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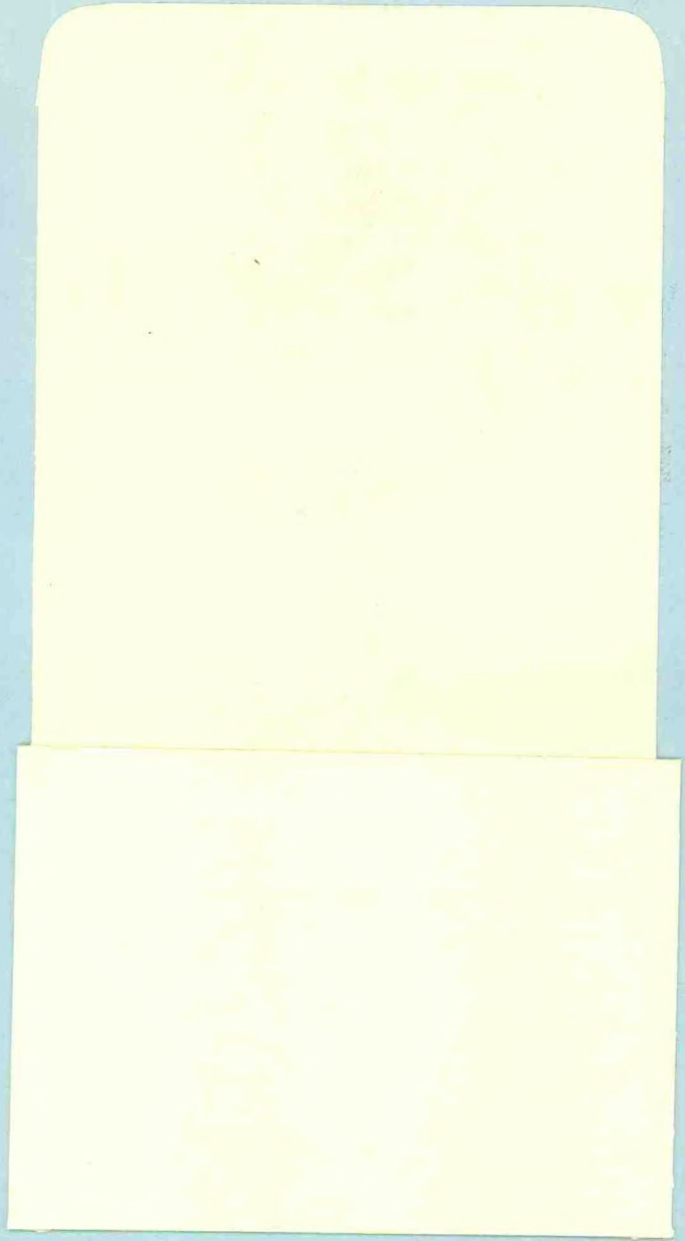
Potential Use of the Andersen-Ursin Multispecies Beverton and Holt Model for Modelling North Pacific Fish Interactions

by
Patricia A. Livingston

March 1983

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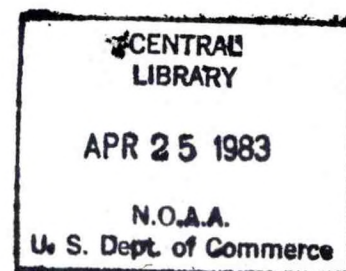
POTENTIAL USE OF THE ANDERSEN-URSIN
MULTISPECIES BEVERTON AND HOLT MODEL
FOR MODELLING NORTH PACIFIC FISH INTERACTIONS

by

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ABSTRACT

The Andersen and Ursin (1977) multispecies Beverton and Holt model includes explicit descriptions of trophic interactions between fish species by age groups. This model is described and evaluated in terms of its formulation and structure. The type of data needed for input along with the availability of data specific to North Pacific fishes is discussed.

Sensitivity analysis of the model produced results which paralleled those of a biomass based model. Similar types of parameters, those involving growth and predation, proved to be the most sensitive in both the number based Andersen-Ursin model and a biomass based model. The implications of this result are discussed in terms of using the Andersen-Ursin model for the North Pacific management areas.

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INTRODUCTION

The management of marine fisheries is a complex task. At the very least, it requires knowledge of resource abundance and its associated rates of fishing and natural mortality. More detailed information is needed in order to understand the observed fluctuations in a population's abundance. For example, age structure, fecundity, and growth rate are parameters used to estimate a species' potential to recover from fishing removal. There is an increasing awareness that this type of data alone is not sufficient to intelligently manage a multispecies resource. Fish species interact with each other through predation and competition for food and these interactions may be a major cause of fluctuations in fish abundance. A multispecies model is usually required to assess the effects not only of fishing but also of fish interactions on fish population size.

Many multispecies models have been developed which include trophic interactions in their calculations. One model which has received an unusual amount of attention in recent years is the Andersen-Ursin (1977) multispecies Beverton and Holt model. This model not only contains a detailed description of fish interactions through predation, but can also include nutrient cycling. It has been suggested that this model be adapted for use at the Northwest and Alaska Fisheries Center. First, the model should be evaluated to determine its suitability as a fisheries management device. It will be my purpose here to describe the model and discuss its attributes as part of the evaluation process.

A BRIEF DESCRIPTION OF THE MODEL

The model is an extension of the Beverton and Holt (1957) theory of fishing which has three basic differential equations for each species i

$$\frac{dw_i}{dt} = H_i w_i^m - k_i w_i^n \quad (1)$$

$$\frac{dN_i}{dt} = - (F_i + M_i) N_i \quad (2)$$

$$\frac{dY_i}{dt} = F_i N_i w_i \quad (3)$$

Equation (1) describes the change in body weight, w_i , as a function of energy taken in by the fish ($H_i w_i^m$) and loss of energy by the fish ($-k_i w_i^n$).

Equation (2) relates the change in numbers, N_i , to fishing (F_i) and natural (M_i) mortalities.

Equation (3) computes the rate of yield to the fishery as a function of fishing mortality (F_i).

Feeding

Andersen and Ursin (1977) have expanded on equation (1) to describe more specifically the energetics of feeding. The rate of food consumption (R_i) by species i is defined as

$$\frac{dR_i}{dt} = f_i h_i w_i^m \quad (0 \leq f_i \leq 1) \quad (4)$$

where h_i is a proportionality constant and f_i is the feeding level. When $f_i = 1$, the fish is eating all it can, otherwise ($f_i < 1$) the fish is eating some fraction, f_i , of the maximum. Andersen and Ursin put an upper bound on f_i , called the critical feeding level f_c . Only a fraction, v_i , of food consumed is actually absorbed by the fish. Therefore, the weight equation (1) can be rewritten as

$$\frac{dw_i}{dt} = v_i \frac{dR_i}{dt} - k_i w_i^n = v_i f_i h_i w_i^m - k_i w_i^n \quad (1A)$$

where v_i is the product of the food fraction which is actually digested (β) and the fraction of food left after energy transfer costs ($1-\alpha$). The feeding level is computed as

$$f_i = \frac{\Psi_i}{\Psi_i + Q_i}; Q_i = \frac{V(\text{or } A)}{q_i w_i^r} \quad (5)$$

where V is the water volume and q_i is a search rate coefficient and r is a search rate exponent. Ψ_i is the sum of all prey j biomass, each weighted by its suitability G_{ij} to the predator

$$\Psi_i = \sum_j \Psi_{ij} = \sum_j G_{ij} w_j N_j \quad (6)$$

G_{ij} is the fraction of prey j 's biomass available as food to i . In order to calculate G_{ij} , Andersen and Ursin defined G_{ij} as a function of predator size and prey size

$$G_{ij} = \rho_{ij} g_{ij} \quad (0 \leq G_{ij} \leq 1)$$

where ρ_{ij} is the coefficient of vulnerability to predation and

$$g_{ij} = \exp - \frac{(\ln(w_i/w_j) - \eta)^2}{2\sigma^2} \quad (7)$$

This assumes that there exists a preferred prey size and that a prey twice the preferred size is as acceptable as a prey half the preferred size. η is the natural log of the preferred predator/prey size ratio and σ is the standard deviation of the distribution (Fig. 1).

Mortality

The mortality equation (2) has also been modified by Andersen and Ursin. The natural mortality coefficient \hat{M} of Beverton and Holt is divided into at least two parts

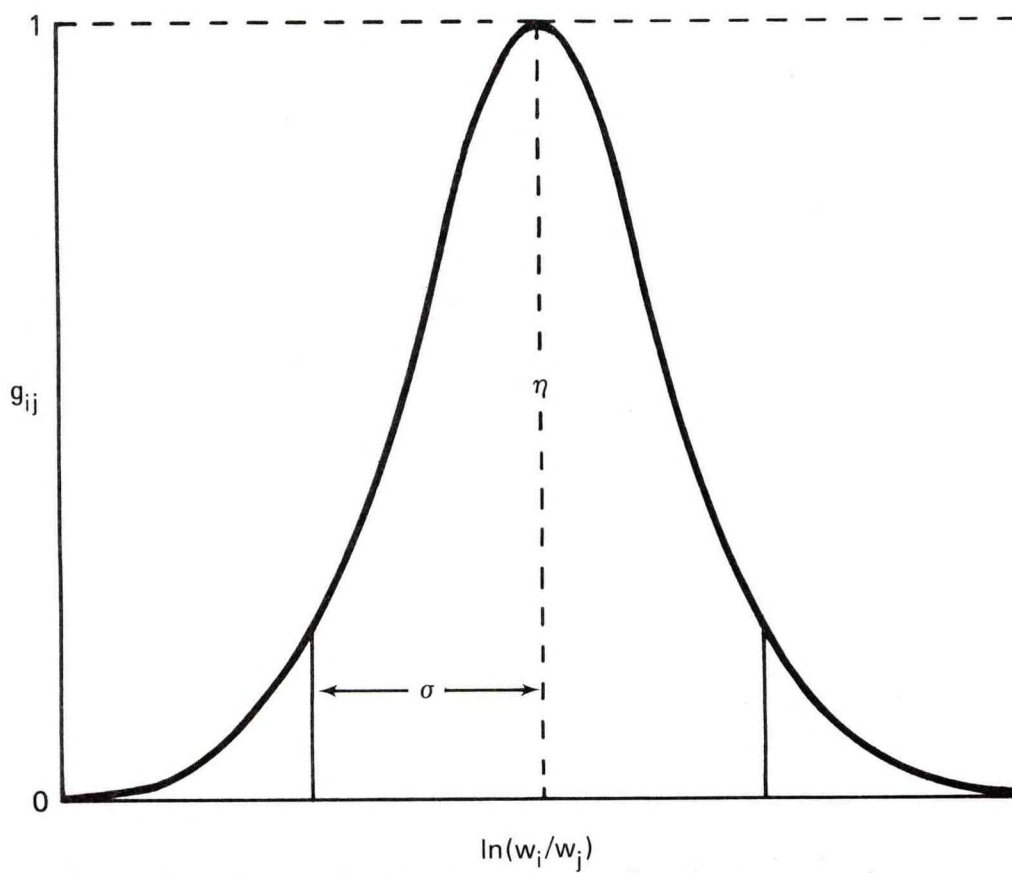


Figure 1.--Shape of the prey size selection curve where η is the mean prey size preference.

$$\frac{dN_i}{dt} = - (F_i + \hat{M}_i + M2_i) N_i \quad (2A)$$

$M2_i$ is defined as predation mortality rate of species i by all groups preying upon i .

$$M2_i = \frac{1}{N_i w_i} \sum_j \frac{dR_j}{dt} N_j \frac{\psi_{ji}}{\psi_j} \quad (8)$$

The remaining natural mortality \hat{M}_i can be further broken down into a density dependent larval mortality $M1_i$. Discard mortality and mortality on fish damaged by fishing gear but not retained by the gear could also be added to fishing mortality.

Age Structure and Reproduction

Each species in the model is broken down into several age groups. The final age group is usually a cumulative one, i.e., it contains all individuals older than a given age. Although the model is basically continuous, spawning occurs at discrete (yearly, half-yearly, or monthly) intervals. At the time of spawning, the mature age groups lose a fraction, π , of their weight. The spawned biomass is divided by the weight of one egg to give the number of eggs, E . The number of eggs hatched, $E1$, is a fraction of the number of eggs laid. The $E1$ larvae then form the youngest age group and each of the older groups are moved into the next older age group.

Parameters Required for the Model

Some parameters for the model are universal, i.e., they are used for all species. For example, the exponents m and n and the coefficient of food absorption, v , in the growth equation are universal parameters. The male fraction of spawning products, π male, and fraction of eggs unhatched, π unhatched, are also the same for all species.

Some parameters are species specific: h_i and k_i of equation (1A), prey size parameters η_i and σ_i , individual egg weight, ω_i and spawning dates. If some species have seasonal variation in feeding rate, then this can be specified in the model also.

Each age group of a species requires several parameters. The age, numbers, and individual weight must be specified for each age group for a given starting point in the model, usually January 1st of a given year. The fraction of body weight lost at spawning, π_i , must be given for each age group. Fishing and discard mortalities are specified for each age group but are tuned in model runs to agree with fishery statistics on landings.

The complete model has many other features not discussed here. The reader is referred to Andersen and Ursin (1977) for a detailed description of the model and methods for parameter estimation.

DISCUSSION OF MODEL ATTRIBUTES

The brief discussion above has at least highlighted the general characteristics of the model. The following questions about the model should be answered in order to evaluate the model's usefulness.

(1) Is the model understandable? In other words, is the model described in terms understandable by the people who will potentially use it, like fishery managers and biologists?

This is an important quality of any model for if it is not easily understood, it will be extremely difficult to convince fishery managers to experiment with the model, let alone use its outputs to formulate management plans. Also, since a model is our view of how an ecosystem works, there are many pitfalls in interpreting model outputs if one does not understand the workings of the model.

Fortunately, Andersen and Ursin (1977) have taken great pains to explain their model in "plain English" and in biological and mathematical language. Because they have tried to model the mechanisms by which ecosystems operate, almost all of their equations can be translated directly into biological terms. Portions of the model which do not function as expected, or where they were unable to incorporate a desired feature, are pointed out by Andersen and Ursin so that no unintended qualities are attributed to the model. Finally, since the model is an extension of the Beverton and Holt theory of fishing, at least that basis of the model should be understandable to fishery managers.

(2) Does the model include the necessary processes to answer the questions being asked about the system?

The model contains the necessary features in order to address questions about the effects of fishing pressure on the species composition of the system. This is accomplished through the detailed description of age structure and the interrelationships of fish species through growth and predation. In the complete model, the flow of a nondegradable compound like DDT can be traced through the food web. This feature could provide insight as to effects of toxic substances on a system. The model can show what could happen if an unusually large year class of fish should appear, but it does not attempt to explain the causes of fluctuations in year-class size.

(3) Are the formulations in the model realistic? Do they correspond to the biological mechanisms of the real system?

One of the strong points of this model is the detailed description of fish growth as related to the fish's activity, feeding level, digestion, and excretion. It is one of the better attempts at realistically describing in mathematical

terms the biological mechanisms of growth. The model also includes a realistic approach to predation by relating it to predator/prey size and prey vulnerability. This could be improved somewhat by incorporating some definition of patchiness in predator and prey distributions over the model area. Also, like other existing models, the Andersen-Ursin model is not equipped with a sufficiently detailed approach to recruitment in order to reproduce observed variations in year-class size in a mechanistic fashion. On the whole, every attempt has been made to incorporate as much biology as possible into the model.

(4) Does the model have precision? That is, can the model produce values comparable to observed values?

Fishing mortality and recruitment parameters are adjusted in the model to produce yields that correspond to observed fishery yields. The model estimates of size at age compare well with observed values. Andersen and Ursin also make periodic checks on the prey item selection by each predator to insure that it is reasonable compared with observed diet information. Ursin (1977) used the model to perform a prognostic assessment of the North Sea for 1977-79. A real test of the model's precision will come when Ursin compares these values with the observations for 1977-79.

(5) Would the model be difficult to parameterize for the management areas of the Northwest and Alaska Fisheries Center?

Table 1 shows a summary and short description of the major parameters required in the Andersen-Ursin model including some notes on the availability of estimates for the parameters. Many of the parameters can be considered universal in the model such as the feeding level (f), the powers of weight in the growth equation (m and n), the search rate coefficient and exponent (q and r), the fraction of food digested (β), and the fraction of food lost in energy transfer

(α). These have been estimated by various methods as discussed in Ursin (1967) and the values used by Andersen and Ursin (1977) are listed in Table 1. The other parameters are specific to a species or age group of a species and thus require data for their estimation.

The coefficients h and k in the growth equation can be estimated from length at age data which should be available for many North Pacific fish. Fishing mortality (F_1) is tuned in the model to agree with observed landings. The other natural mortalities due to disease, old age, and spawning stress ($M_4+M_5+M_6$) can be entered into the model if their values are known though these mortalities have not been estimated for most fishes. The exclusion of these values from the model should not be critical as the magnitude of other natural mortalities should be small relative to fishing and predation mortality.

The initial values for numbers and weights ($N_{1,i}$ and $W_{1,i}$) are more difficult to estimate as they must correspond to the numbers and weights present on January 1st of the model's starting year. Size-at-age data are available for some of the commercial species in the North Pacific. It may be more difficult to obtain this type of information for noncommercial species such as capelin or sandlance, though data from studies in the North Atlantic on similar fish could be used if no other data source is available. A similar problem exists for obtaining numbers at age for more of the North Pacific fish species. Although virtual population analysis (VPA) and cohort analysis are traditionally used to estimate population abundance, these methods usually require a long time series of catch-at-age data which are not available for most North Pacific fish. Some recent innovations to VPA and cohort analysis enable the use of a shorter time series of data (Cook 1981) or catch composition by length instead of age (Jones 1981; Pope 1980), so that it may be possible to use the sparse North Pacific data sets to estimate numbers at age.

Table 1.--Description of major parameters required in the Andersen-Ursin model.

Parameter symbol	Description	Species specific or universal	Availability - data required for estimation
A	Area of model region	-	-
Fl_i	Fishing mortality (fish landed)	Species specific	Specific to each age group - need catch-at-age data
f_c	Critical feeding level	Universal	0.44 (not used in skeleton model)
h	Coefficient in anabolic term of growth equation	Species specific	Can be estimated from feeding experiments. Ursin (1967) estimated H from length at age where $H = (1-\alpha)\beta hf$.
k	Coefficient in catabolic term of growth equation, independent of body size, related to activity level of species	Species specific	1.1 for standard metabolism. Can be estimated from fasting experiments in laboratory. Ursin (1967) estimated k for 81 species of fish from length-at-age data. Range: 0.2-2.0.
m	Power of weight (w) in anabolic term of growth equation which defines the food absorbing surface relationship	Universal	0.56. Estimated from length at age data, respiration experiments, direct measurement of absorbing surface of intestine, or measuring the rate of food consumption. ($m = 2/3$ in skeleton model)
$M4+M5+M6$	"Other" natural mortalities: disease, old age, spawning stress	Can be species specific or universal	$M4 = 0.03/\text{yr}$. (Ursin) ($M4+M5+M6 = 0.1/\text{yr}$ in skeleton model)
n	Power of weight (w) in catabolic term of growth equation	Universal	0.83. Estimated from length-at-age data, respiration experiments, or measuring respiratory surface versus body size. ($n=1$ in skeleton model)
$N_{1,i}$	Initial number of fish in each age group	Species specific	VPA can be used. System will reach the same equilibrium regardless of the values estimated for N. Choice of N's do matter in real-time mode.
q	Search rate coefficient $Q = V(\text{or } A)/q_i w_i$	Universal	$23m^3 - (l+tr)$ pelagic habitat $0.53m^2 - (l+tr)$ demersal habitat Can be estimated from food consumption versus food concentration experiments.

Table 1. (cont.)--Description of major parameters required in the Andersen-Ursin model.

Parameter symbol	Description	Species specific or universal	Availability - data required for estimation
r	Search rate exponent	Universal	0.15
V	Volume of model region	-	-
$w_{1,i}$	Initial individual fish weights	Species specific	System will reach same equilibrium regardless of choice of $w_{1,i}$'s. Choice of w 's do matter in real-time mode.
α	Fraction of digested food lost in energy transfer (in anabolic term of growth equation)	Universal	0.4 Sperber et al. 1977
β	Fraction of consumed food which becomes digested	Universal	0.8 Sperber et al. 1977
η	Mean prey size preference parameter	Species specific	Available for some species. Can be estimated from stomach data. Can be tuned in the model to produce observed diet.
π	Fraction of biomass spawned	Species specific	Requires fecundity at age and mean egg weight. (universal in skeleton model: $\pi_{\text{male}} = 0.25, \pi_{\text{unhatched}} = 0.50$)
ρ	Coefficient of vulnerability to predation	Species specific	Disregarded (ie, = 1.0) unless there is reason to believe decreased vulnerability due to species behavior, ie, burial in sand or schooling. (not used in skeleton model)
σ	Prey size preference parameter which indicates the steepness of the prey size selection curve	Species specific	Available for some species. Can be estimated from stomach data. Can be tuned in the model to produce observed diet. ($\sigma^2 = \eta$ in skeleton model)
ω	Mean egg weight	Species specific	Could be estimated from egg diameter data or by direct measurement.
v	Fraction of food consumed that is assimilated $v = (1-\alpha) \beta$	Universal	

The prey size preference parameters η and σ can be estimated from stomach data as described by Ursin (1973). These parameters have been estimated for some northwest Atlantic fish (Hahm and Langton 1980) and could easily be estimated for North Pacific fishes if the appropriate stomach data are available. These parameters can be adjusted in the model to produce fish diets consistent with those reported in the literature. Also, a species' vulnerability to predation, represented in the model by the coefficient ρ , can be used if there is reason to believe a species has decreased vulnerability due to its schooling behavior or burial in sand, for example.

The remaining parameters which are the fraction of biomass spawned, π , and mean egg weight, ω , require fecundity at age and egg size data. Andersen and Ursin (1977) admit there is a great deal of guesswork in choosing values for π , but do not seem to mention whether or not errors in these estimates have a large effect on model outputs. Overall, it would be useful to obtain an idea on the effects that errors in input values have on output values. This would help prioritize input data needs according to their importance in determining model output values.

SENSITIVITY ANALYSIS

A sensitivity analysis was performed on the "skeleton" version of the Andersen-Ursin model to determine the effect of input errors on model behavior. This skeleton model is a simplified view of an ecosystem consisting of phytoplankton, zooplankton, a herring-like fish, and a cod-like fish. It is much easier to test the model and interpret its behavior using this reduced version. Since most the major parameters described in Table 1 are still included in this version, the behavior of this model should be very much like a more extended version which contains many fish groups.

Overview of Skeleton Model

The basic model equations which were explained earlier remain the same. Another equation is added, however, to stabilize the model. This equation controls the number of eggs hatched (E_1) in a density dependent fashion related to the number of eggs laid (E) and a species specific parameter C .

$$E_1 = E(C/(C+E)) \quad (9)$$

Additionally, in this simplified model the critical feeding level, f_c , along with the coefficient of vulnerability, ρ , is not used; i.e., they are set equal to one. The other natural mortalities, $M_4+M_5+M_6$, of Table 1 are lumped into one mortality called M_1 which is set to 0.1 yr^{-1} for all species. Table 2 shows the species used in the model and their breakdown according to age into separate computational entities, along with the initial parameter values for each entity. The initial numbers N , the mean individual weights w , and fishing mortality F are entity specific parameters. The coefficients h and k of the growth equation, the mean egg weight ω , and the density dependent mortality parameter C are species specific parameters.

Sensitivity Analysis Procedure

The individual parameter perturbation method (IPP) was used where parameters are perturbed singly by a particular amount from their base value - with only one parameter being perturbed per model run. Table 3 lists and describes the parameters which were perturbed for the sensitivity runs. The changes in model outputs are then compared to model outputs from the base run of the model where no parameters are perturbed. The outputs from this model are the numbers, N_i , and individual mean weights, w_i , of each entity i in the model.

Typically, parameters are perturbed either by an amount equivalent to a fixed percentage of the parameter, i.e., $\pm 10\%$ (Kitchell et al. 1977; Francis 1974;

Table 2.--Species in the skeleton model and their breakdown into age categories along with the base parameter values for each age group entity.

Species	Entity	Age (years)	Parameter					
			N	w	h	k	ω	F
Phytoplankton	1	0	1,000,000,000	.001				
	2	0	40,000	.01	10	2.5	.01	2,000,000
	3	.5	10,000	.25	10	2.5	.01	2,000,000
	4	1.0+	10,000	1.00	10	2.5	.01	2,000,000
Herring	5	0	1,000,000	.02	18	1.75	.02	10,000
	6	.5	-	-	18	1.75	.02	10,000
	7	1.0	100	25.00	18	1.75	.02	10,000
	8	1.5+	100	40.00	18	1.75	.02	10,000
Cod	9	0	-	-	35	.40	.05	2
	10	.5	1,000	3.00	35	.40	.05	2
	11	1.0	-	-	35	.40	.05	2
	12	1.5	2	42.50	35	.40	.05	2
	13	2.0	-	-	35	.40	.05	2
	14	2.5+	1	250.00	35	.40	.05	2
								.5

Table 3.--Andersen-Ursin skeleton model parameters used for model sensitivity tests (cf. Table 1 for more complete description).

Parameter	Brief description
F6	Fishing mortality for 0.5 yr old herring (entity 6)
F7	Fishing mortality for 1.0 yr old herring (entity 7)
F8	Fishing mortality for 1.5+ yr old herring (entity 8)
F14	Fishing mortality for 2.5+ yr old cod (entity 14)
H1	Anabolic growth coefficient for species 1 - zooplankton
H2	Anabolic growth coefficient for species 2 - herring
H3	Anabolic growth coefficient for species 3 - cod
K1	Catabolic growth coefficient for species 1 - zooplankton
K2	Catabolic growth coefficient for species 2 - herring
K3	Catabolic growth coefficient for species 3 - cod
m	Power of weight in anabolic term of growth equation (same all species)
n	Power of weight in catabolic term of growth equation (same all species)
ω_1	Mean egg weight species 1 - zooplankton
ω_2	Mean egg weight species 2 - herring
ω_3	Mean egg weight species 3 - cod
C1	Density dependent egg mortality parameter species 1 - zooplankton
C2	Density dependent egg mortality parameter species 2 - herring
C3	Density dependent egg mortality parameter species 3 - cod
v	Fraction of food consumed that is assimilated (same all species)
η	Mean prey size preference parameter (same all species)
π	Fraction of biomass spawned (same all species)
Q	Predator search rate (same all species)
M1	Total other natural mortality (same all species)

Orth 1979), or by an estimate of the standard error of each parameter (Livingston 1980). If one wants to test whether model response is linear or nonlinear, then parameters can be perturbed by varying amounts and linearity of model outputs can be checked by inspection (Miller 1974) or regression techniques (Summers and McKellar 1981).

It was decided that the most information about skeleton model behavior could be gained by varying each parameter successively by +10%, +20%, -10%, and -20%, and then testing model response for linearity over that range of perturbation through regression. The regression model used was $y = \alpha x^\beta$, where the dependent variable y is the change in a model output parameter expressed as a proportion of that output parameter's value in the base model run, and the independent variable x is the change in model input parameter expressed as a proportion of the input parameter's base value. For example, if an input parameter was decreased by 20% of its base value, then x would be 0.8; but if an input parameter were increased by 20%, then $x = 1.2$.

If model response is essentially linear, then $\beta = 1$ and α should be a measure related to the relative sensitivity measure, R , which is explained in more detail by Rivard and Doubleday (1979) and Mohn (1979). Basically, R is the ratio of the fractional change in a model output parameter to the fractional change in a model input parameter. In relation to the x and y variables $R = (y-1) (x-1)^{-1}$ while $\alpha = yx^{-1}$ (if $\beta = 1$). Unfortunately, the relationship between R and α is not that simple and, while it is easy to interpret R values, α values are not readily interpreted. Luckily, in this particular application there is no need to interpret the α 's as is shown in the results section.

β is the important parameter that needs interpretation to understand the sensitivity results in terms of nonlinear model response to perturbations. The types of model response that can be described by the model $y = \alpha x^\beta$ for different values of β are shown in Figure 2. The following interpretations can be assigned to the different β values:

$\beta > 1$ Change in output increases more rapidly when model input is increased above the base input value,

$\beta = 1$ Change in output is linear over the range of input value changes,

$0 < \beta < 1$ Change in output increases more slowly when model input is increased above the base input value, and

$\beta < 0$ Change in output is very high when model input is less than its base value and decreases as the input value is increased above its base value.

Thus, the most nonlinear responses occur as β either gets increasingly larger than one or increasingly negative.

Sensitivity Results

The resulting fit to the sensitivity model $y = \alpha x^\beta$ was good. The values for r^2 , the proportion of the total variation explained by regression, were greater than 0.8 for most of the cases. Some input parameters caused very nonlinear responses that would have required a much more complex sensitivity model. In general, though, the model could have been simplified even further to one parameter, β , instead of both α and β . This is because α was essentially equal to one, except in the cases already mentioned where the sensitivity model could not adequately describe the nonlinearity of response. So β is the variable which best indicates the degree of model sensitivity and nonlinearity.

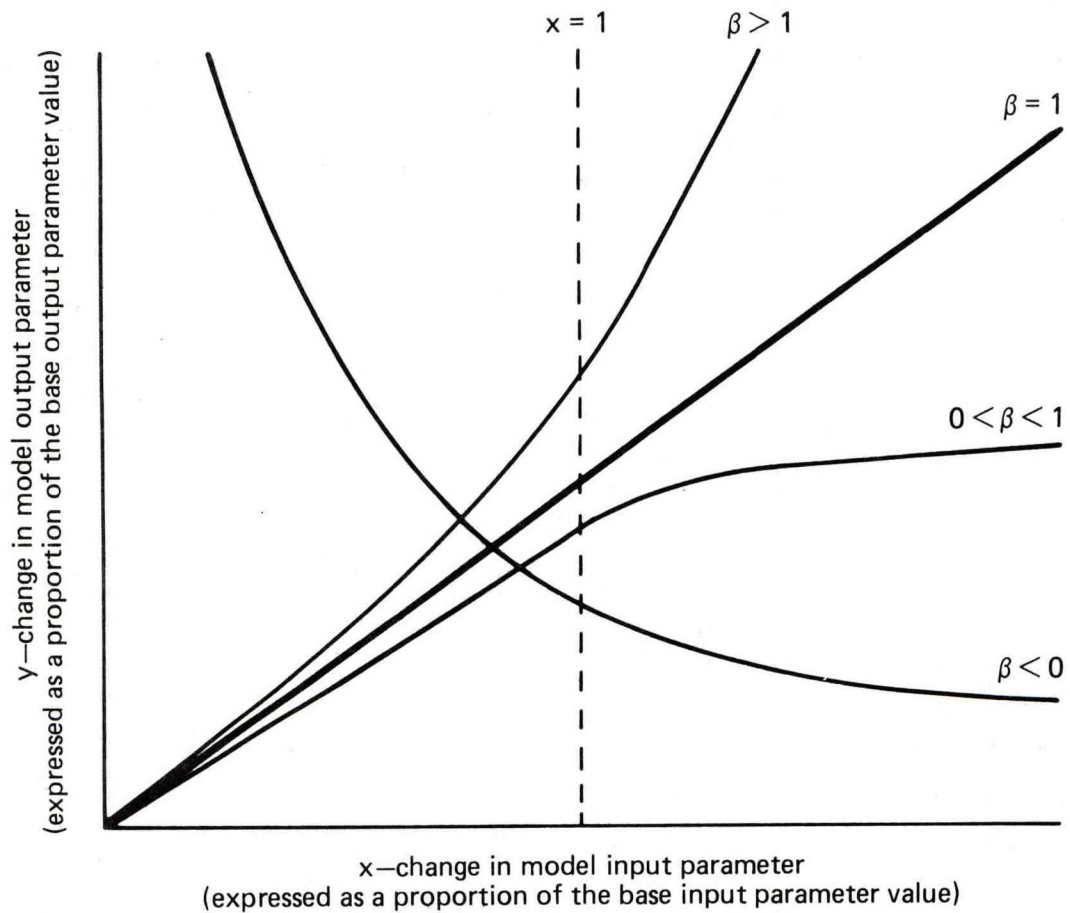


Figure 2.--Shapes of sensitivity curves of the form $y = \alpha x^\beta$ for different values of β .

The results are divided into three degrees of sensitivity - low, moderate, and high depending on the absolute value of β - the indicator of nonlinearity in model response. If none of the absolute values for β were greater than 0.5 when a particular input parameter was perturbed, then that input parameter was classified as one which produced low sensitivity results (Table 4). If the greatest value for $|\beta|$ fell between 0.5 and 1.5 for a given input parameter, then it was designated as a moderate sensitivity result (Table 5). An input parameter was considered to have produced high sensitivity results if $|\beta| > 1.5$ (Table 6).

The input parameters which produced low model response (Table 4) were π , the fraction of biomass spawned; $M1$, the other natural mortality coefficient; $\omega2$ and $\omega3$, the mean egg weight for herring and cod, respectively; and $C1$, the density dependent egg mortality parameter for zooplankton.

The parameter which man has the most control over - fishing mortality F - did not exert much influence over model outputs in the case of herring fishing mortality; $F6$, $F7$, and $F8$.

The model proved to be moderately sensitive to several input parameters (Table 5). For instance Q , which defines the predatory search rate of all the animals, had a direct relationship with the model outputs of animal numbers. When Q was increased, numbers also increased although the fractional increase in numbers was not as great as the fractional increase in Q . The model outputs of mean individual weights were inversely related to Q .

$K1$, the coefficient in the catabolic term in the zooplankton's growth equation which is related to their activity level, had varying effects on model outputs. Zooplankton numbers ($N2$) and weights ($W4$) were most affected and were inversely related to $K1$. Conversely, numbers of zooplankton and herring in

Table 4.--List of model input parameters which produced low sensitivity results ($0 < |\beta| < 0.5$) and the β 's estimated from the model $y = \alpha x^\beta$ where y is the dependent variable-change in model output expressed as a proportion of the base output variable and x is the independent variable-change in model input parameter expressed as a proportion of the base input value.

Species	Output parameter	π	M1	ω_2	ω_3	Input parameter		
						C1	F6	F7
Zooplankton	N2	.50	.00	-.04	.00	.41	.10	.09
	N3	.32	-.01	-.03	.00	.23	.04	.01
	N4	.21	.02	.10	.00	.11	.15	.14
Herring	N5	.04	-.01	.08	-.00	.00	.01	-.01
	N7	.11	.00	-.03	.00	-.03	-.39	.10
	N8	.16	-.17	-.03	-.01	-.02	-.30	-.32
Cod	N10	.06	.01	-.03	.08	.02	.07	.07
	N12	.08	-.07	-.03	.09	.02	.08	.08
	N14	.09	-.28	-.03	.08	.02	.08	.08
Total	NT	.44	.00	-.04	.00	.35	.09	.08
Zooplankton	W3	-.14	-.02	.02	-.00	-.10	-.05	-.05
	W4	-.41	-.02	.02	-.00	-.12	-.04	-.03
Herring	W7	-.08	-.02	.10	-.00	-.06	-.03	-.03
	W8	-.34	-.04	-.01	-.00	.04	.05	.04
Cod	W10	-.01	-.01	-.00	.16	-.01	-.00	-.00
	W12	.03	-.01	-.01	.06	.03	.03	.03
	W14	-.33	-.11	-.00	.01	.01	.01	.01
Total	WT	-.27	-.10	-.00	.02	.01	.01	.01

Table 5.--List of model input parameters which produced moderate sensitivity results ($0.5 < |\beta| \leq 1.5$) and the β 's estimated from the model $y = \alpha x^\beta$ where y is the dependent variable-change in model output expressed as a proportion of the base output variable and x is the independent variable-change in model input parameter expressed as a proportion of the base input value.

Species	Output parameter	Q	K1	K3	Input parameter			F14
					ω_1	C2	C3	
Zooplankton	N2	.12	-.85	-.01	-.57	-.21	.01	-.02
	N3	.26	.63	-.00	-.28	-.10	.01	-.00
	N4	.53	.48	-.02	-.16	-.33	.03	-.03
Herring	N5	-.00	.02	.00	-.00	.98	-.00	.00
	N7	.27	.80	-.01	-.00	.76	.01	-.01
	N8	.43	.70	.05	-.00	.59	-.07	.07
Cod	N10	.14	.10	-.02	-.01	-.14	1.01	-.01
	N12	.18	.09	-.00	-.01	-.16	.98	.02
	N14	.19	.08	.01	-.01	-.15	.96	-.56
Total	NT	.18	-.53	-.01	-.48	-.19	.01	-.02
Zooplankton	W3	-.34	-.58	.01	.31	.11	-.01	.01
	W4	-.40	-1.50	.01	.13	.08	-.01	.01
Herring	W7	-.45	.13	.00	.03	.06	-.00	.01
	W8	-.55	-.14	.01	-.02	-.10	-.01	.01
Cod	W10	-.39	.04	-.11	-.00	-.00	.00	.00
	W12	-.51	-.22	-.30	-.00	-.06	.00	-.00
	W14	-.66	-.56	-.70	.01	-.02	-.00	-.43
Total	WT	-.63	-.50	-.62	.01	-.03	-.00	-.36

Table 6.--List of model input parameters which produced high sensitivity results ($1.5 < |\beta|$) and the β 's estimated from the model $y = \alpha x^\beta$ where y is the dependent variable-change in model output expressed as a proportion of the base output variable and x is the independent variable-change in model input parameter expressed as a proportion of the base input value.

Species	Output parameter	Input parameter						
		v	η	H1	H2	H3	K2	m
Zooplankton	N2	.22	.86	.51	-1.26	.06	.49	.02*
	N3	-.97	.89	-1.80	-.23*	.02	-.13	1.28
	N4	-1.83	1.33	-1.54	-1.71	.11	.58	.40*
Herring	N5	.06	.09	-.05	.10	.01	-.05	.03*
	N7	-1.00	.93	-1.34	.19*	.05	.29	-1.16
	N8	-1.33	1.44	-1.21	-.21*	-.29	.44	-3.19
Cod	N10	-.49	.48	-.11	-.88	.42	.42	-.85
	N12	-.58	.54	-.08	-1.05	.46	.53	-1.66
	N14	-.60	.57	-.07	-1.06	.42	.54	-2.06
	NT	-.15	.90	-.01*	-1.16	.06	.42	.24*
Zooplankton	W3	2.28	-.95	1.77	.57	-.04	-.22	-2.80
	W4	2.46	-.34*	2.08	.34	-.03	-.11	-.57*
Herring	W7	2.48	.21*	-.50	2.84	-.02	-.98	.76
	W8	2.98	1.06	-.09*	2.47	-.04	-2.00	3.86
Cod	W10	2.39	.46	-.27	.00*	2.42	-.01	.92
	W12	2.98	.97	.08*	-.41	2.77	.13	4.69
	W14	3.37	2.09	.46	-.33*	2.45	.04	7.77
Total	WT	3.29	1.88	.39	-.28*	2.44	.02*	7.17
								-3.12

* indicates regressions where $r^2 < 0.8$

the older groups (N3, N4 and N7, N8) were directly related to changes in K1. The catabolic coefficient for cod, K3, was also categorized as a moderately sensitive parameter, although the only real effect it had was on the model output of cod weight for the oldest group of cod - W14.

Mean zooplankton egg weight, w1, mostly affected zooplankton numbers in an inverse fashion for the youngest category - N2. Likewise, C2 and C3, the density dependent egg mortality parameters for herring and cod, respectively, affected the numbers of their own groups the most but in a direct relationship instead. Finally, F14, the fishing mortality for the oldest cod group, most affected both the numbers and mean weight of that group.

Table 6 shows the input parameters which were classified as producing high model sensitivity. Some model responses were very nonlinear for these tests and the sensitivity model could not adequately describe the response (* indicates regressions where $r^2 < 0.8$). However, the sensitivity model was adequate for the majority of responses.

The universal parameter v, the fraction of food consumed that is assimilated, had mostly moderate effects on numbers of animals but rather severe effects on mean individual weights. In the majority of cases, the percent change in output weight was more than double the percent change in v. The response was nonlinear because the percent change in weight was much greater when v was increased by 20% than when v was decreased by 20%. For instance, W12, the mean individual weight of 1.5 yr old cod, increased 75% when v was increased 20% and decreased about 50% when v was decreased by 20%.

The mean prey size preference parameter η did not produce such strong responses as v but the responses were also nonlinear. In most cases, decreasing η had a strong negative effect on numbers and weights while increasing η did not cause a large response.

The model proved to be highly sensitive to changes in the coefficients in the anabolic term of the growth equation for all three species; H1, H2, and H3 for zooplankton, herring, and cod, respectively. When H1 was perturbed it affected not only the numbers of zooplankton in an inverse fashion, but also the numbers of herring. Zooplankton weights were the only outputs that varied directly with H1, though. H2 affected the numbers of zooplankton and cod inversely, while it affected the weight of zooplankton very strongly in a direct relationship. The coefficient for cod H3 had little effect on model outputs with the exception of cod weights for which it had a strong direct effect.

K2, the coefficient in the catabolic term of the growth equation for herring, affected cod numbers to some extent. However, the most obvious response was the inverse relationship with herring weight.

Finally, m and n, the exponents of the anabolic and catabolic terms, respectively, of the growth equation produced the largest estimates of β . Herring and cod numbers had an inverse relationship with m but a direct relationship with n. Zooplankton weight varied inversely, while herring and cod weights varied directly with m. Cod weight, in particular W12 and W14, had an enormous response to variations in m. Changes in n showed a negative relationship to herring and cod weights but a direct relationship with zooplankton weights.

Sensitivity Discussion

In general, model outputs were affected very little by most parameters. Mean egg weights, ω , had little influence on model response. Similarly, natural and fishing mortality, M1 and F, which are the driving parameters for many single-species models, did not exert much influence on outputs.

The density dependent egg mortality parameters, C, had an effect only on the number of animals for the species associated with a particular C. The effect

of C was not as great on the numbers in the older age groups of zooplankton in the case of C1 or the older age groups of herring for C2. Possibly increased predation losses occur in the older age groups of these species when C is increased, thereby offsetting the positive effect of C on numbers of animals. All age groups of cod are equally affected by C3 because the model has no predators on the older cod groups.

It is difficult to explain the influences that K1, the coefficient in the energy loss term of the growth equation for zooplankton, has on model outputs. The direct result of increasing K1 is a decrease in zooplankton mean weight. This seems to shift the predation on zooplankton to the smaller sizes, thus decreasing the numbers in the smallest zooplankton size group (W2) and increasing the numbers in the older size groups (N3 and N4). The only probable explanation for the decrease in older cod weight would be that they were not getting enough older zooplankton of the appropriate size because the mean weight of older zooplankton had decreased so drastically.

The coefficient in the energy loss term of the growth equation for cod, K3, did not have a widespread effect on model outputs. Large cod, at the end of the food chain, decreased in size but did not produce any ill effects on either the numbers or weights of the other species in the model.

The universal parameter, v , the fraction of consumed food that is actually used for growth and maintenance, had a large influence on the weights of all the animals in the system. Since average weight increased, the predation rate also increased. This decreased the numbers of animals, especially in the zooplankton and herring group which are preyed upon by the top predator, cod.

When the preferred prey size, η is increased for all animals, the only negative response in the system is zooplankton weight. This is probably because

the abundant phytoplankton resource is no longer the best size for the zooplankton. Thus some zooplankton weight loss occurs due to insufficient food. The oldest (largest) group for each species seems to benefit more than the younger groups in terms of both numbers and weight. Possibly the preferred prey size distributions for these groups are separated enough from each other to insure they each get sufficient food and are not of a preferred size for other groups.

All of the H's produced high sensitivity results when perturbed. The primary effect of increasing a species' H value is to increase that species' individual mean weight since H is the coefficient in the energy gain term of the growth equation. This weight change will shift that group's preferred prey size and also may put them out of the preferred prey size range of another group. Additionally, a species' ration is also a function of H so that food intake, and thus predation mortality of other species, would increase as H increases.

The energy gain side of the growth equation has the term w^m which makes energy intake a function of the animal's weight raised to the power m. Increasing m has the effect of increasing most of the mean individual weights in the system. Since m is an exponent, the effect is more pronounced for animals of increasing size. In this test, however, zooplankton lost weight, probably because their food source, phytoplankton, is no longer in the right prey size range relative to zooplankton weight. Zooplankton numbers increase, however, probably because their predators, herring and cod, not only decreased in number but also grew very large relative to zooplankton so that zooplankton were no longer of a suitable prey size.

Energy loss in the growth equation is a function of animal weight to the power n. The effect on model outputs of changing n is not as great as that of m. Like m, n is an exponent so model responses were also nonlinear. Since food

intake and thus predation mortality are functions of w^m , m 's influence on the model is widespread in comparison to n .

Thus, the driving parameters in the model are the ones associated with the growth equation and with prey size preference. Particularly, those parameters in the left-hand side, or energy intake side, of the growth equation were most important in determining model output values. Because energy gain, ration, and predation mortality are all functions of these parameters, they have a large-scale effect on model output estimates.

CONCLUSIONS

Evaluation of the model from a theoretical point of view in the first section showed that the model equations have a good biological basis and incorporate many processes in an understandable manner. The sensitivity analysis showed which parameters are most important in determining model output values. The growth equation and predation parameters affected model outputs most and often affected them in a nonlinear manner.

Interestingly, the counterparts of these parameters in a biomass based model, the Bulk Biomass Model (BBM), at NWAFC also proved to have the most influence on that model's outputs (Livingston 1980). As discussed by Livingston (1980), these parameters set up a hierarchy for species response. How a particular species is able to recover from or is affected by predation mortality is determined by its growth rate as well as its predators' growth rates.

Thus, both types of models - the number based and the biomass based - seem to depend on the same type of parameters to estimate model outputs. The number based model of Andersen-Ursin has an advantage in its ability to keep track of the age distribution for each species. This may be a necessary detail for some management purposes. However, some of the biomass based models at NWAFC also

have an advantage in that they incorporate spatial resolution and fish migration which may be important in some management applications, especially in large areas like the eastern North Pacific and Bering Sea. Adding spatial resolution to Andersen-Ursin's model has been attempted, but because of the small time steps necessary for accurate integration of model equations, the computer time becomes excessive even for a "2-box" model. If the biomass-based models could incorporate age structure into the formulation, then they could address most management questions (except economic ones). The Andersen-Ursin model could still be used on areas where geographic resolution is not necessary and where fish migration is not significant.

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