

A COMPARTMENTALIZED SIMULATION MODEL OF THE SOUTHERN NEW ENGLAND YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*, FISHERY

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ABSTRACT

A compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea*, fishery was developed. The population was divided into 10 age-groups, each of which was subdivided into 7 size categories. The model simulated discard mortality as well as natural mortality and fishing mortality. Fishing and discard mortality rates depended on the level of fishing and on gear and market selection factors. Both linear and density independent stock-recruitment functions were considered. Seasonal variations in growth and exploitation were incorporated into the model. The influence of fluctuation in temperature on recruitment and growth was also simulated. The model using a linear stock-recruitment function accounted for 85.5% of the variability in the yield of the fishery for 1943-65; with a density independent stock-recruitment function, the model explained 83.2% of the variability in yield for the same period.

The linear stock-recruitment model was used to investigate the response of the fishery to alternative fishing strategies. Substantial increases in the past yield of the fishery were indicated by the model when fishing effort was concentrated during the second half of the year and when fishing effort and discard mortality were reduced.

This paper describes a compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea* (Storer), population. There is evidence that production of the Southern New England yellowtail flounder population is influenced by environmental temperature (Sissenwine 1974). The model is intended to demonstrate the feasibility of predicting catch under fluctuating environmental conditions based on the rate of exploitation. The model shares many of the characteristics of Walters' (1969) "generalized computer simulation model," which incorporates growth, fishing and natural mortality, and a stock-recruitment relationship, and also incorporates several additional features. These features include 1) temperature dependent growth and recruitment, 2) growth and fishing mortality rates which vary seasonally, and 3) age-groups subdivided into size categories.

More than 600 thousand metric tons of yellowtail flounder valued at over \$120 million have been landed in Southern New England and New York since the onset of fishing in the late

1930's. The magnitude of the fishery has stimulated numerous quantitative investigations. Royce et al. (1959), Lux (1964, 1969a), Brown and Hennemuth,² Brown,³ and Parrack⁴ reported catch and fishing effort data for each of the three major fishing grounds (Lux 1963) since 1943. Until recently, most of the catch has been from the Southern New England ground. Catch and fishing effort data were used by Sissenwine (1974) to estimate the annual recruitment and equilibrium catch produced by the Southern New England ground for 1944-65. The equilibrium catch and recruitment were shown to be highly correlated with the atmospheric temperature record at Block Island, R.I. Lux and Nichy (1969) determined the growth rate of the yellowtail flounder. Lux (1969b) and Pitt (1971) calculated the length-weight and length-fecundity functions of the species, respectively. Mortality rates of the yellowtail flounder were estimated by Lux

²Brown, B. E., and R. C. Hennemuth. 1971. Assessment of the yellowtail flounder fishery in Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 71/14, Ser. No. 2599, 57 p.

³Brown, B. E. 1972. Current status of the yellowtail flounder fishery in ICNAF Subarea 5 - January, 1972. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/23, Ser. No. 2174, 18 p.

⁴Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

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(1969a), Brown and Hennemuth (see footnote 2), and Penttila and Brown.⁵

Some of the research cited above is recorded only in unpublished documents. Any information extracted from these reports must be considered as preliminary. Accordingly, the work reported in this paper was primarily based on the published literature.

Catch data used in this paper include both domestic and foreign landings of yellowtail flounder but exclude the industrial catch. All effort data are expressed in standard days fished as defined by Lux (1964).

DESCRIPTION OF THE MODEL STRUCTURE

A diagram representing the compartments and activities of the system is shown in Figure 1. Since yellowtail flounder greater than 10 yr of age are seldom encountered, fish were divided into 10 age-groups. Certainly, the length of individuals within each age-group is not uniform. Therefore, each age-group was subdivided into seven size categories in which all fish were assumed to be of a uniform length. The number of size categories was limited to seven in order to minimize computer cost. The level (number of fish) of each of the 70 age-size compartments is denoted by $N_{i,j}$ where i indicates the age-group and j the size category. Another attribute of each compartment is its mean length, denoted by $L_{i,j}$ with i and j defined in the same manner.

The yield of the fishery in weight (Y_w) and number of fish (Y_n) landed annually are attributes of the yield compartment. Total fecundity of the population during each spawning season is P_e (number of eggs in the egg compartment).

The important activities affecting the system are: 1) fishing which results in a continuous transfer of fish from age-size compartments to the yield compartment and results in some non-productive mortality (discard mortality) since not all fish captured are actually landed (Brown and Hennemuth see footnote 2); 2) natural mortality which results in a continuous decay of each age-size compartment and loss of fish from the system; 3) aging which results in a discrete advancement

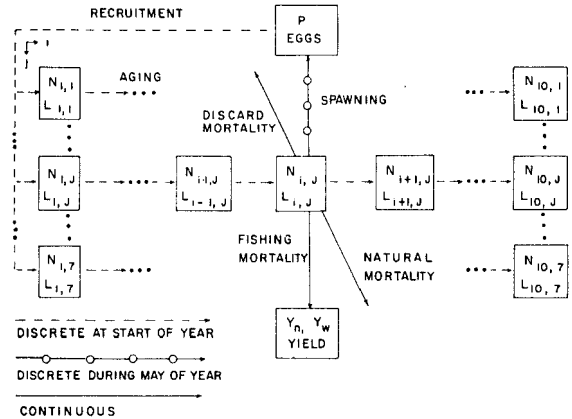


FIGURE 1.—Compartments representing a fish population. Three dots (...) indicate additional compartments. The age-group is indicated by i and the size category by j . $N_{i,j}$ is the number of fish in the j th size category of age-group i , and $L_{i,j}$ is the mean length of the fish of the same compartment. Each compartment (only shown for (i,j)) undergoes continuous loss due to fishing, discard, and natural mortality. Losses due to fishing mortality are added to the yield compartment. At the beginning (or end) of each year, aging occurs, advancing each compartment to the next higher age-group, retaining the same value of j . Recruitment to age-group 1 also occurs at the beginning of each year as a function of the previous year's egg production. Spawning occurs during May of each year (only shown for (i,j)) with egg production a function of the number and size of fish in each compartment.

of fish to the next higher age-group (retaining the same value of j) at the beginning of each year; 4) spawning which is the discrete production of eggs (P_e) during May (Bigelow and Schroeder 1953) of each year; 5) recruitment which is represented as the discrete addition of individuals to the youngest age-group of the model at the beginning of each year according to the magnitude of P_e during the previous year; and 6) growth which results in a continuous increase in $L_{i,j}$.

The dynamic system briefly described above was simulated by a FORTRAN program using finite difference approximation. Details of each activity regulating the system are presented below. The variables used in the model are defined in Table 1.

Fishing, Discard, and Natural Mortality

Each age-size compartment is subject to mortality at a rate proportional to the number of fish of the compartment; that is,

⁵Penttila, J. A., and B. E. Brown. 1972. Total mortality rates for two groups of yellowtail flounder estimates from survey cruise data from ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/22, Ser. No. 2713, 14 p.

TABLE 1.—List of variables of yellowtail flounder, *Limanda ferruginea*, model.

Variable	Description
$N_{i,j}$	Number of fish in size category j of age-group i
$L_{i,j}$	Length of fish in size category j of age-group i
Y_n	Yield of fishery in number of fish
Y_w	Yield of fishery in weight of fish
P_e	Annual egg production of stock
W	Weight of fish as function of length
F_e	Fecundity of fish as function of length
Z	Instantaneous total mortality rate
D	Instantaneous discard mortality rate
F	Instantaneous fishing mortality rate (excluding discard mortality)
M	Instantaneous natural mortality rate
G	Instantaneous gear mortality rate ($G = F + D$)
f	Instantaneous rate of fishing
t	Time
P_1	Relative gear effectiveness as function of length
P_2	Probability of landing a captured fish as function of length
P_4	Probability of a fish being mature as function of length
T	Index of temperature
k	Growth rate coefficient of von Bertalanffy equation
T_r	Recruitment-temperature factor as function of temperature
T_g	Growth-temperature factor as function of temperature
R	Annual recruitment to age 1

$$\frac{d(N_{i,j})}{dt} = -(F + D + M) \cdot N_{i,j} \quad (1)$$

where F , D , and M are the instantaneous fishing, discard, and natural mortality rates, respectively, and t is time in years. Total mortality of fish greater than 10 yr old was assumed. Very few fish reach this advanced age. Lux (1964) reported that fish discarded at sea suffered a high mortality rate. In the model, all discarded fish were assumed lost. The yield rate, in number of fish and biomass, contributed by each compartment is

$$\frac{d(Y_n)}{dt} = F \cdot N_{i,j} \quad (2)$$

and

$$\frac{d(Y_w)}{dt} = F \cdot N_{i,j} \cdot W(L_{i,j}) \quad (3)$$

where $W(L)$ is a function relating the weight of a fish to its length. This function assumes the usual form,

$$W(L) = c_1 \cdot L^3 \quad (4)$$

The letter c with a numerical subscript is used throughout the paper to denote constants. The total yield rate is obtained by summing $d(Y_n)/dt$ and $d(Y_w)/dt$ for all age-size compartments.

The mortality rate inflicted by fishermen ($F + D$) on the yellowtail flounder population is

assumed to be proportional to the instantaneous annual rate of fishing (f) for fish which are fully vulnerable. This mortality is called the gear mortality (G),

$$G = F + D = q \cdot f \quad (5)$$

where q is the catchability coefficient. The number of days fished annually is determined externally to the model and acts as a driving variable. Natural mortality was assumed to decrease with age until maturation and then remain constant through the rest of the life span.

In order to approximate the seasonality of fishing, the instantaneous rate of fishing is estimated by multiplying the total number of days fished annually by quarterly effort adjustment factors (c_3 , c_4 , c_5 , and c_6) where the average value of these factors is 1.

Yellowtail flounder first become available to trawl gear on the Southern New England ground in about 1 yr (Brown and Hennemuth see footnote 2), but they are not captured commercially until they have grown to the minimum size retained by the fishermen's nets, L_{gmin} . Some fish continue to escape the nets because of their small size until they have grown to the length at which the gear obtains its maximum effectiveness, L_{gmax} . It is assumed that the relative effectiveness of the gear from fish with a length between L_{gmin} and L_{gmax} can be calculated by linear interpolation. Accordingly, the relative effectiveness of the gear, P_1 , is defined as follows:

$$P_1 \begin{cases} (L - L_{gmin}) / (L_{gmax} - L_{gmin}) & \text{for } L_{gmin} \leq L \leq L_{gmax} \\ 0 & \text{for } L < L_{gmin} \\ 1 & \text{for } L > L_{gmax} \end{cases} \quad (6)$$

where L is the length for which P_1 is applied.

Since not all of the fish captured are large enough to be marketed (for economic and technological reasons), the probability of landing a captured fish (P_2) as a function of its length must be calculated. Let L_{mmin} be the minimum length landed by the fishermen and L_{mmax} be the length at which all fish are landed. Note that the determination of the marketability of each fish is made by the fishermen on the decks of their vessels. Therefore, a gradual transition from total unacceptability to total acceptability as L increases is expected. Again applying linear interpolation,

$$P_2 \begin{cases} (L - L_{m\min}) / (L_{m\max} - L_{m\min}) & \text{for } L_{m\min} \leq L \leq L_{m\max} \\ 0 & \text{for } L < L_{m\min} \\ 1 & \text{for } L > L_{m\max} \end{cases} \quad (7)$$

Using Equations (5), (6), and (7); G , F , and D are calculated as follows for fish of any length:

$$G = q \cdot f \cdot P_1 \quad (8)$$

$$F = q \cdot f \cdot P_1 \cdot P_2 \quad (9)$$

$$D = q \cdot f \cdot P_1 \cdot (1 - P_2). \quad (10)$$

Since G , F , and D vary with L and f , they are time dependent functions.

Aging

The aging process of yellowtail flounder is simulated by advancing individuals of each age-size compartment to the next higher age-group within the same size category.

Growth

The mechanism used in the model to simulate growth was based on the von Bertalanffy growth function. The von Bertalanffy function can be expressed in many forms, but the following is most applicable to this study:

$$L = L_m + (L_0 - L_m) \cdot e^{-kt} \quad (11)$$

where L_m is the maximum length obtained by the fish of the population, L_0 is the length of a fish at the beginning of a time interval of duration t , k is the growth rate coefficient that applies during the interval, and L is the length obtained by the end of the interval. The derivative of Equation (11) is identical to the growth equation deduced by von Bertalanffy (1938).

A single value of L_m is usually assumed for an entire population. In the model, differences in the mean length of size categories are maintained by assigning a unique maximum value to L for each size category (L_{m1} , L_{m2} , . . . , L_{m7}). Fish are distributed among the size categories in the following manner. Assume L_m is a normally distributed random variable with mean L_{m4} and standard deviation s_m . For G_1 , G_2 , . . . , G_7 , the portion of the population in each size category respectively (in the absence of fishing), the range of values of L_m included in each size category can be determined from a standard normal table. The mean value of

L_m for the j th size category (L_{mj}) is obtained by integrating the product of the normal density function and the random variable L_m over the range of values of L_m included in the size category and then dividing the result by G_j .

Taylor (1962) showed that k of the von Bertalanffy function was related to water temperature for a number of species, and there is evidence (which is discussed later in this paper) that this is also true for the Southern New England yellowtail flounder. The influence of temperature on k is simulated by adjusting k by a multiplicative growth-temperature factor, T_g , defined as

$$T_g = 1 + c_{14} \cdot (T - \bar{T}) \quad (12)$$

where T is an index of temperature and \bar{T} is the average value of the index over the total period for which data are available. T is an exogenous variable of the model.

Different values of k (k_1 , k_2) were necessary to describe the growth of yellowtail flounder less than and greater than 2 yr old (Lux and Nichy 1969). Seasonal variations of growth were incorporated into the model by multiplicative quarterly growth factors K_1 , K_2 , K_3 , K_4 (with an average value of 1.0). The length of age-size compartment i, j after an interval of time t is calculated according to Equation (11) using the length of the compartment at the beginning of the interval L_{mj} , and k as follows:

$$k = k_a \cdot k_n \cdot T_g \quad (13)$$

where n indicates the quarter of the year and a indicates age less than or greater than 2 yr.

Spawning

Spawning occurs during May or at 0.4 of each year. The fecundity-length function of the yellowtail flounder was assumed to be of the usual form,

$$Fe(L) = c_7 \cdot L^{c_8} \quad (14)$$

where Fe is the egg production of a mature female fish of length L . Not all fish mature at the same age or length. Royce et al. (1959) found that maturation was more closely associated with length than age. A relationship of the following form, expressing the probability of a fish of specific length being mature (P_4) was assumed.

$$P_4 = \begin{cases} y_3 & \text{for } 0 \leq P_3 = c_9 + c_{10}L \leq 1 \\ 0 & \text{for } P_3 < 0 \\ 1 & \text{for } P_3 > 1. \end{cases} \quad (15)$$

Equation (15) assumes maturation is a linear function of length in the transition zone between the length below which the entire population is immature and the length above which the entire population is mature. Assuming that the proportion of females in the population is constant, c_{11} , then the egg production of each age-size compartment is the product of $N_{i,j}$, $Fe(L_{i,j})$, P_4 , and c_{11} . The total egg production of the population (P_e) is obtained by summing over all age-size compartments.

Recruitment

The possibilities that recruitment is a linear function of egg production and that recruitment is independent of egg production, under average environmental conditions, were considered. There is evidence (Sissenwine 1974) that recruitment of the Southern New England yellowtail flounder is also related to temperature. In fact, most of the variability in estimated recruitment for 1944–65 was explained by anomalies in air temperature, ignoring egg production. In order to simulate the influence of temperature, a recruitment temperature factor (T_r) was defined as follows:

$$T_r = 1 + c_{12} \cdot (T - \bar{T}). \quad (16)$$

The number of recruitments as affected by temperature is calculated by multiplying the level of recruitment expected at average temperature conditions by T_r .

The total recruitment (R) of a year class (at age 1) is calculated by

$$R = c_{13} \cdot P_e \cdot T_r \quad (17)$$

or

$$R = c_{13} \cdot T_r. \quad (18)$$

The parameter c_{13} has a different value in each equation. Equation (17) is applicable when recruitment is linearly related to P_e for average temperature conditions. Equation (18) is applicable when recruitment is independent of P_e . Equations (17) and (18) will be referred to as the linear and density independent recruitment functions, re-

spectively. The model described in this paper incorporating either Equation (17) or (18) will be referred to as the linear or density independent models, respectively. Recruits are assigned to size categories of age-group 1 by multiplying R by the appropriate value of G_j .

Parameter Estimation

Estimates of the parameters of the model were taken from the literature or based on published or unpublished data sources. The parameter values used in all the simulations reported in this paper (unless otherwise stated) are shown in Table 2 along with citations of the source of the estimate. Special attention is given below to the estimation of some parameters and initial conditions. These estimates of parameters and initial conditions required some subjectivity.

The natural mortality rate of the yellowtail flounder has yet to be precisely estimated. Lux (1969a) estimated that the upper limit on natural mortality of adult yellowtail flounder is 0.20. Beverton and Holt (1957) estimated the natural mortality of a similar species (North Sea plaice) as 0.10. Values of instantaneous natural mortality of 0.10 and 0.20 have been used in the literature in the past. An instantaneous natural mortality rate of 0.10 was assumed for age-groups 3 and older fish in the model. Instantaneous natural mortality rates of 0.4 and 0.2 were applied to age-groups 1 and 2, respectively. Based on a generalized simulation model, Walters (1969) concluded that natural mortality rates, especially in older fish, could vary widely without affecting harvesting strategies.

Brown and Hennemuth (see footnote 2) reported the size-group structure of fish captured and landed by yellowtail flounder fishermen during 1963. According to these data, few fish less than 250 mm long were captured ($L_{g\min} = 250$ mm). The modal value of Brown and Hennemuth's capture curve is about 330 mm. The modal value usually coincides closely with the length of complete functional recruitment. Therefore, gear efficiency was assumed to reach its maximum at this length ($L_{g\max} = 330$ mm). All yellowtail flounder less than 300 mm long were discarded at sea ($L_{m\min} = 300$ mm) and almost all fish captured of greater than 350 mm were landed ($L_{m\max} = 350$ mm). Of course, market conditions will change with time and there are now reports of some fish less than 300 mm being landed.

TABLE 2.—Value of each parameter used to yield best results with yellowtail flounder model. The parentheses indicate values used for the model in which recruitment is independent of spawning stock. L_{mi} for $i = 1, 2, \dots, 7$ are given in Table 3.

Parameter	Value	Description	Source
c1	0.233×10^{-5}	From weight-length function (Equation (4))	Lux (1969b)
c2	3.233	From weight-length function (Equation (4))	
c3	1.26	First quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c4	0.37	Second quarter seasonal effort factor	
c5	0.87	Third quarter seasonal effort factor	
c6	1.49	Fourth quarter seasonal effort factor	
c7	0.725×10^{-6}	From fecundity-length function (Equation (14))	Pitt (1971) for fish from Grand Bank
c8	4.69	From fecundity-length function (Equation (14))	
c9	-1.821	From proportion mature-length function (Equation (15))	Based on percent mature data from Royce et al. (1959)
c10	0.00707	From proportion mature-length function (Equation (15))	
c11	0.50	Proportion of females	Data on 9,268 fish provided by Northeast Fisheries Center
c12	$-0.68 (-0.89)$	Slope of recruitment-temperature factor	
c13	5.8×10^{-6} (60.0×10^{-6})	Slope of stock-recruitment function	Fitted to catch data with the model, see text
c14	-0.466	Slope of growth-temperature factor	From annual growth estimates (Sissenwine 1975), see text
q	1.68×10^{-4}	Catchability coefficient	Sissenwine (1974)
Lgmin	250.0 mm	Minimum size retained by net	From length composition of catch for 1963, see text
Lgmax	330.0 mm	Size of maximum net retention	
Lmmin	300.0 mm	Minimum size at which fish are marketed	
Lmmax	350.0 mm	Size at which all fish are marketed	
T	10.175°C	Mean temperature	National Weather Service data, Block Island
G1	0.05	Proportion entering size-class 1	Arbitrary
G2	0.10	Proportion entering size-class 2	
G3	0.20	Proportion entering size-class 3	
G4	0.30	Proportion entering size-class 4	
G5	0.20	Proportion entering size-class 5	
G6	0.10	Proportion entering size-class 6	
G7	0.05	Proportion entering size-class 7	
sm	33.9 mm	Standard deviation of L_m	Data on 9,268 fish provided by Northeast Fisheries Center
k1	0.56	Growth rate for fish less than 2 yr	
k2	0.285	Growth rate for fish greater than 2 yr	See text
K1	0.0	First quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
K2	0.0	Second quarter seasonal growth factor	
K3	2.0	Third quarter seasonal growth factor	
K4	2.0	Fourth quarter seasonal growth factor	
M1	0.40	Natural mortality of age-group 1	See text
M2	0.20	Natural mortality of age-group 2	
$M_i, i = 3, 10$	0.10	Natural mortality of age-group 3	

The annual average air temperature at Block Island was used as an index of temperature on the Southern New England ground because there are no water temperature records of adequate length (1944 to present). Block Island is located on the southwest edge of the Southern New England ground.

Taylor et al. (1957) concluded that air temperature data are a rough index of the general level of surface water temperature. Colton (1968) reported that trends in offshore water masses paralleled trends in surface water temperature at Boothbay Harbor, Maine. Lauzier (1965) used trends in air temperature from 1875 to 1905 as an index of the water temperature of the Gulf of Maine. Templeman (1965) concluded that air temperature at St. John's, Newfoundland, and water temperature at Cape Spear for 1952-62 agreed extremely well.

A record of the bottom water temperature at Lurcher Lightship off Nova Scotia (Lauzier and Hull⁶) was collected from 1951 to 1969. The water

depth was about 100 m. The correlation between the average annual bottom water temperature at Lurcher Lightship and the average annual air temperature at Block Island is 0.78. The correlation between the annual average air temperature at Block Island and the annual average surface water temperature at Woods Hole, Mass., for data reported by Chase (1967) is 0.87 during the period 1956-66. The correlation between monthly averages of water temperature at Woods Hole and air temperature at Block Island for this 132-month time series is 0.98. Therefore, Block Island air temperature record was used as an index of water temperature on the Southern New England ground.

The annual equilibrium catch of a fishery is the level of catch that results in no change in the biomass of the nominal stock (stock suitable for

⁶Lauzier, L. M., and J. H. Hull. 1969. Coastal station data temperature along the Canadian Atlantic coast 1921-1969. Fish. Res. Board Can., Tech. Rep. No. 150, 5 p.

landing). The equilibrium catch is the sum of recruitment and growth (of the individual fish of the nominal stock) minus loss due to natural mortality. Based on this relationship using earlier estimates of equilibrium catch and recruitment (Sissenwine 1974) and assuming annual natural mortality of 0.1, Sissenwine (1975) estimated the average annual weight gain per fish of the Southern New England yellowtail flounder fishery for 1944–65. These estimates ranged from 72 to 331 g/fish per year and are significantly correlated (Kendall rank correlation coefficient (τ) of -0.60) with annual average air temperature at Block Island. Estimates of k of the von Bertalanffy function derived from growth increments of age-classes for 1962–71 were also significantly correlated ($\tau = -0.42$) with temperature at Block Island. Thus, the model was designed to simulate the effect of temperature on growth.

The instantaneous growth rate of a fish is related to k by the following equation:

$$\frac{dw}{dt} = kc_1c_2(L_m - L)L^{c_2-1}. \quad (19)$$

Equation (19) was derived by substituting Equation (11) into Equation (4) and differentiating with respect to t . For the values of k , c_1 , c_2 , and L_m reported by Lux (1969b) and Lux and Nichy (1969), dw/dt is 143, 172, 182, and 163 g/yr for a length of 250, 300, 350, and 400 mm, respectively. Most of the fish in the catch are within this range of length. Therefore, only a minor proportion of the estimated range in annual growth per fish can be accounted for by changes in size composition of the stock. Thus, within the constraints of the model described here (c_1 , c_2 , L_m do not vary with time), k must be nearly proportional to the rate of weight gain.

During the period 1944–65 there were 4 yr in which the estimated average annual air temperature was greater than 11°C and 7 yr in which it was less than 10°C . For the four warmer years, temperature averaged 11.2°C and growth per fish averaged 88 g. For the seven colder years, temperature averaged 9.5°C and growth 222 g. Assuming k proportional to annual average weight gain per year, c_{14} was estimated as -0.466 by solving:

$$\frac{\{1 + c_{14}(11.2 - \bar{T})\}}{\{1 + c_{14}(9.5 - \bar{T})\}} = 88/222.$$

The proportion of yellowtail flounder recruits entering each size category of age-group 1 was assumed as follows: $G_1 = G_7 = 0.05$, $G_2 = G_6 = 0.10$, $G_3 = G_5 = 0.20$, and $G_4 = 0.30$.

Lux and Nichy (1969) reported a value of 500 mm for parameter L_m of the von Bertalanffy growth function for the yellowtail flounder. They selected this value since it was the maximum length observed. The model described in this paper requires values of L_m for each of the seven size categories. Considering the magnitude of s_m (33.9 mm, see Table 2) a value of 500 mm for L_{m4} may yield fish far in excess of the maximum length observed. Therefore, a more conservative value was used: $L_{m4} = 480$ mm.

The probability density function of L_m was used to calculate values of L_{mi} for $i = 1, 2, 3, 5, 6, 7$. The range of values of L_m represented by each size category (Z_{1i} to Z_{2i}) was calculated based on G_i and the normal density table and found to be as in Table 3. The mean value of L_m for each size category equals the integral of L_m times its density function divided by the integral of the density function (results also shown in Table 3).

TABLE 3.—Range and mean for L_m , the maximum length parameter of the von Bertalanffy growth function, representing each of the size categories of the yellowtail flounder model.

Size category	Range of L_m (mm)	Mean of L_m (mm)	Size category	Range of L_m (mm)	Mean of L_m (mm)
1	0.0–425.1	410.9	5	492.8–514.6	503.0
2	425.1–445.4	436.3	6	514.6–534.9	523.6
3	445.4–467.2	457.0	7	534.9–∞	549.1
4	467.2–492.8	480.0			

Lux and Nichy (1969) estimated the growth rate coefficient (k of the von Bertalanffy growth function) for yellowtail flounder older than 2 yr of age as 0.335. For the period during which Lux and Nichy collected their data, the average annual temperature at Block Island was about 9.8°C . This temperature results in a growth-temperature factor (T_g) of 1.175. Lux and Nichy's estimate was divided by T_g resulting in an estimate of $k_2 = 0.285$. An estimate of $k_1 (=0.56)$ was determined using the model so that fish would grow to a realistic length by age 2.

The seasonal nature of yellowtail flounder growth was exhibited when the average lengths of age-groups were determined quarterly (Lux and Nichy 1969). In general, the mean size of an age-group changes little from the first to the second quarter. Thus, most growth apparently occurs during the second half of the year. In order

to simulate this phenomenon, the following quarterly growth adjustment factors were used: $K_1 = K_2 = 0.0$ and $K_3 = K_4 = 2.0$.

Estimation of c_{12} of the recruitment-temperature factor (T_r , Equation (16)) depends on the form of the recruitment relationship that is assumed. The parameter c_{12} was estimated for both the linear and density independent recruitment functions (Equations (17) and (18)) using estimates of annual recruitment reported by Sissenwine (1974). During 1949-53, recruitment averaged 6.82 million fish (recruits to the stock of marketable fish, about 3 yr and older) with a spawning stock size proportioned to an average relative abundance of 1.4 tons/day and an average annual temperature of 11.08°C. On the other hand, for 1960-63, recruitment averaged 49.7 million fish with a relative abundance and annual average temperature of 2.9 tons/day and 9.65°C, respectively.

For the density independent recruitment function, fluctuations in recruitment result directly from fluctuations in T_g . An increase in recruitment and in T_g by a factor of 7.3 while the temperature anomaly changes from 0.905 to -0.525 provides an estimate of $c_{12} = -0.89$ by solving the following expression:

$$7.3\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525).$$

If egg production is assumed proportional to stock size or relative abundance, then for the linear recruitment function, the increase in recruitment by a factor of 7.3 would reflect an increase in spawning stock size by a factor of 2.05 ($\approx 2.9/1.4$) and an increase of T_g by a factor of 3.56 ($\approx 7.3/2.05$). Therefore, solving the following expression:

$$3.56\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525)$$

$c_{12} = -0.68$ for the linear recruitment function.

Since little is known about the survival of yellowtail flounder eggs and their eventual recruitment to age-group 1, c_{13} of the recruitment function was estimated by fitting the model to data (see Verification). The parameter c_{13} was estimated as 5.8×10^{-6} (fish per egg) for the linear recruitment model and as 60.0×10^6 (fish) for the density independent recruitment model.

Both estimates appear realistic as indicated by the following discussion. The average recruitment to the stock of marketable fish reported by Sissenwine (1974) was 22.8×10^6 fish. Assuming an

instantaneous natural mortality of 0.4 for age-group 1 and a natural mortality of 0.2 with a total gear mortality of 0.5 ($F + D$) for age-group 2, recruitment to age-group 1 may be crudely estimated by multiplying recruitment to the marketable stock by 3.0. Thus, average annual recruitment to age-group 1 could be estimated as 68.4×10^6 fish which is similar to the estimate of c_{13} for the density independent model. For the linear recruitment model, c_{13} is the proportion of eggs that survive to be recruited to age-group 1 under average temperature conditions. Using the average catch per effort for 1943-66 ($U = 2.5 \times 10^6$ g/day), the sex ratio ($c_{11} = 0.5$), the catchability coefficient ($q = 1.68 \times 10^{-4}$), and an estimate of average weight and fecundity (of females) of the nominal stock ($W = 451$ g, $Fe = 700,000$ eggs), c_{13} could be crudely estimated as 5.9×10^{-6} using $c_{13} = (R \cdot W \cdot q)/(Uc_{11} \cdot Fe)$. For the winter flounder, *Pseudopleuronectes americanus*, Saila's (1961) work indicated about 18 recruits to age-group 1 per million eggs (actually reported 18 recruits/100,000 hatched eggs assuming 10% hatching success). The value used here is somewhat lower, but the fecundity of the yellowtail flounder is higher than for the winter flounder.

In order to avoid the possibility of recruitment becoming negative for extremely high temperatures, the additional constraint that recruitment never falls below 5 million fish was incorporated into the model.

The initial length and number of individuals of each age-size compartment had to be specified prior to simulating the fishery. Royce et al. (1959) reported the mean length of age-groups 2-6 for the first quarter of 1943. These values were assumed as the initial length of size category 4 of the appropriate age-groups. For the initial lengths of the other age-groups, reasonable but arbitrary values were selected. The average initial size of each age-group is listed in Table 4. The lengths of size categories 1, 2, 3, 5, 6, and 7 were determined by multiplying the length of size category 4 by 0.856, 0.908, 0.950, 1.050, 1.092, and 1.144, respectively. These factors correspond to the ratio of the maximum length of each size category to the maximum length of size category 4.

The onset of the collection of fishing effort data was 1943; therefore, the model was used to simulate the fishery from that date. The relative abundance of the yellowtail flounder during the first quarter of 1943 was 5,742 fish/day (Royce et al.

TABLE 4.—Initial (1 January 1943) mean total length in millimeters of each age-group for yellowtail flounder model. The lengths of age-groups 2–6 were reported by Royce et al. (1959).

Age-group	Mean length (mm)	Age-group	Mean length (mm)
1	160	6	401
2	271	7	425
3	324	8	440
4	353	9	450
5	372	10	460

1959). Dividing this by q , the mean population size during this quarter was estimated as 34.2×10^6 fish. Because there is little growth and, therefore, little recruitment during the first quarter (since fish are recruited as they grow to the size vulnerable to fishing gear), the population was assumed to undergo exponential decay during this time interval. The effort expended during the first quarter of 1943 was 2,038 days (Royce et al. 1959), resulting in a total maturity $Z = 1.47$ ($Z = M + qf$ where f is the rate of fishery in days per year). Accordingly, the size of the landable stock at the beginning of 1943 was estimated as about 41.1×10^6 fish (using Equation 1.38 of Ricker (1975) modified for an interval of one-quarter of a year).

Royce et al. (1959) also reported the age composition for the first quarter of 1943. The catch primarily comprised fish greater than 3 yr of age. The number of fish captured per day for age-group 3 and older is shown in Table 5. Based on the

TABLE 5.—Catch per day and relative abundance adjusted for fishing vulnerability of age-group 3 and older yellowtail flounder for the first quarter of 1943. These age-groups represented 95% of the catch.

Age-group	Catch/day	Adjusted relative abundance
3	1,793	3,984
4	1,596	1,995
5	1,008	1,061
6	504	504
7+	476	476

length composition assumed for each age-group and Equation (9), the relative level of fishing mortality suffered by fish of age 3, 4, 5, and older was calculated as 0.45, 0.80, 0.95, and 1.00, respectively. By dividing the catch per day of each age-group by the appropriate factor, the relative abundance adjusted for fishing vulnerability was obtained (also Table 5). These values represent the relative abundance of each age-group in the population. Using Table 5,

$$N_4 = 0.50 N_3$$

$$\begin{aligned} N_5 &= 0.55 N_4 = 0.280 N_3 \\ N_6 &= 0.48 N_5 = 0.130 N_3 \\ N_7 &= 0.50 N_6 = 0.065 N_3 \\ N_8 &= 0.50 N_7 = 0.033 N_3 \\ N_9 &= 0.50 N_8 = 0.016 N_3 \\ N_{10} &= 0.50 N_9 = 0.008 N_3 \end{aligned}$$

where the subscript . indicates the summation over all size categories, and the survival of fish older than 7 yr was assumed to be 0.50. The size of the marketable population was estimated by summing N_i times the relative fishing vulnerability of age-group i . This expression was set equal to 41.1×10^6 fish and solved for N_3 ($\approx 32.0 \times 10^6$ fish). Estimates of initial conditions for other age-groups were obtained using the equations in this paragraph. Age-group 2 was assumed to be twice age-group 3 as indicated by a natural mortality of 0.2 and a discard mortality of about 0.5. Based on a natural mortality of 0.40 age-group 1 was assumed to be 1.5 times age-group 2. The initial conditions of each age-group for the beginning of 1943 based on the above discussion are shown in Table 6. The population was distributed among the size categories according to the appropriate values of G_i .

TABLE 6.—Initial size of each age-group of yellowtail flounder population assumed at the beginning of 1943.

Age-group	Number in thousands	Age-group	Number in thousands
1	95,000	6	4,200
2	64,000	7	2,100
3	32,000	8	1,100
4	16,000	9	530
5	8,800	10	260

VERIFICATION

The primary mode of verification of the model was to compare predicted annual levels of catch with published values. Lux's (1969a) record of catch and fishing effort for 1943–66 is in conflict for several years with data reported by Brown and Hennemuth (see footnote 2) in an unpublished form. These conflicts are minor, except for the 1966 catch where the difference is about 40%. Since this year is at the end of the published record and could easily be ignored, 1943–65 were initially used for verification. After c_{13} was fit to the data, the model was then compared with data through 1972.

Before comparing the model with the published data, it was necessary to select a time step or

integration interval that would not result in unreasonable numerical errors being propagated through many years of simulated time. This was done by increasing the time step until the simulation results converged. With an integration interval of 0.005 yr, the results converged sufficiently so that a numerical error of less than 5% is expected after 23 yr of simulation (the length of the data record used for verification). This level of error was considered acceptable in light of the precision of all the data upon which this work was based. It was noted that each decrease in the time step was accompanied by an increase in the simulated catch; therefore, the predictions yielded by the computer simulations are probably slightly lower than would have resulted from an exact solution of the model.

The average length of age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71, and the average length of these age-groups as reported by Lux and Nichy (1969), and of the catch for 1962–71 are compared in Table 7. Age-groups 2–5 were considered because they were most abundant in available samples; and, therefore, their means have smaller standard errors than less abundant age-groups.

Most of the fish measured by Lux and Nichy were collected during 1957–62. Model results for this period compare favorably as expected since the model was designed to simulate the situation reported by Lux and Nichy. The average simulated lengths for 1943–66 are generally lower than for the 1957–62 design period since the design period had a lower temperature (favorable to growth) than the longer time interval.

The model tends to overestimate growth for 1962–71. The mean length of fish of a particular age-group collected from the catch for 1962–71 is lower than is predicted by Lux and Nichy's growth function. This situation cannot be explained as an effect of temperature. As has been the practice throughout this work, the model was designed

TABLE 7.—Average length (millimeters) of yellowtail flounder age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71 according to Lux and Nichy (1969), and for samples from the commercial catch collected January–March 1962–71 (data provided by Northeast Fisheries Center).

Age-group	Model 1943–66	Model 1957–62	Model 1962–71	Catch samples 1962–71	Lux and Nichy
2	275	290	323	306	266
3	303	338	365	342	338
4	351	367	397	365	378
5	378	385	416	387	404

in accordance with the published literature; therefore, some apparent overestimation of growth in later years of the simulations is inevitable. This situation makes application of the model less satisfactory for recent years, but part of the effect of overestimating growth would be compensated for by a shift in age-group structure of the catch. If the model slightly overestimates growth, there is a tendency to catch younger fish; and, therefore, the effect of overestimating growth is partially offset.

The simulated size-category structure of captured (landed and discarded) fish for 1943–65 is compared with unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2) in Figures 2 and 3. Clearly, it would have been

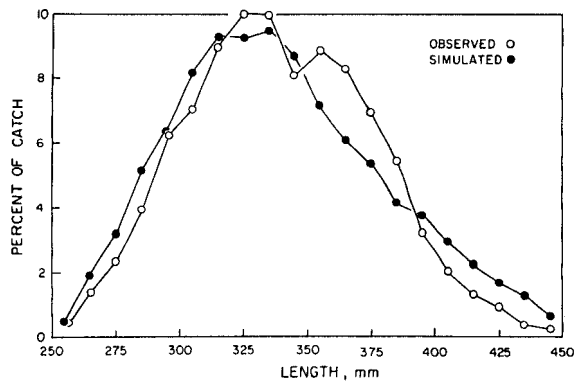


FIGURE 2.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of catch (including discards) of yellowtail flounder.

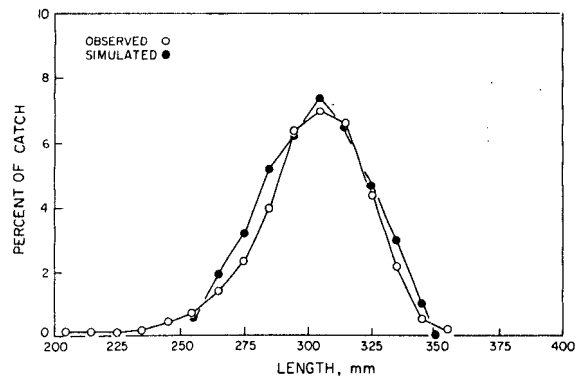


FIGURE 3.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of discards as percentage of catch (including discards) for yellowtail flounder.

better to compare the 1963 simulated size-category structure with these data, but, because of a programming oversight, this information was not available. The comparisons in Figures 2 and 3 are generally favorable and indicate that the assumed linear relationships (Equations (6) and (7)) describing the relative effectiveness of the fishing gear and the marketability of fish as a function of length were adequate. The model indicates that 39.5% of the fish captured by fishermen for 1943-65 were discarded. The average weights of landed and discarded fish based on Figures 2 and 3 are 455 and 249 g, respectively.

The parameter c_{13} of the recruitment function (Equations (17) and (18)) was estimated by running the model for several values of this parameter and selecting the value that explained the greatest proportion of variation in observed yield. Of the values considered, c_{13} equal to 60.0×10^6 and 5.8×10^{-6} for the density independent and linear recruitment models were most successful in explaining variation in yield. Since only a finite number of values of c_{13} were considered, the values selected are probably not the "best least squares" estimates, but the results (Table 8) indicate that the model is not very sensitive to 5-10% fluctuations in this parameter. As noted earlier, these values appear realistic.

TABLE 8.—Percent of variation in yield explained by the yellowtail flounder model with various values of c_{13} for 1943-65.

c_{13}	Linear stock-recruitment (%)	c_{13}	Density independent stock-recruitment (%)
5.4×10^{-6}	73.6	55.0×10^6	81.3
5.6×10^{-6}	82.0	57.5×10^6	82.6
5.7×10^{-6}	84.5	60.0×10^6	83.2
5.8×10^{-6}	85.5	62.5×10^6	83.0
6.0×10^{-6}	82.3	65.0×10^6	82.1
		70.0×10^6	78.1

The model using linear or density independent recruitment explained 85.5 and 83.2% of the variation in yield from 1943-65, respectively. In addition to catch and effort data reported by Lux (1969a), catch data through 1972 and effort data through 1971 were available (at the time when this research was in progress) for the Southern New England ground (Brown and Hennemuth see footnote 2; Brown see footnote 3; and Par-rack see footnote 4). Both the linear and density independent stock-recruitment models were run for 1943-72 (assuming that the level of effort was unchanged from 1971 to 1972), and the

results were compared with the available data in Figures 4 and 5. Both models seem to simulate catch as well since 1965 (although yield is substantially underestimated for 1969 and 1970) in spite of the fact that they were developed independently of the later data and that growth is apparently somewhat overestimated toward the end of the simulation. Since errors for any particular

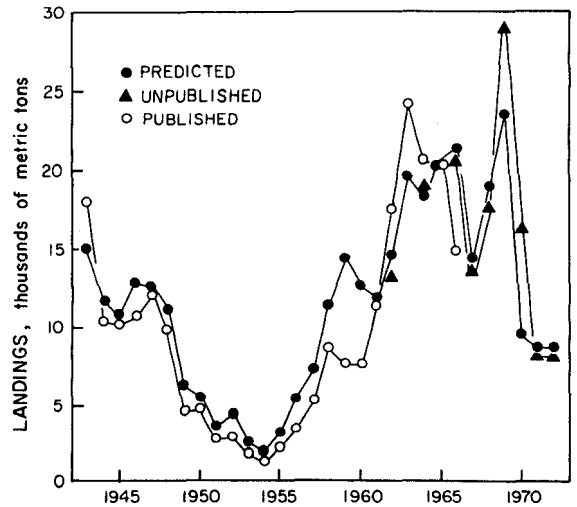


FIGURE 4.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with linear recruitment function (Equation (17)).

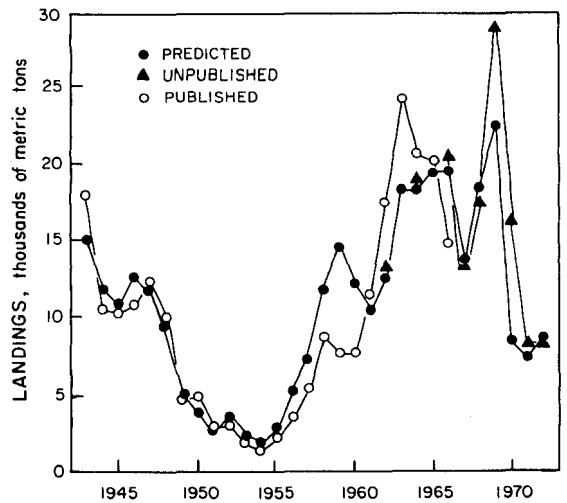


FIGURE 5.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with a density independent recruitment function (Equation (18)).

year are propagated through the simulation, it is surprising that the model seems to recover after occasional substantial deviations from the observed yield.

Sissenwine (1974) explained most of the variability in recruitment of the Southern New England ground even though the size of the spawning stock was ignored. This earlier work noted that spawning stock size may have an important effect on recruitment, but the effect might be obscured by environmental noise. The work reported here demonstrates that models incorporating either linear or density independent recruitment explain most past variability in catch of the fishery. Nevertheless, the model incorporating recruitment linearly dependent on spawning stock size is preferable for the following reasons:

1. While the linear model only explained 2.2% more variation than the density independent model, it did explain 13% of the density independent model's residual variation with no increase in number of parameters.
2. While the density independent model is more simplistic mathematically, a direct linear relationship between stock size and recruitment is a more basic biological relationship. Obviously, recruitment cannot be independent of spawning stock size over its entire range. The density independent situation can only exist as a special case of a more complex non-linear stock-recruitment relationship.
3. It seems unrealistic for recruitment to be unaffected by size of spawning stock when stock size varies by a factor of 3.
4. The linear stock-recruitment model is a more conservative management tool than the density independent model. Management practices designed to prevent a dangerous reduction in stock size of a population regulated by a linear stock-recruitment relationship will also prevent a reduction in stock size of a population regulated by a density dependent stock-recruitment relationship.

No attempt was made to use the Ricker (1954, 1958) stock-recruitment function or other non-linear functions because the results obtained using the linear and density independent functions (Equations (17) and (18)) indicated that most likely these more complicated functions would not significantly increase the accuracy of the model. When using the linear model where the Ricker

function (for example) is more appropriate, the linear model is expected to be accurate at low population levels but overestimates recruitment (and catch) at higher population levels. The reverse situation is expected when the density independent model is used where a Ricker function is more appropriate. In neither case was the more complex Ricker function indicated.

Based on the above discussion, the linear stock-recruitment function (Equation (17)) seemed most appropriate over the observed range of population size. Therefore, only the linear model is used in the remainder of this paper.

The linear stock-recruitment model was run for 1943-65 without temperature dependent growth ($c_{14} = 0.0$), without temperature dependent recruitment ($c_{12} = 0.0$), and without temperature dependent growth or recruitment ($c_{12} = c_{14} = 0.0$). None of these situations explained a significant portion of variation in catch. This fact does not constitute rigorous evidence that incorporation of T_g and T_r into the model is necessary to explain most of the variability in catch because no attempt was made to tune the model for the temperature independent cases. Earlier work by Sissenwine (1974, 1975) demonstrated the influence of temperature on the fishery and supports the incorporation of T_g and T_r into the model.

APPLICATIONS

The effects of several alternative fishing strategies were examined using the model. These examples deal with some aspects of the model which are not common components of other fishery models (such as discard mortality, temperature dependence, and seasonal growth and fishing rate).

The impact of discarding at sea fish shorter than 300 mm was evaluated by running the model with the assumption that the minimum size retained by a net equaled this value. The results for $L_{g\min} = 300$ mm are compared with the model results as described earlier ($L_{g\min} = 250$ mm) in Figure 6. Landings in excess of 30,000 metric tons are not shown because these have not been observed during the history of the fishery; thus simulations indicating these high values are extrapolative in nature. These higher simulated landings result because the model assumes a linear stock-recruitment relationship at all stock sizes, while in reality the relationship probably becomes density dependent as stock size becomes large. By eliminating discard mortality of fish shorter

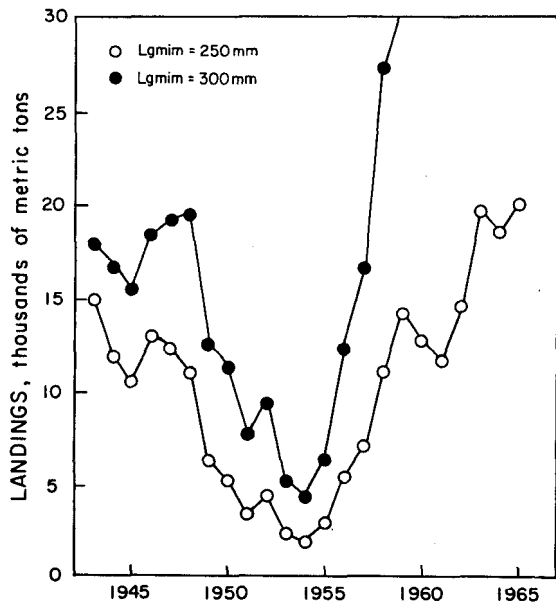


FIGURE 6.—Simulated landings of yellowtail flounder with $L_{gmin} = 250$ mm and 300 mm. Landings greater than 30,000 metric tons are not shown.

than 300 mm, these fish have a higher probability of surviving until they are recruited and spawn. The result was from a 20% to a severalfold increase in landings.

Using the Beverton and Holt yield per recruit (YPR) function, Brown and Hennemuth (see footnote 2) found less than a 40% increase in yield by delaying the age at first capture from 1.75 yr (or 245 mm) to 2.5 yr (or 302 mm) for F less than 1.1. This was the highest simulated fishing mortality rate during 1943-65. The substantially greater increase in yield from the simulation reported in Figure 6 results from increased recruitment which is not considered in the Beverton and Holt YPR function.

The benefit of increasing mesh size to eliminate discard mortality is clearly demonstrated (for the linear recruitment model), but this analysis ignores financial and technological difficulties which may be involved (Gates and Norton 1974).

The effect of the seasonality of fishing mortality was explored by varying seasonal effort adjustment factors ($c_3, c_4, c_5,$ and c_6). Situations where effort was applied uniformly throughout the year and where all effort was applied during a single quarter were considered. These cases are compared with the results reported earlier ($c_3 = 1.26,$

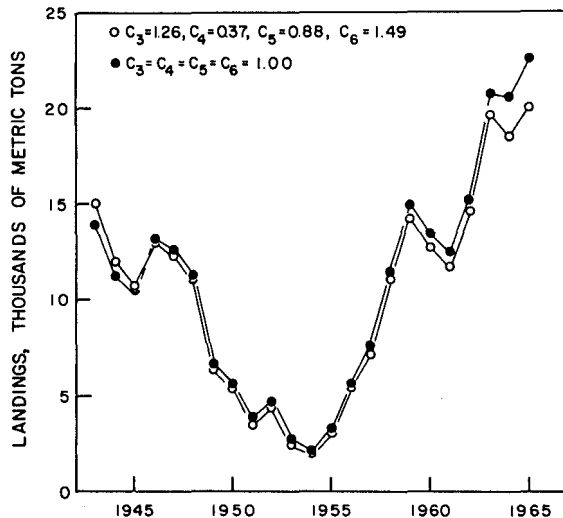


FIGURE 7.—Simulated landings of yellowtail flounder with fishing effort applied uniformly and with c_3-c_6 as assumed for 1943-65.

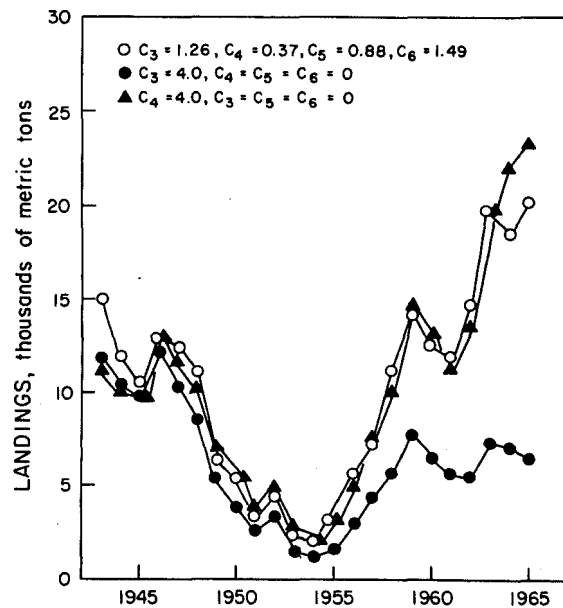


FIGURE 8.—Simulated landings of yellowtail flounder with all fishing effort in the first or second quarter of the year and with c_3-c_6 as assumed to have occurred for 1943-65.

$c_4 = 0.37, c_5 = 0.88,$ and $c_6 = 1.49$) in Figures 7-9 and Table 9.

The simulations reported in Figures 7-9 indicated that the seasonal aspect of the expenditure of effort and resulting fishing mortality could

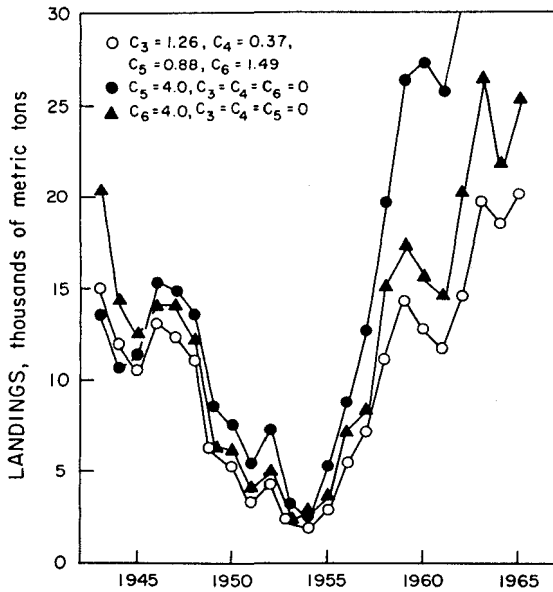


FIGURE 9.—Simulated landings of yellowtail flounder with all fishing effort in the third or fourth quarter of the year and with c_3 – c_6 as assumed to have occurred for 1943–65.

TABLE 9.—Comparison of simulated catches of yellowtail flounder with various values of the seasonal effort factors (c_3 , c_4 , c_5 , c_6). Percentage changes in yield are relative to the simulated yield with c_3 , c_4 , c_5 , and c_6 as in the first line of the table.

c_3	c_4	c_5	c_6	Percentage change in yield		
				1943	1944	1943–65
1.26	0.37	0.88	1.49	—	—	—
1.00	1.00	1.00	1.00	-6.7	-4.5	+3.6
4.00	0.0	0.0	0.0	-20.7	-14.3	-40.6
0.0	4.00	0.0	0.0	-24.0	-16.8	-0.6
0.0	0.0	4.0	0.0	-9.4	-9.3	+92.8
0.0	0.0	0.0	4.0	+36.4	+21.0	+22.6

have a very significant impact on the yield of the fishery. There was little change in yield indicated when fishing mortality was assumed uniform throughout the year. The simulations showed that yield of the simulated fishery would have been reduced if all fishing mortality occurred during the first quarter of the year. If all fishing mortality were applied during the second quarter, yield of the fishery would have been lower during the first few years of the simulation, but little difference in total yield is indicated over 23 yr. The expenditure of effort during the third quarter also tended to reduce the early catch, but in the long run appeared to result in the highest yield. By restricting fishing mortality to the fourth quarter of the year, some initial increase in catch was indicated and long-term yield was also increased.

These results reflect the facts that spawning occurs during the second quarter and growth of fish is limited to the third and fourth quarters of the year according to the model. Clearly, to obtain a short-term gain in yield, it is most advantageous to harvest at or near the end of the growing season (Table 9). Long-term gains were obtained when egg production was optimized by harvesting just after spawning (third quarter). By concentrating effort during the fourth quarter, an increase in yield was indicated for all years of the simulation. Fishing during the first quarter appears to be particularly detrimental because it crops fish just prior to spawning.

The seasonal pattern of effort exhibited by the fishery in the past includes intense fishing during the first quarter and the fourth quarter of the year. Apparently these balance, resulting in yields similar to the case where fishing is uniform through the year. In recent years, the annual catch quota for the United States (established by the International Commission for the Northwest Atlantic Fisheries (ICNAF)) was divided equally among the four quarters. The result is that fishing mortality was probably distributed nearly uniformly through the year. There may be some advantage to increasing the portion of the annual quota captured during the second half of the year. It is important to note that the long-term gains obtained by concentrating fishing just after the spawning season will not be realized if recruitment is independent of spawning stock size (Equation (18)).

Several experiments were conducted with the model in order to determine to what degree the yield of the fishery could be stabilized or increased by regulating the annual expenditure of effort and ultimately F . For a fishery in which recruitment is linearly related to stock size, in the long run it is advantageous to reduce fishing effort (and mortality) in order to increase egg production. Therefore, the fishery was simulated with effort at 80% of observed values (Figure 10). The short-term decrease in yield was rather minor. Considerable long-term advantage was predicted; but even with a reduced level of effort, the simulated fishery declined during the late 1940's and early 1950's. However, the recovery when conditions became favorable was more rapid at the lower level of effort for this particular case.

The Beverton and Holt YPR equation (Brown and Hennemuth see footnote 2) indicates less than a 5% increase in catch with a 20% decrease in

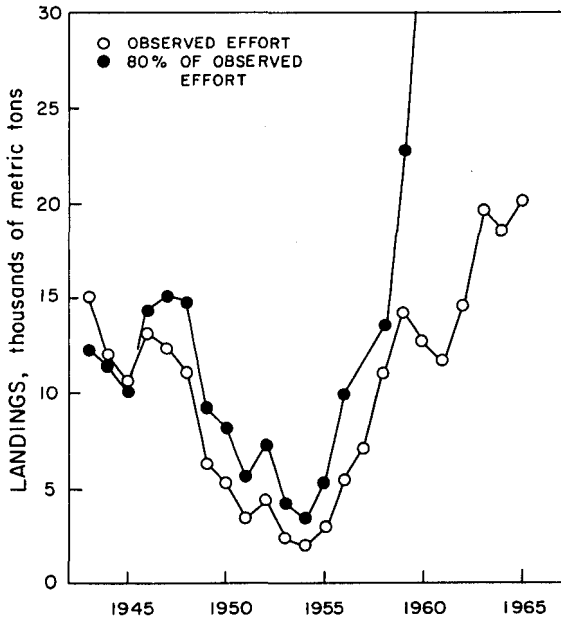


FIGURE 10.—Simulated landings of yellowtail flounder with observed level of fishing effort and with 80% of the observed level.

fishing mortality (for $0.6 \leq F \leq 1.5$ and age at first capture between 1.75 and 3.0). Therefore, most of the increase in yield indicated in Figure 10 must result from improved recruitment at lower levels of F .

Since recruitment and growth appear related to temperature, the possibility of using this environmental variable to predict an appropriate level of effort was considered. The model is such that growth and recruitment are proportional to T_g and T_r , respectively. Therefore, the following relationship between fishing effort and T_g and T_r was utilized:

$$f_i = c_{15} \cdot \{(T_g)_{i-1} + (T_r)_{i-2}\}. \quad (20)$$

Effort for year i was based on the growth-temperature factor for the year $i - 1$ since Equation (20) is of little value unless effort can be set in advance. The recruitment-temperature factor from 2 yr prior ($i - 2$) was used since recruitment lags spawning by about 2 yr. A 3-yr lag could have been used. T_g and T_r could have been weighted in Equation (20) since the latter is usually more important in determining equilibrium yield, but this would have introduced another parameter.

Initially, c_{15} was estimated as 1,870 days of

fishing, which yields about the average level of effort for 1943–65 when T_g and T_r equal 1. A value higher and lower than 1,870 days was also considered. Simulated catches for each value of c_{15} are shown in Figures 11–12, and the simulated catch per unit of effort is shown in Figure 13.

For 1943–65, $c_{15} = 2,200$ days resulted in a decrease in relative abundance while $c_{15} = 1,540$ days permitted the relative abundance to increase. The value of c_{15} (1,870 days) corresponding to the average effort during 1943–65 best stabilized the relative abundance of the fishery, but was only slightly more effective than the voluntary actions of the fishermen who probably responded to fluctuations in fishing success (U). It appears that a function even more sensitive to temperature than Equation (20) is required to better stabilize the population. Since T_r is more sensitive to temperature than T_g , weighting of these factors (in favor of the former) might result in a function more effective in maintaining the population size during the early 1950's. Nevertheless, the yield of the simulated fishery (with the linear recruitment function) could have been substantially increased if fishing effort were regulated by a simple function such as Equation (20) with c_{15} considerably less than 1,870 days.

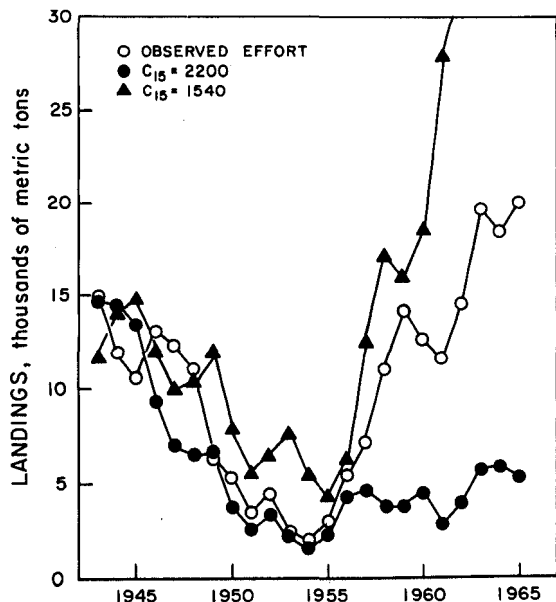


FIGURE 11.—Simulated landings of yellowtail flounder with observed effort and with effort set by Equation (20) using $c_{15} = 2,200$ or 1,540.

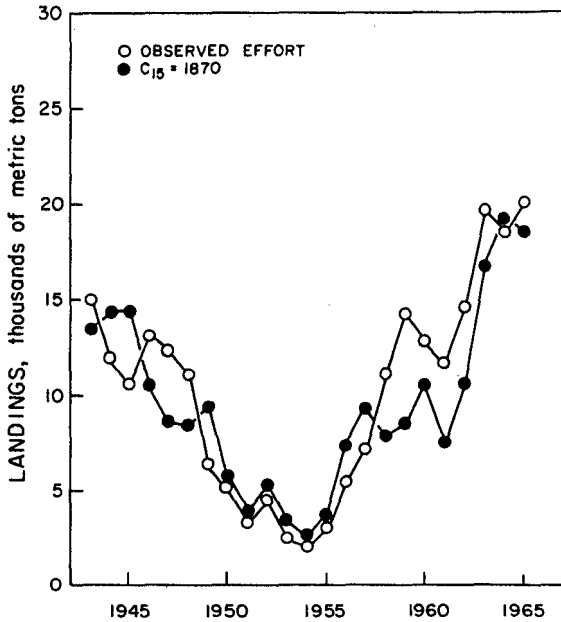


FIGURE 12.—Simulated landings of yellowtail flounder with observed effort and with effort by Equation (20) using $c_{15} = 1,870$.

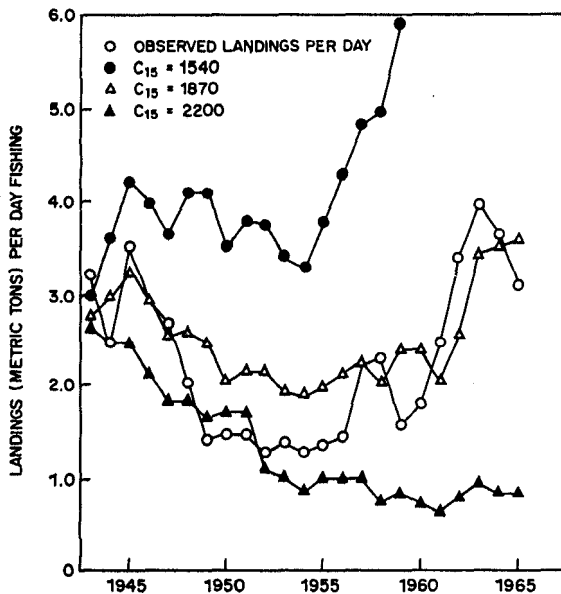


FIGURE 13.—Observed catch of yellowtail flounder per day of fishing and simulated catch per day with effort set by Equation (20) using $c_{15} = 1,540, 1,870, \text{ or } 2,200$.

At present, annual catch quotas for the Southern New England yellowtail flounder stock are based on a prerecruit index (Brown and Henne-

muth 1971). The index is calculated from the catch of 1-yr-old fish in an autumn bottom trawl survey (Grosslein 1969). Thus the major source of variability in production resulting from the influence of temperature on recruitment is accounted for in current stock assessments. This model should not be considered as an alternate method of management of the fishery on a year to year basis without further verification and refinement.

Walters (1969) developed a yield optimization procedure for his generalized fish simulator using the steepest ascent method. The development of an optimization procedure for the model reported in this paper would be more difficult because this model is driven by two exogenous factors, temperature and the rate of fishing, while Walters's model is only driven by fishing mortality. This model is generally more complex than Walters's model and much more expensive to run. Therefore, the development of an optimization procedure is beyond the scope of the present work.

DISCUSSION

A complex compartmentalized simulation model of the Southern New England yellowtail flounder fishery has been described, verified against catch statistics, and used to examine methods of increasing yield. The relationships and parameters upon which the model was based do not appear to be unreasonable since most variability was explained. Nevertheless, in retrospect, some consideration of alternate approaches to estimating parameters and of modifications of the model is appropriate. It is important to remember that there may be numerous other models or parameter values equally as successful at explaining variation in catch as the one proposed here.

An average maximum length (L_{m4}) for the simulated population of 480 mm was assumed. This value was used in order to assure that few fish would exceed 500 mm in length. When fishing pressure was applied to the simulated population, its average maximum length was suppressed. For some years, the average length of the older age-groups converged to about 460 mm. Since the growth rate coefficients (k_i) of adult fish were based on Lux and Nichy's (1969) work where a maximum length of 500 mm was assumed, the model tends to underestimate the length of older fish. In order to compensate for this effect, the growth rate coefficient of fish younger than 2 yr of age was overestimated. The result was that

the mean size of younger fish was higher than observed while the converse applied to older fish. The differences were generally small. The sizes of the most abundant fish in the catch (age-groups 3 and 4) were well simulated. While the model adequately simulates growth, more precise results might have been obtained by assuming an average maximum size in excess of 500 mm. The result, with fishing, would be an average maximum size near the value assumed by Lux and Nichy (1969). Thus the assumed value of k_2 would have been more appropriate.

The parameters of c_{12} and c_{14} specify the temperature dependence of the model. Estimates of these parameters were based on Sissenwine's (1974, 1975) calculations of recruitment and average growth per fish for 1944-65. No attempt was made to improve these estimates by tuning them to the model. While Figures 4 and 5 indicate the adequacy of the model and its parameters, these figures also reveal that catch was generally overestimated during warm years and underestimated during cold years. This implies that the fishery was probably more sensitive to temperature than indicated by estimates of c_{12} and c_{14} . Rather minor adjustment of these parameters would probably account for much of the remaining unexplained variation in catch. On the other hand, since tuning in effect reduces the residual degree of freedom and, more subjectively, reduces confidence in the model, no attempt was made to improve the initial estimates of c_{12} and c_{14} .

Adult female yellowtail flounder are generally longer than males of the same age. The model does not distinguish between sexes. To do so would require doubling the central processing time required to run the model. Fishing pressure would tend to shift the sex ratio in favor of males because of this size difference. Since the sex ratio ($c_{11} = 0.5$) was estimated for the exploited population, the influence of fishing was incorporated into the model through the estimation of this parameter. Variations in c_{11} resulting from changes in level of fishing were not simulated.

Since females are larger than males, the total fecundity of the population is underestimated when based on the mean size of the age-size compartments. This bias is probably compensated for by overestimating mean recruitment per egg (c_{13}). Thus, expansion of the model to segregate fish according to sex should not affect the results reported here, although some revision of c_{13} would be required.

In recent years, several changes have occurred in the Southern New England yellowtail flounder fishery that were not reflected in the model. During the late 1960's, more active industrial and distant water fisheries (using small mesh nets) for the yellowtail flounder developed. The fisheries statistics used in this report do not include the catch of the industrial fishery which in a few years equaled 20% of the total yield. Estimates of the catch of the distant water fishery are included and the fishing effort of the distant water fleet is estimated by assuming that the catch per unit effort was the same as for the domestic fishery. Since 1971, the fishery has been regulated by quotas set by ICNAF. During the 1970's, landings of yellowtail flounder within ICNAF Subarea 6 (south of the Southern New England ground which is within ICNAF Subarea 5) have increased. The relationship between the fisheries in these two areas is unknown (Brown see footnote 3; Parrack see footnote 4). These recent changes necessitate several modifications of the model before it can be used to simulate the present fishery.

The work reported here indicates the potential for predicting future trends of certain well-studied fisheries in which the role of a specific environmental variation can be described. Two important limitations of this approach are demonstrated. Firstly, model parameters may change with time; thus it is important to keep the model up-to-date. This does not imply that the model should be regularly tuned to assure that it successfully predicts each additional year of data but rather that parameters be updated as evidence of change in the fishery becomes available. Secondly, numerous fundamentally different models may be nearly as successful in simulating a specific system. Therefore, it is dangerous to limit consideration to a single model or regulatory mechanism.

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