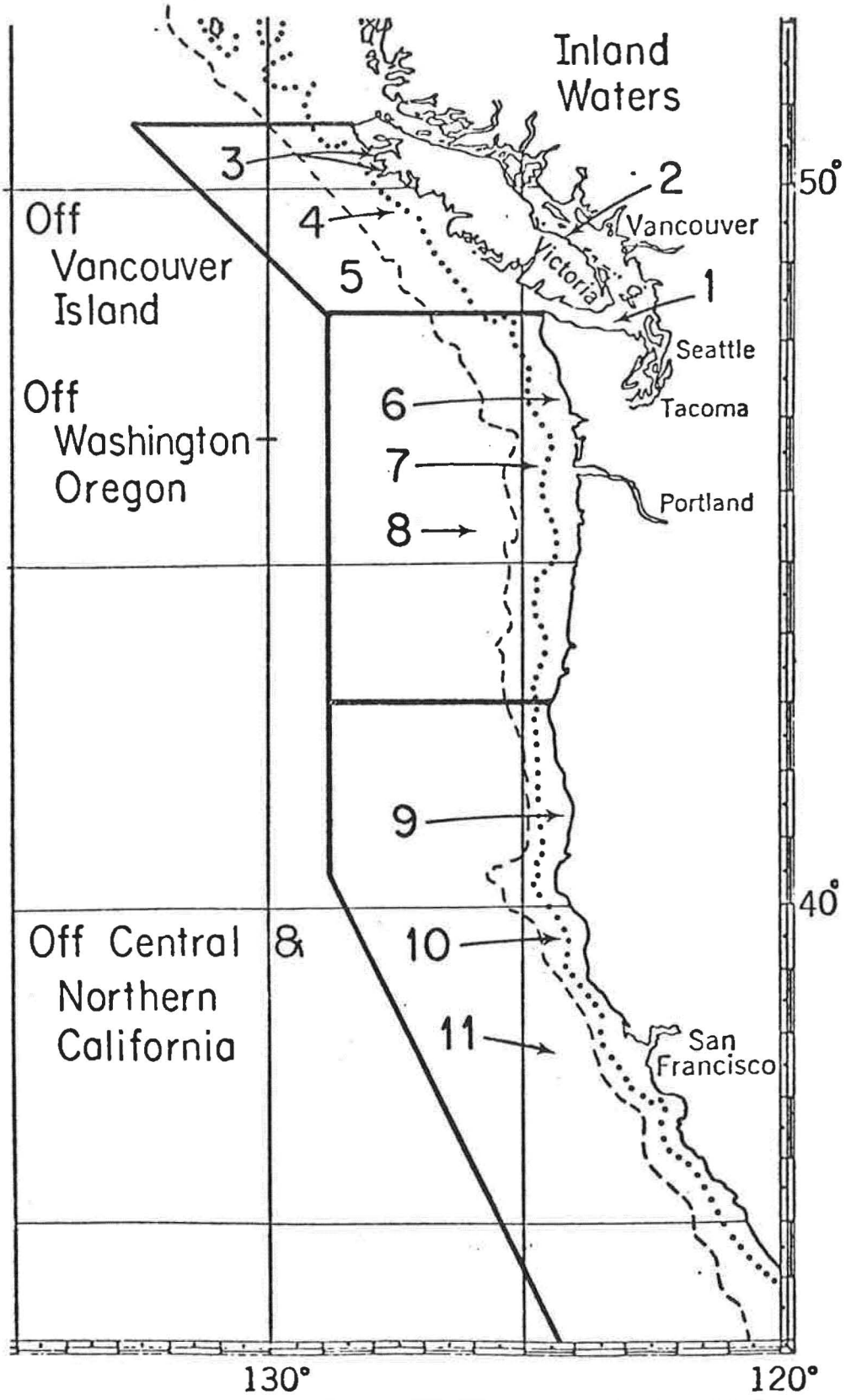

Figure 1. Example of subregions of a BBM model along a section of the west coast of North America.

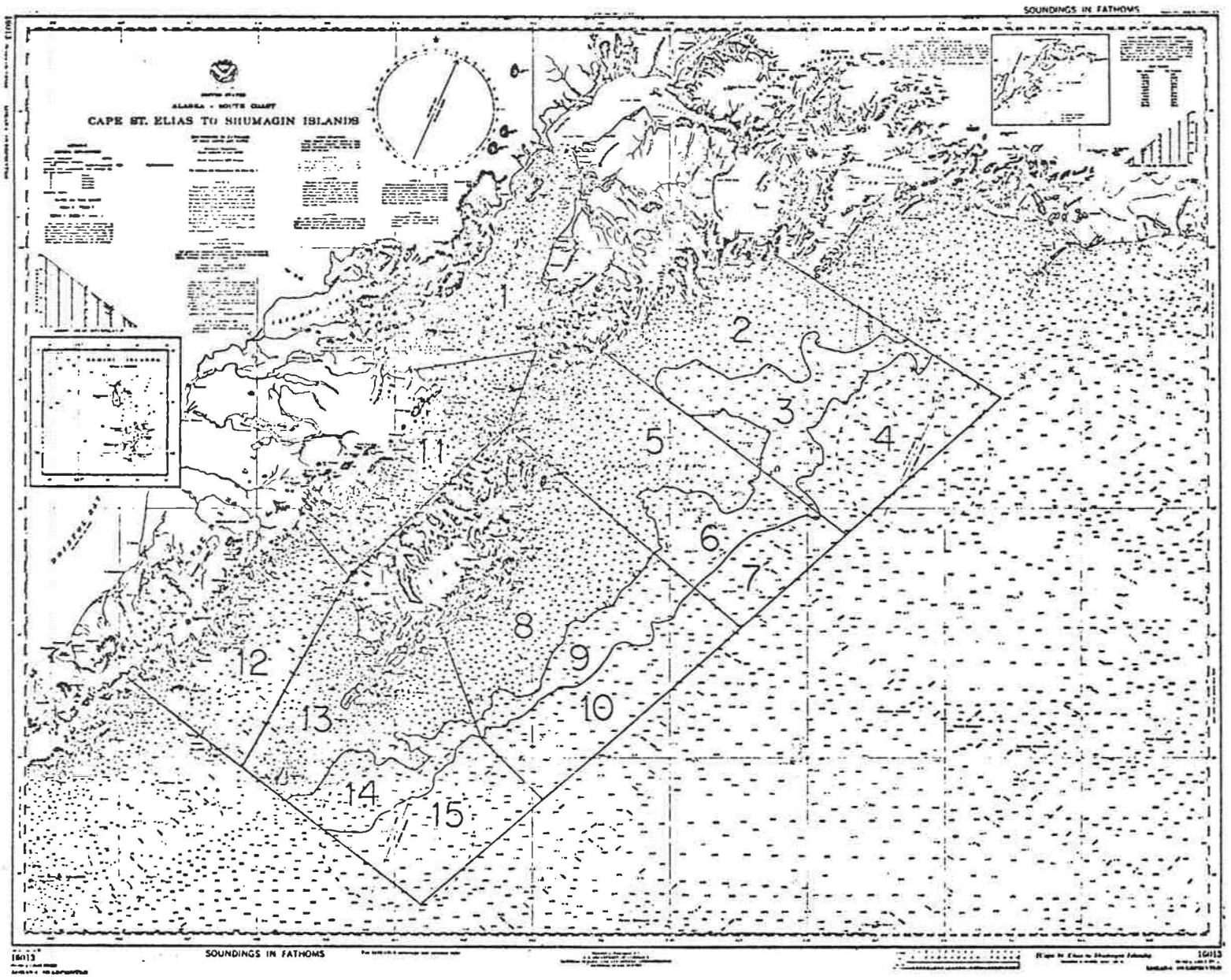

Figure 2. Example of BBM model subregions in the Kodiak area of the Gulf of Alaska.