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On the Population
and Trophic Dynamics
of
Pacific Whiting,
*Merluccius productus*

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ON THE POPULATION AND TROPHIC DYNAMICS

OF PACIFIC WHITING, MERLUCCIUS PRODUCTUS

by

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ABSTRACT

This paper is an attempt to explore the population and trophic dynamics of the coastal stock of Pacific whiting (Merluccius productus). Results of investigations on the basic population biology of whiting are reported. In particular, attempts are made to quantify the biological mechanisms of growth, mortality (natural and fishing), migration, and bioenergetics in such a way that both fishery and trophic dynamics can be examined. The central focus of the analysis is an age-structured computer simulation model. Through the model, the implications of two different representations of individual fish growth and age-specific natural mortality on both stock bioenergetics and fishery dynamics are explored.

## CONTENTS

INTRODUCTION

Pacific whiting, Merluccius productus, is commercially and ecologically one of the most important fish species on the west coast of North America. Since 1966, it has been the target of a large foreign fishery. Estimated catches have ranged from 91 thousand to 236 thousand metric tons (t) (Bailey et al. 1982). A small, rather insignificant, domestic fishery for whiting has existed since at least 1879. In recent years U.S. and Canadian domestic joint ventures for whiting have begun to develop. The U.S. joint-venture catch has been estimated at 3, 13, 41, and 45 thousand t in 1978 through 1981.

Besides being an important resource to man, whiting is also important in the California Current ecosystem. As a large predator, whiting influences other fish and shellfish populations, notably the commercially important stocks of herring, anchovy, and shrimp. Whiting is also important as prey in the diets of marine mammals and large fishes (Bailey and Ainley 1982).

A detailed description of the life history of and fishery for Pacific whiting is given by Bailey et al (1982). Briefly, the coastal stock of Pacific whiting occupies the continental shelf and slope area of the California Current system, ranging from a feeding area off Vancouver Island in the north to a spawning area as far south as the southern tip of Baja California (Figure 1). In autumn, adult whiting make an annual migration from the summertime feeding grounds off the Pacific Northwest coast to the winter spawning grounds off the coasts of southern California and Baja California. In spring and summer large adult fish migrate northward as far as central Vancouver Island and juveniles remain off central and northern California. Oceanographic conditions at the time of spawning appear to play a major role in the recruitment to the exploitable stock of Pacific whiting (Bailey 1981).
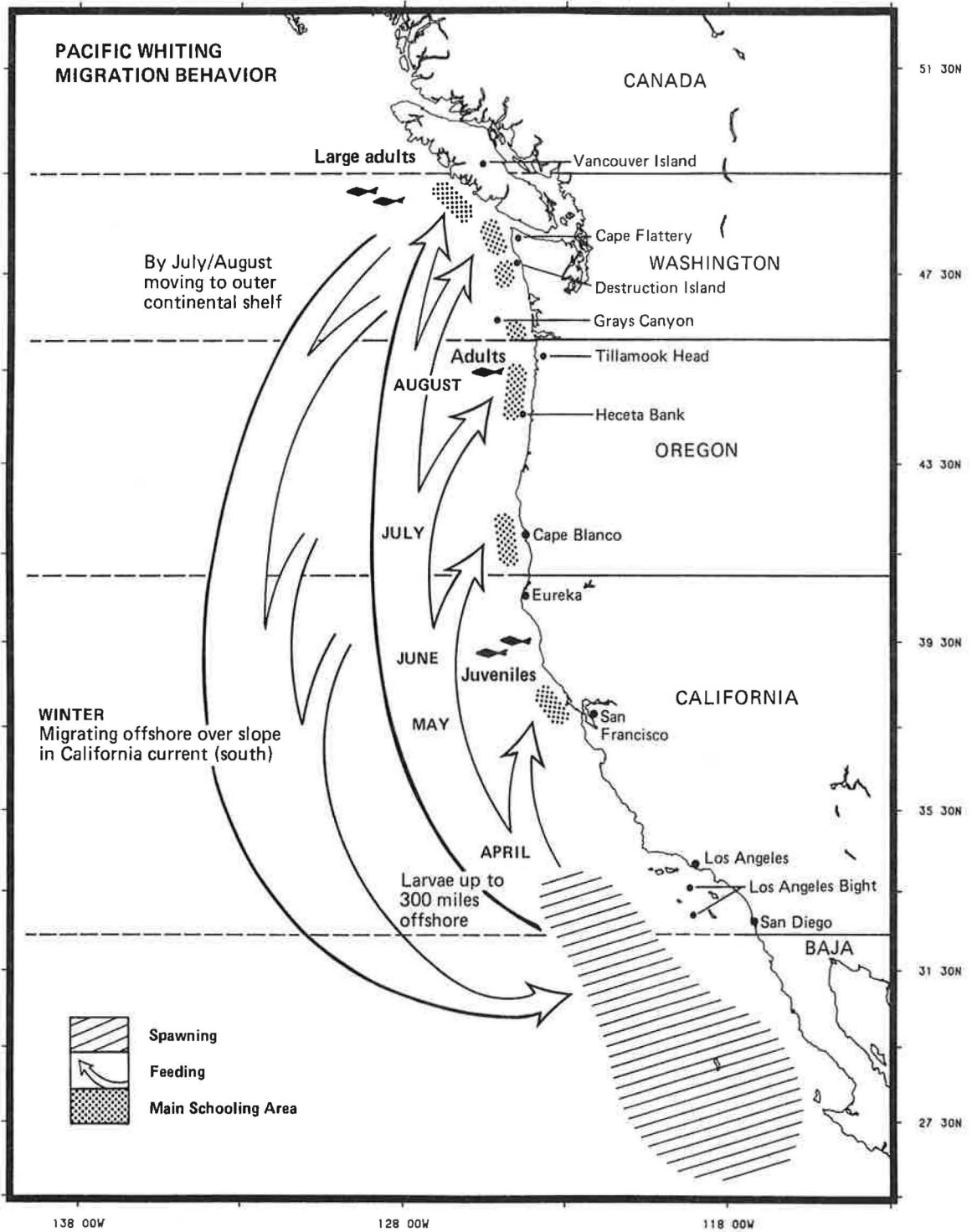
PACIFIC WHITING
MIGRATION BEHAVIOR

CANADA

51 30N

Large adults

Vancouver Island

Cape Flattery

By July/August
moving to outer
continental shelf

WASHINGTON

47 30N

Destruction Island

Grays Canyon

Tillamook Head

Adults

AUGUST

Heceta Bank

OREGON

43 30N

JULY

Cape Blanco

Eureka

39 30N

JUNE

Juveniles

CALIFORNIA

MAY

San
Francisco

WINTER
Migrating offshore over slope
in California current (south)

35 30N

APRIL

Larvae up to
300 miles
offshore

Los Angeles

Los Angeles Bight

San Diego

BAJA

31 30N

Spawning

Feeding

Main Schooling Area

27 30N

138 00W

128 00W

118 00W

Figure 1.--Migratory patterns of Pacific whiting (Merluccius productus).

The intent of studies of the population dynamics of exploited populations is to determine the numbers, biomass, age-structure, and potential yield from a population so that rational management decisions can be made to insure efficient utilization of the resource. Studies of trophic dynamics shed light on the relationships between various components of an ecosystem. Ecologists and fisheries scientists have long recognized the importance of these interactions, in particular their importance on fishery dynamics; however, attempts to quantify these phenomena have been limited until recently.

This paper presents an attempt to explore both the population and trophic dynamics of the coastal stock of Pacific whiting. Results of investigations on the basic population biology of whiting are reported. In particular, attempts are made to quantify the biological mechanisms of growth, mortality, migration, and bioenergetics in such a way that both fishery and trophic dynamics can be explored. The central focus of the analysis is an age-structured computer simulation model, entitled HAKE. Population parameters estimated in this analysis are also subsequently used in a management analysis of the Pacific whiting fishery (Francis et al. 1982).

## THE SIMULATION MODEL

The basic structure of the simulation model (HAKE) is similar to that described by Francis (1974, 1977) and Walters (1969). The primary function of HAKE is to accurately describe the manner in which Pacific whiting population biomass varies over time and area. Operating as a dynamic process, the model is used as a tool in synthesizing, summarizing, and evaluating analyses of whiting growth, mortality, and migration. These are presented in later sections. The model is then used to make estimates of stock bioenergetic demands.

The essential structural units of HAKE are the annual age group, quarter of a year, and International North Pacific Fisheries Commission (INPFC) statistical area. Letting

$i$ = age group $(2,\ldots,12)$,

$j$ = area $(1,\ldots,6)$,

$x \in [t,t+1]$,

$N_{ij}(x)$ = number of fish of age $i$ in area $j$ at time $x$,

$Z_{ij}(t)$ = instantaneous total mortality rate on age group $i$ during $[t,t+1]$,

$\quad = F_{ij}(t) + M_i$,

$\quad = q_{ij}f_j(t) + M_i$,

$F_{ij}(t)$ = instantaneous fishing mortality rate on age group $i$ during $[t,t+1]$,

$M_i$ = instantaneous natural mortality rate on age group $i$,

$q_{ij}$ = catchability coefficient on age group $i$ in area $j$,

$f_j(t)$ = number of standard days effort in area $j$ during $[t,t+1]$,

then

$$\frac{dN_{ij}(x)}{dx} = \left[ -Z_{ij}(t) - \sum_{K(\neq j)=1}^{6} I_i^{jk}(t) \right] N_{ij}(x)$$

$$- \sum_{K(\neq j)=1}^{6} I_i^{kj} N_{ik}(x)$$

where

$I_i^{jk}(t)$ = instantaneous migration rate on age group i from area

j to area k during [t,t+1].

Also

$YN_{ij}(t)$ = catch in numbers of age group i in area j during

[t,t+1]

$$= \int_t^{t+1} F_{ij}(t) N_{ij}(x) dx.$$

$YW_{ij}(t)$ = catch in weight of age group i in area j during

[t,t+1]

$$= \int_t^{t+1} F_{ij}(t) B_{ij}(x) dx$$

where

$B_{ij}(x)$ = biomass of age group i in area j at time x

$$= N_{ij}(x) \, w_i(t) \, e^{G_i(t)(x-t)} \quad ,$$

$w_i(t)$ = average weight of an individual on entry into age group i during [t,t+1], and

$G_i(t)$ = instantaneous growth of age group i during [t,t+1]

$$= \ln \left[ \frac{w_{i+1}(t+1)}{w_i(t)} \right] .$$

In order to compute population bioenergetics, the gross biomass added to the population by the process of individual fish growth, referred to as gross growth, must be calculated:

$GG_{ij}(t)$ = gross growth of age group i in area j during [t,t+1]

$$= GG1_{ij}(t) + GG2_{ij}(t)$$

where

$GG1_{ij}(t)$ = total biomass added to age group i in area j by fish which survive [t,t+1]

$$= N_{i+1,j}(t+1) \left[ w_{i+1}(t+1) - w_i(t) \right]$$

$\text{GG2}_{ij}$ (t) = total biomass added to age group i in area j by fish which die during [t,t+1]

$$= \int_{t}^{t+1} [F_{ij}(t) + M_i] \ N_{ij}(x) \ w_i(1) \left[ e^{G_i(t)(x-t)} \right] dx.$$

Recruitment is assumed to occur in a knife edge fashion at the beginning of age 2, as:

$R_j$ (t) = number of fish recruited into age class 2 at time t

$$= N_{2j}(t).$$

## GROWTH

Growth parameters were calculated from length-at-age and weight-length data taken by U.S. observers aboard Soviet and Polish commercial fishing vessels during the 1976-80 fishing seasons (May-October). The sampling procedures are described by French, Nelson, and Wall (1981). Briefly, length-frequency measurements were taken from random samples of trawl hauls, and otoliths and weight samples were taken from subsamples stratified by length and sex. The determination of age from otolith is described by Dark (1975). The following analyses are based on estimates (George Hirschhorn, Northwest and Alaska Fisheries Center, Seattle, WA 98112. Pers. commun., 1981) of mean lengths and weights at age stratified by:

1) Bimonthly stanzas - Stanza 1 = May, June; Stanza 2 = July, August; Stanza 3 = September, October,

2) Year - 1976-1980,

3) Sex - Male, Female,

4) INPFC Statistical Area - Columbia, Eureka, Monterey.

The estimates are to be used in a model which attempts to represent the trophic dynamics of whiting on an inter-annual and regional areal basis. Since the latitudinal distances that whiting migrate seem to be determined by size (length), and trophic demands determined by growth in weight, an attempt is made to examine the fundamental characteristics of both growth in length and growth in weight.

The following results summarize the problems associated with analysis of whiting growth data.

Figure 2 gives annual length-frequency estimates for the whiting fishery in U.S. waters by INPFC area (Columbia, Eureka, Monterey). Figure 3 gives mean length at age during the July, August stanza by INPFC area (Columbia, Eureka) and sex. And Figure 4 is a plot of mean length at age (2-12) by stanza and sex for all areas combined. These figures indicate several points:

1) Both between (Figure 2) and within (Figure 3) age classes, fish tend to stratify by size on a latitudinal gradient, with the larger fish tending to move farther north than the smaller fish. This tendency is also reported by Dark (1975).

2) The apparent decrease in average length for ages 3-12 between stanza 1 (May, June) and stanza 2 (July, August) (Figure 4) is a result of the larger fish of a given age group migrating into and through a given fishing area before the smaller fish. Therefore, for a given area, fish measured in stanza 2 are not necessarily the same fish that are measured in stanza 1.

These figures reveal the problems inherent in elucidating the factors regulating growth in length of animals taken in a fishery where significant migration is present. Unfortunately, direct measurement of individual animal growth employing such methods as tagging is virtually impossible in this case. One hope, however, is that the quantification of annual growth increments on
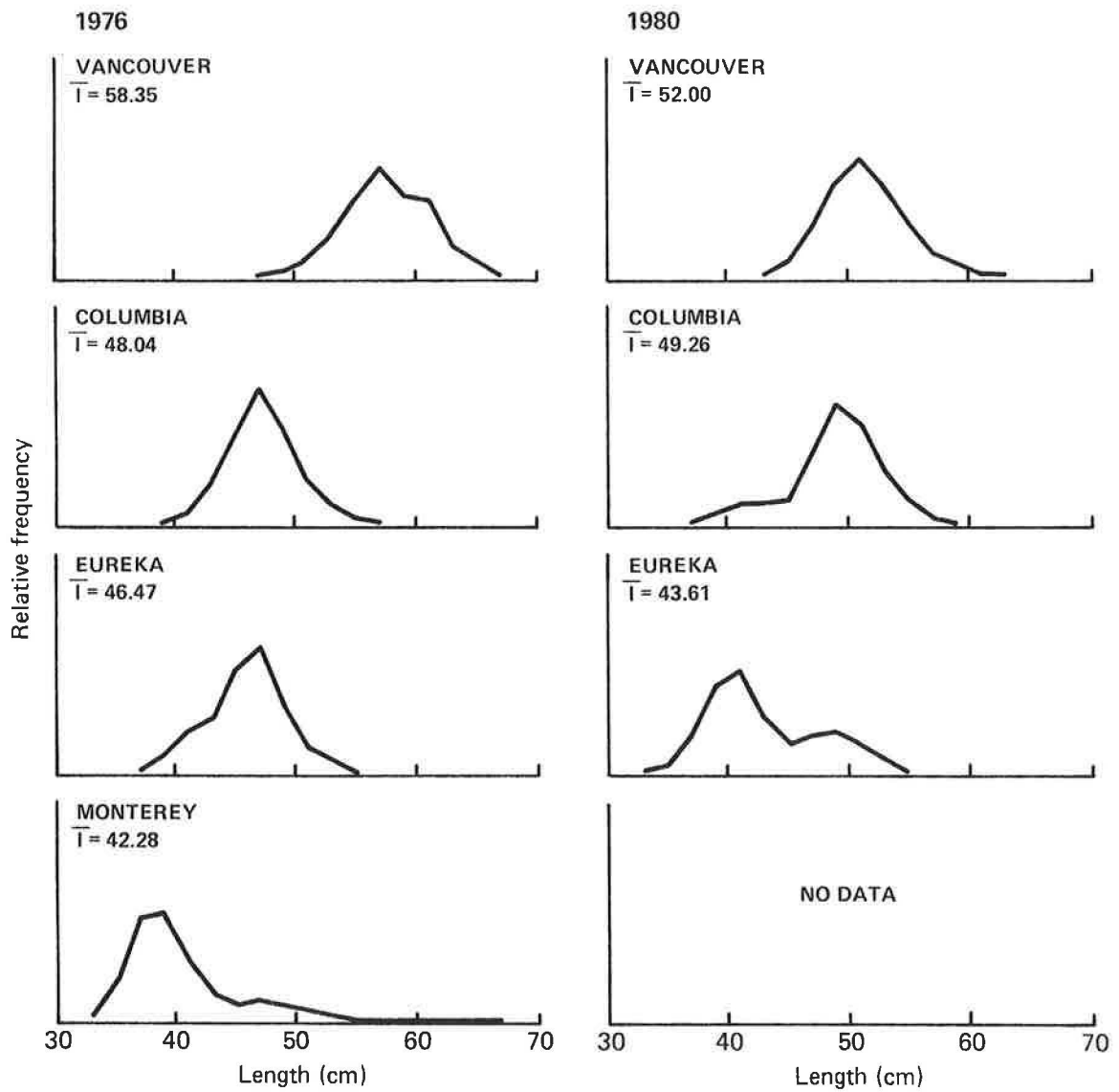
Figure 2.--1976 and 1980 length-frequency estimates for the Pacific whiting fishery in U.S. waters. (INPFC areas).
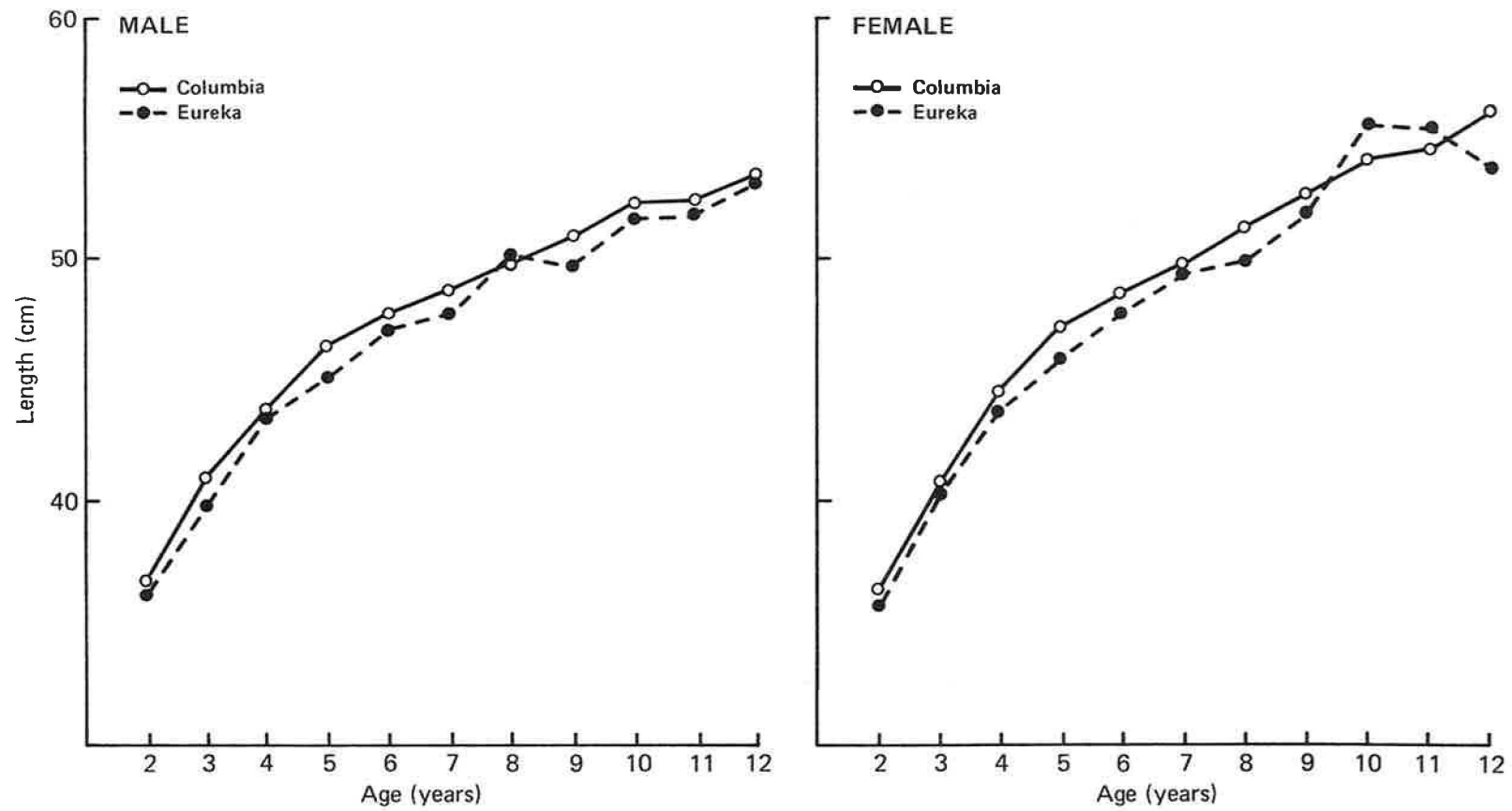
Figure 3.--Mean length of Pacific whiting by age group during July, August, 1976-80. (INPFC Columbia and Eureka areas).
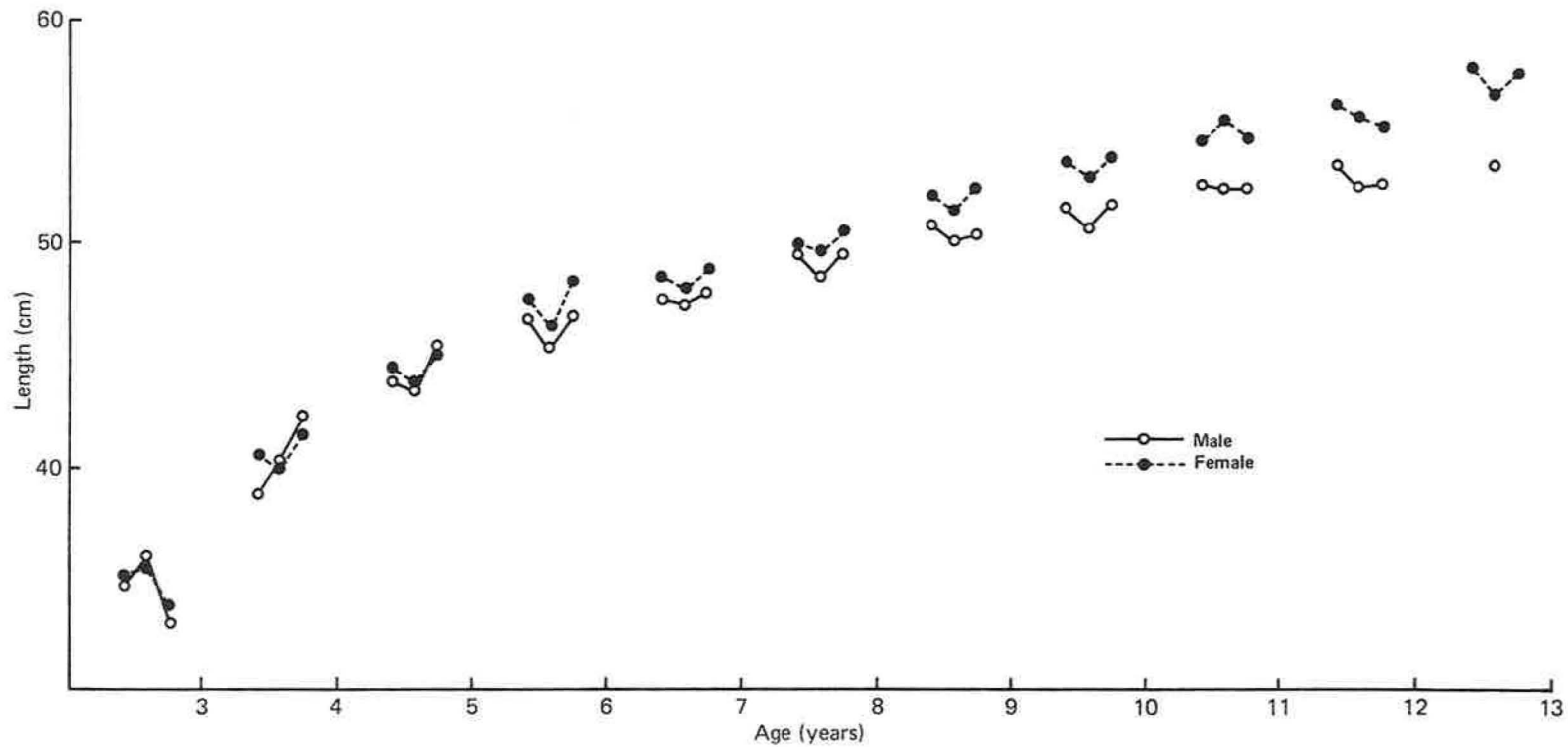
Figure 4.--Mean length of Pacific whiting by age group and sex, 1976-80.

scales might reveal more about the dynamics of growth of whiting than the present use of otoliths (George Hirschhorn, Northwest and Alaska Fisheries Center, Seattle, WA 98112. Pers. commun., 1981).

In order to facilitate this analysis, the data was stratified as follows:

| Year | Stanza | Eureka | | Columbia | |
|------|--------|-----------|------------------------------------|-------------|------------------------------------|
| | | No. Lengths | No. otoliths read and fish weighed | No. Lengths | No. otoliths read and fish weighed |
| 1976 | 1 | - | - | 192 | 1,055 |
| | 2 | 270 | 2,102 | 1,190 | 19,050 |
| | 3 | - | - | 236 | 4,465 |
| 1977 | 1 | 284 | 10,811 | 1,785 | 22,235 |
| | 2 | 1,335 | 46,247 | 2,469 | 42,671 |
| | 3 | - | - | 1,789 | 20,590 |
| 1978 | 1 | 874 | 19,241 | 1,176 | 12,593 |
| | 2 | 576 | 17,007 | 2,227 | 49,008 |
| | 3 | - | - | 980 | 26,872 |
| 1979 | 1 | 883 | 24,790 | 189 | 12,933 |
| | 2 | 411 | 31,896 | 1,142 | 51,762 |
| | 3 | - | - | 501 | 51,804 |
| 1980 | 1 | - | - | 446 | 14,531 |
| | 2 | 231 | 12,851 | 827 | 25,394 |
| | 3 | - | - | - | |

The numbers of males and females examined were approximately equal.

Since Dark (1975) demonstrated that annual growth in length can adequately be described by the von Bertalanffy equation, it was decided to focus this analysis on the dynamics of within season (May-October) growth. Instantaneous growth rates were calculated by taking the natural logarithm of the ratio of lengths in successive stanzas. Calculations were made by cohort, area, and sex. All rates were normalized to a quarterly (3 mo) time unit for comparative purposes. Thus, if for a given area and sex,

$$l_{ijk} = \text{average length of an individual in cohort j at annual age i in stanza k,}$$

then

$$g_{i,j,3\to1} = \frac{3}{8} \ln \left( \frac{l_{ij3}}{l_{i+1,j,1}} \right) \text{, and}$$

$$g_{i,j,1\to2} = \frac{3}{2} \ln \left( \frac{l_{ij2}}{l_{ij1}} \right)$$

The factor 3/8 normalizes an 8-mo growth rate to a 3-mo growth rate and the factor 3/2 normalizes a 2-mo growth rate to a 3-mo growth rate.

These estimates of instantaneous growth were then subjected to analysis of variance using the following linear model.

$$Y_{ijk} = \mu + a_i + b_j + c_k + d_l + e_m + ac_{ik} + cd_{kl} + \varepsilon_{ijklmn}$$

where

$$Y_{ijklm} = \text{quarterly instantaneous growth rate for age i, area j, stanza k, sex l, year m,}$$

$$i = 2, \ldots, 12 \quad - \text{ Age,}$$

$$j = \begin{cases} 1 & \text{Columbia} \\ 2 & \text{Eureka} \end{cases} - \text{Stanza,}$$

$$k = \begin{cases} 1 & \text{(May, June)---(July, August)} \\ 2 & \text{(July, August)---(September, October)} \quad - \text{ Stanza} \\ 3 & \text{(September, October)---(May, June) - over winter,} \end{cases}$$

$$l = \begin{cases} 1 & \text{Male} \\ 2 & \text{Female} \end{cases} - \text{Sex,}$$

$$m = 1976, \ldots, 1980 \quad - \text{ Year, and}$$

$$\varepsilon_{ijklmn} \sim N(0, \sigma^2).$$

From the ANOVA, the only factors which were significant to growth variability were Year ($p < .10$), Area ($p < .05$), and Stanza ($p < .01$). However, an important result was that, taking the estimates of the coefficients of the linear model, the expected values of quarterly instantaneous growth were:

$$
E\,(g_{..k}) \;=\; \begin{cases} -.01332 & K = 1 \\ .02787 & K = 2 \\ .02349 & K = 3 \end{cases}
$$

Thus, if one estimates instantaneous growth by area one obtains an estimated negative growth in length between Stanza 1 (May, June) and Stanza 2 (July, August), a result also reflected in Figure 2. This implies that, on the average, the fish which are harvested in an area in July, August are not among the fish that are harvested in that area in May, June.

In order to remove this apparent effect of migration on the estimates of instantaneous growth, I re-estimated these rates under the following assumption: fish which are exploited in Eureka in Stanza 1 (May, June) are exploited in Columbia in (July, August). Thus,

$$
_m\hat{g}_{i,j,1\to2} \;=\; \frac{3}{2}\; \ln\; \left[ \frac{l_{ij2}\ (\text{Columbia})}{l_{ij1}\ (\text{Eureka})} \right]
$$

Since there were no estimates of average length ($l_{ijk}$) for Eureka in Stanza 3,

$$
_m\hat{g}_{i,j,3\to1} \;=\; \frac{3}{8}\; \ln\; \left[ \frac{l_{ij3}\ (\text{Columbia})}{l_{i+1,j,1}\ (\text{Columbia})} \right] .
$$

A similar ANOVA was done on these <u>modified</u> growth rates with Area no longer a factor and 1980 not included in years (no suitable data). The only significant factor was Year (p <.01), for which the expected values of quarterly instantaneous growth were

| | | | June-Aug mean upwelling at 45°N (from Bakun, pers. com.) |
|---|---|---|---|
| | .04440 | 1976 | 32 |
| $E\ (_m\hat{g}...)$ | .00179 | 1977 | 62 |
| | .01792 | 1978 | 46 |
| | .00881 | 1979 | 49 |

It is interesting to relate these estimates of relative annual growth to the June-August mean upwelling index at 45°N latitude (Andrew Bakun, Southwest Fisheries Center, Monterey, CA 93940. Pers. commun.). Although very little can be drawn from four data points, it appears that annual whiting growth could be inversely related to the magnitude of upwelling in the feeding area off the northwest coast.

Figure 5 is a plot of mean length at age for 1976-79, with Stanza 1 in Eureka and Stanzas 2 and 3 in Columbia, taken from the same raw data that generated the modified growth rates above. Based upon this plot, I decided to look for ages where there might be differences in growth between stanzas by: 1) removing ages 2 and 12 due to a lack of data and 2) partitioning the analysis into two parts - one on ages 3-7 (ages where whiting become mature and where sexual dimorphism should occur) and another on ages 8-11. ANOVAs on these two subsets reveal both Year (p <.01) and Stanza (p < .10) to be significant for ages 3-7 and Year (p <.05) only to be significant for ages 8-11. Furthermore individual orthogonal contrasts reveal that for ages 3-7,
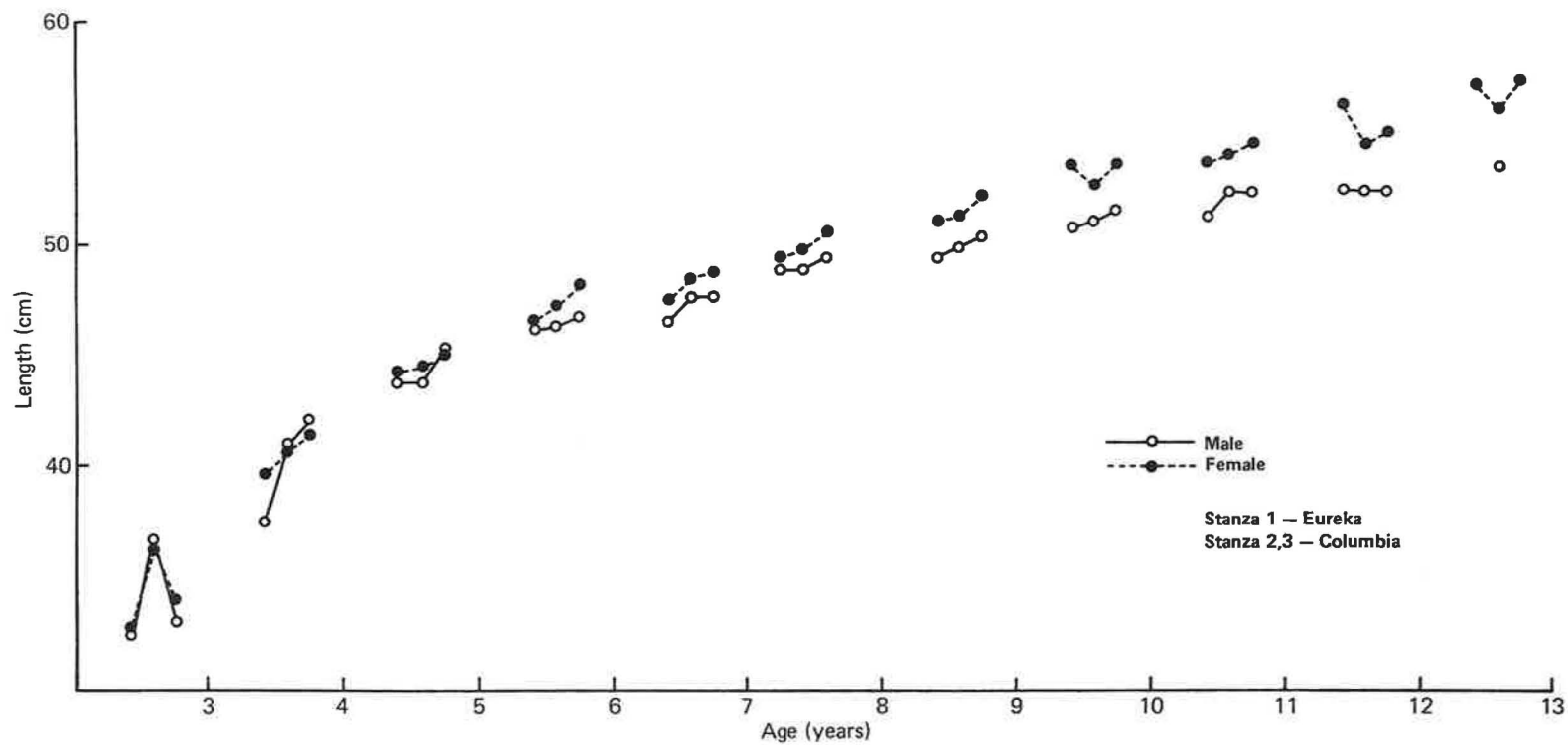
Figure 5.--Mean length of Pacific whiting in Eureka (Stanza 1) and Columbia (Stanzas 2 and 3) by age group and sex, 1975-79.

differences in growth occur between what I will call spawning (September, October $\longrightarrow$ May, June) and feeding (May, June $\longrightarrow$ September, October) stanzas. The expected values of instantaneous quarterly growth for ages 3-7 are

$$E\left(_m\hat{g}_{i.k}\right) = \left\{ \begin{array}{ll} 0.02666 & k = 1\rightarrow2,\ 2\rightarrow3 \\ 0.01152 & k = 3\rightarrow1 \end{array} \right\} \quad i = 3,\ \ldots,\ 7,$$

and for ages 8-11 is

$$E\left(_m\hat{g}_{i..}\right) = 0.00278 \qquad i = 8,\ \ldots,\ 11\ .$$

The implications of this analysis in terms of estimates of model parameters are that:

1) Between ages 3 and 7, growth is seasonal. Using the estimates of instantaneous growth coefficients given above as indicators of relative growth during different parts of the year, then

$$f_q = \text{fraction of annual growth in length occurring during quarter q.}$$

$$= \left\{ \begin{array}{lll} .17391 & \text{Quarter 1} & \text{(Jan-Mar)} \\ .25000 & \text{Quarter 2} & \text{(Apr-June)} \\ .40218 & \text{Quarter 3} & \text{(July-Sept)} \\ .17391 & \text{Quarter 4} & \text{(Oct-Dec)} \end{array} \right. ,$$

2) Fish older than 7 are probably growing so slowly that any differences are slight.

One aspect that was rather disappointing in this analysis was the inability to detect any significant differences in instantaneous growth between sexes. Sex-Age and Sex-Stanza interactions were examined in the ANOVAs but never were significant. Because the differences in growth between sexes appears around ages 4-5 (Figure 4), the apparent time of full maturity (Nelson and Larkins 1970), a more careful examination of the growth in length data around the ages of 4-5 might reveal the mechanisms involved in the dimorphism.

In order to get annual increments in growth in length, the von Bertalanffy equation was fit to the mean values of length during September, October for ages 3 through 10 for 1976-79, averaged over sex and area, using a Fabens fit (Fabens 1965). The resultant equation and parameters are

$$l_t = \text{length in cm at annual age t}$$

$$= 55.402849 \ [ \ 1 - e^{-0.260831 \ (t - 1.605444)} \ ] \ .$$

Partitioning the estimated annual instantaneous growth rates from the von Bertalanffy fit for ages 3-7 into quarterly values according to the estimates of $f_q$ given above, a modified von Bertalanffy fit is obtained. Estimates of quarterly length at age for both of these fits are given in Table 1 and Figure 6.

Weight-at-age has been traditionally obtained from length-at-age (1) by employing the weight-length equation

$$(1) \qquad w = a \ l^b$$

Table 1.--Von Bertalanffy and modified von Bertalanffy estimates of length (cm) of Pacific whiting at age, and standard and modified length estimates of weight (kg) at age.

| | Length | | Weight | |
|---|---|---|---|---|
| Age | von Bertalanffy | Modified von Bertalanffy | Standard | Modified |
| 2.00 | 33.8 | | .274 | .258 |
| 2.25 | 35.1 | SAME | .304 | .285 |
| 2.50 | 36.4 | | .336 | .340 |
| 2.75 | 37.6 | | .367 | .386 |
| 3.00 | 38.7 | 38.7 | .397 | .381 |
| 3.25 | 39.8 | 39.4 | .429 | .403 |
| 3.50 | 40.8 | 40.3 | .459 | .460 |
| 3.75 | 41.7 | 41.9 | .487 | .533 |
| 4.00 | 42.6 | 42.6 | .516 | .508 |
| 4.25 | 43.4 | 43.1 | .543 | .527 |
| 4.50 | 44.1 | 43.8 | .567 | .590 |
| 4.75 | 44.8 | 45.0 | .592 | .661 |
| 5.00 | 45.5 | 45.5 | .618 | .610 |
| 5.25 | 46.1 | 45.9 | .640 | .628 |
| 5.50 | 46.7 | 46.5 | .663 | .697 |
| 5.75 | 47.3 | 47.4 | .687 | .758 |
| 6.00 | 47.8 | 47.8 | .707 | .703 |
| 6.25 | 48.3 | 48.1 | .727 | .717 |
| 6.50 | 48.7 | 48.5 | .744 | .782 |
| 6.75 | 49.1 | 49.2 | .761 | .838 |
| 7.00 | 49.5 | 49.5 | .778 | .758 |
| 7.25 | 49.9 | 49.8 | .795 | .773 |
| 7.50 | 50.2 | 50.1 | .808 | .838 |
| 7.75 | 50.6 | 50.6 | .826 | .887 |
| 8.00 | 50.9 | | .840 | .813 |
| 8.25 | 51.2 | SAME | .853 | .829 |
| 8.50 | 51.4 | | .862 | .894 |
| 8.75 | 51.7 | | .876 | .931 |
| 9.00 | 51.9 | | .885 | .846 |
| 9.25 | 52.1 | SAME | .895 | .856 |
| 9.50 | 52.3 | | .904 | .922 |
| 9.75 | 52.5 | | .914 | .954 |
| 10.00 | 52.7 | | .923 | .871 |
| 10.25 | 52.9 | SAME | .933 | .882 |
| 10.50 | 53.0 | | .938 | .941 |
| 10.75 | 53.2 | | .947 | .977 |
| 11.00 | 53.3 | | .952 | .882 |
| 11.25 | 53.5 | SAME | .962 | .892 |
| 11.50 | 53.6 | | .967 | .953 |
| 11.75 | 53.7 | | .972 | .981 |
| 12.00 | 53.8 | | .977 | .890 |
| 12.25 | 53.9 | SAME | .982 | .895 |
| 12.50 | 54.0 | | .987 | .953 |
| 12.75 | 54.1 | | .992 | .986 |
| 13.00 | 54.2 | SAME | .996 | .892 |
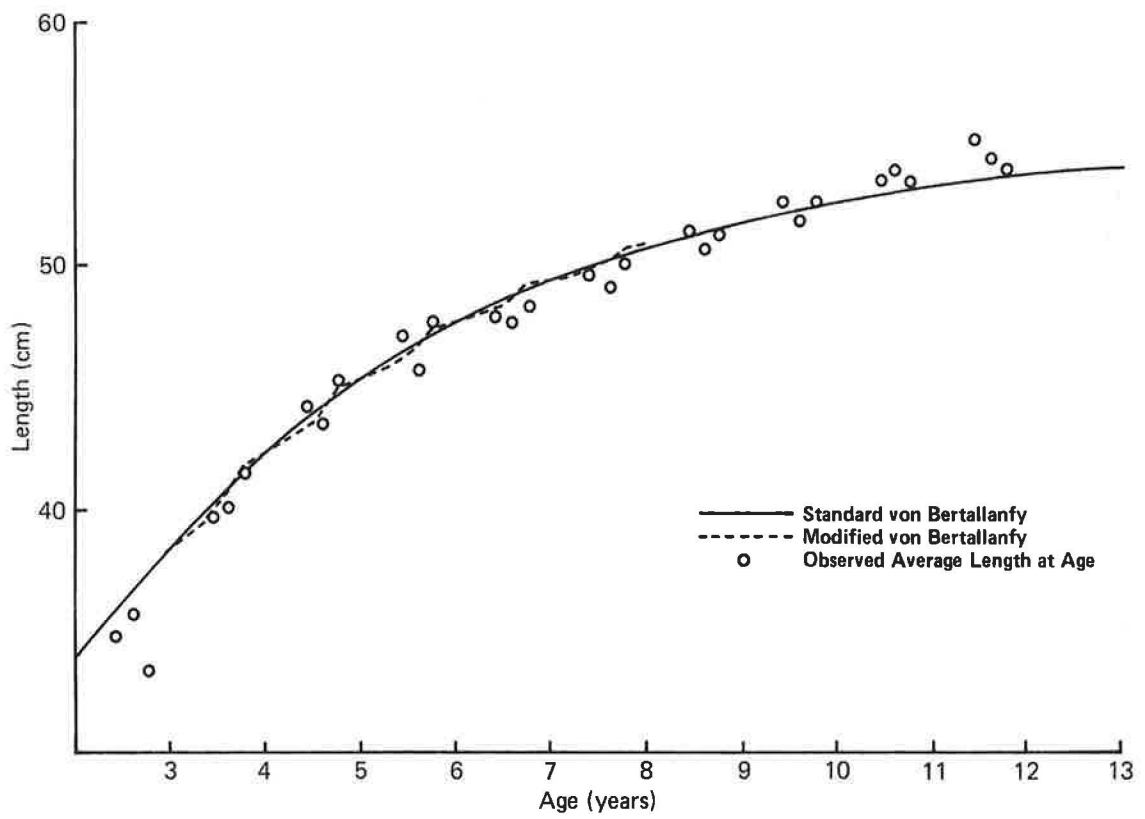
Figure 6.--Estimated length-age (sexes combined) of Pacific whiting.

Figure 7 is a plot of mean weight at age (2-12) by Stanza and Sex for the 1975-80 U.S. observer data. Figure 8 is a plot of mean weight at age against mean length by Age, Sex, and Stanza of the growing season. These two figures reveal a significant amount of variability in weight within a given growing season which cannot be explained by a simple weight-length equation. An analysis of covariance was applied in an attempt to account for some of this variability. The model was a linear version of the weight-length equation (1),

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_l + e_m + b_{ik} X_{ijklm} + \varepsilon_{ijklm}$$

$Y_{ijklm}$ = natural logarithm of average weight of age i, area j, stanza k, sex l, year m

$X_{ijklm}$ = natural logarithm of average length

$i$ = 2, ..., 11

$$j = \begin{cases} 1 & \text{Columbia} \\ 2 & \text{Eureka} \\ 3 & \text{Monterey} \end{cases}$$

$$k = \begin{cases} 1 & \text{(May, June)} \\ 2 & \text{(July, August)} \\ 3 & \text{(September, October)} \end{cases}$$

$$l = \begin{cases} 1 & \text{Male} \\ 2 & \text{Female} \end{cases}$$

$m$ = 1975, ..., 1980.

The model was first tested for differences in slopes ($b_{ik}$) and none were significant. An analysis of covariance (intercepts) was then performed under the assumption that there is one common slope (see the following table).

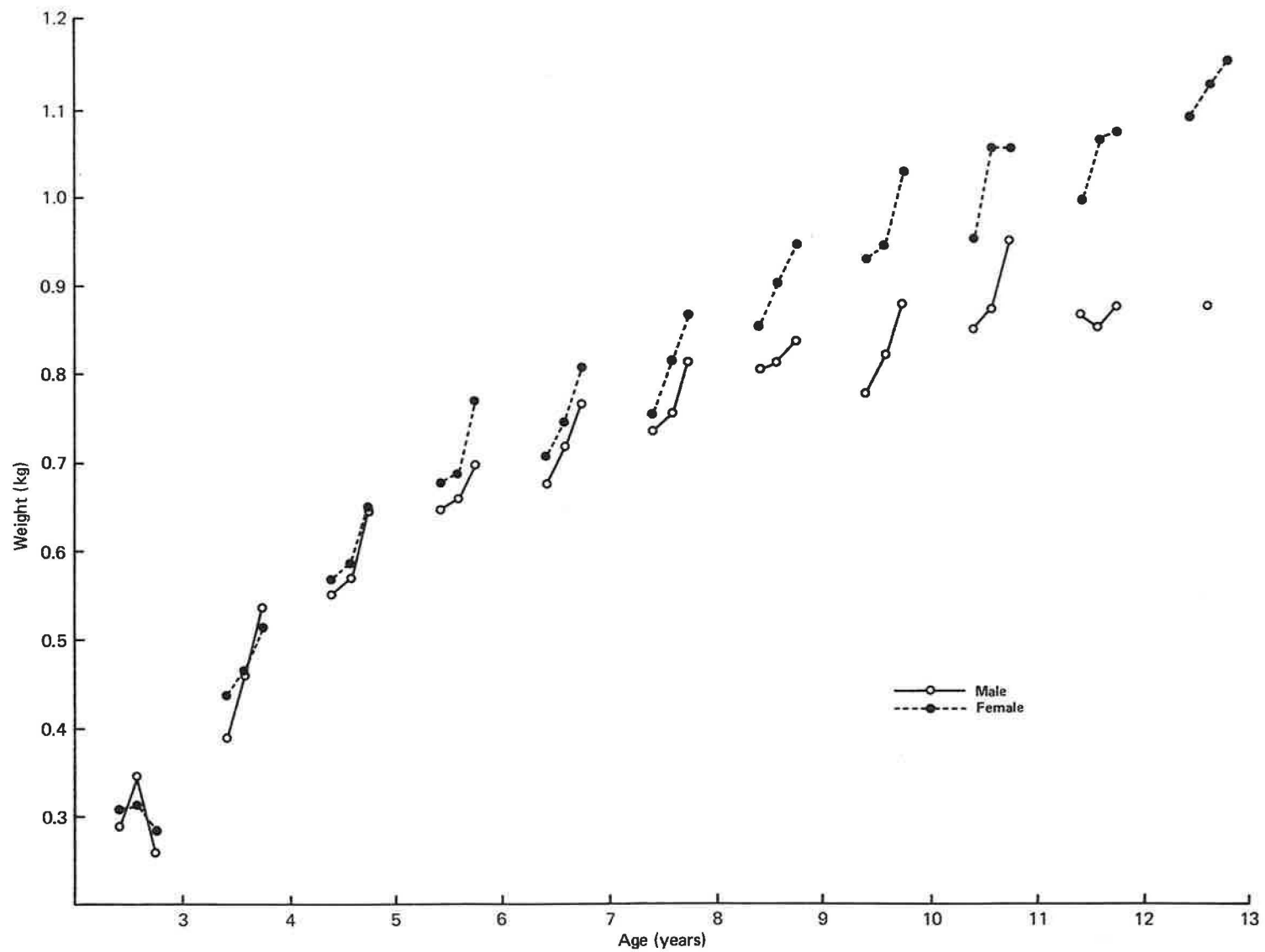Figure 7.--Mean weight of Pacific whiting by age group, 1976-80.
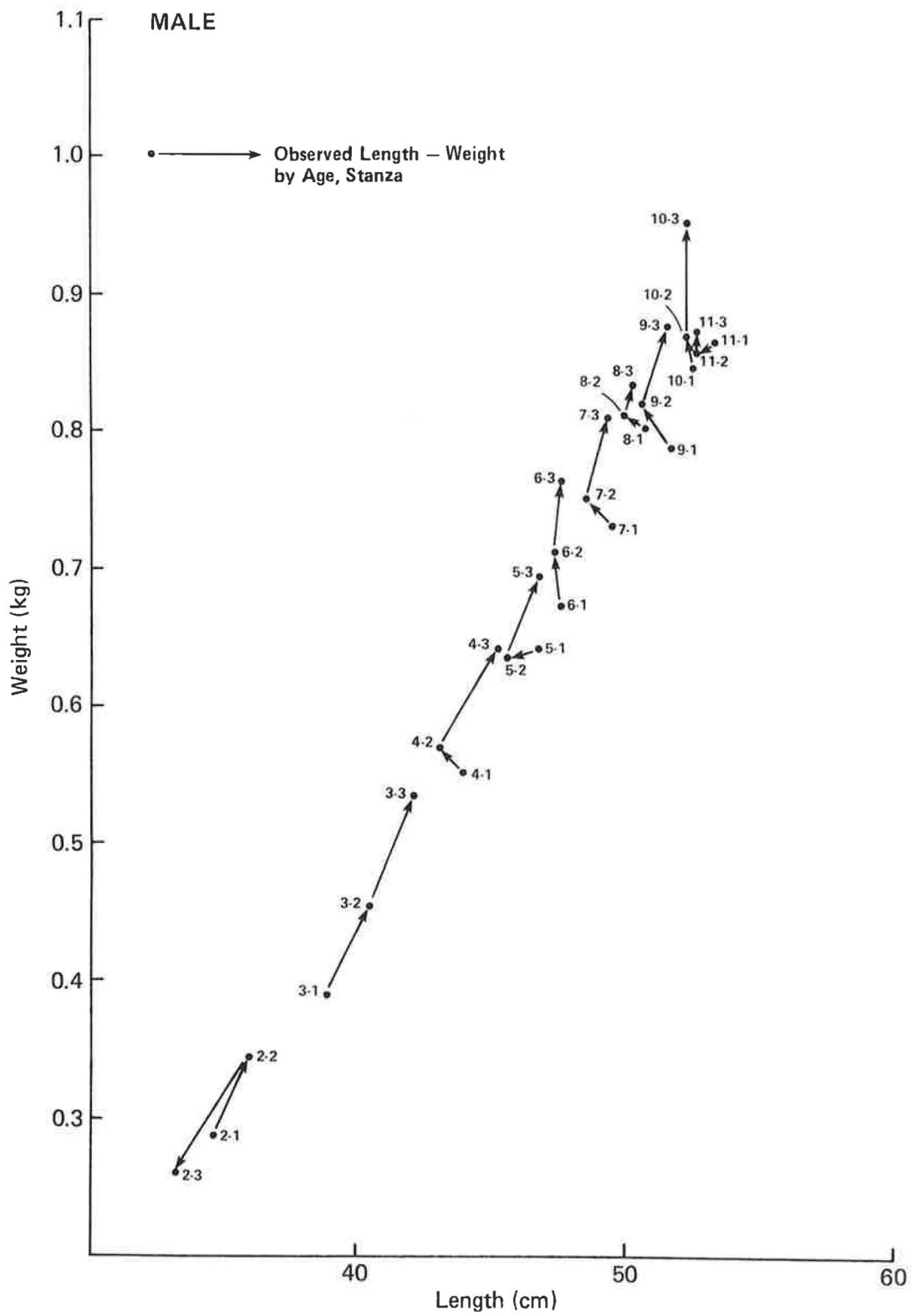
Figure 8.--Mean observed length-weight of Pacific whiting by age, stanza, and sex, 1976-80.
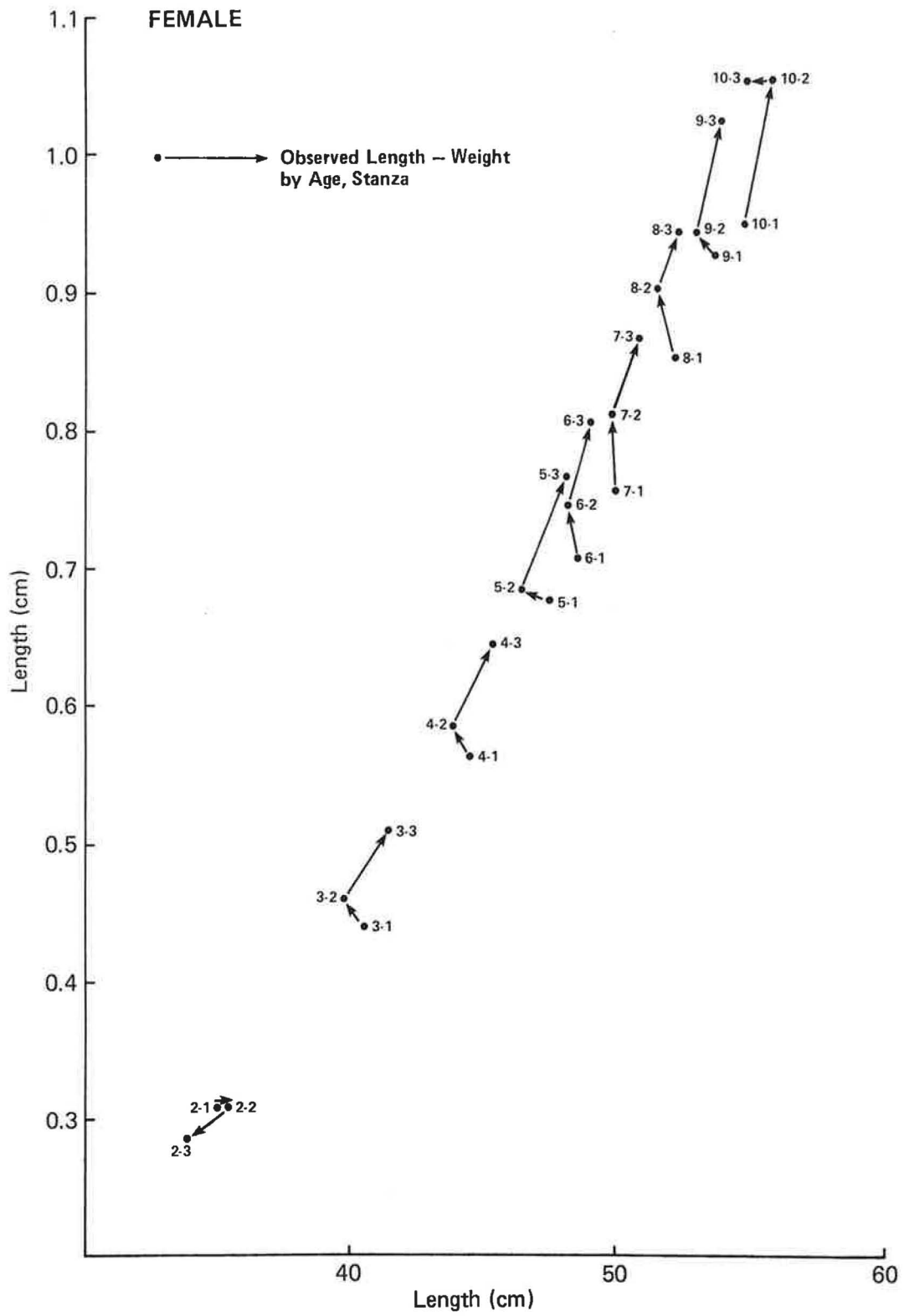
Figure 8.--(Continued).

| Source | df | SS | MS | F |
|--------|-----|---------|---------|-------------|
| Year | 5 | .71316 | .14263 | 67.39*** |
| Area | 2 | .02285 | .01142 | 5.40*** |
| Sex | 1 | .00039 | .00039 | .18 |
| Age | 9 | .40587 | .04510 | 21.31*** |
| Stanza | 2 | .39121 | .19561 | 92.42*** |
| Covariate | 1 | 8.39019 | 8.39019 | 3,964.25*** |
| Error | 392 | .82965 | .00212 | |

*** $\longrightarrow$ p<.01

It is important to note from the analysis that both Age and Stanza are highly significant, which implies that an accurate representation of the within-season dynamics of weight necessitates use of the following weight-length equation (Modified) for sexes combined.

$$w_{ik} = a_{ik} \, l^{3.21976}$$

where the values of $a_{ik}$ are given in Table 2. A single weight-length equation (Standard) was also fit to the data and had the form

$$w = .001815 \, l^{2.73343}$$

Figure 9a shows the observed weight-lengths and a plot of the standard weight-length equation. Notice how most of the observations in Stanza 3 fall above the line and in Stanza 1 below the line. Figure 9b shows the expected weight-lengths by age employing the modified von Bertalanffy length-age relationship and the modified weight-length equation. Finally, Figure 10 shows the standard and modified quarterly weight-age relationships used in the simulation model in addition to the mean observed values. The representation of within-season growth in weight is noticeably different between the two curves. Later I will examine the impact of these two representations of whiting growth on the estimated trophic demands of the stock.

Table 2.--Parameters for modified equation on the weight-length of Pacific whiting.

$$w_{ik} = a_{ik} l^{3.21976}$$

$$i = 2, \ldots, 12; \quad k = 1, 2, 3$$

$$a_{ik}$$

| | Stanza | | |
|---|---|---|---|
| Age | 1 | 2 | 3 |
| 2 | .000301 | .000320 | .000327 |
| 3 | .000294 | .000312 | .000319 |
| 4 | .000288 | .000306 | .000314 |
| 5 | .000280 | .000298 | .000305 |
| 6 | .000275 | .000292 | .000299 |
| 7 | .000265 | .000282 | .000289 |
| 8 | .000260 | .000277 | .000283 |
| 9 | .000254 | .000270 | .000276 |
| 10 | .000249 | .000264 | .000271 |
| 11 | .000243 | .000258 | .000264 |
| 12 | .000238 | .000252 | .000259 |
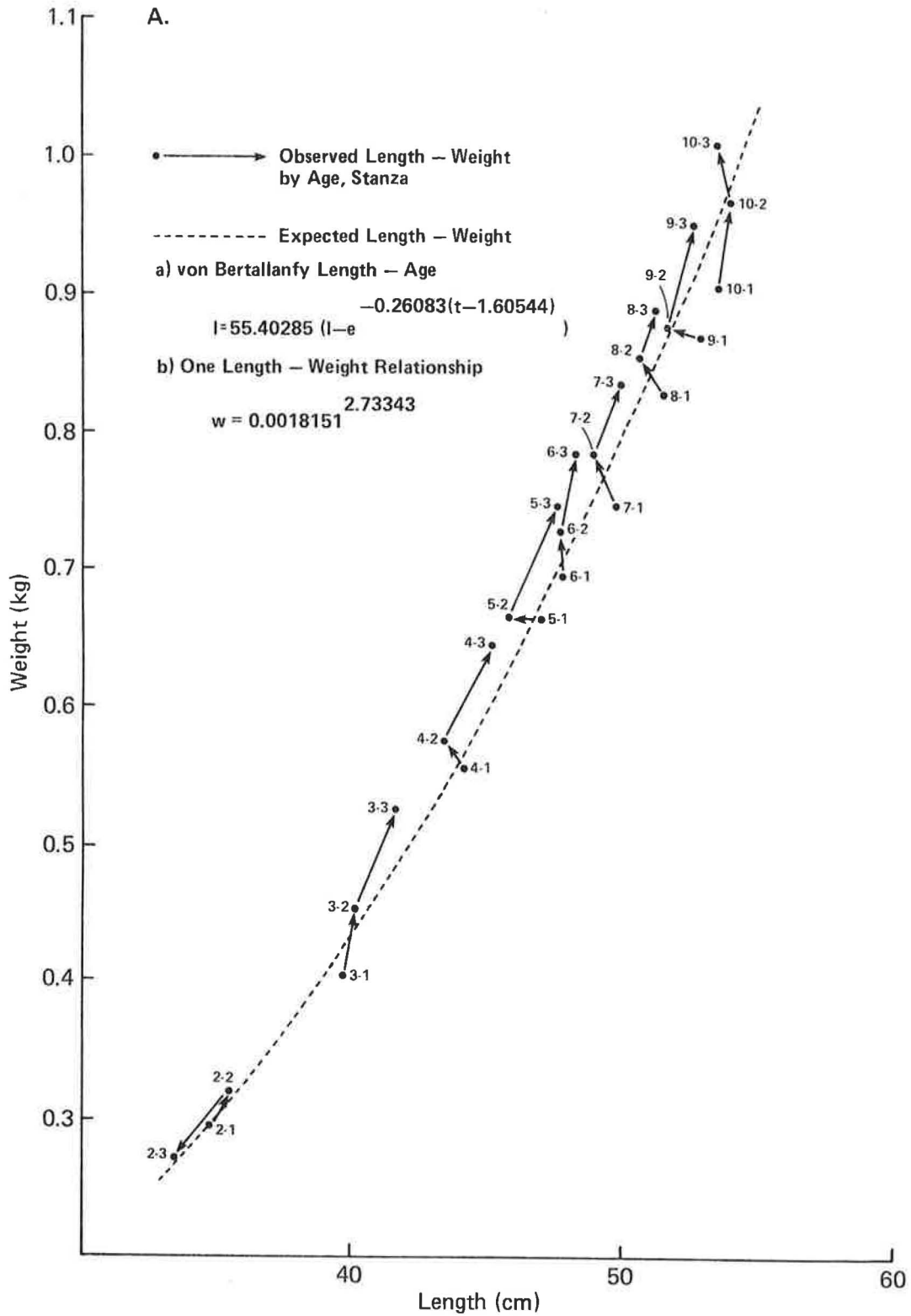
Figure 9.--Standard (A) and modified (B) length-weight of Pacific whiting by age group (sexes combined).
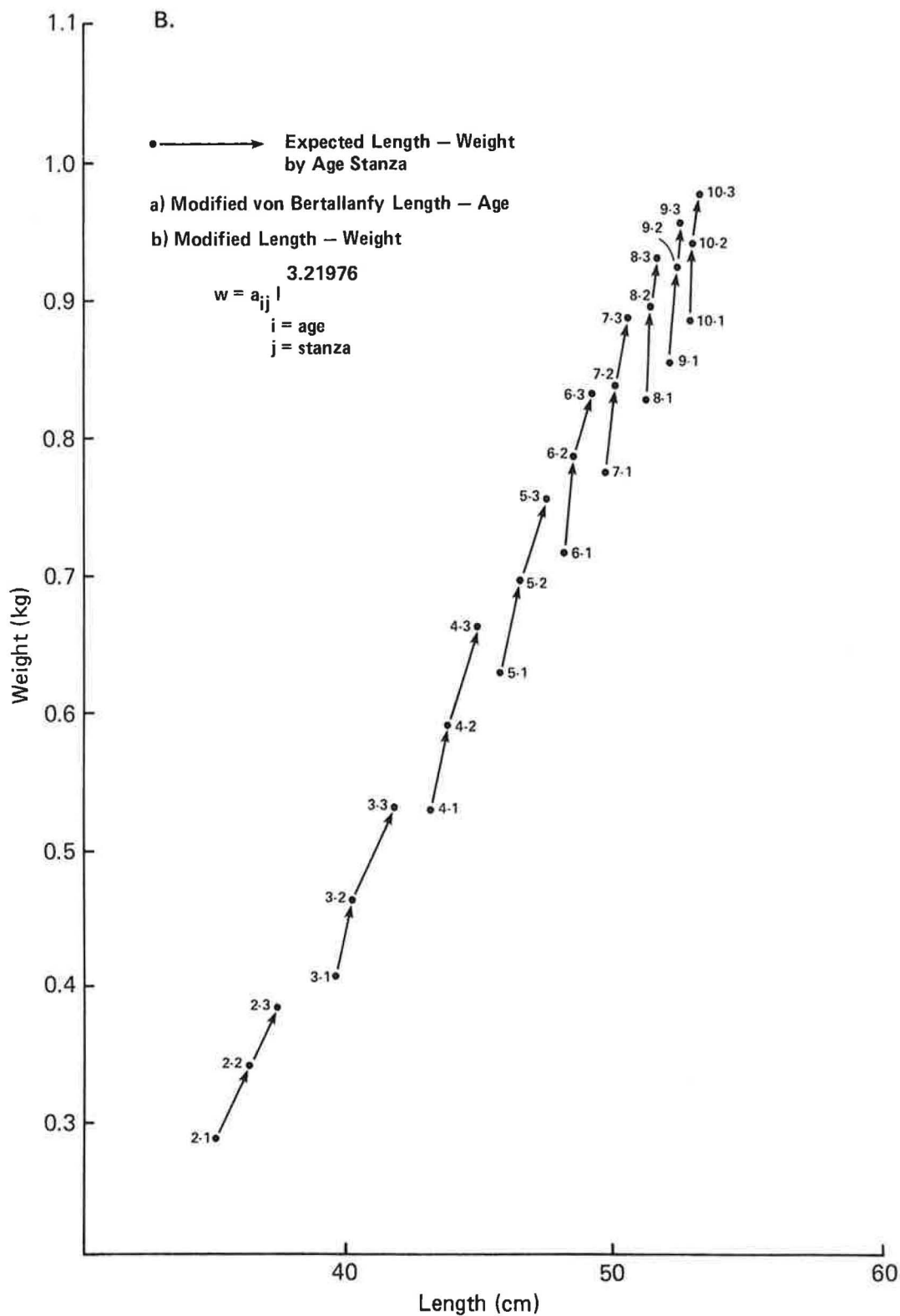
Figure 9.--(Continued).
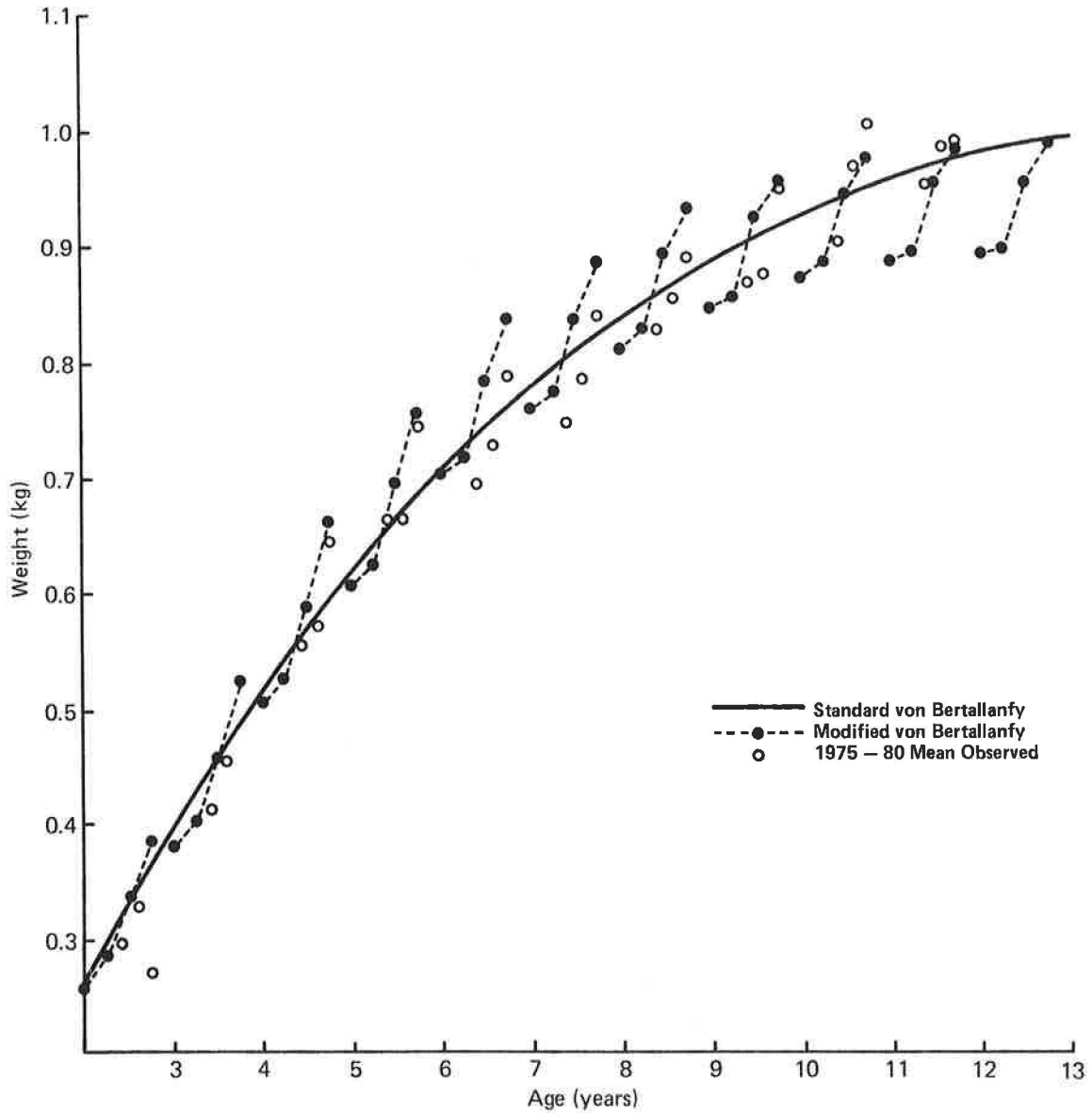
Figure 10.--Standard and modified weight-age for Pacific whiting.

MORTALITY

Two sets of natural mortality rates are used in the simulation. The first assumes that the annual instantaneous natural mortality rate $M_i = 0.45$; $i = 2, \ldots, 12$. This is the average value of M presented in the Pacific Fishery Management Council (PFMC) Pacific Coast Groundfish Plan (Pacific Fishery Management Council 1981). The second uses the assumptions of Granfeldt (1979), Cushing (1973), and Laevastu and Larkins (1981):

a) Between hatching and the critical age (age at which most of the stock is fully mature), natural mortality is a density dependent function of age (size).

b) After the critical age, natural mortality shows a rather steady increase with age [approximately 10% per yr - Laevastu and Larkins (1981)] for 4 to 5 yr due to an increase of spawning stress, after which it undergoes irregular fluctuations.

Average age-specific natural mortality was thus estimated assuming that the critical age was age 5. This certainly seems reasonable from the literature (Bailey et al 1982). The average increase rate in post-critical age natural mortality was estimated from the 1973-1980 mean age-structure of the commercial catch given below.

| Age | Mean Composition of Catch in Numbers | $\hat{Z}$ |
|---|---|---|
| 1 | .011 | |
| 2 | .040 | |
| 3 | .081 | |
| 4 | .144 | |
| 5 | .150 | |
| 6 | .188 | .193 |
| 7 | .155 | .256 |
| 8 | .120 | .583 |
| 9 | .067 | .947 |
| 10 | .026 | .860 |
| 11 | .011 | .788 |
| 12 | .005 | .916 |
| 13 | .002 | |

The table also gives estimates of $Z_i$; i = 6, ..., 12, the average total annual instantaneous mortality rate. Figure 11 gives a plot of $Z_i$ against age. If one is willing to assume that on the average age-specific fishing mortality is constant from age 6 on, then one can fit the regression.

$$Z_t = F + M_O + \Delta M (t-6); \quad t = 6, ..., 12$$

where

F = constant annual instantaneous fishing
    mortality rate.

$M_O$ = baseline annual instantaneous natural
    mortality at age 6.

$\Delta M$ = average annual increase in natural
    mortality.

Using the above data, $(\hat{F}+M_O)$ = .127 and $\Delta \hat{M}$ = .146. The following two factors lead one to believe that this estimate of $\Delta M$ might be an overestimate.

1) Preliminary cohort analyses indicate that on the average fishing mortality increases with age past age 6, and

2) Survey results (Dark et al. 1980, Beamish 1981) indicate that there is a tendency for larger, older fish to move into Canadian waters where they are unavailable to the U.S. fishery.

Both of these factors would tend to bias the estimate of $\Delta M$ upwards. Annual age-specific M was therefore estimated assuming a) and b) above, that the annual increase factor in postcritical M was 0.1 (Laevastu and Larkins, 1981) and that

$$\sum_{i=2}^{12} \hat{M}_i = 11 \times 0.45 = 4.95$$
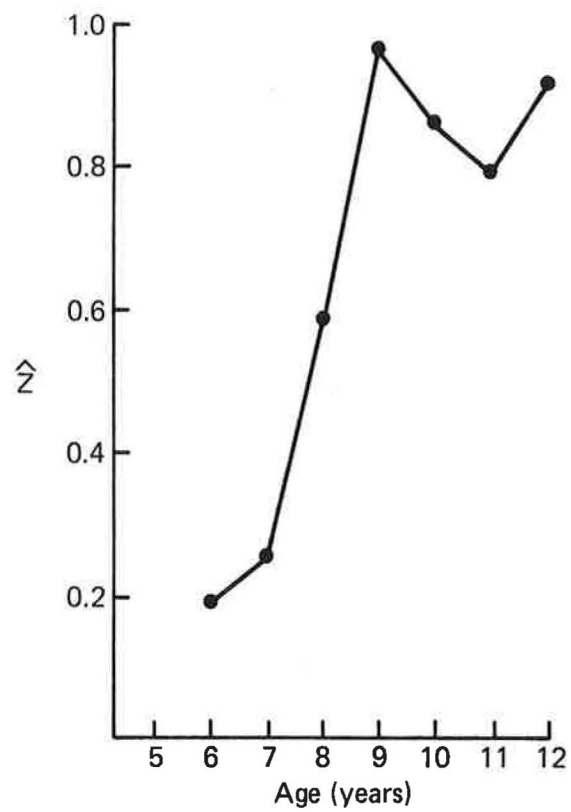
Figure 11.--Annual instantaneous total mortality for Pacific whiting.

Thus the total natural mortality of the simulated (ages 2-12) population is the same under both options. The estimates of $\hat{M}_i$ are given below.

| Age i | $\hat{M}_i$ |
|:-----:|:-----------:|
| 2 | .377 |
| 3 | .268 |
| 4 | .210 |
| 5 | .195 |
| 6 | .257 |
| 7 | .357 |
| 8 | .457 |
| 9 | .557 |
| 10 | .657 |
| 11 | .757 |
| 12 | .857 |
| $\Sigma$ | 4.949 |

It is interesting to plot the growth and decay of an average unexploited whiting cohort using the two options for growth and mortality used in the simulation model (Figure 12). These options are

Option 1 -  Standard weight-age, with

$$M_i = 0.45; \ i = 2, \ \ldots, \ 12,$$

Option 2 -  Modified weight-age, with

Laevestu-Cushing natural mortality.

A cohort analysis using the analytic formulation of Pope (1972) and Tomlinson (1970) was performed on the estimates of annual whiting catch by age for 1973-80 to estimate age-specific fishing mortality rates and catchability coefficients. Separate cohort analyses were carried out for growth-mortality options 1 and 2. The basic input data for the analyses are given in Table 3. The data limited the estimable ages to 3-11. The catch-effort data
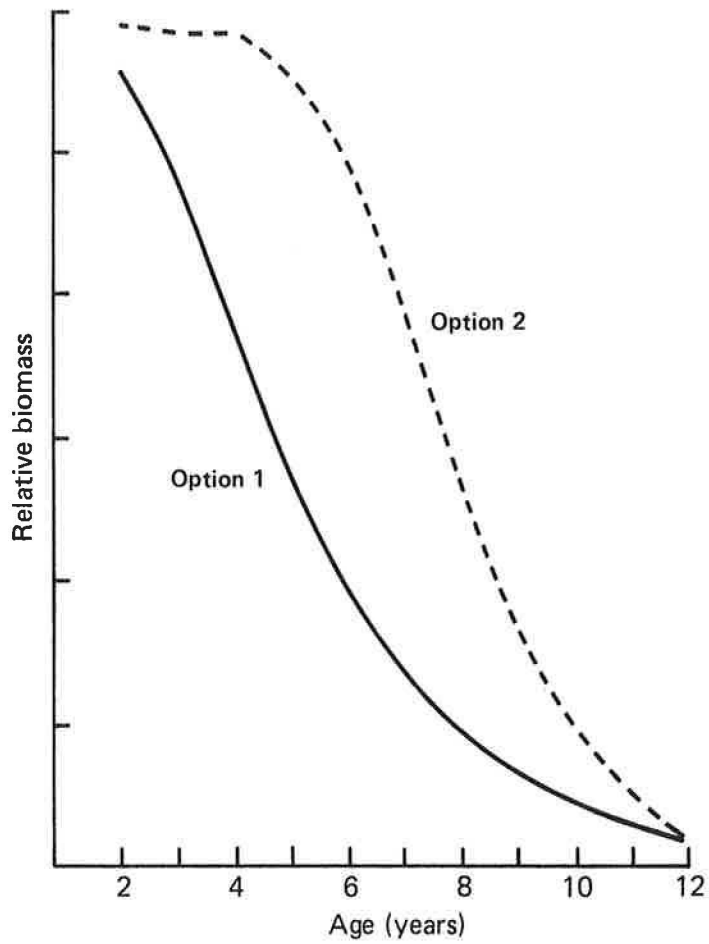
Figure 12.--Growth and decay of an average Pacific whiting cohort under two growth-mortality options.

Table 3.--Input data on Pacific whiting for cohort analysis.

a) Option 1 - Standard weight-age
Constant natural mortality

| | | | | | Age | | | | | | Effort |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | ($10^3$ days) |
| Catch | 73 | 54.94 | 9.51 | 21.34 | 39.52 | 24.72 | 22.61 | 21.13 | 10.14 | 4.44 | 6.31 |
| in | 74 | 0.94 | 162.41 | 22.24 | 38.49 | 48.02 | 27.89 | 12.36 | 3.88 | 1.77 | 8.68 |
| numbers | 75 | 2.71 | 3.72 | 129.12 | 21.98 | 23.67 | 38.22 | 17.25 | 7.44 | 3.72 | 11.52 |
| in | 76 | 37.37 | 29.70 | 30.03 | 188.20 | 28.03 | 14.02 | 5.01 | 1.00 | 0.33 | 9.21 |
| millions | 77 | 3.84 | 54.87 | 11.34 | 20.12 | 68.59 | 11.16 | 5.85 | 2.74 | 1.46 | 4.24 |
| | 78 | 4.28 | 8.15 | 49.57 | 9.39 | 19.88 | 37.28 | 5.39 | 2.35 | 1.11 | 2.99 |
| | 79 | 11.23 | 17.93 | 10.14 | 54.71 | 19.20 | 34.06 | 20.83 | 3.26 | 1.81 | 5.27 |
| | 80 | 18.36 | 10.75 | 10.39 | 11.48 | 25.01 | 11.72 | 18.00 | 9.18 | 2.66 | 3.20 |
| M | | 0.45 | 0.45 | 0.45 | 0.45 | 0.45 | 0.45 | 0.45 | 0.45 | 0.45 | |

b) Option 2 - Modified weight-age
Laevastu-Cushing natural mortality

| | | | | | Age | | | | | | Effort |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | ($10^3$ days) |
| Catch | 73 | 52.66 | 9.11 | 20.46 | 37.87 | 23.70 | 21.67 | 20.25 | 9.72 | 4.25 | 6.31 |
| in | 74 | 1.00 | 153.94 | 21.09 | 36.48 | 45.51 | 26.44 | 11.71 | 3.68 | 1.67 | 8.68 |
| numbers | 75 | 2.58 | 3.54 | 123.03 | 20.93 | 22.54 | 36.39 | 16.43 | 7.09 | 3.54 | 11.52 |
| in | 76 | 32.25 | 28.01 | 28.32 | 177.49 | 26.43 | 13.22 | 4.72 | 0.94 | 0.32 | 9.21 |
| millions | 77 | 3.65 | 52.11 | 10.77 | 19.11 | 65.14 | 10.60 | 5.56 | 2.61 | 1.39 | 4.24 |
| | 78 | 4.07 | 7.74 | 47.08 | 8.92 | 18.88 | 35.41 | 5.11 | 2.23 | 1.05 | 2.99 |
| | 79 | 10.70 | 17.09 | 9.67 | 52.12 | 18.30 | 32.45 | 19.85 | 3.11 | 1.73 | 5.27 |
| | 80 | 17.65 | 10.33 | 9.99 | 11.03 | 24.03 | 11.26 | 17.30 | 8.82 | 2.55 | 3.20 |
| M | | .268 | .210 | .195 | .257 | .357 | .457 | .557 | .657 | .757 | |

corresponds to that reported in Bailey et al. (1982). Analyses were made using the backward solution (Tomlinson 1970) for each cohort assuming that each year ages 10 and 11 were exploited at the same rate. Pope (1972) shows that for a given cohort the error in the estimate of fishing mortality $F_i$ for some age i (and subsequently catchability $q_i$) is proportional to the expression

$$\rho(F_i) = \left( \frac{1 - e^{F_i}}{F_i} \right) e^{-\sum\limits_{k=i}^{t-1} F_k}$$

where

$F_k$ = estimates of fishing mortality for that cohort at ages k = i, ..., t-1, and

t = maximum age represented in the cohort analysis.

Letting

$W_{ij}$ = weighting factor for age i in year j

= $1 / \rho^2 (F_{ij})$,

the cohort analysis was performed by setting initial catchability coefficients.

$q_{i,1980}$; i = 3, ..., 10 such that if

$$\overline{q}_{i.} = \sum_{j=1973}^{1980} W_{ij} \, \hat{q}_{ij},$$

$$\text{Var}(\overline{q}_{i.}) = \frac{\sum\limits_{j=1973}^{1980} W_{ij} (q_{ij} - \overline{q}_{i.})^2}{7 \sum\limits_{j=1973}^{1980} W_{ij}} \, .$$

$$\overline{CW}_{i.} = \sum_{j=1973}^{1980} CW_{ij}, \text{ and}$$

$$CW_{ij} = \text{catch in weight of age } i \text{ in year } j.$$

then

$$\overline{CV} = \sum_{i=3}^{11} \overline{CW}_{i.} \sqrt{\frac{Var(\overline{q}_{i.})}{\overline{q}_{i.}}}$$

is minimized. Since the primary objective of the analysis is to estimate age-specific catchability coefficients for the simulation, the cohort analysis was performed to minimize the average coefficients of variations of these age-specific catchability coefficients. The weighting factors ($W_{ij}$) were chosen to give greater weight to the more precise estimates of $q_{ij}$. The results of the analyses are given in Table 4. It is interesting to note that the estimates of mean stock biomass for Option 1 are about two times what they are for Option 2. The estimates of total whiting biomass from the NWAFC trawl-hydroacoustic surveys of July-September 1977 and 1980 are 1.199 million t (Dark et al. 1980) and 1.519 million t (Marty Nelson and Thomas Dark, Northwest and Alaska Fisheries Center, Seattle, WA 98112. Pers. commun.), respectively. Certainly the survey estimates tend to correspond to the cohort analysis estimates of mean stock biomass much better when Option 2 is employed than when Option 1 is employed. It is apparent that if age-specific catchability has been relatively constant between 1973 and 1980 the cohort analysis

Table 4.—Summarized results of cohort analyses of Pacific whiting data.

| Year | Recruitment (millions) at age 3 | Mean stock biomass ($10^6$ mt) | Age i | $\overline{q}_i.$ |
|------|------|------|------|------|
| a) Option 1 — Standard weight-age Constant natural mortality | | | | |
| 1973 | 4,100 | 2.302 | 3 | .00197 |
| 1974 | 2,126 | 2.474 | 4 | .00620 |
| 1975 | 1,248 | 2.190 | 5 | .00829 |
| 1976 | 3,916 | 2.916 | 6 | .01993 |
| 1977 | 936 | 2.386 | 7 | .03044 |
| 1978 | 1,295 | 2.131 | 8 | .04897 |
| 1979 | 1,115 | 1.858 | 9 | .05329 |
| 1980 | 3,575 | 2.593 | 10 | .04835 |
| Mean | 2,289 | 2.356 | | |
| CV | 0.593 | 0.135 | | |
| b) Option 2 — Modified weight-age Laevastu-Cushing natural mortality | | | | |
| 1973 | 1,736 | 1.125 | 3 | .00450 |
| 1974 | 673 | 1.265 | 4 | .01185 |
| 1975 | 388 | 1.210 | 5 | .01416 |
| 1976 | 1,255 | 1.454 | 6 | .03072 |
| 1977 | 300 | 1.275 | 7 | .04290 |
| 1978 | 434 | 1.182 | 8 | .07121 |
| 1979 | 410 | 1.062 | 9 | .07711 |
| 1980 | 1,582 | 1.450 | 10 | .06982 |
| Mean | 847 | 1.253 | | |
| CV | 0.691 | 0.113 | | |

indicates that stock biomass has remained relatively constant over that time interval. Finally it is interesting to correlate the estimates of recruitment at age 3 ($R_3$) provided by the cohort analyses with Bailey's corresponding year class index (YCI) (Kevin Bailey, University of Washington, Seattle, WA 98195. Pers. commun.) based on environmental conditions at the time of spawning.

| Year class | YCI | Option 1 | $R_3$ ($10^6$ individuals) Option 2 |
|---|---|---|---|
| 1970 | 71.3 | 4,100 | 1,736 |
| 1971 | 11.7 | 2,126 | 673 |
| 1972 | 13.6 | 1,248 | 388 |
| 1973 | 117.7 | 3,916 | 1,255 |
| 1974 | 19.5 | 936 | 300 |
| 1975 | 14.2 | 1,295 | 434 |
| 1976 | 14.1 | 1,115 | 410 |
| 1977 | 38.9 | 3,575 | 1,582 |

The linear correlations are $r = 0.804$ for Option 1 and $r = 0.691$ for Option 2.

## MIGRATION

The annual migration cycle of Pacific whiting is described by Alverson and Larkins (1969) and Bailey et al (1982). Adults spawn during the winter and early spring, primarily in waters beyond the continental shelf of southern California (south of Point Conception) and Baja California. Adult feeding takes place inshore along the coasts of northern California, Oregon, Washington, and Vancouver Island during the spring, summer, and early autumn.

Figure 13 gives a schematic representation of the whiting migration as it is represented in the simulation model. The simulated spawning migration takes place over a 2 mo period (November, December) and the simulated feeding migration over a 6 mo period (February-July). It is assumed that animals migrating north migrate through the inshore fishing grounds over the continental shelf. The average distance an animal of a given age migrates is a function of its average size with the larger animals tending to migrate farther to the north.

For a given age i, the instantaneous migration rate is calculated after a model of Bledsoe (L. J. Bledsoe, University of Washington, Seattle, WA 98195. Pers. commun.) for North Pacific albacore (reported in Kume and Bartoo 1981) as follows.

$I_i^{j-1,j}(t)$ = instantaneous migration rate of age group i from area j-1 to area j at time t

$$= \frac{a_i^j}{b_i^j \sqrt{2\pi}} \, e^{-\frac{1}{2} \frac{(t - t_{oi}^j)}{(b_i^{j-1})^2}}$$

$a_i^j$ = total instantaneous migration of age i from area j-1 to area j

$t_{oi}^j$ = time of maximum migration from area j-1 into area j (mean of t)

$b_i^j$ = standard deviation of t

$$= \sqrt{\sum_{k=2}^{j-1} \left( \frac{MR_i^k}{4} \right)^2}$$

$MR_i^k$ = mean residence of age i in area k.

Southern Spawning
Migration
November — December

Continental Shelf Area
Northern Feeding Migration
February — July

Vancouver (6)

Columbia (5)

Eureka (4)

Feeding Ground
March — October

Monterey (3)

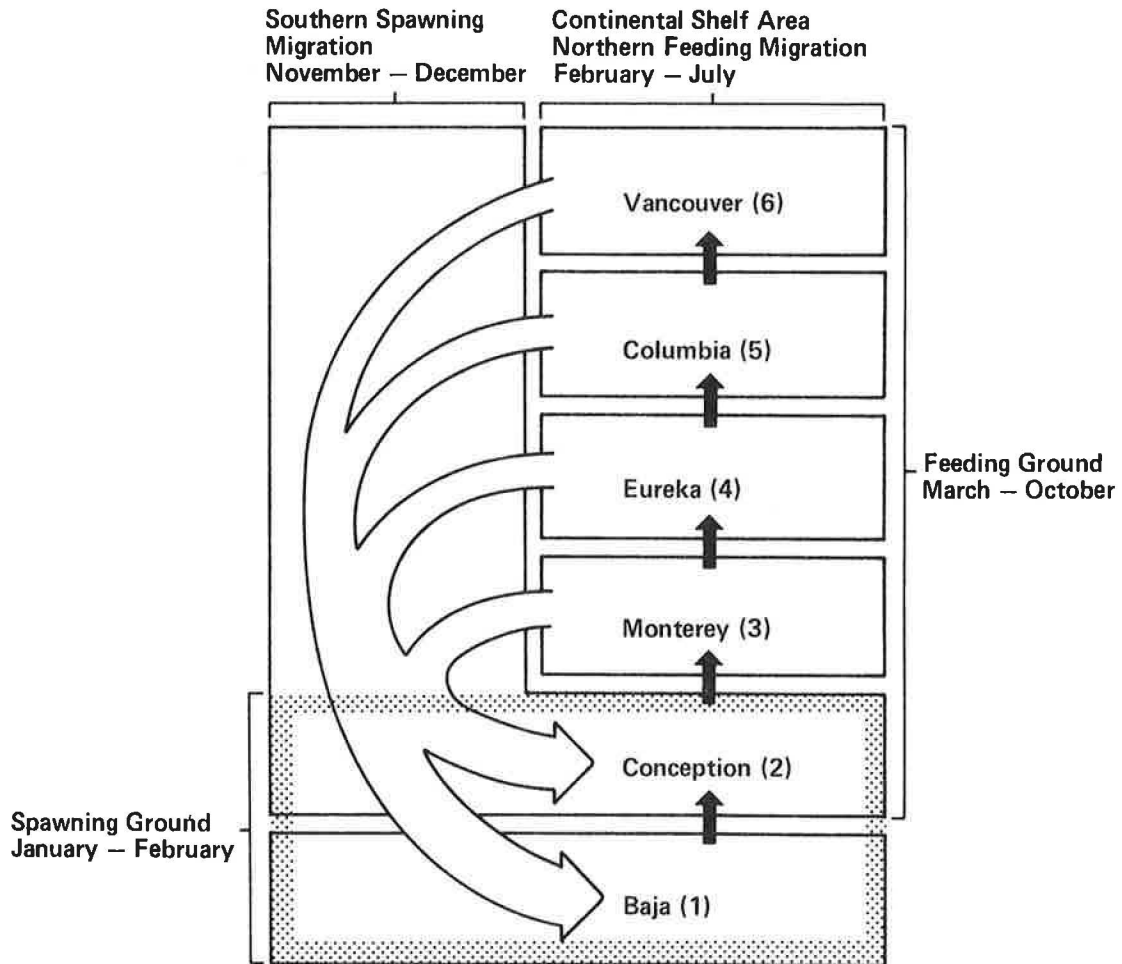Conception (2)

Spawning Ground
January — February

Baja (1)

Figure 13.--The annual migration cycle of Pacific whiting.

Thus northern feeding migration between two adjacent areas j-1 and j is normally distributed with a specified time of peak migration and a variance based on the mean residence times in those and previously occupied areas. The parameters of the model were estimated from results of the July-September 1977 NWAFC groundfish survey (Dark et al. 1980). The relative whiting distribution over area by age for the survey is given in Table 5. From these, and the estimated distances between areas ($m_j$), the mean distance traveled for each age ($d_i$) can be calculated. Then, assuming that on the average it takes an animal 120 days (4 months) to travel that distance, the mean swimming speed ($s_i$) was calculated. These are also given in Table 5. Parameters for the model were then calculated (Table 6) assuming that the areal distributions reflected by the survey are indicative of stable distributions on the feeding grounds after the feeding migration is complete.

Plots of the relative areal distribution of ages 3 and 7 whiting (unexploited) as a function of time of the year are given in Figures 14 and 15. The spawning migration for all ages is assumed to start at the beginning of November and last through December. Little is known about the relative distribution of the spawning population between the southern California (Conception) and Baja California (Baja) spawning grounds. To accommodate the hypothesis of Smith[1], that large adults spawn farther south, the age-specific distribution of whiting on the Baja ground was assumed to be the same (mirror image) as the distribution of those same adults on the Vancouver feeding ground.

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[1]   Smith, P.  Pacific hake larval distribution and abundance, 1951-1975.
      Southwest Fish. Cent. Admin. Rep. LJ-75-83.  Southwest Fish. Cent., Natl.
      Mar. Fish. Serv., NOAA, P. O. Box 271, La Jolla, CA 92038.

Table 5.--The 1977 groundfish survey data used to estimate migration parameters of Pacific whiting.

| Age | Vancouver | Columbia | Eureka | Monterey | Conception | $\bar{d}_i$ | $\bar{s}_i$ |
|-----|-----------|----------|--------|----------|------------|-------------|-------------|
| 2 | .000 | .003 | .216 | .768 | .012 | 356 | 2.967 |
| 3 | .000 | .049 | .431 | .477 | .042 | 427 | 3.558 |
| 4 | .141 | .153 | .446 | .257 | .003 | 585 | 4.875 |
| 5 | .273 | .227 | .433 | .066 | .001 | 703 | 5.858 |
| 6 | .276 | .331 | .320 | .072 | .000 | 725 | 6.042 |
| 7 | .366 | .297 | .275 | .062 | .000 | 756 | 6.300 |
| 8 | .306 | .408 | .232 | .052 | .001 | 757 | 6.308 |
| 9 | .365 | .379 | .213 | .042 | .001 | 777 | 6.475 |
| 10 | .189 | .483 | .256 | .071 | .002 | 723 | 6.025 |
| 11 | .282 | .380 | .224 | .112 | .003 | 726 | 6.050 |
| 12 | .021 | .767 | .087 | .125 | .001 | 703 | 5.858 |
| $m_j$ | 957 | 777 | 567 | 303 | 0 | | |

$m_j$ = estimated distance from spawning ground to center of area j (nautical miles)

$\bar{d}_i$ = mean distance traveled for age i (nautical miles)

$\bar{s}_i$ = mean swimming speed (nautical miles/day)

Table 6.--Migration parameter estimates for Pacific whiting.

| Age | | Conception $j = 2$ | Monterey $j = 3$ | Eureka $j = 4$ | Columbia $j = 5$ | Vancouver $j = 6$ |
|---|---|---|---|---|---|---|
| 2 | $MR_2^j$ | 38 | 128 | 51 | 83 | |
| | $a_2^j$ | | 4.423 | 0.252 | 0.014 | 0.000 |
| | $b_2^j$ | | 9.50 | 33.38 | 35.73 | 41.32 |
| | $t_{o2}^j$ | | 79 | 162 | 252 | 319 |
| 3 | $MR_3^j$ | 32 | 107 | 42 | 76 | |
| | $a_3^j$ | | 3.170 | 0.697 | 0.108 | 0.000 |
| | $b_3^j$ | | 8.00 | 27.92 | 29.83 | 35.37 |
| | $t_{o3}^j$ | | 76 | 146 | 220 | 279 |
| 4 | $MR_4^j$ | 23 | 77 | 31 | 55 | |
| | $a_4^j$ | | 5.809 | 1.356 | 0.506 | 0.653 |
| | $b_4^j$ | | 5.85 | 20.30 | 21.71 | 25.75 |
| | $t_{o4}^j$ | | 72 | 122 | 176 | 219 |
| 5 | $MR_5^j$ | 19 | 65 | 26 | 46 | |
| | $a_5^j$ | | 6.908 | 2.717 | 0.768 | 0.790 |
| | $b_5^j$ | | 4.87 | 16.89 | 18.06 | 21.42 |
| | $t_{o5}^j$ | | 70 | 112 | 157 | 193 |
| 6 | $MR_6^j$ | 19 | 63 | 25 | 45 | |
| | $a_6^j$ | | 4.605 | 2.631 | 1.064 | 0.606 |
| | $b_6^j$ | | 4.72 | 16.37 | 17.51 | 20.77 |
| | $t_{o6}^j$ | | 69 | 110 | 154 | 189 |

Table 6.--(Continued)

| Age | | Conception $j = 2$ | Monterey $j = 3$ | Eureka $j = 4$ | Columbia $j = 5$ | Vancouver $j = 6$ |
|---|---|---|---|---|---|---|
| 7 | $MR_7{}^j$ | 18 | 60 | 24 | 43 | |
| | $a_7{}^j$ | | 4.605 | 2.781 | 1.227 | 0.803 |
| | $b_7{}^j$ | | 4.50 | 15.66 | 16.77 | 19.92 |
| | $t_{o7}{}^j$ | | 69 | 108 | 150 | 183 |
| 8 | $MR_8{}^j$ | 18 | 60 | 24 | 43 | |
| | $a_8{}^j$ | | 6.908 | 2.956 | 1.406 | 0.560 |
| | $b_8{}^j$ | | 4.52 | 15.69 | 16.77 | 19.89 |
| | $t_{o8}{}^j$ | | 69 | 108 | 150 | 183 |
| 9 | $MR_9{}^j$ | 18 | 59 | 23 | 42 | |
| | $a_9{}^j$ | | 6.908 | 3.169 | 1.503 | 0.675 |
| | $b_9{}^j$ | | 4.40 | 15.28 | 16.34 | 19.38 |
| | $t_{o9}{}^j$ | | 69 | 107 | 148 | 180 |
| 10-12* | $MR_i{}^j$ | 17 | 57 | 23 | 41 | |
| | $a_i{}^j$ | | 7.601 | 3.507 | 1.558 | 0.680 |
| | $b_i{}^j$ | | 4.27 | 14.84 | 15.87 | 18.82 |
| | $t_{oi}{}^j$ | | 69 | 106 | 145 | 177 |

* assumed $\left.\begin{array}{l} \bar{d}_i = 800 \\ \bar{s}_i = 6.667 \end{array}\right\}$ $i = 10, \ldots, 12$
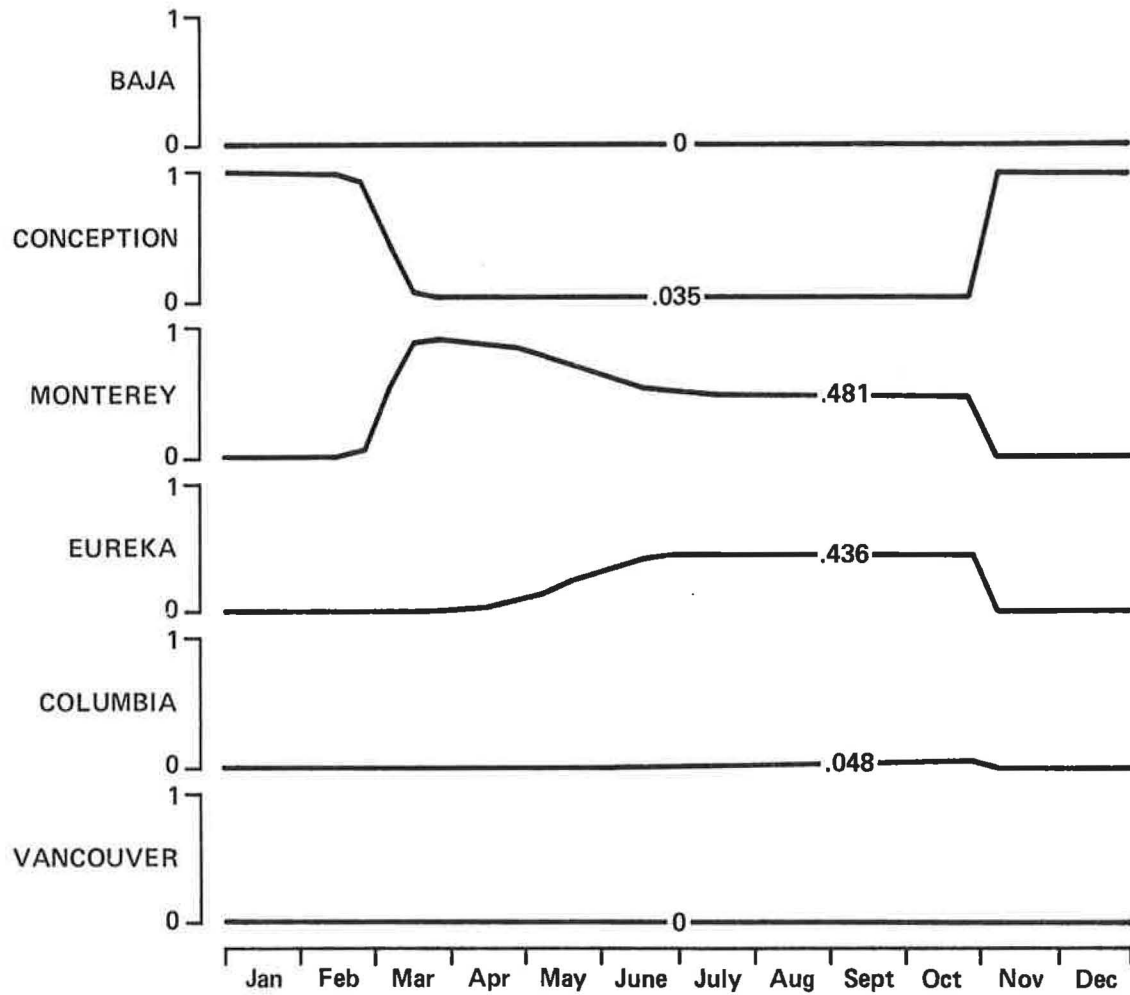
Figure 14.--Simulated relative areal distribution of age 3 Pacific whiting.
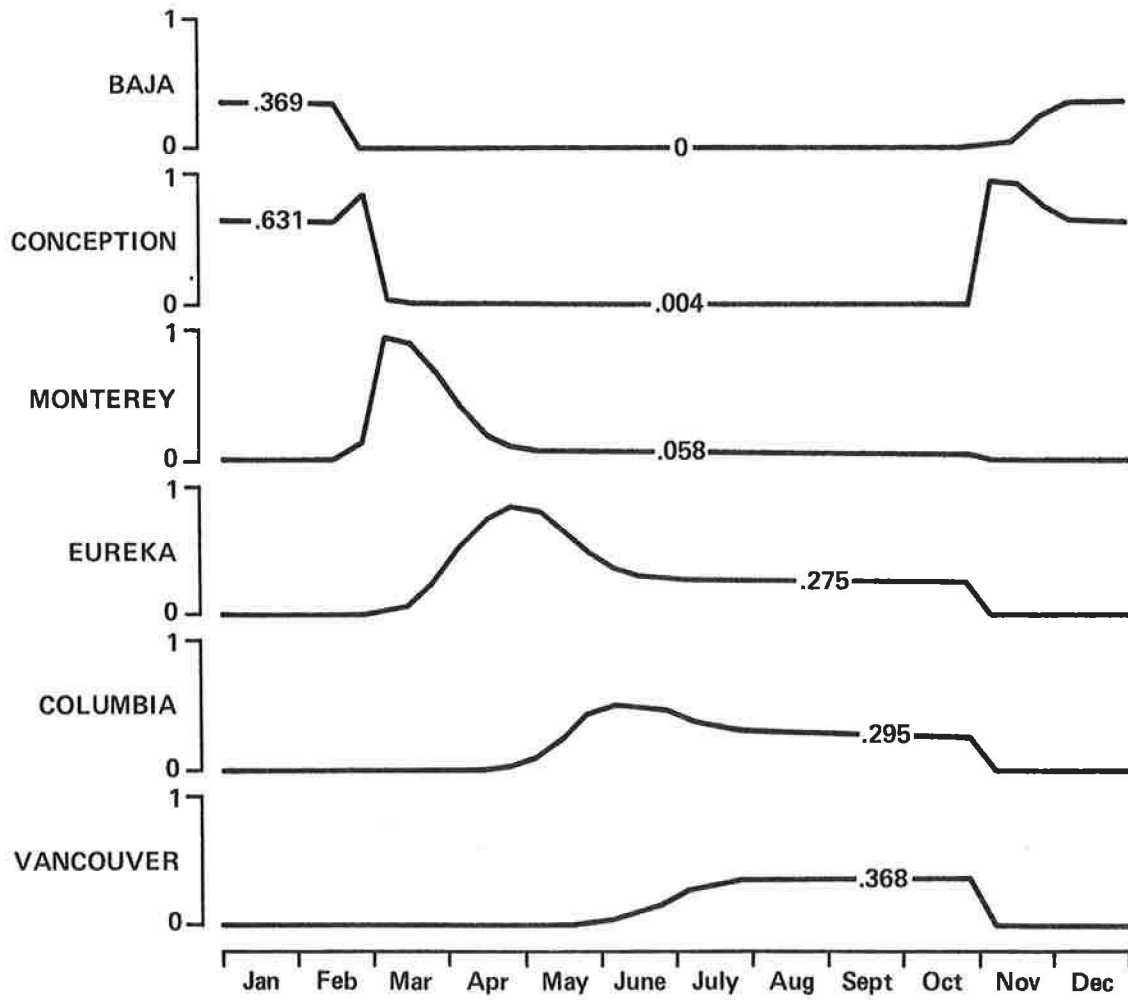
Figure 15.--Simulated relative areal distribution of age 7 Pacific whiting.

## MODEL CALIBRATION AND VALIDATION

Francis (1977) describes the process of model validation as a subjective pursuit which, more than anything else, helps display the modeler's intuition concerning the most suitable analytic form or parameter values for attaining specific objectives. In the case of HAKE, the primary calibration and validation criteria are the ability of the model to mimic the areal, time, and age distribution of the observed catch during 1977-80, the only years for which these statistics are available in any reliable detail. The calibration-validation run of the model was made for 1977-80 with:

1) Initial age-specific population numbers (1977) derived from the cohort analysis.

2) Recruitment numbers derived from the cohort analysis back calculated to the beginning of age 2.

3) Effort taken from Table 7.

4) Estimates of average age-specific catchability from the cohort analysis adjusted as follows:

For a given year 1 let

$_1q_{ij'k}$ = catchability of age i in area j´ during quarter k.

  j´ = 1 for the southern two fishing areas (Monterey, Eureka)

  j´ = 2 for the northern two fishing areas (Columbia, Vancouver),

$_1\hat{q}_i$ = estimated catchability from the cohort analysis;

$_1YN_{ij'}$ = yield in numbers,

$_1YN_{i\cdot}$ = $\sum\limits_{j} YN_{ij'}$,

$_1f_{j'}$ = effort in area j´,

$_1f_{\cdot}$ = $\sum\limits_{j} f_{j'}$ , and

$\rho_{ij'}$ = fraction of age i whiting contained in area j´ (from 1977 survey)

Table 7.--Observed total catch (1000s of metric tons), effort (1000 standard BMRT[1]/ days on ground), and CPUE for Pacific whiting, 1977-80.

| Year | Quarter | | Vancouver | Columbia | Eureka | Monterey | Total |
|------|---------|-----|-----------|----------|--------|----------|-------|
| 1977 | 2 | C | - | 20.738 | 1.774 | - | 22.512 |
|      |   | f | - | 0.506 | 0.064 | - | 0.570 |
|      |   | C/f | | 40.98 | 27.72 | | 39.50 |
|      | 3 | C | 2.590 | 54.406 | 39.775 | - | 96.771 |
|      |   | f | 0.084 | 2.146 | 1.082 | - | 3.312 |
|      |   | C/f | 31.02 | 25.35 | 36.76 | | 29.22 |
|      | 4 | C | 2.590 | 10.339 | - | - | 12.929 |
|      |   | f | 0.084 | 0.275 | - | - | 0.359 |
|      |   | C/f | 31.02 | 37.60 | | | 36.01 |
|      |   | C | 5.180 | 85.483 | 41.549 | - | 132.212 |
|      |   | f | 0.168 | 2.927 | 1.147 | - | 4.242 |
|      |   | C/f | 31.02 | 29.21 | 36.22 | | 31.17 |
| 1978 | 2 | C | - | 13.502 | 13.523 | 0.750 | 27.775 |
|      |   | f | - | 0.331 | 0.289 | 0.031 | 0.651 |
|      |   | C/f | | 40.79 | 46.79 | 24.13 | 42.67 |
|      | 3 | C | 3.225 | 46.924 | 12.367 | - | 62.516 |
|      |   | f | 0.091 | 1.526 | 0.321 | - | 1.938 |
|      |   | C/f | 35.44 | 30.75 | 38.53 | | 32.26 |
|      | 4 | C | 3.225 | 10.563 | - | - | 13.788 |
|      |   | f | 0.091 | 0.309 | - | - | 0.400 |
|      |   | C/f | 35.44 | 34.19 | | | 34.47 |
|      |   | C | 6.450 | 70.989 | 25.890 | 0.750 | 104.079 |
|      |   | f | 0.182 | 2.166 | 0.610 | 0.031 | 2.989 |
|      |   | C/f | 35.44 | 32.77 | 42.44 | 24.13 | 34.82 |
| 1979 | 2 | C | - | 10.237 | 20.838 | 0.214 | 31.289 |
|      |   | f | - | 0.603 | 0.443 | 0.004 | 1.050 |
|      |   | C/f | | 16.97 | 47.04 | 53.50 | 29.80 |
|      | 3 | C | 6.065 | 60.729 | 26.292 | 0.071 | 93.157 |
|      |   | f | 0.201 | 2.701 | 0.830 | 0.002 | 3.734 |
|      |   | C/f | 30.25 | 22.48 | 31.68 | 35.50 | 24.95 |
|      | 4 | C | 6.065 | 5.334 | - | - | 11.399 |
|      |   | f | 0.201 | 0.279 | - | - | 0.480 |
|      |   | C/f | 30.25 | 19.12 | | | 23.75 |
|      |   | C | 12.130 | 76.300 | 47.130 | 0.285 | 135.845 |
|      |   | f | 0.402 | 3.583 | 1.273 | 0.006 | 5.264 |
|      |   | C/f | 30.25 | 21.30 | 37.02 | 47.50 | 25.81 |

Table 7.--(Continued)

| Year | Quarter | | Vancouver | Columbia | Eureka | Monterey | Total |
|------|---------|-----|-----------|----------|--------|----------|-------|
| 1980 | 2 | C | - | 7.320 | 1.655 | - | 8.975 |
| | | f | - | 0.322 | 0.034 | - | 0.356 |
| | | C/f | | 22.73 | 48.68 | | 25.21 |
| | 3 | C | 9.560 | 37.990 | 9.545 | - | 57.095 |
| | | f | 0.173 | 1.235 | 0.592 | - | 2.000 |
| | | C/f | 55.26 | 30.76 | 16.12 | | 28.55 |
| | 4 | C | 9.560 | 12.780 | 2.290 | - | 24.630 |
| | | f | 0.173 | 0.432 | 0.237 | - | 0.842 |
| | | C/f | 55.26 | 29.58 | 9.67 | | 29.25 |
| | | C | 19.120 | 58.090 | 13.490 | - | 90.700 |
| | | f | 0.346 | 1.989 | 0.863 | - | 3.198 |
| | | C/f | 55.26 | 29.21 | 15.63 | | 28.36 |

1/ BMRT = Soviet type factory trawler

If

$$_1YN_{ij'} = {_1q_{ij'}} \cdot {_1f_{j'}} \; \rho_{ij'} \; {_1\overline{N}_{i\cdot}}$$

$$_1YN_{i\cdot} = {_1q_{i\cdot\cdot}} \; {_1f_{\cdot}} \; {_1\overline{N}_i},$$

then

$$_1\hat{q}_{ij'\cdot} = \frac{_1YN_{ij'} \; {_1q_{i\cdot\cdot}} \; {_1f_{\cdot}}}{_1YN_{i\cdot} \; \rho_{ij'} \; {_1f_{j'}}},$$

and

$$_{\cdot}\hat{q}_{ij'\cdot} = {_1\hat{q}_{ij'\cdot}}.$$

This gives an estimate of average age-specific catchability for the southern and northern two fishing areas.

The model was then run for 1977 and 1978 and calibrated by employing time-specific availability factors for each of the two areas in such a manner that

$$q_{ij'k} = {_{\cdot}\hat{q}_{ij'\cdot}} \; a_{j'k}.$$

The values of $\{a_{j'k} : j' = 1,2, \; k = Q2, Q3, Q4\}$ were adjusted (calibration) to give the best fit of the simulated to the observed catches and age-structures for 1977 and 1978. For validation purposes, the model was then allowed to run for 1979 and 1980 with the observed effort  The observed and simulated catches, in particular for the Eureka and Columbia areas, are given in Tables 7, 8, and 9. The final parameter values of catchability and availability are given in Table 10. The model was run in two modes--HAKE/MØD1 uses standard weight-age and constant natural mortality; HAKE/MØD2 uses modified weight-age and Laevastu-Cushing natural mortality. The relative fit for the two modes is approximately the same. If the availability factors are adjusted for the number of months effort is applied for a given quarter (assuming the fishery operates from May through October each year), the following results:

Table 8.--Observed age-composition of Pacific whiting catch in Columbia and Eureka, 1977-80.

| Year | Age | Columbia | Eureka | Year | Age | Columbia | Eureka |
|------|-----|----------|--------|------|-----|----------|--------|
| 1977 | 2 | .006 | .018 | 1978 | 2 | -- | -- |
|  | 3 | .014 | .034 |  | 3 | .016 | .067 |
|  | 4 | .245 | .403 |  | 4 | .043 | .096 |
|  | 5 | .054 | .076 |  | 5 | .332 | .424 |
|  | 6 | .114 | .104 |  | 6 | .061 | .084 |
|  | 7 | .416 | .301 |  | 7 | .156 | .117 |
|  | 8 | .077 | .030 |  | 8 | .311 | .176 |
|  | 9 | .037 | .022 |  | 9 | .048 | .020 |
|  | 10 | .020 | .007 |  | 10 | .019 | .011 |
|  | 11 | .012 | .003 |  | 11 | .010 | .004 |
|  | 12 | .004 | .002 |  | 12 | .004 | .002 |
| 1979 | 2 | .047 | .039 | 1980 | 2 | -- | -- |
|  | 3 | .034 | .098 |  | 3 | .080 | .370 |
|  | 4 | .037 | .181 |  | 4 | .056 | .191 |
|  | 5 | .036 | .081 |  | 5 | .091 | .079 |
|  | 6 | .289 | .318 |  | 6 | .085 | .128 |
|  | 7 | .123 | .084 |  | 7 | .247 | .100 |
|  | 8 | .225 | .139 |  | 8 | .118 | .040 |
|  | 9 | .170 | .042 |  | 9 | .182 | .061 |
|  | 10 | .022 | .012 |  | 10 | .094 | .029 |
|  | 11 | .015 | .003 |  | 11 | .029 | .001 |
|  | 12 | .002 | .003 |  | 12 | .018 | -- |

Table 9.--Simulated total catch of Pacific whiting, 1977-80.

| Year | Quarter | Vancouver | Columbia | Eureka | Monterey | Total |
|------|---------|-----------|----------|--------|----------|-------|
| a) HAKE/MØD1 | | | | | | |
| 1977 | 2 | - | 19.055 | 2.351 | - | 21.406 |
| | 3 | 1.775 | 55.922 | 41.810 | - | 99.507 |
| | 4 | 3.278 | 8.893 | - | - | 12.171 |
| | Total | 5.053 | 83.870 | 44.161 | - | 133.084 |
| 1978 | 2 | - | 14.647 | 11.598 | 0.486 | 26.730 |
| | 3 | 2.164 | 43.520 | 12.848 | - | 58.532 |
| | 4 | 3.839 | 11.182 | - | - | 15.021 |
| | Total | 6.003 | 69.349 | 24.446 | 0.486 | 100.283 |
| 1979 | 2 | - | 24.856 | 16.384 | 0.072 | 41.313 |
| | 3 | 4.127 | 68.174 | 29.382 | 0.036 | 101.720 |
| | 4 | 7.188 | 8.485 | - | - | 15.674 |
| | Total | 11.316 | 101.516 | 45.766 | 0.109 | 158.707 |
| 1980 | 2 | - | 13.874 | 1.230 | - | 15.104 |
| | 3 | 4.109 | 32.700 | 22.474 | - | 59.283 |
| | 4 | 7.092 | 14.686 | 2.050 | - | 23.828 |
| | Total | 11.201 | 61.260 | 25.754 | - | 98.216 |
| b) HAKE/MØD2 | | | | | | |
| 1977 | 2 | - | 19.573 | 2.384 | - | 21.956 |
| | 3 | 1.910 | 58.139 | 40.367 | - | 100.416 |
| | 4 | 3.678 | 9.424 | - | - | 13.102 |
| | Total | 5.588 | 87.135 | 42.750 | - | 135.474 |
| 1978 | 2 | - | 14.310 | 11.321 | 0.437 | 26.068 |
| | 3 | 2.199 | 43.699 | 12.108 | - | 58.006 |
| | 4 | 4.079 | 11.440 | - | - | 15.519 |
| | Total | 6.278 | 69.450 | 23.429 | 0.453 | 99.593 |
| 1979 | 2 | - | 22.910 | 15.477 | 0.065 | 38.452 |
| | 3 | 3.947 | 64.467 | 26.995 | 0.032 | 95.440 |
| | 4 | 7.157 | 8.120 | - | - | 15.278 |
| | Total | 11.104 | 95.496 | 42.471 | 0.097 | 149.169 |
| 1980 | 2 | - | 12.226 | 1.124 | - | 13.350 |
| | 3 | 3.808 | 30.220 | 20.691 | - | 54.719 |
| | 4 | 6.871 | 13.875 | 2.084 | - | 22.830 |
| | Total | 10.679 | 56.321 | 23.898 | - | 90.898 |

Table 10.--Estimates of catchability and availability of Pacific whiting.

$q_{ij'}.$

| Age i | $j' = 1$ Monterey, Eureka | | $j' = 2$ Columbia, Vancouver | |
|---|---|---|---|---|
| | MØD1 | MØD2 | MØD1 | MØD2 |
| 2 | .005 | .010 | .001 | .002 |
| 3 | .010 | .020 | .002 | .005 |
| 4 | .018 | .040 | .013 | .029 |
| 5 | .031 | .058 | .014 | .027 |
| 6 | .050 | .076 | .018 | .028 |
| 7 | .107 | .133 | .054 | .066 |
| 8 | .179 | .210 | .085 | .098 |
| 9 | .131 | .152 | .073 | .084 |
| 10 | .124 | .143 | .054 | .068 |
| 11 | .079 | .082 | .058 | .067 |
| 12 | .080 | .091 | .060 | .067 |

Availability (Raw)

$a_{j'k}$

| | Quarter (k) | $j' = 1$ Monterey, Eureka | $j' = 2$ Columbia, Vancouver |
|---|---|---|---|
| MØD1 | Q2 | 0.679 | 4.677 |
| | Q3 | 1.332 | 2.164 |
| | Q4 | - | 10.898 |
| MØD2 | Q2 | 0.700 | 4.770 |
| | Q3 | 1.238 | 2.199 |
| | Q4 | - | 11.449 |

Standard availability

|        | Quarter | Monterey, Eureka | Columbia, Vancouver |
|--------|---------|------------------|---------------------|
| MØD1   | 2       | 0.453            | 3.118               |
|        | 3       | 1.332            | 2.164               |
|        | 4       | --               | 3.633               |
| MØD2   | 2       | 0.467            | 3.180               |
|        | 3       | 1.238            | 2.199               |
|        | 4       | --               | 3.816               |

The trend of these standard availability factors over time of the year reflects the movement of the fishing fleet. The fishery begins in May, June, and July in southern Columbia and Eureka and then moves north into Columbia and Vancouver in August, September, and October until the fish start their spawning migration moving offshore and then south from the fishing grounds. The Soviet hydro-acoustic survey of 1978 (Stepanenko 1979) certainly reflects this with an estimated order of magnitude increase in biomass of whiting in Columbia between June-July and August-September.

## BIOENERGETICS

The design of HAKE makes it useful for examining the bioenergetics of the coastal stock of Pacific whiting. The model incorporates sufficient resolution to reflect the interaction between age structure and migration, important factors in bioenergetic calculations.

For a given time interval, dt, and area, i, knowledge of the age-structure and growth of the whiting occupying that area drives the calculation of biomass consumed by whiting. Suppose we have a fish of average weight Wg (grams). Then, based on Jones and Johnston (1977) and Sharp and Francis (1976):

$$FE = \text{food energy intake (Kcal/dt)}$$

$$= GE + ME, \text{ and}$$

$$GE = \text{energy demands for growth and reproduction (Kcal/dt)}$$

$$= GG/\varepsilon$$

where

$$GG = \text{gross growth (g/dt)}$$

$$\varepsilon = \text{gross growth efficiency (g/Kcal)}$$

$$= .79\ \overline{Wg}^{-.15} \quad \text{(Jones and Johnston 1977),}$$

$$ME = \text{energy for maintenance}$$

$$= (.01904)\ DDT\ \overline{Wg}^{.8}\ \text{(Kcal/dt)} \quad \text{(Jones and Johnston 1977), and}$$

$$DDT = \text{number of dt's per day}$$

Then, if 1 g wet food intake = 1 Kcal (Sharp and Francis 1976),

$$FC = \text{wet weight of food ingested (g/dt)}$$

$$= FE$$

Typical values for daily consumption of 2-, 4-, 6-, and 8-yr old whiting during the spring-summer (April-September) growth period, using MØD2 parameters are given below:

| Age | Wg (grams) | GG (yr/day) | (g/Kcal) | GE (Kcal/day) | ME (Kcal/day) | FC (g/day) | BWD(%) |
|-----|-----|-----|-----|-----|-----|-----|-----|
| 2 | 336 | 0.553 | .33 | 1.676 | 3.675 | 3.675 | 1.094 |
| 4 | 594 | 0.734 | .30 | 2.423 | 3.153 | 5.575 | 0.939 |
| 6 | 778 | 0.663 | .29 | 2.278 | 3.912 | 6.190 | 0.796 |
| 8 | 880 | 0.559 | .29 | 1.956 | 4.318 | 6.274 | 0.713 |

Note that these estimates are only for the portion (April-September) of the year where significant feeding occurs.

It is interesting to compare the estimated percentage body weight consumed per day (BWD) from the above table with published values of other gadids. Remember that the above whiting values are for their feeding-growing season whereas the values given below are annual.

| Source | Species | | BWD(%) |
|--------|---------|---|--------|
| Cohen et al. (1979) | Silver hake | 1964-1966 | 1.324 |
| | | 1973-1975 | 1.342 |
| Cohen et al. (1979) | Cod | 1964-1966 | 0.777 |
| | | 1973-1975 | 0.904 |
| Jones & Johnston (1977) | Cod  -  | Wg = 987 | 1.134 |
| | | Wg = 594 | 1.397 |
| | | Wg = 363 | 0.715 |
| | | $\overline{\text{Wg}}$ = 648 | 1.150 |

In order to make estimates of whiting population bioenergetics, annual production (P), production to average biomass ratio ($P/\overline{B}$), consumption (C), and consumption to average biomass ratio ($C/\overline{B}$) similar to Cohen et al. (1979) were calculated from HAKE for 1973 through 1980. In this paper, production is defined as the addition of biomass due to growth and reproduction (gross growth). Annual computations were made by INPFC area. Geometric mean annual $P/\overline{B}$, $C/\overline{B}$, and $R/\overline{B}$ (recruitment to biomass) ratios were calculated for the 8-year period. Parallel runs of the model were made in exploited (E) and unexploited (U) modes. The exploited mode starts in January 1973 with the initial conditions estimated by the cohort analysis and imposes the observed 1973-1980 fishing effort on the stock. The unexploited mode starts in January 1973 with the stock in unexploited equilibrium, based on average observed recruitment from the 1973-1980 cohort analysis (MØD2), and runs an unexploited simulation inputting the appropriate estimated recruitment values derived from

the cohort analysis. In order to compare bioenergetic estimates using the two different representations of growth (standard and modified weight-age), two separate sets of simulations were made. The results of the analysis are summarized in the following table.

| | | | | Mean percent composition | | | | |
|---|---|---|---|---|---|---|---|---|
| Mode | Growth | | Total (1000 t) | Baja-Conception | Monterey | Eureka | Columbia | Vancouver |
| Exploited | Standard | $\overline{B}$ | 1,532 | 35 | 32 | 22 | 7 | 4 |
| | | $\overline{P}$ | 322 | 37 | 40 | 18 | 4 | 1 |
| | | $\overline{R}$ | 260 | 100 | - | - | - | - |
| | | $\overline{C}$ | 2,206 | 36 | 36 | 20 | 5 | 3 |
| | Modified | $\overline{B}$ | 1,548 | 35 | 31 | 23 | 7 | 4 |
| | | $\overline{P}$ | 356 | 3 | 55 | 33 | 8 | 1 |
| | | $\overline{R}$ | 260 | 100 | - | - | - | - |
| | | $\overline{C}$ | 2,337 | 19 | 42 | 28 | 8 | 3 |
| Unexploited | Standard | $\overline{B}$ | 1,945 | 35 | 27 | 22 | 10 | 6 |
| | | $\overline{P}$ | 331 | 36 | 38 | 18 | 5 | 3 |
| | | $\overline{R}$ | 260 | 100 | - | - | - | - |
| | | $\overline{C}$ | 2,567 | 36 | 32 | 21 | 8 | 3 |
| | Modified | $\overline{B}$ | 1,964 | 34 | 27 | 23 | 10 | 6 |
| | | $\overline{P}$ | 353 | - 4 | 53 | 37 | 11 | 3 |
| | | $\overline{R}$ | 260 | 100 | - | - | - | - |
| | | $\overline{C}$ | 2,749 | 18 | 37 | 29 | 11 | 5 |

The following points are of interest to note:

1) Average biomass would have been 27% greater under virgin (unexploited conditions) than under the observed fishing patterns. Most of that increased biomass would have occurred in the northern areas.

2) Production due to growth would have been approximately the same in the exploited and unexploited situation; however, it is estimated to be, on the average, 9% greater under modified growth than under standard growth.

3) The distribution of production is weighted much more heavily toward the feeding areas (Monterey, Eureka, Columbia, and Vancouver) under modified growth than under standard growth.

4) Consumption would have been 17% greater under unexploited conditions than under the observed exploited condition and only 7% greater under modified growth than under standard growth.

5) As with production, the distribution of consumption is weighted more heavily toward the summer feeding areas under modified growth than under standard growth.

I believe that the simulations of bioenergetics under the modified growth are a much more realistic representation than under standard growth. This is further indicated because whiting do not feed extensively on the winter spawning grounds off the Conception and Baja California areas. Thus they must lose weight in winter and regain it during the spring-summer-fall feeding period. Under modified growth, the average (geometric mean of exploited and unexploited ratios) ratio of total production to biomass (P+R/B) is 35% per year (around 600 thousand t total production under both exploited and unexploited conditions). It is interesting that, apparently, only about one-third of that production can be diverted into the fishery. It is of further interest to speculate on the relationship and implications of these estimates to those of

Laevastu and Favorite (1977). They calculate an ecosystem internal consumption at minimum sustainable equilibrium levels for west coast roundfish, of which whiting is the major component, at 82% per year. In an unexploited population of 1,964 thousand t, this would translate into an ecosystem internal consumption of post-recruit (ages 2+) of around 1.6 million t. Since total production of the unexploited 2+ stock is estimated to be only around 600 thousand t per year and the fishery is capable of taking, at most, around 200 thousand t on a sustained basis (Francis et al. 1982), this implies an ecosystem internal consumption of 2+ whiting of no more than 400 thousand t, or about 20% of the average biomass, per year. The most likely reason for the discrepancy between these two approaches for estimating production is that Laevastu and Favorite (1977) are estimating ecosystem internal consumption of both adults and juveniles (50% of their roundfish biomass is in pre-fishing juveniles) and that the consumption of juveniles is much higher than that of adults, whereas I am estimating consumption of adults only. It is interesting to note that if ecosystem internal consumption of a particular species is approximately equal to that which it consumes, corrected for trophic efficiency, then if an unexploited population of whiting consumes 2,749 thousand t, then the ecosystem internal consumption of that population should be between 275 and 550 thousand t per year, which seems to be "in the ballpark." In addition, under modified growth the average annual consumption-biomass ratio is 1.454 which translates to an average daily consumption of .398% BWD, considerably less than the estimates from the literature for similar species given in an earlier table. My guess is that I may be low on my estimate of energy requirements for maintenance as well as on my estimate of weight loss due to spawning.

In terms of total consumption, it is interesting to compare the estimated whiting consumption by area under unexploited ($\hat{\bar{C}}_u$) to that under exploited ($\hat{\bar{C}}_E$) conditions.

| | BC-Conc. | Monterey | Eureka | Columbia | Vancouver | |
|---|---|---|---|---|---|---|
| $\hat{\bar{C}}_u - \hat{\bar{C}}_E$ (1000 t) | 51 | 36 | 143 | 115 | 67 | 412 |

Thus, the estimated difference in total consumption by whiting between un-exploited and exploited conditions is around 412 thousand t per year. The most pronounced impact of this difference would be felt in the INPFC Eureka and Columbia areas. It is interesting to speculate on what impact this difference has on the pandalid shrimp fishery off the coasts of northern California, Oregon, and southern Washington, basically the Eureka and Columbia areas. Livingston (Patricia Livingston, Northwest and Alaska Fisheries Center, Seattle, WA 98112. Pers. commun.) reports a range of from 0.3 to 4.4 percent as the fraction of pandalid shrimp in the diets of whiting collected off Oregon and Washington in 1977 and 1980. Extrapolating this would imply that, between 1973 and 1980, the removal of whiting through fishing has on the average reduced the ecosystem internal consumption of pandalid shrimp in the Eureka and Columbia areas by 800 to 11,000 t. Assuming that no other predators pick up the slack, this shrimp would be available to the fishery. Figure 16 gives the trends of catch and CPUE for the pink shrimp (Pacific Fishery Management Council 1979) off the coasts of Washington, Oregon, and California. The following table which gives the average catches (1000 t) and catch per unit of effort (CPUE) (lb/h trawled) for pink shrimp during the pre- and post-whiting fishery periods.

| | 1952-65 | 1966-77 |
|---|---|---|
| Avg. catch (1000 t) | 1.8 | 12.0 |
| Avg. CPUE (lb/h) | 605 | 594 |

Assuming that effort was standardized properly, these results indicate that the pink shrimp fishery could have replaced whiting as a predator on shrimp.
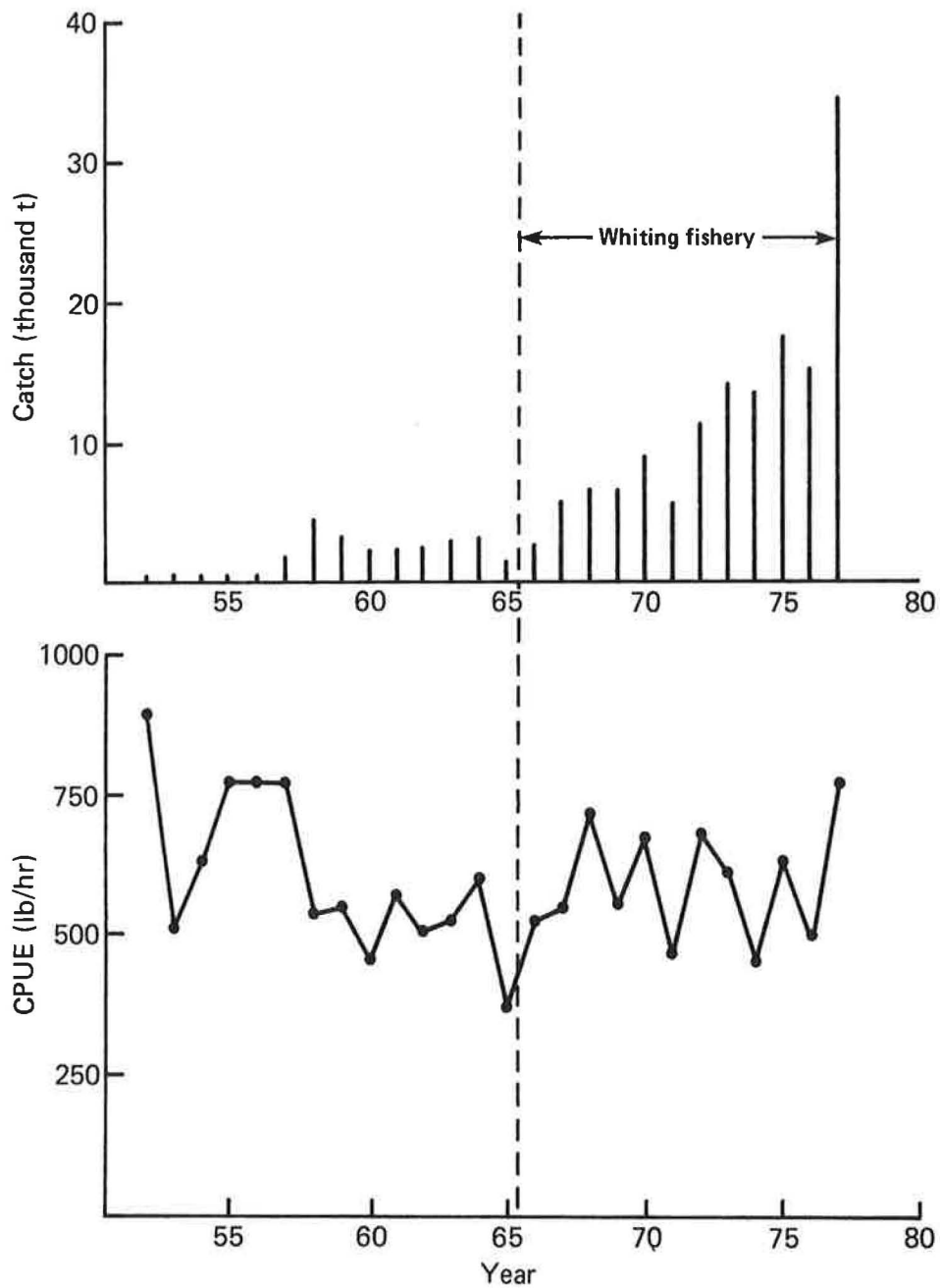
Figure 16.--Catch and catch-per-unit-effort (CPUE) of pink shrimp off
Washington, Oregon, and California, 1952-77.

An interesting point to note is that this could happen with shrimp being a rather minor item in the whiting diet.

SUMMARY

This paper presents an attempt to explore both the population and trophic dynamics of the coastal stock of Pacific whiting. An attempt was made to investigate and quantify certain facets of the basic population biology of the stock. An age-structured computer simulation model, entitled HAKE, was used as the central focus of this analysis. The results can be summarized as follows:

1) Both between and within age classes, whiting stratify by size on a latitudinal gradient, with the larger fish tending to move farther north than the smaller fish.

2) Two growth relationships of weight on age are derived for whiting, one assuming that growth is uniform throughout the year and a second assuming that growth is seasonal (during the winter, November-March, spawning season adults between ages 4 and 11 lose a minimum of between 5 and 10% of their total body weight and during the April-October feeding season gain a minimum of between 11 and 30% of their initial body weight). These two relationships provide markedly different estimates of trophic demands.

3) Two representations of age-specific natural mortality (M) are explored. One assumes that M is constant as a function of age. The other assumes that between hatching and the critical age M is a density dependent function of age and, after the critical age, M increases with age for 4 to 5 yr, after which it undergoes irregular fluctuations. Comparisons of results of cohort analyses employing these two representations of M indicate that the latter is more realistic.

4) Results of simulations of adult (ages 2-12) stock bioenergetics indicate that

a) Whereas production due to growth does not seem to vary much as a function of exploitation, it is greater under the seasonal growth option than the uniform growth option.

b) The distribution of both production and consumption is weighted more heavily toward the summer feeding areas (off northern California, Oregon, and Washington) under seasonal growth than under uniform growth.

c) The average ratio of total annual production (growth + recruitment) to average biomass is 0.35 (around 600 thousand t total annual production).

d) Average daily consumption is around 0.4% BWD which is considerably less than estimates from the literature for similar species.

e) The increased pink shrimp catch off the Washington-Oregon-California coast since the inception of the whiting fishery in 1966 could be attributable to an increase in shrimp production as a result of decreased whiting predation on shrimp.

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