Synthetic Estimates of Historical Abundance and Mortality for Northern Anchovy

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Abstract.—The stock synthesis model combines the analyses of catch, abundance, and agecomposition data. The model seeks the most likely time series of abundance and mortality, and distributes the residual error among all types of data according to each type's consistency with the synthetic estimates. The data base for northern anchovy *Engraulis mordax* includes two independent fisheries, an auxiliary source of age-composition data, a 6-year time series of accurate spawning biomass measurements by the egg-production method (EPM), and two longer time series of biomass indices. Specific biological relationships in the northern anchovy model are an influence of chub mackerel *Scomber japonicus* on natural mortality, and an influence of ocean temperature on patterns in age-specific availability and the fraction of 1-year-old fish that are mature. The synthetic estimates of spawning biomass since 1980 typically are within 15% of the measurements made by the EPM. This high precision demonstrates the consistency between changes in biomass measured by the EPM and changes expected from recruitment information in the age-composition data. Consistency between the other biomass indexes and age-composition data were lower. Nevertheless, the other biomass indexes are valuable for defining trends in the estimated 33-year time series.

Knowledge of the abundance of a harvested population is invaluable for an accurate assessment of the population's potential yield. Fisheryindependent measurements of abundance are desirable, but precise estimates may be unavailable or prohibitively expensive. Much population assessment methodology involves the inference of abundance from fishery data. When fishery and survey data are available, we usually lack objective means of integrating them in a comprehensive analysis.

Separate virtual population analysis (VPA; Doubleday 1976) treats catch-at-age data, and was developed from the assumption that fishing mortality of each age-group in each year could be estimated as the product of an age-dependent availability to the fishery and an annual value for fishing effort. Separable VPA simultaneously analyzes all year classes in the fishery, resulting in a more determinate overall solution than conventional VPA (Murphy 1965); although the catch of each age in each year is no longer exactly reproduced by the model. Recent advances in catchat-age analysis (Fournier and Archibald 1982; Deriso et al. 1985) include more careful attention to the error structure and establishment of a framework for inclusion of auxiliary information (fishing effort, survey estimates of age composition, stock-recruitment relationships).

The stock synthesis model (SS), like the models above, brings auxiliary data directly into the catch-at-age analysis. Synthesis of fishery and survey data into a coherent whole can provide a more accurate evaluation of the history and current status of the population. In this synthesis, the age-composition data describe vear-to-vear changes in relative abundance, whereas these data by themselves are inadequate for estimating trends or current abundance. Data from biomass surveys typically are too imprecise for estimating year-to-year changes in abundance, but they are invaluable for establishing the mean and trend. In its simultaneous examination of all data, the SS model distributes the residual error among the various types of data according to the specified level of confidence in each data type and the consistency of the data with the synthetic estimates.

The approach of the SS model is more similar to that of Fournier and Archibald (1982) than to that of Deriso et al. (1985) or to VPA. In the SS model, the numbers at age calculated by the deterministic population model are transformed to provide expected values for comparison to the varied data

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sources; the data are not manipulated into a number-at-age format. The user must be directly involved in specifying the relation between the model's estimates of numbers at age and the types of quantities that have been measured. Thus, it is a modeling approach, rather than a packaged model, that can be transferred to other species. Here, an application of the SS model to northern anchovy *Engraulis mordax* is described. Important aspects of this implementation are the breadth of the auxiliary information about northern anchovy and environmental effects on the species' age-specific availability.

Deterministic Population Model

A deterministic description of a homogeneous, fished population with annual recruitment is as follows:

y is time (years, measured quarterly); a is age (years, measured quarterly); t is type (here, U.S. or Mexican fishery); P(y,a) is the age-specific abundance;

 $P(y+1,a+1) = P(y,a)e_{-Z(y,a)}$ is survivorship;

$$P(y,0) = R(y)$$
 is the recruitment in year y; (2)

$$C(y,a,t) = P(y,a)\frac{F(y,a,t)}{Z(y,a)}[1-e^{-Z(y,a)}]$$

is catch at age; (3)

$$Z(y,a) = M + \sum_{t=1}^{\infty} F(y,a,t) \text{ is total mortality;} \quad (4)$$

M is natural mortality;

F(y,a,t) = E(y,t) Q(a,t) is fishing mortality; (5) E(y,t) is nominal fishing effort;

Q(a,t) is age-specific availability.

With estimates of M, E(y,t), Q(a,t), and R(y), the above equations calculate F(y,a,t), P(y,a)and C(y,a,t). The important questions are (1) How well do the estimated abundances, P(y,a), and catches, C(y,a,t), conform to data on the population and its fishery? and (2) How can we estimate values for the parameters defining M, E(y,t), Q(a,t), and R(y) to maximize the likelihood of the available data base?

The important problem is that the data for northern anchovy, and for most other species, are not collected in the form P(y,a) and C(y,a,t). For example, northern anchovy abundance is measured as spawning biomass without age structure. Specification of the relationship between the estimated age-structured population, equations (1-5), and the available data base is critical for accurate estimation of the population's abundance and mortality. In addition, changes in observed age composition for northern anchovy (Mais 1981) indicate that M or Q or both changed during the late 1970s. The following sections first describe the data base for northern anchovy (Methot 1986), and then describe the incorporation of environmental effects on M and Q and the relationships between the estimated age-structured population and the expected values for quantities that can be compared to data collected for the northern anchovy.

Northern Anchovy Data

Abundance Observations

Three types of abundance observations are available for northern anchovy (Table 1). Spawning biomass measured by the egg-production method (EPM) is the quotient of two measured quantities: daily rate of egg appearance in the sea, and daily rate of egg production by mature females (Parker 1980). It is the most precise and accurate of available techniques (Bindman 1986), but has only been used during 1980-1985. Historical egg production (HEP) observations are the average abundances of newly spawned eggs during January-April (Lo 1985) and are available since 1951 (but triennial during 1966-1978). Here, the HEP is considered as an index of spawning biomass. Acoustic observations (sonar) of schooled northern anchovy abundance are available since 1969 (Mais 1974). None of these types of abundance observations are age structured, although measurements of age composition were made during the acoustic surveys.

Fishery

(1)

There are four components to the northern anchovy fishery: the reduction fishery in southern California, the reduction fishery in northern California, the bait and nonreduction fishery, and the reduction fishery in Ensenada, Baja California, Mexico. Age-composition data were available from the two largest components, the southern California and Mexican reduction fisheries. The fishery data described below were not expanded into a number-at-age format. The data were kept as catch biomass and, when available, age composition of the aged fish.

Prior to 1966, only annual harvest data were available from the U.S. fishery, and no agecomposition data were collected (PFMC 1983; Methot 1986). Annual landings were split into 50%

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TABLE 1.—Abundance of and auxiliary data for northern anchovy. The egg-production method (EPM) is a measurement of spawning biomass and the historical egg production (HEP) is the production of eggs during January-April as estimated by Lo (1985). Sonar is a measurement of schooled northern anchovy biomass made by the California Department of Fish and Game. The HEP and sonar observations are treated as indexes with arbitrary units. The biomass of chub mackerel *Scomber japonicus* influences the natural mortality of northern anchovy. Temperature was measured at the Scripps Institution of Oceanography pier, La Jolla, California, during January and February. The model was fitted to quarterly fishery data, not to the annual values presented here.

Year		Northern anchovy					
	A	bundance		Fishery	landings	Chub	
	EPM (10 ³ tonnes)	HEP	Sonar	USA (10 ³ tonnes)	Mexico (10 ³ tonnes)	mackerel (10 ³ tonnes)	Temperature (°C)
1954		0.168		25.3		79	14.2
1955		0.316		25.8		77	13.2
1956		0.146		31.6		84	12.8
1957		0.364		22.1		52	14.6
1958		1.274		9.1		27	16.1
1959		0.992		7.6		59	15.6
1960		1.765		6.5		65	13.9
1961		0.653		8.9		104	14.6
1962		1.314		6.9		125	13.5
1963		2.275		6.1		87	14.4
1964		4,147		7.0	4.6	53	15.0
1965		4.019		8.3	9.2	18	13.3
1966		5.256		34.4	13.2	9	13.8
1967				36.5	20.1	5	14.0
1968				20.7	14.3	5	14.5
1969		3.821	438	66.3	3.9	5	14.3
1970			275	92.9	28.0	5	13.6
1971			233	46.5	20.1	5	13.1
1972		1.657	822	68.0	30.1	5	12.8
1973			1,671	126.0	15.4	5	15.0
1974			947	80.2	42.8	5	13.1
1975		19.691	3,086	149.4	55.0	10	13.2
1976				119.5	72.0	10	13.9
1977			1.984	107.5	142.0	97	16.0
1978		2.330	392	17.5	130.0	132	15.7
1979		5.426	292	53.2	198.0	292	13.9
1980	870	2.671	604	49.0	240.0	252	15.0
1981	635	4.376	567	56.2	258.7	333	14.6
1982	415		250	49.0	173.0	359	14.1
1983	652		532	8.5	87.0	244	15.9
1984	309	2.850	573	7.0	101.1	157	15.0
1985	521		1,015	5.3	118.8	457	13.8
1986						400	15.2

for the first semester and 50% for the second semester of the year, although data since 1966 show wide variation in the semester percentages. The weights at age for these early landings were assumed to be equal to the average weights at age in the U.S. fishery during 1966–1979 (Table 2).

The U.S. fishery data since 1966 were available as reduction harvest (PFMC 1983) and combined bait and nonreduction harvest (e.g., Thomson et al. 1985). These data were available as monthly or semesterly values, except annual landings of bait plus nonreduction fish for 1966–1978 were split into two semesters by the 40%:60% average partition for 1979-1984.

Age-composition and weight-at-age data from the U.S. northern anchovy reduction fishery are available in Methot (1986). These data were assumed to apply to the total harvest (reduction +nonreduction + bait) because the reduction fishery contributed about 90% of the total harvest. Only trivial numbers of age-0 fish occur in the U.S. fishery. Since 1966, the first- and secondquarter total U.S. harvests have been combined, as have the third- and fourth-quarter harvests.

TABLE 2.—Mean weight at age and fecundity of northern anchovy for all available years of data. Tabulated values were used in the model for years with no observations. "Total" categories include data from U.S. and Mexican waters.

	Age								
Quarter	0	1	2	3	4	≥5			
		U.	S. fishery weight at a	ge (g)					
2 4	11.2	12.9 16.6	17.5 19.4	21.0 21.8	24.5 24.4	28.8 26.3			
		То	tal survey weight at a	ige (g)					
1		8.7	14.6	18.3	21.2	24.3			
		Το	tal survey fecundity (eggs/g)					
1		2,464	4,867	7,599	9.030	9,030			
		Mex	ican fishery weight at	age (g)					
2 3	8.5	11.2 12.5	13.4 14.4	15.0 16.0	16.5 17.6	18.6 18.6			
4	8.2	12.8	14.6	18.1	19.2	18.6			

This compression is reasonable because the reduction fishery is closed during July and August and has been closed during February and March since 1978. Age-composition data have ceased to be collected since 1983, when the fishery declined to a low level (Table 1).

Annual landings by the reduction fishery for northern anchovy in Ensenada, Baja California, were first recorded in 1962 (PFMC 1983; Methot 1986). Chavez et al. (1977) estimated age composition and catch by quarter in 1975 as the fishery increased (Table 1). Sunada and Silva (1980) provided age composition and catch for 1976 and 1977. Recent unpublished quarterly data were provided by Living Marine Resources, Inc. (Methot 1986). The first-quarter Mexican harvest typically was very small and was combined with the second-quarter harvest. Third-quarter agecomposition data were not used because of variable availability of age-0 fish. Fish of age 4 and older contributed little to this fishery, and age-0 fish often dominated the fourth-quarter fishery.

Survey Age Composition

Midwater-trawl surveys of northern anchovy have been conducted by the California Department of Fish and Game nearly annually since 1966 and provide fishery-independent observations of age composition (Mais 1974; Parrish et al. 1985). Here, cruises were categorized into either a firstquarter (primarily February) or second-quarter (primarily April) period (Methot 1986). Also, separate age-composition estimates were made for U.S. and Mexican regions because most cruises were made only in U.S. waters, and younger fish tend to be relatively more common south of the USA-Mexico border. Surveys for which less than 100 fish were aged were not included in the SS analysis.

Northern Anchovy Model Specification

Equations (1-5) defined a deterministic description of an age-structured population and its fishery. This section describes a relaxation of the assumptions of constant natural mortality and availability, and the conversion of estimated numbers at age into expected values for quantities that can be compared to the four types of age-composition data and three types of abundance data.

Natural Mortality

Average instantaneous total mortality (Z) of northern anchovy, age 2 and older, during 1966–1980 has been estimated to be 0.97–1.09 per year (MacCall 1974; Hanan 1981). Hanan (1981) noted that total mortality has increased since 1977, and Mais (1981) noted that older fish are now rare in the population.

Gut contents of chub mackerel indicate that northern anchovy are commonly eaten by this predator. Chub mackerel abundance increased from less than 10,000 tonnes during 1966–1976 (Table 1) to more than 300,000 tonnes in 1985 (MacCall et al. 1985). It seems likely that natural mortality of northern anchovy has increased as a consequence of increased predation by chub mackerel, but the magnitude of this increase could not be estimated from available data. The SS model was used to explore likely magnitudes by defining natural mortality as

$$M = M_{o} + M_{n} \cdot \text{Pred}.$$

- Pred is chub mackerel biomass on July 1, in 10⁶ tonnes;
- M_o is the natural mortality without chub mackerel;
- M_p is the rate at which M increases with increasing chub mackerel biomass.

Investigated values of M_o were 0.4, 0.6, and 0.8. Investigated values of M_o were 0.0, 0.4, and 0.8.

Recruitment

Age-0 northern anchovy begin appearing in the Mexican fishery during July-September and sometimes dominate the Mexican fishery during the fourth quarter. Recruitment is defined to occur on July 1 at a nominal age of 0.5 years. The parameters that define the recruitments are independently estimated for each year. These recruitments are not constrained to follow any stockrecruitment relationship, and the SS model is not used as a technique for direct estimation of the stock-recruitment relationship. Recruitments and spawning-stock abundances estimated by the SS model can, however, be used to explore the relationship between parent stock, environment, and recruitment (Peterman et al. 1988).

Abundance

Biomass estimates were calculated on February 15 from estimated numbers at age at that time, observed body weight at age in the trawl survey for the first quarter of that year, and age-specific contributions (availabilities) to each type of survey. February 15 is consistent with the approximate mean date of the EPM and other first-quarter surveys. The expected values for the three biomass measurements are

$$B(y,t) = S(t) \sum_{a=1}^{n} Q(y,a,t) W(y,a) P(y,a);$$

A is 5 years and includes all older ages;

- B(y,t) is biomass in year y measured by technique t for t = 5-7 (5 = EPM, 6 = HEP, 7 = sonar), t = 1-4 specify age-composition data; W(y,a) is weight at age;
- P(y,a) is the number at age calculated by the model;
- Q(y,a,t) is age-specific availability;



FIGURE 1.—Temperature effects on spawning by age-1 northern anchovy (Methot, unpublished data). Temperature is the mean temperature during January and February at the Scripps Institution of Oceanography pier, La Jolla, California. Mature northern anchovy are those with yolked eggs as disclosed by histological examination during 1979-1985. Active northern anchovy are those not classified as unsexable or immature by visual examination (Parrish et al. 1986) during 1966-1985.

S(t) is a scaling factor: 1.0 for the calibrated EPM, and adjusted for the other data types to maintain a mean lognormal deviation of 1.0.

The abundance measurements are not agestructured, so the availability vector, Q, cannot reasonably be estimated within the model. For EPM and HEP, there is biological information that is used below to specify Q for those two types of abundance data. For sonar, Q is crudely estimated by the model.

The relation, Q(y,a,5), between EPM spawning biomass and estimated age-specific abundance depends on the age-specific fraction of fish that are mature. Parrish et al. (1986) found that nearly all age-2 and older northern anchovy were mature during the major spawning season (January-April), and that the fraction mature was lower at age 1. Methot (unpublished data) found that the fraction of age-1 northern anchovy mature during late January-early March was related to temperature (Figure 1). Thus, the availability is 1.0 for ages 2 and older in all years, and the availability for age 1 is defined as

$$Q(y,1,5) = \frac{e^{A+BT(y)}}{1+e^{A+BT(y)}};$$

$$A = -33.40; B = 2.44;$$

T(y) is temperature at Scripps Institution pier during January and February.

The measured HEP values must be compared to quantities that are proportional to the estimated population's total egg production during January-April. Therefore, Q(y,a,6) depends on the agespecific fraction of fish spawning and the agespecific fecundity of the spawners during this period. Methot (unpublished data) found that the temperature-specific fraction of age-1 female northern anchovy that were actively spawning during late winter was less than the fraction that were mature (Figure 1). Mean egg production by spawners during January-April was calculated from Parrish et al. (1986; Table 2). The availability, Q(y,a,6), of spawners for HEP for ages 2 and older in all years is equal to the eggs per gram for that age because 100% of the fish are actively spawning. The availability for age 1 involves the fraction of fish active as well as fecundity:

$$Q(y,1,6) = \frac{e^{A+BT(y)}}{1 = e^{A+BT(y)}} \cdot 2,464$$
$$A = -17.51; B = 1.21.$$

There is no information to define the availability to a sonar survey. Fish of ages 3 and older are assumed to be fully and equally available to the sonar survey. The availability at age 1, Q(y,1,7), was assumed to be time-invariant and was defined as a parameter, AGE-1 SONAR, to be estimated by the model. Age-2 availability was the mean of the age-1 availability and 1.0.

Mean body weight at age was calculated from estimated mean length at age in first-quarter surveys and a length-weight relationship (PFMC 1983). In years without a sufficient sample to calculate mean body weight, the mean from other years was used (Table 2).

Deviations from expected biomass were calculated as

$$D(y,t) = \log_e \frac{\text{observed } B(y,t)}{\text{estimated } B(y,t)}$$
.

The log-likelihood (1) for each type of abundance measurement is

$$l(t) = \frac{\sum_{y} -D(y,t)D(y,t)}{2 s(t)^{2}} - n(t)\log_{e} s(t);$$

s(t) is the standard deviation of the D(y,t);

n(t) is the number of observations of that type.

Magnitude of the Harvest

The total harvest is

$$H(y,t) = \sum_{a=0}^{A} W(y,a,t)C(y,a,t);$$

for the U.S. fishery t = 1, and for the Mexican fishery t = 2. The catches, C(y,a,t), were calculated from equation (3), and the weights at age were observed or taken from Table 2. If there were measurements of the fishery's effort, the log-likelihood function would include deviations between the observed and estimated fishery efforts, and the E(y,t) would be included in the vector of parameters to be estimated. Similarly, if there were constraints on permissable values for the E(y,t), it would be appropriate to consider deviations between observed and estimated harvest. With northern anchovy, there are no measurements or constraints on the fishery effort, so the estimated E(y,t) can be manipulated to match each H(y,t) with the corresponding observed harvest. Consequently, the E(y,t) were not included in the list of parameters to be estimated. As derivatives of the likelihood function are calculated for the other parameters, the efforts are constantly adjusted to match the magnitude of each observed harvest. Note that calculated survivorship (equation 1) depends on the model's current estimate of fishing mortality for a given age and year, not directly on the observed landings from that age and year.

Age-Specific Availability

There are four types (t) of age-composition data: U.S. fishery, Mexican fishery, U.S. survey, and Mexican survey (U.S. survey in Mexican waters). Age-specific availabilities, Q(y,a,t), for each type were defined to follow the general form depicted in Figure 2 with parameters listed in Table 3. Three-parameter continuous functions were explored and judged too inflexible for the northern anchovy. Availability is defined as a function of time, y, to allow introduction of environmental effects. The estimated availabilities in each quarter and for each type of age composition were interpolated from the compound relationship (e.g., Figure 2), the actual age of the fish being measured in quarter years. For each type of age composition, the parameter AVAIL1(t) specified availability at age 1.0 in the first quarter for survey age composition and at age 1.25 in the second



FIGURE 2.—Forms of age-specific availability functions for northern anchovy. The parameter AVAIL1 defines availability at age 1.0 (first quarter of year) for survey age composition, or at age 1.25 (second quarter) for fishery age composition. AVAIL1 can be more or less than 1.0. The parameter AGEFULL defines the age at which availability is 1.0. Availability remains at 1.0 for 1.0 year following AGEFULL, and availability of older fish declines at an exponential rate specified by the parameter OLDAV. K(Mex) and K(US) are parameters (for Mexican and U.S. fish) that define the rate at which availability increases from 0.0 at age 0.25 to AVAIL1 at age 1.25. AVAIL1 and AGEFULL are modified annually as a function of ocean temperature.

quarter for fishery age composition data. The parameter AGEFULL(t) specified the age at which availability was 1.0. Other parameters and environmental effects on AVAIL1 and AGE-FULL are described below.

Young northern anchovy are less available to the U.S. fishery than to the Mexican fishery. The parameter K(t) was introduced to specify the rate at which availability increased from 0.0 at age 0.25 to the estimated value AVAIL1(t) at age 1.25:

TABLE 3.—List of parameters included in the stock synthesis model for northern anchovy. Emphasis (userspecified) on the abundance data was set at 20. Common and availability parameters were estimated only from data and recruitments beginning in 1964. Pre-1964 recruitments and 1954 age composition were estimated with the common and availability parameters fixed at values shown here.

Parameter or age	Value	Year	Value		
Соттол*		Recruitmentb.c			
		(number at age 0			
Ma	0.6	on J	uly I)		
M _n	0.4				
OĽDAV	0.312	1954	0.070		
SPRINGAV	0.503	1955	0.083		
% MISAGED	0.310				
AGE-1 SONAR	0.237	1956	0.484		
		1957	0.317		
Availability	1	1958	0.076		
		1959	0.001		
AVAIL1		1960	0.347		
U.S. fisherv	0.052				
Mexican fishery	0.264	1961	0.804		
U.S. survey	0.010	1962	0.985		
Mexican survey	0.010	1963	0.745		
AGEFULI		1964	0.772		
IIS fishery	3 465	1965	0.268		
Mexicon fishery	3 142				
II S survey	3 860	1966	0.267		
Maxiann survey	3 199	1967	0.558		
MEXICAL SULVEY	5.177	1968	0.396		
II S fichery	0.496	1969	0.662		
U.S. History Manicon fishery	0.490	1970	1 467		
	0.341	17/0	1.402		
U.S. Survey	1 266	1071	2 467		
MEXICAN SUIVEY	1.500	1072	3 084		
AGEFULL _a	1 905	1972	3.004		
U.S. fishery	1.095	1973	0.457		
Mexican insnery	2.110	17/4	0.052		
U.S. survey	2.464	1975	0.200		
Mexican survey	1.999	1076	1 1 4 2		
K	2.055	19/0	1.143		
U.S. fishery	3.933	19//	0.131		
Mexican fishery	0.231	1978	2.285		
		19/9	1.639		
Initial age compo	sition	1980	1.480		
(number on Jan. 1	. 1954)				
		1981	0.393		
Age 1	0.099	1982	1.835		
2	0.024	1983	0.724		
3	0.006	1984	1.839		
4	0.003	1985	1.145		
≥5	0.003				

 ${}^{*}M_{o}$ = natural mortality in the absence of chub mackerel (fixed at 0.6); M_{p} = natural mortality in the presence of chub mackerel (fixed at 0.4); OLDAV = exponential decline in availability for ages greater than AGEFULL (age at which availability is 1.0) plus 1.0 year; SPRINGAV = adjustment for "excess" availability of fish older than AGEFULL during the second quarter of the year; % MISAGED = percentage of fish age 5 and older that were misaged by 1 year; AGE-1 SONAR = availability of age-1 fish to sonar surveys.

^bMultiply by 50 × 10⁹ to obtain absolute values.

Not reliable prior to 1964 due to lack of age-composition data.

dAVALL1_c and AVALL1_w = cold- and warm-temperature availability of age-1 fish in the first quarter and of age-1.25 fish in the second quarter; AGEFULL_c and AGEFULL_w = age at which availability is 1.0 for cold and warm periods; K = rate at which availability increases from 0.0 at age 0.25 to AVALL1 st are 1.25

at age 1.25. ^eMinimum permissible value.



FIGURE 3.—Recruitment index for northern anchovy defined as the percentage of youngest fish in an age-composition observation. MX-F-4: percentage of age-0 fish in the fourth-quarter Mexican fishery (age = 0.75 years). US-S-1,2: percentage of age-1 fish in the first- or second-quarter trawl surveys conducted north of the USA-Mexico border (mean, if surveys were conducted in both quarters in same year). US-F-2: percentage of age-1 fish in the second-quarter U.S. reduction fishery. MX-F-2: percentage of age-1 fish in the second-quarter U.S. reduction fishery. MX-F-2: percentage of age-1 fish in the second-quarter Mexican fishery trend is indicated with a dashed line to emphasize the temporal shift from entirely U.S. data to dominance by Mexican age-composition data. Data from the few surveys in Mexican waters are omitted for clarity. Age-0 fish in the fourth-quarter U.S. fishery are not presented because of their extremely low availability.

$$Q(y,0,t) = \text{AVAIL1}(t)(\text{age} - 0.25)^{K(t)};$$

age is age in years measured quarterly for ages less than 1.25.

Older northern anchovy have been underrepresented in the age-composition samples if one assumes constant mortality and availability. Mac-Call (1974) suggested that natural mortality increased for older northern anchovy, but such a trend is indistinguishable from decreased availability of these fish. Older northern anchovy tend to be found offshore and to the north (Parrish et al. 1985), so they certainly are less available to the Mexican fishery, and probably to the U.S. fishery as well. Reduced availability of older fish was modeled as an exponential decline for ages greater than AGEFULL(t) plus 1.0 year (Figure 2). The same exponential decline parameter, OLDAV, was used for all four types of age composition. When AGEFULL(t), the age at full availability, is

greater than about 3.5 years, the OLDAV parameter has little effect on the expected age composition.

In the second quarter, the availability of older age-groups was greater than expected. This was especially apparent when there were U.S. trawl surveys in the first and second quarter of the same year. This phenomenon is probably due to some consistent, but undescribed, seasonal migration pattern. The model attempted to mimic this pattern by including a parameter, SPRINGAV, which was added to AGEFULL(t) in the second quarter.

The observed pattern of age-specific availability changed during the mid 1970s. In the early 1970s, the age-1 fish were highly unavailable to agecomposition samples (Figure 3). Since 1976, and especially since autumn 1978, age-0 and age-1 fish became more common in the fishery and surveys (Mais 1981), and ocean temperatures warmed (Table 1). Earlier surveys suggested that young fish were more common in southern California during warm periods (Baxter 1967). Such a shift in apparent availability could be due to a latitudinal gradient in stock structure. Off Mexico, size at age was smaller and young fish were more common (Parrish et al. 1985). During El Niño periods, the stock has shifted north, causing a decrease in size at age in southern California (Fiedler et al. 1986).

The above patterns suggest that availability can be modeled as a function of water temperature. A 4-year, linearly weighted average of temperature at the Scripps Institution of Oceanography pier during January and February (Table 1) was used as the temperature index I(y). The current year had a weight of 4 and the value 4 years ago had a weight of 1. The temperature effect was imposed on the AVAIL1(t) and AGEFULL(t) by splitting each into a cold (c) and a warm (w) level (Table 3):

$$AVAIL1(t) = AVAIL1_{c}(t) \quad \text{for } I(y) < I_{\min};$$

$$AVAIL1(t) = AVAIL1_{c}(t) + \frac{I(y) - I_{\min}}{I_{\max} - I_{\min}} \cdot [AVAIL1_{w}(t) - AVAIL1_{c}(t)]$$

$$for I_{\max} > I(y) > I_{\min};$$

 $AVAIL1(t) = AVAIL1_{y}(t)$ for $I(y) > I_{max}$;

$$I_{\min} = 13.7^{\circ}C$$
 (U.S. data types);
 $I_{\min} = 14.2^{\circ}C$ (Mexican data types);
 $I_{\max} = 15.0^{\circ}C$.

The AGEFULL_c(t) and AGEFULL_w(t) were defined similarly.

Age-Determination Variability

Variance in age determination cannot be avoided and has the effect of smearing the sampled age composition as it becomes the observed age composition. A small misaging percentage, say 10%, has little effect on a good year class, but could double the apparent abundance of an adjacent small year class. In the SS model, the percentage of fish misaged into the adjacent age groups was assumed to increase linearly with age and to double from age 0 to the estimated value at ages of 5 and more. It was further assumed that no fish were misaged by more than 1 year. These estimated misaging percentages were used to adjust the estimated available age compositions before they were compared to the observed age compositions. Percentage misaged at ages 5 and more, %MISAGED, was estimated by the model.

Age-Composition Likelihood

Each of the four types of age-composition data was treated as a sample of the population's age composition, and a multinomial error structure was assumed (Fournier and Archibald 1982; Deriso et al. 1985). The probability of observing a particular sample age composition was expressed as the logarithm of the likelihood function.

$$D(y,t) = \sum_{a=0}^{A'} n(y,a,t) \cdot \log_a f(y,a,t);$$
$$l(t) = \sum D(y,t);$$

- n(y,a,t) is observed number of fish assigned to age a in a sample of type t collected during period y;
- A' includes all older ages, and is the oldest age for which n(y,A',t) is greater than five fish;
- f(y,a,t) is estimated proportion of fish of age a during period y in sample of type t.

The estimated age composition, f(y,a,t), was calculated from the model's estimate of numbers at age during period y, P(y,a); the age-specific availability to that type of sample, Q(y,a,t); and estimated age-determination error.

Relative Emphasis on Data Types

The overall log-likelihood function, L, is a weighted sum of the log-likelihoods for each type of data (four age-composition types, three abundance types):

$$L = \sum_{t=1}^{7} \text{EMPHASIS}(t)l(t).$$

EMPHASIS(t) is specified by the user.

The problem is quantification of confidence in the age-composition data relative to the abundance data. The objectivity with which the relative emphasis can be specified depends on the correctness of the error structure in the likelihood function. The multinomial formulation for error in age composition is incomplete because it deals only with the stochastic component of variation in age composition; inaccuracy in the age-specific availability functions is not explicitly modeled. Fournier and Archibald (1982) used a multinomial for-

mulation, but recognized the problem of specifying the correct error structure. Deriso et al. (1985) evaluated the multinomial and two other error structures, and found that the selection mattered little to the end result. The SS model follows Fournier and Archibald by setting an arbitrary upper limit on the number of fish aged per time period. This de-emphasizes large age-composition samples, and prevents the model from attempting a perfect fit to these observations at the expense of other types of data. In recognition of the inherent subjectivity of the relative emphasis, the effect of increasing the relative emphasis on abundance data was explored.

Parameter Estimation

The complexity of the SS model for northern anchovy, and the philosophy which demands that the interface between model and data be tailored to each application, made application of standard statistical techniques, such as Marquardt's algorithm, impractical. Here, the search for the best parameter estimates depended on numerical evaluation of derivatives of the total log-likelihood function, L, instead of on derivatives of the expected values at each point in the data set.

The search for the best parameter values was based on quadratic hill climbing (Goldfeld and Quandt 1972), which is a modification of Newton's method, and included a Hessian matrix scaling described by Conway et al. 1970. The vectors of first (dX) and second (d^2X) derivatives of L with respect to each value of the parameter Xwere numerically evaluated in the region around the current estimates of the parameters ($\pm 5\%$ of X). The Hessian matrix, H, of mixed partial derivatives, which includes the d^2X on its main diagonal, also was calculated. The vectors of calculated parameter changes was calculated as follows.

 $DIAG_i$ = square root $-d^2X_i$ for each *i*th parameter;

$CORR_{ij} = H_{ij}/[DIAG_iDIAG_j]$ for each *i*th, *j*th parameter;

- $GRAD_i = dX_i/DIAG_i$ for each *i*th parameter; DEL = CORR⁻¹GRAD (matrix algebra);
 - $DEL_i = DEL_i/DIAG_i$ for each *i*th parameter:

The above calculations of the DEL_i are equivalent to $-dX_i/d^2X_i$ if all off-diagonal elements of H are zero. New parameter values were calculated by

$$X_{\text{new}i} = X_{\text{old}i} - \text{DEL}_i$$

In practice, when the X_{new} did not increase the total log likelihood L, the off-diagonal elements of CORR were multiplied by a fraction (0.0 < fraction < 1.0) to emphasize the steepest ascent approach. Each evaluation of the overall loglikelihood function, L, takes about 3 s on an IBM PC/AT computer. Convergence of the complete model takes about 4 h, even if the numerous mixed partial derivatives are recalculated only when the absolute value of the previous estimate of CORR (i,j) was greater than a uniform random value (0-0.3). Second derivatives and large mixed partial derivatives typically changed less than 20% as the parameter vector moved towards convergence. Computation time and number of parameters would be much less for a model that did not include environmental effects on the availabilities.

There are two major classes of parameters (Table 3). One class includes all those parameters necessary to define the age-specific availabilities and environmental effects on these availabilities. The other set includes the recruitments for each year and the numbers at age in the first year of the time series. The fishing efforts are not included as parameters. Instead, they are constantly tuned; that is, efforts are adjusted so that estimated harvest equals observed harvest every time a parameter is tweaked to calculate a derivative and every time the parameters are changed as a result of the calculated derivatives.

The full model (recruitments and availabilities) was fitted to data from 1964 to 1986. This model was used to investigate the appropriate level of emphasis on abundance data and to define the availability functions. Then, with the availability parameters fixed, the model was run on data extending from 1954 to 1986 to estimate the full time series of abundance, recruitment, and fishing mortality.

Results and Discussion

Data Consistency

Before the SS model was fitted to data, the internal consistency of the age-composition and abundance data was investigated. An index of the information in the age-composition data is the percentage of fish in the youngest age-group (Figure 3). The incoming year class has been well represented in the fourth-quarter Mexican fishery at an age of about 9 months; a year class's percentage in that sample was highly correlated

TABLE 4Correlations among recruitment indexes (percentage at age 0 or 1) for northern anchovy during
1966–1985. Data sources are MX-F, Mexican fishery; US-F, U.S. fishery; US-S, U.S. trawl survey; MX-S, Mexican
trawl survey. Mean percentages and correlations were calculated after values were transformed to arcsine square
root: N observations is the number of years in which an age-composition observation was available for the indicated
type and quarter.

				Data sour	ce and quart	er of year								
Variable or source	MX-F 3	US-F 4	MX-F 4	US-S I	MX-S 1	US-F 2	MX-F 2	US-S 2	US-F 4					
Age (years)	0.5	0.75	0.75	1.00	1.00	1.25	1.25	1.25	1.75					
Mean % at age	19.6	6.1	41.5	32.4	48.1	27.5	45.5	16.3	32.2					
		Correl	ations (decim	als) and sam	ple sizes (who	le numbers)								
MX-F-3		0.89	0.65ª	0.15*	0.73	0.70	0.05°	0.82	0.68					
US-F-4	5		0.76	0.82	0.58	0.88	0.75	0.75	0.82					
MX-F-4	9	7		0.72	0.82	0.89	0.62	0.99	0.92					
US-S-1	8	10	10		0.95	0.93	0.80	0.85	0.81					
MX-S-1	4	4	5	5		0.99	0.93		0.94					
US-F-2	5	14	6	9	3	-	0.95	0.93	0.80					
MX-F-2	7	6	8	8	5	5			0.92					
US-S-2	3	7	3	5	ī	7	2		0.93					
US-F-4	4	13	6	10	3	12	5	8						

"Low correlation because of unusually high MX-F-3 values in 1984 and 1985.

with its percentage in other age-composition samples during the following year (Table 4). In contrast, the correlations among abundance data were not significant if the high HEP and sonar observation for 1975 were deleted (Table 5). These patterns of correlation among the agecomposition and abundance data support the original goal: HEP and sonar data are best for constraining trends, and high-frequency variation in abundance must be inferred from the recruitment information in the age-composition data. the three abundance data types, the root-meansquare lognormal error for EPM data was 0.175; that is, 95% of the EPM observations fell within 71 to 140% of the model's estimated values. This level of precision is satisfyingly close to the estimated coefficients of variation for EPM observations (0.15–0.20: Bindman 1986). This result suggests that application of the SS model has filtered out the small amount of measurement error in the EPM observa-

Fit to Biomass

The synthetic estimates of spawning biomass provided an excellent fit to the EPM spawning biomass observations (Figure 4). Varying the emphasis on abundance data affected the goodness of fit to EPM data (Table 6), but the general trend in spawning biomass was largely unaffected except for the early 1970s. With an emphasis of 20 on each of

TABLE 5.—Correlations among three types of abundance data for northern anchovy. Sonar is an index of schooled biomass, HEP is an index of January–April egg production, and EPM is a measurement of spawning biomass by the egg-production method.

N	r	
3	-0.003	
6	0.14	
8	0.94	
7	-0.68	
	N 3 6 8 7	

"The 1975 values were excluded.



FIGURE 4.—Time series of estimated spawning biomass of northern anchovy. Measurements (''observed'') of spawning biomass by the egg-production method (EPM) are represented by solid circles. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed and estimated EPM values; mt is tonnes.

TABLE 6.—Log likelihoods for the northern anchovy stock synthesis model as functions of the specified level of natural mortality (M_{o}) , the chub mackerel influence on natural mortality (M_{o}) , and the emphasis on the goodness of fit for abundance data (EMPHASIS). Goodnesses of fit to spawning biomass (EPM), egg-production index (HEP), and an index of schooled biomass (sonar) are first presented as the root mean square lognormal error (s) between the observed and predicted values. "All abundance data" are the sums of the log-likelihoods (L) for the three types of abundance data listed above. "All age composition" are the sums of the log likelihoods for the four types of age composition data. "All data" combines log-likelihoods for abundance and age-composition data after the abundance log-likelihood was multiplied by the emphasis factor.

		M_{ρ} (upper) and M_{ρ} (lower)										
EMPHASIS	0.4 0.0	0.4 0.4	0.4 0.8	0.6 0.0	0.6 0.4	0.6 0.8	0.8 0.0	0.8 0.4	0.8 0.8			
		Egg production method (s)										
1	0.48	0.42	0.36	0.36	0.33	0.33	0.29	0.29	0.33			
10	0.28	0.27	0.26	0.22	0.22	0.23	0.20	0.21	0.23			
20	0.23	0.22	0.20	0.19	0.18	0.19	0.17	0.16	0.17			
40	0.20	0.19	0.17	0.16	0.12	0.10	0.09	0.07	0.06			
				Historie	al egg produ	ction (s)						
I	0.70	0.71	0.75	0.78	0.78	0.78	0.97	0.98	0.98			
10	0.57	0.58	0.58	0.60	0.61	0.62	0.64	0.64	0.64			
20	0.50	0.51	0.51	0.50	0.50	0.50	0.51	0.50	0.51			
40	0.41	0.40	0.40	0.37	0.36	0.36	0.34	0.34	0.35			
	Sonar (s)											
1	0.62	0.65	0.67	0.86	0.86	0.86	1.11	1.13	1.16			
10	0.54	0.54	0.56	0.61	0.63	0.64	0.70	0.71	0.71			
20	0.50	0.50	0.51	0.51	0.52	0.53	0.58	0.57	0.59			
40	0.46	0.45	0.45	0.45	0.45	0.45	0.45	0.46	0.47			
	All abundance data (log,L)											
1	1.1	0.5	0.4	~6.3	-5.8	-5.9	- 19.9	-21.2	-23.3			
10	8.8	8.7	8.4	7.5	6.9	6.4	5.1	4.4	3.6			
20	12.5	12.7	12.8	13.7	13.4	12.8	11.9	12.5	11.1			
40	16.8	17.7	18.6	19.9	21.8	22.9	23.9	24.3	24.3			
	All age-composition data $(\log L)$											
1	-98	-92	-90	-92	90	90	-99	-97	-97			
10	-136	-133	-131	-151	- 144	-141	-188	- 182	-182			
20	-190	- 193	~ 197	-241	-240	-236	-287	-303	-297			
40	-313	-336	-365	-416	-476	-502	- 574	- 595	-604			
	All data, with emphasis $(\log_{e}L)$											
1	-96	-91	-90	-99	-%	-%	-119	-119	-121			
10	-48	-47	-47	-76	-76	-79	-138	- 140	- 149			
20	60	60	59	34	28	19	-50	- 53	-76			
40	358	372	379	382	397	414	382	3/0	300			

tions, and has resulted in an improved estimate of historical spawning biomass.

The trend in spawning biomass was rather insensitive to the level of natural mortality (Figure 5), and the goodness of fit to the EPM observations improved at higher levels of natural mortality (Table 6). This improved fit occurred because higher levels of natural mortality placed a larger fraction of the total biomass in the first age-group. This juvenation enabled the SS model to more easily track changes in observed EPM biomass by adjusting the estimated recruitment values. However, if the changes in observed EPM spawning biomass had not been basically consistent with the recruitment information in the age-composition data, the improved fit at higher levels of natural mortality could not have been realized without greatly degrading the fit to the age-composition data.

The variabilities of the HEP and sonar data were greater than that of the EPM data (Figures 6, 7) and increasing the emphasis on the abundance data did little to improve the fit to the observed HEP and



FIGURE 5.—Time series of estimated spawning biomass of northern anchovy, showing the effects of three levels of natural mortality (M). All three runs were made with an abundance emphasis of 20. Measurements ("observed") of spawning biomass by the egg-production method (EPM) are represented by solid circles; mt is tonnes.

sonar data (Table 6). The estimated lognormal error of about 0.5 for HEP and sonar was greater than the average coefficient of variation (SE/mean = 0.42) calculated from the standard errors of each HEP observation (Lo 1985). This increase was expected because the former value includes structural and measurement error, and the latter value includes only measurement error.

Natural Mortality

A goal of the SS model was to estimate the natural mortality for northern anchovy and the



FIGURE 6.—Time series of observed and estimated historical egg production (HEP) by northern anchovy. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed (solid circles) and estimated HEP values.



FIGURE 7.—Time series of the observed (solid circles) and estimated sonar index for northern anchovy. Increasing the emphasis (E) on all abundance data during parameter estimation decreases deviations between observed and estimated sonar values.

contribution of predation by chub mackerel to this mortality. This goal was not realized because (1) the age-specific availability functions were sufficiently flexible to obtain a good fit to the observed agecomposition data, regardless of the model's estimate of the true age composition; (2) different types of data were better fitted with high (or low) levels of natural mortality, so the level of emphasis on abundance data determined the "best" level of natural mortality (Table 6); and (3) the overall goodness of fit was insensitive to the level of chub mackerel mortality, probably because the increase in chub mackerel abundance was nearly coincident with the increase in temperature, which changed the shape of the availability functions, and with the increased Mexican fishery. Early attempts to estimate the mortality rates as parameters of the model were stymied by large mixed partial derivatives (i.e., high correlations) between the mortality parameters and some of the availability parameters.

The final version of the SS model had instantaneous natural mortality set at 0.6. This is less than the value of about 0.9 estimated by MacCall (1974), but larger values of M were highly inconsistent with the large abundance of old fish in 1975 and 1976. The effect of chub mackerel was set at a level, $0.4/10^6$ tonnes of chub mackerel, that increased natural mortality to 0.76 at the current abundance of chub mackerel (400,000 tonnes).

Availabilities and Aging Error

The SS model estimated that age-1 northern anchovy have been only 24% available to the sonar

TABLE 7.—Estimated age-specific availabilities for northern anchovy as a function of ocean temperature at the Scripps Institution pier. When the 4-year weighted temperature index, I(y), was greater than 15.0°C or less than 13.7°C (14.2°C in Mexico) the indicated availabilities were used. At intermediate temperatures, availabilities were based on interpolated parameter values. The 20 parameters that define these availabilities are listed in Table 3; MX is Mexican.

	Temperatura	Age					
Data type	index (°C)	0	1	2	3	4	5
				First	quarter		
US survey	13.7		0.010	0.356	0.702	1.00	0.849
-	15.0		0.341	0.785	1.00	0.548	0.171
MX survey	14.2		0.010	0.460	0.911	1.00	0.393
	15.0		1.00	0.732	0.731	0.228	0.071
				Second	quarter		
US fisherv	13.7		0.052	0.401	0.749	1.00	0.720
	15.0		0.496	0.935	1.00	0.371	0.116
MX fishery	14.2		0.264	0.571	0.878	1.00	0.495
	15.0		0.921	0.979	1.00	0.479	0.150
US survey	13.7		0.084	0.378	0.672	0.967	1.00
	15.0		0.424	0.755	1.00	0.737	0.230
MX survey	14.2		0.102	0.468	0.834	1.00	0.528
	15.0		1.00	0.813	0.766	0.321	0.100
				Fourth	quarter		
US fisherv	13.7	0.003	0.266	0.694	1.00	0.717	0.224
	15.0	0.032	0.887	1.00	0 369	0.115	0.036
MX fishery	14.2	0.225	0.459	0.847	1.00	0 493	0.154
	15.0	0.785	0.966	1.00	0.478	0.149	0.046

surveys. This result depended primarily on the lag between the large recruitments in 1970 and 1978 and the respective low sonar observations in 1971 and 1979. No independent evidence for age-specific availability is known. Reduced availability of young fish may be due to the concentration of young fish in shallow water where the side-looking sonar is less effective, and to a lesser tendency for young fish to aggregate into detectable schools.

The SS model estimated that about 30% of older fish (\geq 5 years) were misaged under the assumption that the percentage misaged increased linearly with age and doubled from age 0 to age 5.

The patterns of availability to age-composition samples (Table 7) were defined by 20 estimated parameters: four parameters for each type of age composition and four common parameters (Table 3). As ocean temperature increased, young fish became more available to each type of age-composition sample.

Full Time Series: 1954-1986

Extension of the model to the beginning of the northern anchovy data base was hampered by the lack of age-composition data. Prior to 1964, the only data were U.S. fishery landings and the HEP index of spawning biomass. Running the model back to 1954 required the assumption that the temperature-specific availability to the U.S. fishery was the same during this early period as it was during the post-1964 period. The trend in estimated biomass prior to 1964 probably was accurately described by the model (Table 8). However, high-frequency variation in recruitments prior to about 1964 should not be considered reliable. Without other data, the model fit itself very well to the HEP observations, even though the post-1964 data indicated high variability in the HEP index. Thus, the good fit prior to 1964 is misleading, and the estimated high-frequency variation in recruitment must contain a large component due to the measurement error in the HEP index.

Fishing Mortality

Annual instantaneous fishing mortality (Table 8) has varied due to changes in the level of the fishery and the abundance of the estimated population. During 1954–1957, annual fishing mortality, F, of fish in fully available ages was high, ranging from 0.3 to 0.9. Two factors may have inflated estimated F during this period. Temperature was very cold, so few of the age-1 fish were contributing to the spawning biomass during the

<u> </u>	Biomass on F	Feb 15 (tonnes)	Recruitmen	t" (in 10° fish)	Total
Үеаг	Total	Spawning	jui j	Feb 15	effort
1954	63 570	54 760	3.5	2.4	0.785
1955	53,610	37,920	4.2	2.6	0.869
1956	45,990	25,420	24.2	15.0	0.296
1957	153,920	141,160	15.9	10.8	0.474
1958	213.410	213,150	3.8	2.6	0.031
1959	182.370	182,160	<0.1	<0.1	0.027
1960	118,580	118,470	17.4	11.7	0.054
1961	170,820	160,900	40.2	26.9	0.073
1962	357,500	214,170	49.2	32.9	0.030
1963	563.040	520,210	37.3	25.1	0.012
1964	647,770	639,210	38.6	26.1	0.013
1965	695,280	531,520	13.4	9.1	0.024
1966	576,170	541,880	13.3	9.1	0.077
1967	434,270	409,170	27.9	18.8	0.127
1968	416.100	396.260	19.8	13.4	0.096
1969	395,650	374,300	33.1	22.6	0.168
1970	430,560	321,880	73.1	49.1	0.282
1971	678,390	333,600	123.3	83.9	0.131
1972	1,243,670	588,460	154.2	105.0	0.125
1973	1,848,680	1,812,900	114.9	78.6	0.094
1974	2,033,300	1,481,160	32.6	22.2	0.070
1975	1,606,570	1,458,430	14.3	9.7	0.118
1976	1,086,980	1,050,180	57.2	37.9	0.190
1977	870,170	868,890	6.5	3.8	0.387
1978	435.660	435,370	114.3	68.6	0.162
1979	869.270	582,890	82.0	46.3	0.209
1980	804,720	798,280	74.0	40.4	0.202
1981	814,930	782,770	19.7	9.5	0.422
1982	391,780	369,170	91.7	51.1	0.536
1983	552,200	534,590	36.2	21.4	0.157
1984	383.860	378.000	91.9	54.7	0.125
1985	767,490	589,060	57.3	34.0	0.096
1986	754,670	747,440			

TABLE 8.—Estimated biomass and recruitment of northern anchovy for the final stock synthesis model with emphasis of 20 on abundance data. Effort is the sum of the annual instantaneous fishing mortality rates, which were calculated quarterly (semesterly prior to 1966) then summed over the year for the values presented here.

"Recruitment estimates prior to 1964 are not based on any age-composition data, so they are much less precise than subsequent estimates.

early 1950s. If some of the age-2 fish were not spawning because of the cold temperatures, the total biomass would have been underestimated and the fishing mortality overestimated by the SS model. The second possibility is that age-0 fish were more available to the pre-1964 fishery than they were observed to be during the post-1964 period. If true, then the estimated fishing mortality rate necessary to obtain the observed landings would be reduced.

MacCall (1974) estimated that average F was 0.026 during 1964–1970, but this estimate was biased by the high biomass value $(2.3 \times 10^6$ tonnes) used in his calculations. If his calculations are redone with the new estimate of average

spawning biomass for this period, 460,000 tonnes, the average F for ages 2 and older is 0.128. The average annual F for fully available ages was estimated by the SS model to be 0.112 during the same period. Since 1975, the population has declined and the Mexican fishery has increased. Annual F in this period peaked at 0.54 in 1982.

Fit to Age Composition

Interannual variation in recruitment was estimated with high precision (Figure 8) because of the high consistency among the age-composition data sources and consistency with changes in EPM spawning biomass. However, the estimated recruitment index during 1970–1975 was consis-



FIGURE 8.—Time series of estimated recruitment of northern anchovy, and the observed (solid circles) and estimated recruitment indexes. The observed recruitment index is the average of the recruitment indexes in Figure 2. The estimated recruitment index is the average of the estimates for which there was a corresponding observation.

tently larger than the observed index. There is no doubt that these year classes were abundant because of the large increase in biomass between 1972 and 1975 (indicated by HEP and sonar) and the high frequency of age-4 and older fish in 1975 and 1976. The discrepancy between the observed and estimated recruitment indexes for these years would have been greater were it not for the environmental effects built into the interface between estimated numbers at age and the expected values for the observations. The relation between temperature and the fraction of fish mature made the low 1972 HEP value more likely; the high egg production by older fish (Parrish et al. 1986) made the large HEP value in 1975 more likely; and the temperature effect on age-specific availability made the low recruitment indexes of these good year classes more likely. In addition, the recruitment index is a relative measure, so the first good recruitment masked the magnitude of subsequent good recruitments.

The above factors were not quite sufficient to resolve all of the discrepancy. The large abundance of old fish in 1975 could not be achieved without slightly overestimating the recruitment index in 1971 and 1972 (Figure 8) and overestimating the abundance observations during the same period. At higher levels of natural mortality, this discrepancy was exaggerated because recruitments during the early 1970s had to be even greater to make a large contribution to the biomass and age composition in 1975. The level of emphasis placed on the abundance observations critically determined the absolute level of spawning biomass during the early 1970s. Levels ranging from 1×10^6 to 3×10^6 tonnes were easily obtained (Figure 4).

The unresolved discrepancy between abundance and age-composition data during the early 1970s is not a problem with the SS model: rather, the model identified a shortcoming in our knowledge of northern anchovy. A plausible scenario is that the total biomass actually was large during the early 1970s and that age 1 and age 2 northern anchovy were not spawning in 1972, which was a very cold year. Preliminary examination of the fraction of fish mature in samples taken from the reduction fishery indicates that only about 50% of the age-2 northern anchovy were spawning in 1972 (Methot, unpublished data).

The stock synthesis model is a flexible tool that has enabled a comprehensive review of historical abundance and mortality of northern anchovy. Patterns in deviations indicate shortcomings in our knowledge and identify areas for future investigation. For the present, the stock synthesis model is a valuable management tool because it provides a framework in which diverse types of data can contribute to current stock assessment.

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