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No. 20

RATES OF ATTRITION, COHORT ANALYSIS, AND STOCK PRODUCTION MODELS FOR SKIPJACK TUNA, KATSUWONUS PELAMIS, IN THE EASTERN PACIFIC OCEAN

By
Eric D. Forsbergh

La Jolla, California
1987

PREFACE

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These reports are not to be considered as publications. Because they are in some cases preliminary, and because they are subjected to less intensive editorial scrutiny than contributions to the Commission's Bulletin series, it is requested that they not be cited without permission from the Inter-American Tropical Tuna Commission.

PREFACIO

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Estos informes no deben considerarse como publicaciones, debido a que en algunos casos son datos preliminares, y porque están sometidos a un escrutinio editorial menos intenso que las contribuciones hechas en la serie Boletines de la Comisión; por lo tanto, se ruega que no sean citados sin permiso de la Comisión Inter-Americana del Atún Tropical.

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ABSTRACT

Attempts were made to estimate natural and fishing mortalities and emigration for skipjack from the eastern Pacific but the estimates obtained are unreliable. The results of cohort analysis are also unreliable. About one third of the variation in the catch per unit of effort can be attributed to the wind-mixing index in the spawning area; one third can also be attributed to fishing effort if the assumptions of the asymmetrical general production model are true, but this is not likely. About one third to one half of the variation can be attributed to both of these influences combined if the assumptions of the model are true.

INTRODUCTION

Estimates of the rates of mortality of skipjack in the eastern Pacific have been made by Joseph and Calkins (1969) and Bayliff (1977) from data obtained from tagging experiments. Bayliff (1977) Because of the large variation in these estimates from different experiments another method for estimating mortality rates was attempted in the present study, based on the rate of total attrition of untagged fish obtained from age-specific catch rates.

Cohort analysis and the general production model require the assumption of a closed system where the entire population remains in the fishing area during the time that the catches are made (see references under ANALYSES). Skipjack in the eastern Pacific, however, are generally believed to migrate to the fishing areas of the eastern Pacific from the spawning areas of the central and/or western Pacific, and most of the survivors are generally believed to migrate back to the spawning areas, completing the cycle (Forsbergh, 1980; Matsumoto, Skillman, and Dizon, 1984). If so, the system is not closed, and cohort analysis and the general production model are not applicable (Anonymous, 1986: 76). However, since so little is certain about skipjack in the eastern Pacific, and the system may in fact be closed (R. E. Kearney, formerly with the Inter-American Tropical Tuna Commission, p.c.; see Forsbergh, 1987: Section 3.4) these methods were applied to see whether any useful information might result.

The sources and processing of the data on which the present analyses are based are described by Forsbergh (1987).

ANALYSES

Rates of attrition

Exploited fish populations are reduced by fishing and natural mortality; many stocks in fishing areas are reduced by emigration as well, as is presumed to be the case for skipjack in the eastern Pacific. Using the notation of Ricker (1975), the combined reduction caused by all three factors is the rate of attrition (A), which is related to the rate of survival (S), and the instantaneous rate of attrition (Z) as follows: $(1 - A) = S = e^{-Z}$.

Tagging is one of the most commonly used methods for estimating rates of attrition. Tagged fish are subject to possible immediate mortality from capture, handling, and tagging, and to possible subsequent attrition from mortality due to carrying the tags (and also natural and fishing mortality and emigration). Estimates of mortality are affected by possible immediate shedding of the tags (Type-1 losses) and possible shedding of the tags subsequent to tagging (Type-2 losses).

From double-tagging experiments on yellowfin (*Thunnus albacares*) Bayliff and Mobrand (1972) assumed that the Type-2 shedding rate was constant. Kirkwood (1981), however, from double-tagging experiments on southern bluefin (*T. maccoyii*) proposed that the shedding rate decreases with time. Kleiber, Argue, and Kearney (1983) assumed that the shedding rate for skipjack from the central and western Pacific was constant, and the same assumption is made here for tagged skipjack in the eastern Pacific.

The following notation from Bayliff (1977) is used here in an attempt to estimate some of the components of the instantaneous rates of attrition for skipjack in the eastern Pacific:

q = coefficient of catchability;
f = fishing effort;
F = qf = coefficient of fishing mortality;
G = coefficient of mortality due to carrying the tags;
L = coefficient of loss due to shedding of the tags;
Q = $G + L$;

$\underline{M}$ = coefficient of natural mortality;

$\underline{E}$ = coefficient of net emigration;

$\underline{X}$ = $\underline{M} + \underline{E}$ = natural attrition of untagged fish;

$\underline{X}'$ = $\underline{G} + \underline{L} + \underline{M} + \underline{E} = \underline{Q} + \underline{M} + \underline{E}$ = "natural" attrition of tagged fish;

$\underline{Z}$ = $\underline{F} + \underline{M} + \underline{E} = \underline{F} + \underline{X}$ = total attrition of untagged fish;

$\underline{Z}'$ = $\underline{F} + \underline{G} + \underline{L} + \underline{M} = \underline{F} + \underline{Q} + \underline{M}$ = total attrition of tagged fish exclusive of emigration; and

$\underline{Z}'''$= $\underline{F} + \underline{G} + \underline{L} + \underline{M} + \underline{E} = \underline{F} + \underline{X}'$ = total attrition of tagged fish.

The subscripts $\underline{m}$, $\underline{q}$, and $\underline{a}$ to the rates and coefficients indicate values on monthly, quarterly, and annual bases, respectively.

Rates of total attrition for skipjack tagged in the eastern Pacific during 26 experiments initiated from 1957 to 1973 have been estimated by Bayliff (1977: Table 11) using the method of Robson and Chapman (1961: 182-185). Bayliff's $\underline{Z}'$ is based on data for the first month tagged fish were recaptured and the next five months (truncated data) under the assumption that fish did not emigrate from the eastern Pacific during this period; values of $\underline{Z}_m'$ ranged from -0.090 to 1.244. Bayliff's $\underline{Z}'''$ is based on all tagged fish returned and is assumed to include the effects of emigration after the first six months; values of $\underline{Z}_m'''$ ranged from 0.290 to 1.236. He noted that $\underline{Z}'''$ would be expected to be consistently higher than $\underline{Z}'$, but values were higher in only half of the experiments, and he believed that the test was not valid because there were insufficient returns of fish recaptured after 6 months. The mean values, $\underline{Z}_a' = 6.85$ and $\underline{Z}_a''' = 7.10$, are nearly the same. Mean values of $\underline{Z}'$ and of $\underline{Z}'''$ for each of the four areas of skipjack tagging and recapture were weighted by the proportion of the total logged catch for the entire fishery comprised by each area for the years during which tags were returned (Table 1) to obtain mean values more representative of the skipjack fishery of the eastern Pacific in its entirety. The weighted mean values of $\underline{Z}_a' = 6.71$ and $\underline{Z}_a''' = 6.86$ differ little from the simple means. Because values of $\underline{Z}_a'$ and $\underline{Z}_a'''$ are similar only $\underline{Z}_a'''$ will be considered here.

Table 1 shows that $\underline{Z}_m'''$ for areas at the northern and southern extremes of the skipjack fishery (Baja California and Revillagigedo Islands; Peru) is roughly two to three times the magnitude of $\underline{Z}_m'''$ for areas near the center of the fishery (Gulf of Panama; Gulf of Guayaquil). The weighted mean for the extreme areas was $Z_a''' = 10.20$; that for the central areas was $Z_a''' = 4.59$. Bayliff (1977: Table 13) shows estimates of F to be highest off Peru, next highest in the area off Baja California and the Revillagigedo Islands, lower in the Gulf of Guayaquil area, and lowest in the Gulf of Panama area. The higher values of Z_a''' at the extremes of the fishery, therefore, may be attributed, in part, to higher values of F. It is also likely that these higher values of Z_a''' may be caused, in part, by more rapid emigration (E) at the extremes of the fishery than at the center.

These estimates of Z_a''' for skipjack from Bayliff's (1977) data include Type-2 losses ($Q = G + L$). For yellowfin, Bayliff (1971) arbitrarily assumed G_a to be 0.1, and Bayliff and Mobrand (1972) estimated L_a to be 0.278 based on returns from 7,326 double-tagged yellowfin. Adding the values results in $Q_a = 0.378$, here rounded to 0.4. Assuming that Q_a is the same for skipjack as for yellowfin, this value was subtracted from mean values of Z_a''' from Bayliff (1977) to obtain Z_a (Table 2). For skipjack tagged in the area of the South Pacific Commission (SPC) in the western and central Pacific, Kleiber, Argue, and Kearney (1983: Figure A) assumed G to be zero, and estimated $L_m = 0.0073$, equivalent to $L_a = 0.088$, based on returns from 5,399 double-tagged fish. For skipjack tagged in the eastern Atlantic, Bard (1986) did not assume any value for G, and assumed $L_a = 0.1\text{-}0.2$ after Anonymous (1981: 3) where L_a was estimated to be 0.0759.

For skipjack tagged in the SPC area, Kleiber, Argue, and Kearney (1983) calculated an aggregate estimate of $Z_m = 0.17$ (equivalent to $Z_a = 2.04$) with 95% confidence limits from 0.15 to 0.20. From the combined data from the eastern Pacific from Bayliff (1977) $Z_a = 6.46$, over three times the SPC value (Table 2). It may be expected that Z should be greater for the eastern Pacific skipjack since little spawning occurs in the fishing areas, and fish departing for the spawning areas would cause E to be greater. Because spawning occurs throughout the central and western Pacific where the SSTs exceed 24°C the fish do not have to leave the area to spawn (with the exception of the New Zealand fishery where temperatures are too low for spawning) and E should be less, causing Z to be less.

For skipjack tagged in the eastern Atlantic by Japanese vessels, Bard (1986) estimated $\underline{Z}_a'$ for fish tagged in 1980 and recaptured during the first 6 months (truncated data, equivalent to Bayliff's $\underline{Z}_a'$) to be 4.32 for returns unadjusted for catch, and 4.92 for returns adjusted for catch. For fish tagged during 1981 and recaptured during the first seven months (truncated data) $\underline{Z}_a'$ was 2.28 for unadjusted returns, and 2.52 for adjusted returns. The mean of the two values of $\underline{Z}_a'$ for adjusted returns was 3.72. The method of Robson and Chapman (1961: 182-184), used by Bayliff (1977) to estimate $\underline{Z}_a'''$ for skipjack in the eastern Pacific, was applied to the entire tag return data for skipjack tagged by Japanese vessels in the Atlantic, including 20 months for those tagged in 1980 and 21 months for those tagged in 1981 (Bard, 1986: Tables 2 and 6). $\underline{Z}_a'$ was estimated to be 3.27 for fish tagged in 1980 and unadjusted for catch; adjusted data were not given for 1980. For fish tagged in 1981 $\underline{Z}_a'$ was estimated to be 2.88 for the unadjusted data, and 2.96 for the adjusted data, showing little difference. The mean of the two values of $\underline{Z}_a'$ unadjusted for catch was 3.08 (Table 2).

Comparison of the estimates of some of the components of the instantaneous rates of attrition for skipjack in the eastern Pacific show that there is considerable variability depending upon the area and the time of tagging experiments, and the methods used.

Because of the small numbers of skipjack returned in most of the tagging experiments analyzed by Bayliff (1977) and the great variation in values of $\underline{Z}'''$ obtained, an attempt was made to estimate $\underline{Z}$ from the catch rates of fish of different ages captured in the eastern Pacific. The method used was that of Robson and Chapman (1961: 186-188) for analyzing a segment of a catch curve. The catch rates for eight consecutive quarterly intervals (QIs) for each of the 1961-1983 cohorts were obtained from Forsbergh (1987) and are given in Table 3. Cohorts are designated by the year during which the age-1+ (12-24 months) fish are captured. The catch-rate curve is the catch rate plotted against QI (Figure 1). The beginning of the descending segment of the catch-rate curve, when the fish are assumed to be fully recruited, was selected subjectively from the plots; the end of the segment of the catch-rate curve used was always the eighth QI, effectively truncating any remaining data, hence the use of the Robson-Chapman (1961) method for a segment of a catch-rate curve.

$\underline{Z}_q$ was estimated for each cohort of skipjack from the descending segment of the catch-rate curve (Table 3). The segments of the catch-rate curves used included from three to five QIs, including fish of age 1+ in QI6, in QI5 and QI6, or in QI4 to QI6, and fish of age 2+ (24-36 months) in QI7 and QI8. Estimates of $\underline{Z}_a$ based on a linear growth rate of 24 cm/yr are given in Table 3; estimates based on the von Bertalanffy (vB) growth function were also made and ranges and the mean are given in Table 4. Estimates of $\underline{Z}$ appeared to be higher when based on three and four QIs than when based on five QIs. The estimates for three and four QIs combined, and those for five QIs were tested using the rank test (Tate and Clelland, 1957) and found to differ significantly ($\underline{P}$ <0.01). Median values of $\underline{Z}_a$ were obtained from three and four QIs combined, and from five QIs. The ratios of the two median values to their mean were used as adjustment factors for cohort values of $\underline{Z}_a$. The mean adjusted value differed little from the mean unadjusted value, so the latter was accepted as unbiased by the number of QIs used.

Values of $\underline{Z}$ estimated from tagging studies may be regarded as more precise than those based on relative abundance of fish of estimated ages, as in the present study, because fewer assumptions (such as the rate of growth) need be made. Although the assumptions may be questionable, values of $\underline{Z}$ obtained by the latter method have the advantage of being based on more data. The coefficient of variation ($\underline{C}$) for Bayliff's (1977: Table 11) 26 estimates of $\underline{Z}_m'''$ for skipjack was 0.49; for $\underline{Z}_a$ obtained from rates of attrition in the present study $\underline{C}$ = 0.37, showing the variation to be less than for the tagging data. These high values of $\underline{Z}$ and $\underline{A}$ estimated in Table 4 indicate that $\underline{F}$ or $\underline{M}$ or $\underline{E}$, or some combination of these, is very large. Values of $\underline{Z}_a$ obtained for skipjack by various methods and investigators are given in Table 2 for comparison. Because all of them are so high, it makes little difference whether they were obtained using $\underline{Q}$ = 0.4, 0.2, or 0.1. For the SPC area of the central and western Pacific $\underline{Z}_a$ = 2.04, and for the eastern Pacific $\underline{Z}_a$ = 6.46 from Bayliff's (1977) data for all areas combined and $\underline{Z}_a$ = 3.35 in the present study.

Estimates of $\underline{Z}$, however, are not often useful in analyses of population dynamics, unless some of the components can be estimated. Estimates of $\underline{M}$, $\underline{F}$, and $\underline{E}$ are required for population dynamics studies, but it is questionable whether these can be separated for skipjack from the eastern Pacific.

Murphy and Sakagawa (1977), using previously published estimates of $\underline{M}$ and $\underline{K}$, a parameter of the von Bertalanffy (vB) growth function, for albacore (Thunnus alalunga), bluefin (T. thynnus), and yellowfin assumed that a linear relationship existed and derived the following equation for tunas for estimating $\underline{M}$ from $\underline{K}$: $\underline{M}_a = 1.879\underline{K}$. For skipjack from the eastern Pacific, where $\underline{K}$ was estimated from the grouped data to be 0.79 (Anonymous, 1984: 33; see Forsbergh, 1987: Section 3.5), this equation yields $\underline{M}_a = 1.48$ (Table 5). For skipjack from the SPC area, where K was estimated to be 2.00, $\underline{M}_a = 3.76$, which is unrealistic since it is larger than $\underline{Z}_a = 2.04$. For skipjack from the eastern Atlantic, where $\underline{K}$ was estimated to be 0.322, $\underline{M}_a = 0.61$.

From data for 175 stocks of 84 species of fish Pauly (1980) derived the following equation from which $\underline{M}$ can be estimated for any stock: $\log\underline{M}_a = -0.0066 - 0.279 \log\underline{L}_\infty + 0.6543 \log\underline{K} + 0.4634 \log T$, where $\underline{L}_\infty$ is a parameter of the vB growth function, and T is the mean annual water temperature in degrees Celsius. Fishable concentrations of skipjack in the eastern Pacific have been found where sea-surface temperatures (SSTs) were as low as 17°C and as high as 30°C (Broadhead and Barrett, 1964; Blackburn, 1969). Temperatures at the average swimming depth of skipjack would be lower, but this depth is unknown, so the temperature cannot be estimated. The mean SST in the 22 5-degree skipjack areas of the eastern Pacific (Forsbergh, 1987: Figure K2) is 26°C. Substituting $\underline{K}$ and $\underline{L}_\infty$ for the grouped data and 26°C into Pauly's (1980) equation results in $\underline{M}_a = 1.10$. Stevens and Neill (1978) believed that the temperature in the muscles of skipjack is usually 2°-4°C higher than ambient temperature; and they measured values up to 9°C above ambient in fish that were feeding or swimming rapidly. The mean SST therefore was increased by 3°C to 29°C to adjust for the higher body temperature and substituted for T in Pauly's equation, which resulted in $\underline{M}_a = 1.16$, only 5% higher than $\underline{M}_a$ for 26°C.

For comparison $\underline{M}$ was also estimated for skipjack in the SPC area and the eastern Atlantic from Pauly's equation by adding 3°C to the mean SSTs from each area: for the SPC area $\underline{M}_a = 2.29$, which is unrealistic since it is larger than $\underline{Z}_a$; for the eastern Atlantic $\underline{M}_a = 0.66$ (Table 5).

Where $\underline{f}$ varies sufficiently, it has been shown that $\underline{X}$ and $\underline{q}$ can be estimated by the relationship $\underline{Z} = \underline{X} + \underline{qf}$, where $\underline{X}$ is the intercept and $\underline{q}$ is the slope, in the regression of $\underline{Z}$ and $\underline{f}$ (Beverton and Holt, 1956). Applying this method to the present study, $\underline{Z}_q$ for each skipjack cohort was plotted against the mean value of $\underline{f}_q''$ (see Forsbergh, 1987: Section 4.3) for the quarters used to estimate $\underline{Z}_q$ for the descending segment of each catch-rate curve (Table 3 and Figure 1). The scatter of the plots was so great and the correlations so far from significance that no estimates of $\underline{X}$ or $\underline{q}$ could be made, nor was there any indication that $\underline{Z}$ increased with $\underline{f}$.

Bayliff (1977) attempted to estimate $\underline{X}_m'$ for skipjack from the eastern Pacific, but could only conclude that it was probably less than 0.25, and used the value of 0.23 from Joseph and Calkins (1969) to estimate $\underline{F}$. Using the equivalent value of $\underline{X}_a' = 2.76$, and subtracting $\underline{Q}_a = 0.4$ results in $\underline{X}_a = 2.36$; subtracting $\underline{M}_a = 1.48$ (from the Murphy and Sakagawa 1977 equation) from $\underline{X}_a$ results in $\underline{E} = 0.88$; subtracting $\underline{M}_a = 1.16$ (from the Pauly 1980 equation) from $\underline{X}_a$ results in $\underline{E} = 1.20$. Subtracting $\underline{X}_a$ from $\underline{Z}_a$ results in $\underline{F}_a$; values are given in Table 2. The estimate of $\underline{F}_a = 7.44$ thus obtained from Bayliff's (1977) data for Baja California and Peru appears extremely high, resulting in a high exploitation rate ($\underline{F}/\underline{Z}$) of 0.76. Returns of skipjack tagged off Baja California often have been very high: of 8,098 fish tagged in October 1976, 67% were returned (Anonymous, 1978: 26). Corresponding values for Panama and Ecuador are much lower, with $\underline{F}_a = 1.83$ and $\underline{F}/\underline{Z} = 0.44$. In the present study based on length-frequency distributions $\underline{F}_a = 0.89$ and $\underline{F}/\underline{Z} = 0.27$. Although these calculations have been performed as an exercise in attempting to quantify the various components of $\underline{Z}$ for skipjack in the eastern Pacific, little confidence can be placed in any of the values obtained, because the estimate of $\underline{X}_a'$ from Joseph and Calkins (1969) is based on only one tagging experiment and because the estimates of $\underline{M}$ from Murphy and Sakagawa (1977) and Pauly (1980) are both questionable, and better estimates are not available.

Estimates of $\underline{X}_a' = 1.98$ and $\underline{F}_a = 0.54$ from skipjack tagged from Japanese vessels in the eastern Atlantic in 1981 were made by Bard (1986).

For skipjack in the SPC area Kleiber, Argue, and Kearney (1983) estimated F_a = 0.076 for the aggregate data. Lower tag-return rates for skipjack from the Atlantic and from the western and central Pacific relative to those from the eastern Pacific (Table 6) suggest that F is lower in these regions than in the eastern Pacific.

Cohort analysis

For cohort analysis it is assumed that there is a closed system, where the entire population remains within the geographical limits of the fishery throughout the time the catches are made (Ricker, 1948; Gulland, 1965; Murphy, 1965; Pope, 1972). Skipjack fished in the eastern Pacific are believed to have been spawned in the central Pacific, and then to have migrated to the eastern Pacific fishery area before reaching catchable size. Then, after spending some time there, the survivors are believed to return to the central Pacific to spawn and complete the cycle (see references in Forsbergh, 1987: Section 3.4). In addition, the possibility that there is some emigration of fish of catchable size from the central to the eastern Pacific cannot be ruled out. It is not assumed that all the fish hatched in the central Pacific migrate to the eastern Pacific; some may remain in the spawning area and others may migrate to other areas of the Pacific. Cohort analysis is probably not applicable to this fishery because the population is not a closed system, and it is not possible to differentiate between actual natural mortality (M) and migration into or out of the fishery, but only to estimate the combined effects as apparent natural mortality (M'). Because of lack of data on the age-specific distribution of M, it is normally assumed to be constant for all ages, but if M does vary and/or migration into or out of the fishery varies with age, M' will also vary with age, effectively violating the assumption and invalidating the results. Nevertheless, cohort analysis was performed with the skipjack data of the eastern Pacific to satisfy those who would insist that it be applied. Also, it provides some insight into the difficulties of estimating population size.

A computer program (Abramson, 1971) was prepared based on the method given by Tomlinson (1970) for estimating the numbers in a cohort at the beginning of each time interval when M is known for each interval, following Murphy's (1965) method. A modification of this method, described in Anonymous

(1972: 17-18), was used with the skipjack data. The basic data consisted of quarterly age-specific catches from logbooks of baitboats and purse seiners in numbers of fish (n) in each of the 1961-1982 cohorts calculated according to a growth rate of 24 cm/yr (Forsbergh, 1987: Section 4.3). Total quarterly age-specific catches (Table 7) were estimated by multiplying quarterly age-specific logged catches by a factor for each year. Factors were obtained by dividing total catches from all gears by length-frequency catches (LFC; Forsbergh, 1987: Section 4.3) from baitboats and purse seiners in all areas east of 150°W (Table 8). The data input consisted of total quarterly age-specific catches for eight consecutive quarterly intervals (QIs) for each cohort, from age-0+ (<12 months) fish in the third quarter of a year to age-2+ fish in the second quarter two years later. For most cohorts catches in QIs preceding or following this period were regarded as too small to be meaningful, and in many cases were zero, and therefore were excluded from the analyses for all cohorts.

Since $\underline{F}$ for QI8 on an annual basis ($\underline{F}_{a8}$) and $\underline{M}'$ are not known, various trial values were substituted, and the analysis performed using the backward solution. The resulting estimates of numbers of skipjack at the beginning of QI1 ($\underline{N}_1$, Table 9) for various input values of $\underline{F}_{a8}$ appeared particularly sensitive to $\underline{F}_{a8}$ for high values of $\underline{M}'$. A characteristic of the method is that for varying input values of $\underline{F}$, computed estimates of $\underline{F}$ tend to converge with successively younger ages, until they become similar in the first interval. Estimates of $\underline{N}_1$ for various values of $\underline{F}_{a8}$ should also converge to a similar value, since $\underline{N}_1$ is a function of $\underline{F}_{a1}$. In the present analysis, however, estimates of $\underline{N}_1$ infrequently converge to a similar value (Table 9). Mean values of $\underline{N}_1$ (in millions of fish) for all cohorts, and mean values of average $\underline{F}_a$ for 8 QIs for all cohorts are given in Table 10. The mean values of $\underline{N}_1$ for $\underline{M}_a' = 1.00$ vary by a factor of 2 and those for $\underline{M}_a' = 2.00$ vary by a factor of 3 for $\underline{F}_{a8}$ ranging from 0.20 to 2.00, and the large differences between values of $\underline{N}_1$ for the two values of $\underline{M}_a'$ indicate that the results of this analysis of the skipjack data are unreliable.

The coefficient of variation ($\underline{C} = \underline{s}/\bar{x}$) was calculated for skipjack catches for each QI for all cohorts and was found to be higher (0.88-1.64) during QI1 to QI3, lower (0.54-0.72) during QI4 to QI7, and higher (1.12) during QI8 (Table 7). This may indicate variable immigration and recruitment during the first three quarters, and variable emigration during the last quarter, any of which would invalidate the results of cohort analysis with these data. Any other estimates from these data of cohort strength using methods based on catches by time intervals, such as that of Paloheimo (1980), would also be invalidated.

Because of periodic variations in oceanic properties and their distributions such as temperature, salinity, oxygen concentrations, and possibly skipjack forage in large areas of the central and eastern Pacific, such as occur during El Niño events, it is likely that $\underline{M}$ is variable among cohorts, as well as among age groups within cohorts. If so, cohort analysis could not yield reliable estimates of $\underline{N}_1$ for comparing relative abundance.

Some possible additional reasons for the unreliable results of cohort analysis with the skipjack data are: 1) that the variation of the catches between successive quarters is too great; 2) that the time series are too short; and 3) that the quarterly intervals may be too large. The length-frequency data for skipjack have been compiled by quarterly intervals, and to recompile them by monthly intervals would require more time and effort than is now available. Also it is doubtful that using monthly intervals would improve the results, because the variation in the catches in successive months would be even greater than that in successive quarters.

Stock production models

The annual catch per unit of effort for skipjack captured by purse seiners in the eastern Pacific and adjusted for the successful set ratio (CPUE'), the cube of the wind speed in the spawning area at the time of spawning (W^3SP), and the annual estimated total fishing effort in the eastern Pacific ($\underline{f}'''$) are shown by Forsbergh (1987: Figure 2). Values of CPUE' were generally higher during the 1961-1971, period with a mean of 4.63, and lower during the 1972-1983 period, with a mean of 2.38. For W^3SP and $\underline{f}'''$ the pattern is reversed, with generally lower values in the earlier period and higher values in the later period. It has been shown by Forsbergh (1987: Section 4.533) that the logarithm of the catch rate of age-1+ skipjack in numbers per day (logCR") is inversely correlated with W^3SP. Since age-1+ fish are the major part of the catch in most years, it was expected that logCPUE' in the 1961-1983 period would also be correlated with W^3SP, and it was: $\underline{r}_s = -0.582$ and $\underline{r} = -0.617$ ($\underline{P}$ <0.01 for both). However $\underline{f}'''$ and W^3SP are themselves correlated with $\underline{r}_s = 0.549$ ($\underline{P}$ <0.01) and $\underline{r} = 0.468$ ($\underline{P}$ <0.05), and the apparent relationship of CPUE' with W^3SP may really have been caused by $\underline{f}'''$. One could test the correlation between CPUE' and $\underline{f}'''$, but the coefficients would have to be extremely high to indicate a functional correlation, since they are already mathematically correlated: $\underline{f}'''$ = total catch/CPUE'. In general, the greater the range of $\underline{f}$ the greater the mathematical correlation with CPUE. Here $\underline{f}'''$ varies by a factor of 5, from 13,200 to 63,700 Class-3 days, so a high mathematical correlation would be expected. To estimate the expected mathematical correlation 23 values ranging from 2 to 9 were picked from a table of random numbers to simulate $\underline{f}$ with a range factor close to 5, 23 values were picked for catches, and the CPUE calculated and tested for correlation with $\underline{f}$. For 10 such tests the mean value for $\underline{r}$ was -0.652 ($\underline{P}$ <0.01). For the actual fishery data $\underline{r} = -0.567$ ($\underline{P}$ <0.01) for CPUE' and $\underline{f}'''$, even lower than the value for the simulated data, indicating that this method is inadequate for evaluating this correlation.

Another approach in attempting to determine whether catch and CPUE are influenced by $\underline{f}$ is by the application of stock production models (Schaefer, 1957; Pella and Tomlinson, 1969). Some of the assumptions in production models are: 1) that there is little interchange, which is unrelated to the population size, of fish between the fishing area in question and other areas; 2) that there are no large environmental effects on the size of the population, or on availability, or on vulnerability; and 3) that $\underline{F}$ be sufficiently large relative to $\underline{M}$. Because these conditions did not appear to exist (Anonymous, 1986: 76; Forsbergh, 1987) production models had not previously been applied to skipjack from this fishery. However, since so little is certain about the behavior and population dynamics of skipjack, it was here assumed that these conditions could possibly exist, or at least be approximated, so the production models were applied. Two models were used: the symmetrical, or Schaefer model (Schaefer, 1957) where $\underline{m} = 2.0$, and the asymmetrical generalized model where $\underline{m} \neq 2.0$ (Pella and Tomlinson, 1969). The symmetrical model requires that the stock size at maximum equilibrium catch be exactly half of the maximum stock size. Because the curve of equilibrium catch versus stock size is believed likely to be skewed with the maximum occurring at less than half the maximum stock size (Pella and

Tomlinson, 1969), the asymmetrical production model is regarded as more realistic. For the latter model $\underline{m}$ was set at 0.8, as it has been for yellowfin in the eastern Pacific fishery (Anonymous, 1984: 75).

The limits by which the input parameters were constrained were selected to reduce the computation time. Several trials were made using different limits until the sum of squares was reduced, indicating a better fit between models and the data. Results of the final trials are given in Table 11. For the symmetrical model maximum equilibrium catch ($\underline{C}_{max}$) was 110,000 tons at an optimum effort ($\underline{f}_{opt}$) of 44,000 Class-3 days. For the asymmetrical model the corresponding values were 78,000 tons and 50,000 Class-3 days (the lower limit set). The equilibrium catch curves are shown in Figure 2; and the CPUE' observed and CPUE' expected from the models ($CPUE'_e$) are shown in Figure 3, Panels A and B. It is apparent that $CPUE'_e$ from the asymmetrical model fits the data better than $CPUE'_e$ from the symmetrical model. Correlation coefficients for CPUE' and $CPUE'_e$ for the symmetrical model are $\underline{r}_s = 0.441$ and $\underline{r} = 0.435$ ($\underline{P} < 0.05$ for both), and for the asymmetrical model $\underline{r}_s = 0.700$ and $\underline{r} = 0.593$ ($\underline{P} < 0.01$ for both). Values obtained for logCPUE' and W^3SP are $\underline{r}_s = -0.582$ and $\underline{r} = -0.623$ ($\underline{P} < 0.01$ for both, Figure 3, Panel C). While $\underline{r}^2$ from the asymmetrical model is similar to that from W^3SP, for the asymmetrical model $\underline{r}_s^2 = 0.490$, and for W^3SP $\underline{r}_s^2 = 0.339$, indicating that the asymmetrical model is a better predictor of CPUE' than is W^3SP. However, the catch rate of age-1+ fish in numbers per day (CR") is regarded as a better index of cohort strength than CPUE' of all ages in tons per day (Forsbergh, 1987: Section 4.533) and for logCR"24 and W^3SP $\underline{r}_s^2 > 0.569$ and $\underline{r}^2 > 0.540$ (from Forsbergh, 1987: section 4.533). Thus it appears that CPUE' is best related with $\underline{f}'''$ using the asymmetrical production model, if the assumptions are fullfilled; while CR" is best related to W^3SP, if wind-mixing in the spawning areas of the central Pacific actually is determining cohort strength by influencing the survival of skipjack larvae (Forsbergh, 1987: Section 4.51).

Previous investigations of age-structured models (Anonymous, 1986: 77) have indicated that the yield per recruit for skipjack in the eastern Pacific is maximum at a size of entry of about 35 cm with fishing effort several times that of recent years. It was concluded that the best way of maximizing catches was to exert maximum effort on fish over 35 cm (Anonymous, 1986: Figure 52). Since few fish less than 35 cm are caught maximum effort could be exerted on all sizes presently caught. Examination of the yield-per-recruit curves show that the yield per recruit would not increase proportionally with $\underline{f}$, but would increase at progressively slower rates, such that with sufficiently large $\underline{f}$ the catch would also increase at progressively slower rates, approaching an upper limit, where increased effort would not increase the catch. At some fairly high value of $\underline{f}$ the CPUE would reach the point where the CPUE was so low that the fishery was barely profitable, and $\underline{f}$ would stabilize at that level. These results are regarded as compatible with those of the asymmetrical model where equilibrium catch decreases only gradually with $\underline{f}$ increasing beyond optimum $\underline{f}$.

Results of the production models are highly questionable because some of the assumptions are not fulfilled, and results of the yield-per-recruit model are also questionable because they are based on estimates of growth which vary with area (Forsbergh, 1987: Section 3.5), and on estimates of $\underline{M} + \underline{E}$ and $\underline{F}$ which vary with the data used and with the methods used to obtain the estimates (Forsbergh, 1987: Section 4.3).

Having assumed in this section that the major influence on the catch and CPUE' is $\underline{f}'''$, the ratios CPUE'/CPUE'$_e$ calculated by the two production models were examined for possible correlations with environmental variables in an attempt to explain some of the residual variation in the CPUE'. The ratios were converted to logarithms because the effects of environmental variables are believed to be multiplicative (Ricker, 1975). Correlation coefficients for log(CPUE'/CPUE'$_e$) for the two production models and the four environmental variables are given in Table 11. None are significant at $\underline{P} = 0.05$ for two-sided tests, with the exception of $\underline{r}$ for W^3SP. However, since the corresponding $\underline{r}_s$ value is not significant, and $\underline{r}_s$ is the preferred correlation coefficient here, it is concluded that W^3SP does not explain any of the variation in the ratios from either of the production models. $\underline{f}'''$ therefore remains as the only variable that can account for changes in total catch of skipjack and in CPUE', when production models are applied first to the data, and environmental models are applied second.

Those who prefer $\underline{r}$ over $\underline{r}_s$, however, may conclude that W^3SP explains some of the variation in the production models. Expected values of CPUE' due to the effect of W^3SP superimposed on CPUE'$_e$ from the asymmetrical model were calculated from the regression equation of log(CPUE'/CPUE'$_e$) and W^3SP and are designated as $CPUE'_{ee}$. They are shown in Figure 3, Panel D, and the fit with CPUE' for this combined model is slightly improved over that for the asymmetrical model alone, or W^3SP alone. $r^2 = 0.351$ for the asymmetrical model, $r^2 = 0.388$ for W^3SP, and $r^2 = 0.462$ for the combined model.

The alternative hypothesis is that W^3SP is the major influence on CPUE' of skipjack by determining the recruitment, and that f has a lesser influence. Under these assumptions the environmental model should be applied first, and the production model second. logCPUE' and W^3SP earlier were shown to be significantly correlated at the 1% level. The regression equation is:

$$\log CPUE' = 1.006 - 0.0003006 W^3SP$$

$CPUE'_e$ was calculated from this equation. The production model, however, uses only f and total catch as input data, so either f or total catch must be adjusted for the effect of W^3SP on CPUE'. The estimates of total catch are far more reliable than those of f, so it is preferable to manipulate the latter to conform to $CPUE'_e$ by dividing total catch by $CPUE'_e$ to obtain f'''', adjusted for the effect of W^3SP. The asymmetrical production model was then applied using f'''', and C_{max} is 81,500 tons with $f_{opt}'''' = 70{,}000$ Class-3 days, and the equilibrium catch curve is almost flat with further increases in f''''; at 100,000 Class-3 days the equilibrium catch is 77,200 tons. Although the sum of squares ($SS = 1.744 \times 10^9$) is slightly larger for this second application of the model than that from the first application of the asymmetrical model using f''' ($SS = 1.555 \times 10^9$), meaning a slightly poorer fit, the flatness of the equilibrium catch curve to the right of f_{opt}'''' agrees well with the yield-per-recruit model showing catches leveling off asymptotically with increasing effort.

Expected values of CPUE' ($CPUE'_{ee}$) due to the effect of the asymmetrical model superimposed on $CPUE'_e$ from the W^3SP model are shown in Figure 3, Panel E. Compared to the previous combined model where the asymmetrical model was applied first (Figure 3, Panel D), the fit appears to be poorer, and although r_s values are similar, r is lower, and $r^2 = 0.367$ compared to $r^2 = 0.462$ for the previous model.

Correlation coefficients for expected and observed values of CPUE' from the five models (Figure 3, Panels A-E) show the symmetrical model to have a poorer fit ($\underline{P}$ <0.05) than the other four models ($\underline{P}$ <0.01). The fit among the latter models is similar, with the combined model where the asymmetrical model is applied first being the best, but the differences are so small that it is concluded that all four models are equally probable.

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SYMBOLS AND ABBREVIATIONS

(Others are listed on pages 4-5.)

*	statistical significance at $0.01 < \underline{P} \leq 0.05$
**	statistical significance at $\underline{P} \leq 0.01$
$\underline{A}$	rate of attrition
age 0+	estimated age <12 months
age 1+	estimated age 12 to 24 months
age 2+	estimated age 24 to 36 months
$\underline{C}$	coefficient of variation
$\underline{C}_{max}$	maximum equilibrium catch
CPUE	catch per unit of effort
CPUE'	catch per unit of effort adjusted for changes in the successful set ratio
$CPUE'_e$	expected CPUE' from the asymmetrical production model or W^3SP
$CPUE'_{ee}$	expected CPUE' from the asymmetrical production model and W^3SP combined
CR''	age-specific catch rate, in numbers of fish divided by length-frequency fishing effort
$\underline{f}''$	length-frequency fishing effort
$\underline{f}'''$	total fishing effort
$\underline{f}''''$	total fishing effort estimated for stock production models
$\underline{f}_{opt}$	optimum fishing effort
IATTC	Inter-American Tropical Tuna Commission
$\underline{K}$	growth coefficient in the von Bertalanffy growth function
$\underline{L}$	asymptotic length in the von Bertalanffy growth function
LFC	length-frequency catch - catch used in the calculation of length-frequencies
$\underline{m}$	a parameter of the production models
$\underline{N}_1$	number of fish in cohort analysis at the beginning of each interval
n	age-specific logged catches by baitboats and purse seiners in numbers of fish
n'	n converted to total catch by all gears
n.s.	not statistically significant ($P > 0.05$)
$\underline{P}$	the probability of making a Type-1 error

QI	quarterly interval
Qr	quarter of the year
$\underline{r}$	product-moment coefficient of correlation
$\underline{r}^2$	coefficient of determination
$\underline{r}_{\underline{s}}$	Spearman's coefficient of correlation for ranks
$\underline{r}_{\underline{s}}^2$	coefficient of determination for ranks
$\underline{s}$	standard deviation
SPC	South Pacific Commission
SS	sum of squares
SST	sea-surface temperature
T	water temperature
vB	von Bertalanffy growth function
W^3SP	wind-mixing index in the spawning area where SST >82°F (27.8°C)
$\underline{\bar{x}}$	arithmetic mean

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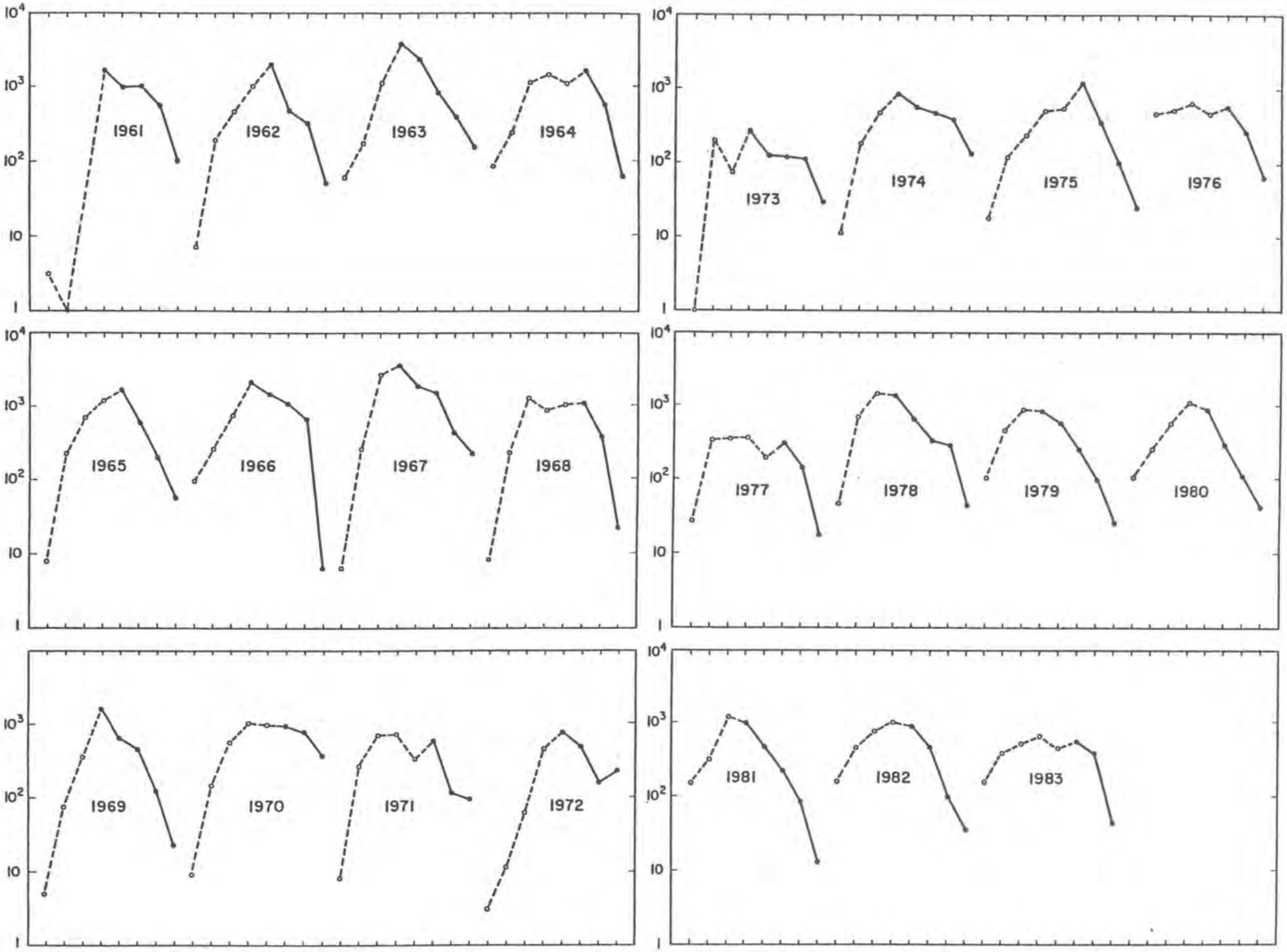

FIGURE 1. Catch-rate curves for skipjack cohorts in the eastern Pacific based on a linear growth rate of 24 cm/yr. The solid lines indicate the portions of the curves used in the Robson and Chapman (1961) method.

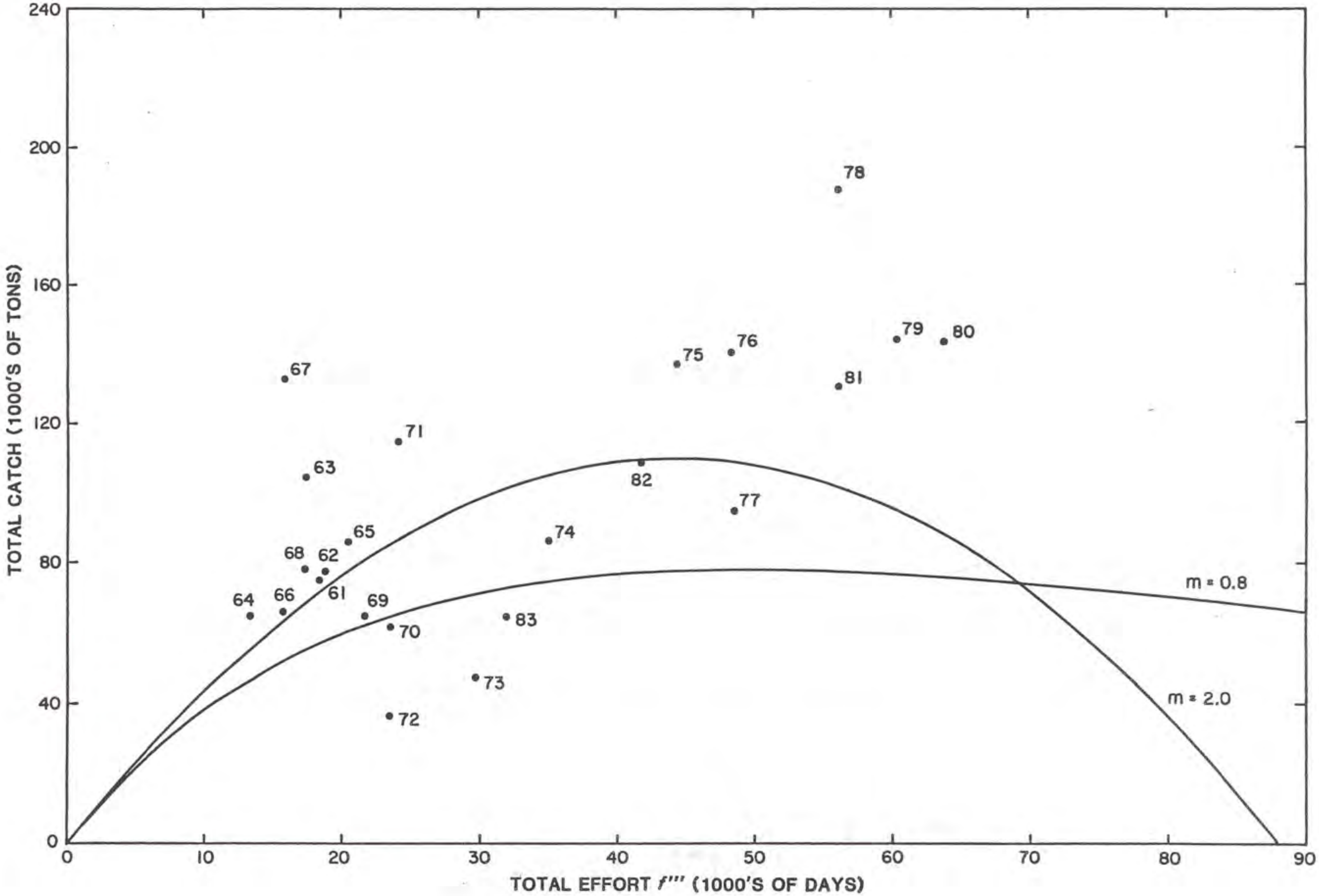

FIGURE 2. Equilibrium catch curves for skipjack in the Pacific east of 150°W for the symmetrical ($\underline{m}$ = 2.0) and the asymmetrical ($\underline{m}$ = 0.8) production models.

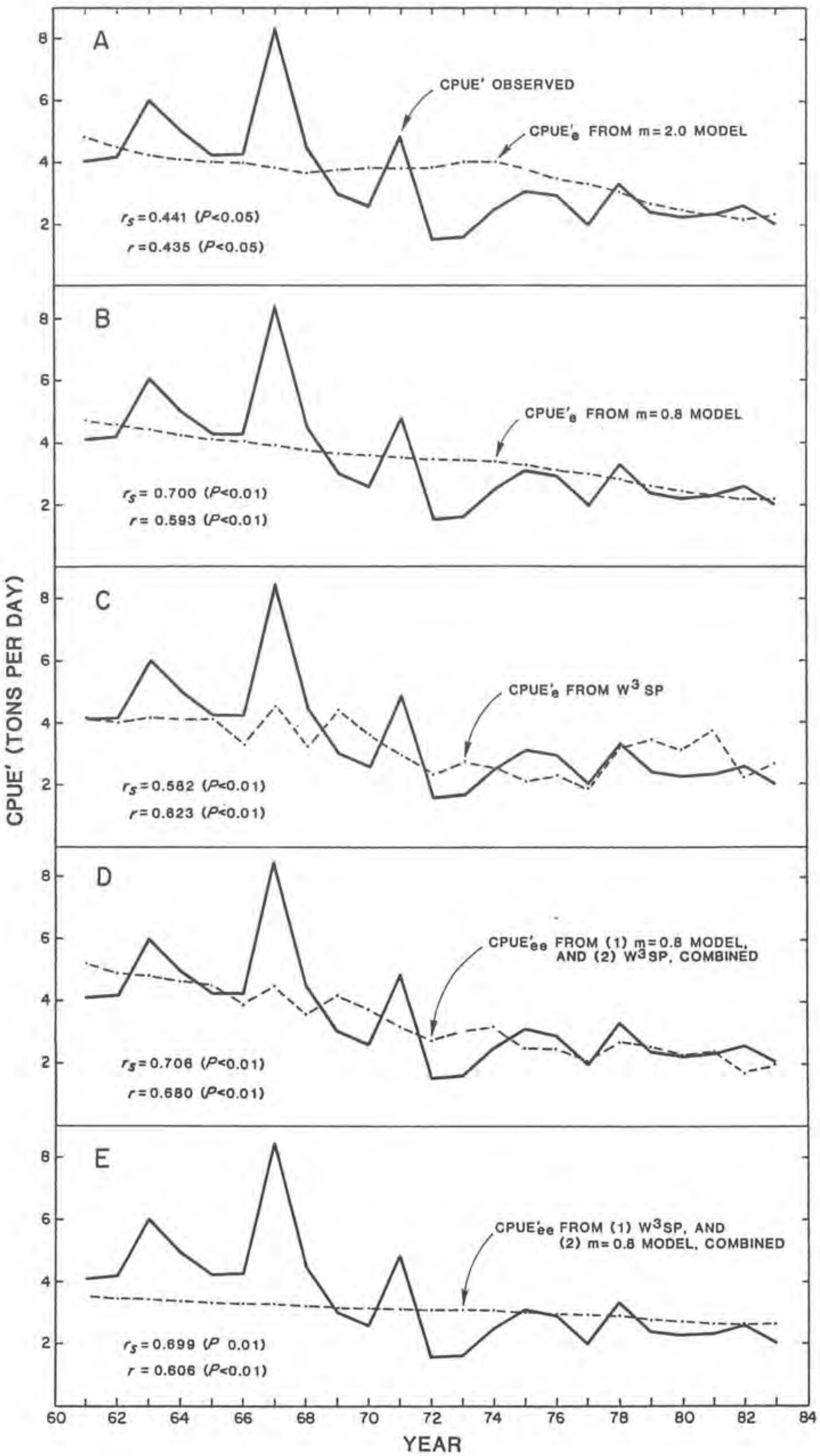

FIGURE 3. CPUE' observed for skipjack in the eastern Pacific. Expected CPUE' from: A. symmetrical (m = 2.0) production model; B. asymmetrical (m = 0.8) model; C. W^3SP; D. from the asymmetrical model and W^3SP; E. from W^3SP and the asymmetrical model (order reversed).

TABLE 1. Mean values of $\underline{Z}_m$' and $\underline{Z}_m$''' for skipjack in four areas of the eastern Pacific from estimates in Bayliff (1977: Table 11), the mean proportion of the total logged catch for the entire fishery comprised by each area for the years during which tags were returned, and weighted mean values of $\underline{Z}$' and $\underline{Z}$''' for all areas combined from area means and proportions.

Area	Numbers of experiments	Proportion	Mean $\underline{Z}_m$'	$\underline{Z}_a$'	Mean $\underline{Z}_m$'''	$\underline{Z}_a$'''
Baja California and Revillagigedo Islands	8	0.185	0.812		0.763	
Gulf of Panama	2	0.313	0.338		0.344	
Gulf of Guayaquil	12	0.366	0.320		0.414	
Peru	4	0.276	0.956		0.909	
		weighted mean	0.559	6.71	0.572	6.86

TABLE 2. Means of estimates of annual instantaneous rates of total attrition and components thereof for skipjack in the eastern Pacific in the present study from catch rates in Table 3; means from tagging experiments in the eastern Pacific and in the South Pacific Commission (SPC) area; and estimates from two tagging experiments in the eastern Atlantic. Symbols are explained in the text.

	SPC area	Eastern Pacific				Eastern Atlantic					
	Kleiber *et al.*, 1983	Bayliff, 1977			Present study	Bard, 1986: Japanese data					
						Adjusted			Unadjusted		
	Aggregate data	Panama Ecuador	Baja Cal. Peru	Comb.		1980 1-6 mo.	1981 1-7 mo.	Mean	1980 20 mo.	1981 21 mo.	Mean
Z_a'''		4.59	10.20	6.86		4.92	2.52	3.72	3.27	2.88	3.08[a]
Q_a		0.4	0.4	0.4[b]		0.2	0.2	0.2[c]	0.2	0.2	0.2[c]
Z_a	2.04	4.19	9.80	6.46	3.25	4.72	2.32	3.52	3.07	2.68	2.88
X_a'		2.76	2.76	2.76[d]	2.76[d]	1.98					
X_a		2.36	2.36	2.36	2.36						
M_a		1.48	1.48	1.48[e]	1.48[e]						
E_a		0.88	0.88	0.88	0.88						
F_a	0.076	1.83	7.44	4.10	0.89	0.54					
F/Z	0.037	0.44	0.76	0.63	0.27	0.23					

a - calculated from data in Bard (1986)
b - from data for yellowfin from Bayliff and Mobrand (1972)
c - from Bard (1986)
d - from Joseph and Calkins (1969)
e - from Murphy and Sakagawa (1977) equation (Table 5)

TABLE 3. Quarterly catch rates of skipjack by age groups caught by purse seiners in the Pacific east of 150°W estimated according to a growth rate of 24 cm/yr in number of fish per Class-3 day (from Forsbergh, 1987: tables for Section 4.3). The means ($\bar{x}$), standard deviations (s), and coefficients of variation (C) are listed at the bottom of the table. The estimates of Z_a were obtained from the underlined values by the method of Robson and Chapman (1961: 186-188).

		Age 0+		Age 1+				Age 2+		S_q	Z_q	Z_a
Cohort	Quarter	3	4	1	2	3	4	1	2			
	QI	1	2	3	4	5	6	7	8			
1961		3	1	--	1,621	957	1,014	522	102	0.62	0.48	1.92
1962		7	187	465	1,010	2,004	465	316	51	0.33	1.11	4.44
1963		57	181	1,125	3,765	2,373	818	379	153	0.47	0.75	3.00
1964		85	238	1,226	1,419	1,084	1,592	559	70	0.27	1.31	5.24
1965		8	230	704	1,201	1,669	589	193	57	0.34	1.08	4.32
1966		93	247	727	2,138	1,466	1,040	652	6	0.59	0.53	2.12
1967		6	248	2,758	3,609	1,861	1,502	428	214	0.54	0.62	2.48
1968		8	222	1,258	859	1,036	1,059	372	21	0.25	1.39	5.56
1969		5	77	348	1,623	659	451	127	23	0.44	0.82	3.28
1970		9	146	527	977	947	927	774	366	0.66	0.42	1.68
1971		8	261	685	720	325	585	113	92	0.33	1.11	4.44
1972		3	11	60	438	739	471	156	218	0.60	0.51	2.04
1973		1	197	74	260	124	118	112	30	0.68	0.39	1.56
1974		11	184	469	861	545	466	392	136	0.70	0.36	1.44
1975		18	121	237	498	523	1,196	356	99	0.29	1.24	4.96
1976		25	470	513	641	473	579	275	66	0.38	0.97	3.88
1977		27	331	350	352	191	296	142	17	0.34	1.08	4.32
1978		45	692	1,427	1,328	641	328	280	42	0.52	0.65	2.60
1979		102	445	835	806	554	240	94	25	0.49	0.71	2.84
1980		100	245	533	1,072	870	284	107	42	0.35	1.05	4.20
1981		153	315	1,197	1,030	482	226	85	14	0.43	0.84	3.36
1982		160	461	785	1,050	921	476	97	39	0.37	0.99	3.96
1983		167	426	567	714	498	595	415	47	0.42	0.87	3.48
1984		59	763	974	1,175	570	281					
1962-1983	$\bar{x}$	50	270	766	1,199	908	650	292	83	1961-83	$\bar{x}$	3.35
	s	56	153	585	913	608	409	194	88		s	1.23
	C	1.12	0.57	0.76	0.76	0.67	0.63	0.66	1.06		C	0.37

Table 4. Statistics for $\underline{Z}_a$ and annual rates of attrition ($\underline{A}_a$), based on a linear growth rate of 24 cm/yr and the von Bertalanffy (vB) growth function ($\underline{L}_{\infty}$ = 86.0, $\underline{K}$ = 0.79, from Anonymous, 1984: 33) from the 1961-1983 cohorts of skipjack caught in the eastern Pacific.

Growth		Range	$\bar{x}$	s	C	A_a
24 cm/yr	Z_a	1.56-5.56	3.35	1.23	0.37	0.965
vB	Z_a	1.44-5.24	3.24	1.19	0.37	0.961

TABLE 5. Estimates of M for skipjack derived from the Murphy and Sakagawa (1977) equation (M & S), and from the Pauly (1980) equation. Three degrees C has been added to the mean SST for each of the skipjack areas to adjust for the higher body temperature of skipjack.

Area	Source of L_∞ and K	L_∞ cm	K	T °C	M_a M & S	M_a Pauly
SPC area	Kleiber, Argue, and Kearney (1983)	62.5	2.04	28	3.83	2.32
Eastern Pacific	Anonymous (1984: grouped data)	86.0	0.79	29	1.48	1.16
Eastern Atlantic	Bard and Antoine (1986)	80.0	0.322	29	0.61	0.66

Murphy and Sakagawa (1977) equation: $M = 1.879\ K$
Pauly (1980) equation: $\log M = -0.0066 - 0.279 L_\infty + 0.6543 \log K + 0.4634 \log T$

TABLE 6. Ranges and means of percentages of return of skipjack captured by pole and line and tagged during various experiments (N) in several oceanic regions. This list excludes experiments from which less than 100 tagged fish were released.

Region	Year tagged	N	Percentages of return		Sources
			Range	Mean	
SPC area	1977-1980	9	0.6-14	6.8	Kleiber, Argue, and Kearney (1983: Table 2)
Eastern Atlantic	1980-1981	2	5.8-9.8	7.8	Bard (1986: Table 3)
Eastern Pacific	1957-1973	31	0.6-49	12	Bayliff (1977: Table 1)
Eastern Pacific	1975-1981	14	5.7-67	30	William H. Bayliff (p.c.)

TABLE 7. Estimated numbers of skipjack (in thousands: 10^3n) caught by baitboats and purse seiners in the eastern Pacific in eight consecutive quarterly intervals (QI) from each cohort, calculated according to a growth rate of 24 cm/yr, and numbers converted to total catch by all gears ($10^3n'$) using annual factors from Table 8. The standard deviations (s), means ($\bar{x}$), and coefficients of variation (C) for $10^3n'$ for the eight QIs are listed at the bottom of the table.

Cohort		Age 0+		Age 1+				Age 2+	
		1	2	3	4	5	6	7	8
1961	10^3n	20	135	609	4,560	3,454	3,256	1,867	358
	$10^3n'$	37	251	1,113	8,336	6,277	5,952	2,528	485
1962	10^3n	20	558	1,674	3,696	6,313	1,646	1,202	128
	$10^3n'$	37	1,020	2,267	5,004	8,548	2,229	1,730	184
1963	10^3n	203	758	4,331	9,210	5,273	3,514	778	317
	$10^3n'$	275	1,026	6,232	13,253	7,588	5,057	1,124	458
1964	10^3n	171	956	2,468	3,113	3,303	2,922	1,143	315
	$10^3n'$	246	1,376	3,566	4,498	4,773	4,222	1,552	428
1965	10^3n	26	396	1,443	5,052	6,911	2,454	787	142
	$10^3n'$	38	572	1,960	6,861	9,385	3,333	1,047	189
1966	10^3n	331	877	2,842	5,701	3,950	1,945	1,485	43
	$10^3n'$	449	1,191	3,780	7,582	5,254	2,587	1,862	54
1967	10^3n	22	537	6,048	12,987	8,449	2,673	655	1,098
	$10^3n'$	29	714	7,584	16,286	10,595	3,352	941	1,577
1968	10^3n	38	395	1,927	4,625	3,066	2,382	1,344	100
	$10^3n'$	48	495	2,767	6,642	4,403	3,421	2,215	165
1969	10^3n	16	179	1,261	7,464	1,502	965	679	88
	$10^3n'$	23	257	2,078	12,301	2,475	1,590	963	125
1970	10^3n	21	320	2,534	5,143	4,051	1,643	5,619	2,723
	$10^3n'$	35	527	3,593	7,293	5,744	2,330	6,984	3,385
1971	10^3n	42	456	5,294	6,416	593	957	1,004	199
	$10^3n'$	60	647	6,580	7,975	737	1,190	1,839	365

TABLE 7. (continued)

Cohort		Age 0+		Age 1+				Age 2+	
		1	2	3	4	5	6	7	8
1972	10^3n	7	26	552	1,437	600	982	1,212	1,555
	$10^3n'$	9	32	1,011	2,633	1,099	1,799	1,850	2,373
1973	10^3n	0	325	595	2,393	748	667	1,031	316
	$10^3n'$	1[a]	595	908	3,652	1,141	1,018	1,538	471
1974	10^3n	34	738	4,720	9,274	1,094	2,068	4,379	2,120
	$10^3n'$	52	1,126	7,042	13,837	1,632	3,085	5,539	2,682
1975	10^3n	38	478	3,019	7,683	1,441	6,022	4,366	1,355
	$10^3n'$	57	713	3,819	9,719	1,823	7,618	5,960	1,850
1976	10^3n	58	2,528	6,628	9,286	2,115	3,579	2,912	549
	$10^3n'$	73	3,198	9,047	12,675	2,887	4,885	4,493	847
1977	10^3n	175	2,521	3,886	3,587	958	1,944	1,875	238
	$10^3n'$	239	3,441	5,996	5,535	1,478	3,000	2,393	304
1978	10^3n	218	4,291	18,418	19,361	4,533	3,034	3,227	421
	$10^3n'$	336	6,621	23,501	24,705	5,784	3,871	3,989	520
1979	10^3n	705	3,869	11,238	10,637	7,608	2,211	1,510	358
	$10^3n'$	900	4,937	13,890	13,147	9,403	2,733	1,901	451
1980	10^3n	1,284	2,322	8,824	15,710	10,243	2,245	1,362	615
	$10^3n'$	1,587	2,870	11,109	19,779	12,896	2,826	1,637	739
1981	10^3n	1,790	2,487	15,269	15,171	3,562	2,458	915	135
	$10^3n'$	2,254	3,131	18,353	18,236	4,282	2,955	1,100	162
1982	10^3n	1,034	4,815	8,350	10,232	5,714	2,940	597	352
	$10^3n'$	1,243	5,786	10,037	12,299	6,868	3,546	737	435
	$\bar{x}$	365	1,842	6,647	10,557	5,231	3,300	2,451	830
	$\underline{s}$	600	1,910	5,855	5,675	3,455	1,555	1,775	931
	$\bar{C}$	1.64	1.04	0.88	0.54	0.66	0.47	0.72	1.12

a - increased to 1 to avoid having a zero in the interval

TABLE 8. Total catch of skipjack by all gears in the eastern Pacific east of 150°W, length-frequency catches by baitboats and purse seiners in the same area, and annual factors for converting purse-seiner catches to total catches (in short tons).

Year	Total catch	Length-frequency catch	Factor
1960	46.2	27.7	1.668
1961	75.5	41.3	1.828
1962	78.3	57.9	1.352
1963	105.3	73.1	1.440
1964	65.3	45.9	1.423
1965	86.2	63.5	1.357
1966	66.7	50.1	1.331
1967	133.0	105.6	1.259
1968	78.3	54.5	1.437
1969	65.1	39.5	1.648
1970	61.7	43.5	1.418
1971	115.4	92.9	1.242
1972	36.8	20.1	1.831
1973	48.4	31.7	1.527
1974	86.8	58.2	1.491
1975	136.7	108.7	1.258
1976	140.1	103.2	1.358
1977	95.6	62.0	1.542
1978	186.7	147.1	1.269
1979	145.6	117.7	1.237
1980	144.1	114.5	1.259
1981	131.0	109.0	1.202
1982	108.8	90.6	1.201
1983	63.9	52.4	1.219
1984	66.5	56.4	1.179

TABLE 9. Estimates of $\underline{N}_1$ in millions of fish and mean estimates of $\underline{F}_{\underline{a}}$ for eight quarterly intervals, for skipjack cohorts, using the Murphy (1965) cohort analysis assuming two values of $\underline{M}_{\underline{a}}$ and three values of $\underline{F}_{\underline{a}8}$. The means ($\bar{x}$), standard deviations ($\underline{s}$), and coefficients of variation ($\underline{C}$) for the six sets of estimates are listed at the bottom of the table.

	$\underline{M}_{\underline{a}}' = 1.00$						$\underline{M}_{\underline{a}}' = 2.00$					
$\underline{F}_{\underline{a}8}$	0.20		1.00		2.00		0.20		1.00		2.00	
Cohort	$\underline{N}_1$	$\underline{F}_{\underline{a}}$	$\underline{N}_1$	$\underline{F}_{\underline{a}}$	$\underline{N}_1$	$\underline{F}_{\underline{a}}$	$\underline{N}_1$	$\underline{F}_{\underline{a}}$	$\underline{N}_1$	$\underline{F}_{\underline{a}}$	$\underline{N}_1$	$\underline{F}_{\underline{a}}$
1961	142	0.42	91	1.06	85	1.44	684	0.27	355	0.80	313	1.16
1962	86	0.65	66	1.38	64	1.78	354	0.43	228	1.07	212	1.45
1963	155	0.49	107	1.16	101	1.55	671	0.29	360	0.84	321	1.20
1964	116	0.38	71	0.99	65	1.37	559	0.43	269	0.73	233	1.07
1965	93	0.68	73	1.41	70	1.81	374	0.44	245	1.09	228	1.47
1966	70	1.16	64	1.98	63	2.39	240	0.85	201	1.62	196	2.02
1967	315	0.23	150	0.72	130	1.06	1,653	0.12	591	0.47	458	0.76
1968	82	0.68	64	1.42	62	1.82	340	0.46	226	1.12	212	1.50
1969	69	0.73	55	1.48	54	1.88	256	0.46	171	1.12	160	1.50
1970	538	0.11	186	0.44	142	0.72	3,237	0.08	959	0.33	675	0.57
1971	97	0.37	59	0.98	54	1.35	456	0.21	209	0.68	178	1.04
1972	344	0.07	97	0.29	67	0.52	2,147	0.05	550	0.23	352	0.42
1973	89	0.20	40	0.66	34	0.99	496	0.13	179	0.48	139	0.77
1974	450	0.14	171	0.52	136	0.82	2,619	0.09	813	0.36	588	0.62
1975	344	0.19	151	0.64	127	0.97	1,949	0.13	702	0.48	546	0.77
1976	215	0.35	127	0.94	116	1.31	1,056	0.21	483	0.68	411	1.02
1977	98	0.47	67	1.13	63	1.52	442	0.29	236	0.83	209	1.19
1978	235	0.63	180	1.36	173	1.76	897	0.37	544	0.98	498	1.36
1979	174	0.56	127	1.26	121	1.65	700	0.32	395	0.89	356	1.26
1980	231	0.45	153	1.10	144	1.49	1,000	0.25	500	0.76	437	1.12
1981	136	0.95	119	1.74	116	2.14	427	0.58	316	1.29	302	1.69
1982	154	0.51	109	1.20	103	1.59	630	0.28	336	0.83	298	1.19
$\bar{x}$	192	0.47	106	1.08	95	1.45	963	0.31	403	0.80	333	1.14
$\underline{s}$	130	0.27	45	0.42	38	0.46	829	0.19	217	0.34	149	0.39
$\underline{C}$	0.68	0.57	0.42	0.39	0.40	0.32	0.86	0.61	0.54	0.42	0.45	0.34

TABLE 10. Mean values of $\underline{N}_1$ and $\underline{F}_a$ obtained for various combinations of $\underline{F}_{a8}$ and $\underline{M}_a'$ from analysis of 1961-1982 skipjack cohorts.

	$\underline{M}_a'$	$\underline{F}_{a8}$		
		0.20	1.00	2.00
$\underline{N}_1 \times 10^6$	1.00	192	106	95
$\underline{N}_1 \times 10^6$	2.00	963	403	333
$\underline{F}_a$	1.00	0.47	1.08	1.45
$\underline{F}_a$	2.00	0.31	0.80	1.14

TABLE 11. Values of $\underline{q}$, $\underline{C}_{max}$, and $\underline{f}_{opt}$, for skipjack in the eastern Pacific fishery, estimated from the symmetrical production model ($\underline{m}$ = 2.0), and the asymmetrical production model ($\underline{m}$ = 0.8), and correlation coefficients ($\underline{r}_s$ and $\underline{r}$) for log(CPUE'/CPUE'$_e$) from production models and environmental variables.

$\underline{m}$	$\underline{q}$	$\underline{C}_{max}$ 10^3t	$\underline{f}_{opt}$ 10^3d	Sum of squares 10^9		SSTSP	W^3SP	SSTFA	W^2FA
2.0	0.0000063	110	44	1.935	$\underline{r}_s$	0.349	-0.410	-0.333	-0.275
					$\underline{r}$	0.377	-0.488*	-0.245	-0.265
0.8	0.0000021	78	50	1.555	$\underline{r}_s$	0.253	-0.247	-0.349	-0.198
					$\underline{r}$	0.368	-0.422*	-0.270	-0.218

SSTSP = SST in the spawning area at the time of spawning; W^3SP = wind-mixing index (wind speed in knots cubed) in the spawning area at the time of spawning: SSTFA = SST in the fishing area at the time of fishing; W^2FA = wave-height index (wind speed in knots squared) in the fishing area at the time of fishing; see Forsbergh (1987) for further explanation of these variables. * $P \leq 0.05$ for two-tailed test