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# CLIMATIC VARIATION AND EXPLOITATION IN THE PACIFIC MACKEREL FISHERY 

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#### Abstract

This bulletin provides an in-depth analysis of the California Current Pacific mackerel (Scomber japonicus) fishery. It includes descriptions of the fishery and the species population biology, a cohort analysis, density and environmental-dependent spawner-recruit models, and yield simulations. The cohort analysis (1928-1968), using an instantaneous natural mortality rate of $\mathrm{M}=0.5$, shows a fluctuating stock size with a maximum total biomass of 965 million pounds ( $438,000 \mathrm{MT}$ ) in 1933 and a minimum of 3.3 million pounds ( 1500 MT ) in 1968. The number of recruits-perspawner shows large fluctuations with considerable coherence between adjacent years. There was no marked downward trend in recruits-perspawner over the 1928-1968 period. Density-dependent spawner-recruit models accounted for a maximum of 24 percent of the observed variation in recruitment. Multiple regression models, including both population and environmental variables, were fitted to the data available for two time periods; 1931-68 and 1946-68. The 1931-68 model accounted for 59 percent of the variation in recruitment; increased recruitment was associated with increased sea surface temperature, reduced sea level and reduced atmospheric pressure during the spaw ning season. The 1946-68 model accounted for 76 percent of the variation in recruitment; increased recruitment was associated with increased coastal upwelling and decreased offshore convergence during the spawning season. Maximum yield-per-recruit occurs with an age at recruitment of 1 or less, and with instantaneous fishing mortalities ( F ) in excess of 1.0. A dynamic pool model incorporating a Ricker spawner-recruit model predicts that extinction of the stock will occur with the above fishing strategy. Maximum sustained yield (MSY) with the steady state dynamic pool model is above 94 million pounds ( $41,000 \mathrm{MT}$ ). This MSY occurs with an age-at-recruitment of 4 and with an exploitation rate of 0.25 . Simulations incorporating the density and environmental-dependent spawner-recruit functions predict that the above MSY cannot be attained when there is serial coherence in the annual recruitment fluctuations. Mean longterm annual yield with the above fishing strategy, under the environmental conditions occurring between 1931-1968, would have been only 56 million pounds ( $25,000 \mathrm{MT}$ ). With an age-at-recruitment of 1 , maximum steady state yield ( 69 million pounds, $31,000 \mathrm{MT}$ ) occurs at an exploitation rate of 0.2 . Maximum longterm yield with this fishing strategy, under the 1931-68 environmental conditions, would have been 45 million pounds ( $20,000 \mathrm{MT}$ ).


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## INTRODUCTION

The objectives of this work are to assess the role of environmental variation in the decline of the California stock of Pacific mackerel (Scomber japonicus) and to evaluate the merits of using environmental data in management policies for this species. The study is principally focused upon three areas. The first is a cohort analysis of the stock. The second is the development of density and environmental-dependent regression models that describe recruitment in the above stock. The third is the use of these regression models in dynamic pool computer simulations to describe the types of management policies that are likely both to decrease the possibility of another recruitment failure and to maximize the longterm yield from the stock.

The Pacific mackerel fishery has been monitored extensively and studied since its beginning in the 1920's. Unfortunately the proper tools and background information for analysis of the fishery were not available until the mid 1960's, by which time the fishery was undergoing its final collapse. Now that the population biology and fishery dynamics are sufficiently understood, there is a real possibility of eventually rehabilitating the fishery and sustaining a reasonable level of exploitation.

This study is based on a cohort analysis of catch data similar to that developed by Murphy (1966) for analysis of the sardine fishery. Necessary steps leading to use of this technique and interpretation of the results include delimitation of the stock, compilation of catches of each year-class, and estimation of important population parameters. These parameters are rates of growth, natural mortality, maturity, and age of recruitment. Cohort analysis produces estimates of fishing mortality rates and population sizes which then can be applied to comprehensive models of the population and its fishery.

Many of these investigations have been undertaken by previous workers, and due credit must be given. Unfortunately little of the previous work reached publication, although Blunt and Parrish (1969) and Parrish (1974) incorporated some of those previous findings. Patrick Tomlinson did extensive work using cohort analysis and Norman Abramson later continued the research. The present study uses few data and parameter estimates from those studies; however, many assumptions, methods, and techniques which were developed and tested by Tomlinson and Abramson are used, directly or indirectly.

Over the last decade increased attention has been focused on the stock and recruitment problem of commercially important fishes. If any consensus exists in the large amount of published data it is that the major factor affecting recruitment is larval survival. The mechanisms controlling larval survival, of course, may vary from stock to stock. Some workers suggest that a critical stage occurs at the time of first feeding (Hjort 1926; Lasker 1965). Other workers feel that the critical period extends for up to 45 days (Jones and Hall 1973).

Most of the recent research into the recruitment problem has been divided into two phases: laboratory and field experiments on harval fish
biology, and population dynamics models. The development of models has been dominated by conceptual work; a statistical approach to the problem has been limited by the lack of long-term data on both fish populations and environmental conditions. Long-term data are becoming available for statistical analyses and workers are beginning to develop multiple regression models utilizing environmental and density-dependent variables (Nelson et al. 1976). One of the best long-term data bases available for statistical analyses of the associations between recruitment of pelagic fishes and environmental conditions is that of the California Current region. This extensive data base is largely the result of the multidisciplinary approach of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).
We have used the CalCOFI data base to determine associations between the recruitment of Pacific mackerel and environmental variables. Recruitment models including density parameters and both density and environmental parameters were then developed with regression procedures. These recruitment models were incorporated in computer simulation models to assess the differences in their predicted yields. The results of the simulations were analyzed to examine the relative merits of managing the fishery on two different policies; that is, a policy based on a yield per recruit model and a policy based on dynamic pool simulations incorporating both density-dependent and environmental-dependent factors.

Previous work on recruitment in Pacific mackerel has been limited to density-dependent recruitment models. Ricker spawner-recruit models were described by Blunt and Parrish (1969) and Parrish (1974). The present work is the first to incorporate long-term environmental data in recruitment models of a California Current stock and to use observed environmental data as inputs to simulations using such models.

## THE FISHERY

## STOCK DEFINITION

Scomber japonicus occurs on both sides of the North Pacific and on its eastern edge ranges from the Gulf of Alaska to the Gulf of California. The bulk of the Northeastern Pacific population resides off southern California and Baja California. As the fishery for Pacific mackerel has been pursued mainly in southern California rather than over the entire range of the species, the problem of geographically defining the stock being exploited is difficult. Rather than being a set fraction or geographical subset of the entire population, the stock is defined vaguely by rates of migration and diffusion of fish along the coast, rates which vary both seasonally and annually.

A tagging study (Fry and Roedel, 1949) showed a progressive decrease in likelihood of returns as the area of release became more distant from the fisheries which recovered the tags. Assuming that the rate of local tag returns from fish released in the same area as the main fishery represents full availability, relative rates of returns from fish released in more distant areas provide measures of relative availability (RA) of fish from those areas (Table 1). Thus we find that most of the fish from central California are available to the southern California fishery ( $\mathrm{RA}=0.88$ ), while the converse is not true; fish from southern California are much less available to the central California fishery ( $\mathrm{RA}=0.23$ ). Availability of fish from Mexican water declines steadily with distance, showing no abrupt edge to the exploitable population. Relative changes in availability with distance for these southern fish show close agreement between central and southern California fisheries. Unfortunately the years in which this tagging study was done (1939-41) correspond to a period of warm water conditions in the northeastern Pacific. Such warm conditions are conducive to strong northward migrations of many southern species of fish (Radovich 1961), and the Pacific mackerel, a known migrant, probably was affected. Thus these return rates may overestimate availability of southern fish to the California fisheries in years of normal oceanic conditions.
Another approach to stock definition was attempted by Roedel (1952), who studied both vertebral meristics and proportional measurements of head and fork lengths. Based on vertebral characters, populations from the Gulf of California and from the Cape San Lucas area were distinguishable from more northerly fish. The northern samples showed significant statistical differences for the Sebastian Vizcaino Bay, Soledad Bay (Ense-

TABLE 1. Tag Refurn Rates by Geographical Area as an Index of Relative Availability of Fish to the Fishery (Based on Fry and Roedel, 1949).

| Area of release | Number released | Southern Calif. fishery |  | Central Calif. fishery |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0,00 returned | Relative avail. | $0 / 00$ returned | Relative avail. |
| Central Calif. (Monterey Bay) | 6,986 | 24.6 | 0.88 | 11.0 | 1.00 |
| Southern Calif. <br> Northern Baja Calif. (San | 32,696 | 28.1 | 1.00 | 2.5 | 0.23 |
| Quintin Bay) | 3,937 | 20.3 | 0.72 | 0 |  |
| Central Baja Calif. (Sebastian Vizcaino Bay) | 8,117 | 13.3 | 0.47 | 0.9 | 0.08 |
| Southern Baja Calif. (Thurloe and San Roque Bays) | 7,869 | 6.9 | 0.25 | . 04 | 0.04 |

nada) and Southern California areas when samples for individual regions were combined and compared by analysis of covariance. Roedel concluded that there was probably little mixing between these areas. As Roedel (1952) admits, these conclusions are not compatible with information from tagging studies.
Two reasons for this inconsistency can be postulated. First, as Roedel (1952) showed, even schools from the southern California area showed significant statistical differences, suggesting that populations tend to be much more heterogeneous than are individual schools. Such a condition is consistent with a north-south migration wherein schools retain their identity. Also, the presence of significant statistical difference between schools within geographic regions makes it difficult to interpret differences between geographic regions from combined samples. The second sources of possible inconsistency relates to the season in which sampling was done. If migration of Pacific mackerel follows a pattern of northward movement in early summer and southward movement in late fall, the samples on which measurements were made tend to be biased against migratory members of the population. Most of the southern California samples were taken in the winter and spring when migrants would be at the southern end of their range, and Sebastian Vizcaino Bay samples were taken in the fall when migrants would be north. Roedel's samples suggest a clinal variation in relative head length, and apparent discontinuities possibly would be smoothed if sampling were distributed over the entire year.

Combined evidence, from both meristic and tagging studies indicates that the spawning stock fished by the California fleet extends from British Columbia to Point Abreojos. Mixing of fish throughout this range is incomplete, so that fish at the ends of the range tend to be unavailable to the localized California fisheries. Since the fishery in Sebastian Vizcaino Bay was viable after the decline of the stock in California waters, there is also de facto evidence that fish at the southern end of the stock are effectively isolated from the California fishery.

## HISTORY OF THE FISHERY

The development and subsequent decline of the Pacific mackerel fishery has been well documented in the literature. Croker (1933) discussed the early history of the fishery including fishing areas and the development of mackerel canning in California. Descriptions of the fishery during and after its peak include those by Croker (1933, 1938), Roedel (1952), Fitch (1952), and Roedel and Joseph (1954). The fishing gear used in the fishery was principally round-haul gear, primarily purse seine, and scoop gear (Fry 1931; Croker 1933; and Scofield 1947, 1951). More recent reviews of the fishery include Blunt and Parrish (1969), Kramer (1969), and MacCall (1973). Recent status reports showing current condition of the stock were prepared by Frey and Knaggs (1973) Knaggs (1974), Knaggs and Sunada (1975) and Klingbeil (1976).

Prior to the 1928-29 fishing season Pacific mackerel was primarily a fresh fish item and was fished both in Monterey and in southern California. Market demand was too small to generate interest among the round-haul net fishermen. After several attempts, a successful pack was made in the late 1920's and increasing cannery demand resulted in large catches by boats which had been fishing for sardines (Figure 1). The economic depression of the early 1930's caused a large drop in fishing effort, but a recovery of demand and prices made fisheries profitable once again and the fishery expanded from 1932-35, reaching a peak catch of 73,000 tons in 1935. Thereafter the fishery went through a long fluctuating decline, with periodic decreases in abundance followed by recoveries. In the 195354 season the fishery was nearly exhausted, but good recruitment in the 1950's rejuvenated the fishery until a series of poor recruitment years in the 1960 's brought the fishery to a close. In the early 1970 s a moratorium was placed on the fishery.

Two independent fleets fished for Pacific mackerel: the purse seine fleet, which was nearly identical with the sardine fleet, and the scoop fleet which was a mixture of specialized mackerel fishermen and off-season albacore fishermen. The purse seine fleet used no specialized techniques, but the scoop fleet had unusual fishing methods. These small boats began fishing in the early 1930's with lift poles and jigs (known as "striker gear"), but soon discovered that the fish could be chummed to such a concentrated frenzy that quantities could be scooped out of the water with a large dip net, hence the name. This fleet was a major component of the fishery, often accounting for over half the annual catch. The scoop fleet, severely affected by the shortage of fish in the early 1950's, fell from 348 full-time boats ( 6 or more days fished in the peak month) in 1949 to 10 full-time boats in 1952. As the fishing technique was highly specialized for this one species, the scoop fleet never fully recovered, and it finally disappeared in the mid 1960's. The purse seiners, which were able to switch to other species and were interested in Pacific mackerel as an altemative to the more lucrative sardine, survived the shortages of mackerel and sardines and continued fishing the species until a moratorium was imposed in 1970.

The fishing season followed a fairly set pattern until the mid 1950's. Fish


FIGURE 1. Pacific mackerel landings in California (1928-1970)
were relatively unavailable in southern California from January through May, and then increased in availability until late fall. Purse seiners accounted for most of the catch up to September when the sardine season began. A few scoop boats would fish all year, supplying fresh fish markets, which preferred scoop-caught fish to purse seined fish as they sustained less injury. The main scoop fishing season was in the fall, from August through December. In the declining years of the fishery catches became sporadic, losing any definitive seasonal pattern.

The sport landings of Pacific mackerel have been of relatively minor importance in the total marine sport landings. Young (1969) ranked them as the eleventh most important species in the southern California partyboat fishery. The mean catch from 1947-1967 was 127,921 fish. Only trace amounts of Pacific mackerel occur in the northern California partyboat catch.

Pinkas, Oliphant and Haugen (1968), ranked the most important sport fish caught in southern California marine waters from 1963-1966. They found Pacific mackerel to be the eighth most common species in the total marine sport fish catch; it comprised $3.2 \%$ of the fish caught. Since the commercial fishing moratorium was declared in 1970, the sport fishery has become the largest exploiter of the Pacific mackerel resource in California (MacCall, 1973).

## MANAGEMENT OF THE FISHERY

Attempts to control or manage the Pacific mackerel fishery were unsuccessful until the stock had collapsed. A moratorium was then enacted by the California Legislature. During the period of 1936-1970 research personnel, principally from the California Department of Fish and Game and later the National Marine Fisheries Service and Scripps Institution of Oceanography, made several major attempts to control the fishery. Management proposals generally concerned both the Pacific mackerel and sardine. Blunt and Parrish (1969) have discussed the past management proposals for Pacific mackerel. An excellent review of the sardine-anchovy regulation controversy was given by Talbot (1973) and much of his account of the sardine is equally true for Pacific mackerel. Messersmith's (1969) treatment of the anchovy controversy provides considerable documentation of the problems of managing the pelagic fisheries of California.

The most recent attempt to regulate the Pacific mackerel fishery was associated with the anchovy-sardine controversy and began about 1967. The spawning biomass of Pacific mackerel had declined rapidly due to a long series of years with poor recruitment. Warnings of this decline (Parrish 1968; Blunt and Parrish 1969) and of the continuing critical situation with the sardine (Aasen 1967) accompanied the descriptions of underexploited species such as the anchovy (Messersmith et al. 1969; Ahlstrom et al. 1967), squid, (Longhurst 1969) and saury (Smith and Ahlstrom 1970). The scientific community was in the politically unenviable position of arguing for increased harvest of the anchovy at the same time it was recommending complete closure of the commercial fishery for sardine and Pacific mackerel.

In response to continuing requests to enact moratoriums on Pacific mackerel and to halt the bait fishery on sardine, the California Legislature requested the California Department of Fish and Game to arrange meetings with Mexican scientists to determine the exact status of the resource (MacCall 1973). In the fall of 1972 cooperative research was undertaken. However, the continued decline of Pacific mackerel off California and the increasing fishing mortality, which had by then become very heavy even
on age 0 Pacific mackerel, encouraged the California Legislature to enact a unilateral moratorium on the commercial fishery for Pacific mackerel. This moratorium allowed an $18 \%$ tolerance for Pacific mackerel in mixed loads.

In 1972 the California Legislature enacted a bill that imposed a quota based on the spawing biomass of the Pacific mackerel. The regulation maintains a moratorium until the spawning biomass exceeds 20 million pounds. If the spawning biomass exceeds 20 million pounds (lower quota level) the annual quota consists of $20 \%$ of the excess over 20 million pounds. If the spawning biomass exceeds 40 million pounds (upper quota level) the quota consists of $20 \%$ of the amount between 20 million and 40 million pounds plus $30 \%$ of the excess over 40 million pounds.

The California Department of Fish and Game began monitoring the spawning biomass of the Pacific mackerel stock in 1973, as required by the above legislation. The subsequent trends are given in Frey and Knaggs (1973), Knaggs (1974), Knaggs and Sunada (1975), and Klingbeil (1976). The spawning biomass declined from 1973 to 1975 due to continued poor recruitment. The 1974 and 1976 year classes were relatively strong, and the spawning biomass has increased since 1975. A preliminary estimate of the spawning biomass for 1977 is 14,200 tons with an expected increase later in the year due to maturation of fish from the 1976 year class (Klingbeil, 1977). A tentative 1500 ton quota for the fall of 1977 has been recommended.

Fishery complications arose in 1977, and further legislation has complicated the management of the Pacific mackerel. The southern Califormia purse seine fleet has expanded its jack mackerel (Trachurus symmetricus) fishery and the 1976 year class of Pacific mackerel was schooling extensively with jack mackerel. Although the previous legislation allowed an $18 \%$ tolerance of Pacific mackerel incidentally caught in harvests of other species, the purse seine fleet was consistently exceeding this tolerance limit. Compromise legislation was quickly passed, allowing a $40 \%$ incidental catch, with the fraction in excess of $18 \%$ applying toward filling the quota prior to the opening of the fishing season. A clause was included whereby pure loads of less than three tons could be landed anytime, and be applied toward filling the quota. This latter provision has allowed the reappearance of a scoop fishery which has begun to harvest Pacific mackerel. Fishing pressure is increasing alarmingly, considering that the spawning biomass is probably still smaller than at any time before 1965. On the other hand, the strong 1976 year class may be able to withstand this assault and maintain the trend toward recovery.

The emergency legislation referred to in the preceding paragraph was designed as an interim measure and it expired on Jamary 1, 1978. Unless further legislation is passed, the 1972 regulations will automatically be in effect after January 1, 1978. For the purposes of this report the 1972 regulations will be referred to as the present regulations and the emergency 1977 regulations will be referred to as the interim regulations.

## CATCHES

Pacific mackerel are landed by three separate fisheries: the California commercial fishery, the Mexican commercial fishery, and a diverse sport fishery which is based primarily in southern California. Documentation of catches of these fisheries is variable in format, and in some cases is lacking, making rough conversions and estimates necessary to compile total season catches (Table 2). A fishing season of May through the following April is used in published age compositions, and therefore will be used in estimation of total catch. California commercial landings have accounted for the majority of catch and fortunately are well documented. While some prob-

TABLE 2. Season Catches of Pacific Mackerel from 1926-27 to 1969-70 (Weights in 1000 lb )

| Season | Calif. | Mexico | Sport | Total |
| :---: | :---: | :---: | :---: | :---: |
| 1926-27 | 3594 |  | 50 | 3644 |
| 1927-28 | 6455 |  | 50 | 6505 |
| 1928-29 | 39405 |  | 50 | 39455 |
| 1929-30 | 56695 |  | 50 | 56745 |
| 1930-31 | 12806 |  | 100 | 12906 |
| 1931-32 | 15152 |  | 100 | 15252 |
| 1932-33 | 10850 |  | 100 | 10950 |
| 1933-34 | 72874 |  | 100 | 72970 |
| 1934-35 | 113464 |  | 200 | 113664 |
| 1935-36 | 146387 |  | 200 | 146587 |
| 1936-37 | 100745 |  | 200 | 100945 |
| 1937-38 | 70446 |  | 200 | 70646 |
| 1938-39 | 76065 |  | 200 | 76265 |
| 1939-40 | 99961 |  | 200 | 100161 |
| 1940-4] | 107555 |  | 200 | 107755 |
| 1941-42 | 71755 |  | 100 | 71855 |
| 1942-43 | 48220 |  | 100 | 48320 |
| 1943-44 | 77804 |  | 100 | 77904 |
| 1944-45 | 80786 |  | 100 | 80886 |
| 1945-46 | 52003 |  | 100 | 52103 |
| 1946-47 | 58896 | 1877* | 100 | 60833 |
| 1947-48 | 39628 | 2783 * | 296 | 42707 |
| 1948-49 | 38203 | $1135{ }^{*}$ | 406 | 39744 |
| 1949-50 | 50062 | 2980 * | 190 | 53232 |
| 1950-51 | 33890 | 4473 * | 134 | 38497 |
| 1951-52 | 31905 | 2911* | 94 | 34910 |
| 1952-53 | 20218 | 2320 * | 154 | 22692 |
| 1953-54 | 8829 | 2595* | 122 | 11546 |
| 1954-55 | 27210 | 12524 * | 630 | 40364 |
| 1955-56 | 26897 | 21601* | 302 | 48800 |
| 1956-57 | 57184 | 23644 * | 242 | 81070 |
| 1957-58 | 56238 | 4485* | 304 | 61027 |
| 1958-59 | 24777 | 989** | 274 | 26040 |
| 1959-60 | 41282 | 1092* | 178 | 42552 |
| 1960-61 | 39074 | 6573 * | 158 | 45805 |
| 1961-62 | 44301 | 13149 * | 228 | 57678 |
| 1962-63 | 45254 | 7124 | 234 | 52612 |
| 1963-64 | 34211 | 17561 | 294 | 520666 |
| 1964-65 | 24875 | 18999 | 202 | 44076 |
| 1965-66 | 7589 | 16788 | 304 | 24681 |
| 1966-67 | 4075 | 11662 | 410 | 16147 |
| 1967-68 | 1382 | 2091 | 216 | 3689 |
| 1968-69 | 3289 | 236 | 158 | 3683 |
| 1969-70 | 1783 | 443 | 240 | 2466 |

- Estimated
lems exist in estimating the poundage of Pacific mackerel in deliveries of mixed species (i.e., mixed with jack mackerel, Trachurus symmetricus, and Pacific sardine, Sardinops caerulea), the records are reasonably correct with a slight bias toward underestimation of actual poundage landed.

Catch statistics on Mexican commercial landings are incomplete. Landings from 1962 to 1969 were furnished by the Instituto Nacional de Pesca (INP) of Mexico, filling in the information for a critical period in the fishery. Earlier data on Mexican landings (Blunt and Parrish, 1969, Table 2) were reported as annual rather than seasonal catch, and for the years 1946 through 1953, and 1957 through 1970 Pacific and jack mackerel were undifferentiated. The latter problem was resolved by considering Pacific mackerel to be a constant fraction of the combined landings. Based on the years 1954-1956 and 1961-1963, this fraction is 0.611 , with a high value of 0.958 (1954) and a low value of 0.457 (1963). Since combined Mexican landings were small for the years in which the problem exists, errors in estimation of Pacific mackerel landings will be small relative to total landings of all fisheries combined. A more difficult problem is the conversion of annual landings to season landings. As information on monthly catches is unavailable, we assumed the distribution of monthly catch of the Mexican fishery to be identical to that for the California fishery for the same year. Based on these proportions, annual catches were divided into estimated catches from January through April, and May through December, and were re-combined as season catches. Values prior to 1955 (except for 1947) were changed very little since about $95 \%$ of the annual California catch was made later than April. In later years this value was less, reaching a low of $70 \%$ in 1958.

Sport fishing landings were inconsequential prior to 1970, however, they have been included to complete the record. The California partyboat fleet has reported catches of all species since 1947 (Young, 1969). The partyboat fishery accounts for the majority of sport-caught mackerel. The total of all other segments of the sport fishery combined may roughly equal the partyboat catch (Pinkas, Thomas and Hanson, 1967; Pinkas, Oliphant and Haugen, 1968; unpublished data). Therefore the total sport catch was estimated to be twice the reported partyboat catch. All fish were assumed to weigh one pound when estimating landings in weight.

## AGE COMPOSITION

Age composition of the California commercial landings since 1939 have been published (Fitch, 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Parrish and Knaggs, 1971, 1972; Knaggs, 1972). Mexican commercial landings, the sport catch, and late reports from the Californta commercial fishery lack age composition information, making it necessary to assume that these catches had the same age composition as the published data. Total landings by age were estimated for each season by increasing each value by the season ratio of total catch of all fisheries to total catch used in the corresponding age composition article. Total pounds catch used in age composition articles was not documented for the 1939-40 through

1951-52 seasons, as the poundage for age $6+$ fish was omitted and total poundage was not recorded. For seasons 1941-42 through 1948-49, the missing information was recovered from the original worksheets. For the remaining five seasons, 1939-40, 1940-41, and 1949-50 through 1951-52, the estimated number of age $6+$ fish (corresponding to a mean length of 38.5 cm ) gave estimated weights for this age group. From this the total weight of the aged landings was estimated and the appropriated proportion of increase could be derived (Table 3 ).

TABLE 3. Pacific Mackerel Ratios of Total Catch to Aged Catch
(Weights in 1000 lb )

| Season | Age composition ages 0-5 | Reports age $6+$ | Estimated total from age composition | Total all fisherjes | Increase factor |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1939-40 | 82783 | $9760^{*}$ | 92543 | 100161 | 1.0823 |
| 1940-41 | 100864 | 2646* | 103510 | 107755 | 1.0410 |
| 1941-42 | 65105 | 1054 | 66159 | 71855 | 1.0861 |
| 1942-43 | 43621 | 469 | 44090 | 48320 | 1.0959 |
| 1943-44 | 69552 | 597 | 70149 | 77904 | 1.1106 |
| 1944-45 | 75199 | 715 | 75914 | 80886 | 1.0655 |
| 1945-46 | 46532 | 2339 | 48871 | 52103 | 1.0661 |
| 1946-47 | 50533 | 3887 | 54420 | 60833 | 11173 |
| 1947-48 | 32709 | 2303 | 35012 | 42707 | 1.2198 |
| 1948-49 | 35245 | 503 | 35748 | 39744 | 1.1118 |
| 1949-50 | 46800 | 491 * | 47191 | 53232 | 1.1256 |
| 1950-51 | 31617 | $224^{*}$ | 31841 | 38410 | 1.2090 |
| 1951-52 | 31037 | $246 *$ | 31283 | 34910 | 1.1159 |
| 1952-53 | 18691 | 71 | 18762 | 22692 | 1.2095 |
| 1953-54 | 6857 | 756 | 7613 | 11546 | 1.5166 |
| 1954-55 | 26656 | 63 | 26719 | 40364 | 1.5107 |
| 1955-56 | 26656 | 230 | 26756 | 48800 | 1.8239 |
| 1956-57 | 57128 | 0 | 57128 | 81070 | 1.4191 |
| 1957-58 | 54843 | 1345 | 56188 | 61027 | 1.0861 |
| 1958-59 |  |  | 24776 | 26040 | 1.0510 |
| 1959-60 |  |  | 41282 | 42552 | 1.0308 |
| 1960-61 |  |  | 39074 | 45805 | 1.1723 |
| 1961-62 |  |  | 44192 | 57678 | 1.3052 |
| 1962-63 |  |  | 45252 | 52612 | 1.1626 |
| 1963-64 |  |  | 34210 | 52066 | 1.5220 |
| 1964-65 |  |  | 24875 | 44076 | 1.7719 |
| 1965-66 |  |  | 7589 | 24681 | 3.2522 |
| 1966-67 |  |  | 4075 | 16147 | 3.9625 |
| 1967-68 |  |  | 1381 | 3689 | 2.6713 |
| 1968-69 |  |  | 3289 | 3689 | 1.1198 |
| 1969-70 |  |  | 1439 | 2466 | 1.7137 |

- Estimated by assumed weight of age $6+$ fish.

The period before 1939 presents special problems, as no refined data have been published. Some otolith readings were made by D. Fry for the 1933-34 and 1934-35 seasons (unpublished), and length frequencies were taken regularly starting in 1929 (unpublished). A comparison of the early otolith readings with those in Fitch (1951) shows that lengths-at-age are consistent (Table 4). The samples appear to be occasional entire clusters of fish which were selected for usual length frequency measurements, and are therefore presumably unbiased.

TABLE 4. Validation of Unpublished Otolith Readings.

| Age | Mean length-at-age** |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Unpublished readings |  |  |  | Fitch (1951) |  |  |  |
|  | 1933 |  | 1934 |  | 1939-40 |  | 1940-41 |  |
|  | $n$ | $L$ | $n$ | $L$ | $n$ | $L$ | $n$ | $L$ |
| 0 | 0 | - | 0 | - | 26 | 101.2 | 56 | 99.7 |
| 1 | 13 | 113.5 | 19 | 105.3 | 335 | 109.3 | 323 | 111.1 |
| 2 | 84 | 123.6 | 221 | 121.6 | 342 | 122.5 | 1040 | 120.2 |
| 3 | 130 | 130.6 | 159 | 130.7 | 486 | 131.5 | 483 | 130.0 |
| 4 | 115 | 137.4 | 192 | 139.9 | 160 | 141.1 | 298 | 136.9 |
| 5 | 37 | $148.9$ | 125 | $143.8$ | 91 | $147.8$ | 44 | 145.0 |
| $6+$ | 21 | 154.3 | 49 | 151.1 | 84 | 154.5 | 14 | 151.6 |

- $\sigma_{L}$ is approximately 5.0 for all ages.

A reconstruction of the age structure of the landings from 1929-30 through 1939-40 was made by separating length frequencies into component normal curves. This was first attempted by Tomlinson (unpublished MS) using the computer program NORMSEP which he modified for the purpose. Tomlinson's modifications (Abramson, 1971) tend to introduce some bias into the estimating procedure, but increase the consistency of the estimated mean lengths-at-age with those from otolith readings, and thus presumably increase the accuracy of the percentage compositions estimated from the samples. Comparison of age composition estimated from length frequency with age compositions estimated from otolith readings is shown for 1933-34, 1934-35, and 1939-40 (Table 5). NORMSEP estimates show general agreement with overall age distribution, but estimates of landings for individual age groups may be considerably different. The 1933-34 season, in which the fewest otolith samples were examined ( 5 clusters with a total of 400 otoliths) shows the poorest agreement, particularly in ages 2 and 5 . The other two seasons show remarkably good agreement in view of the fact that NORMSEP estimates do not stratify the

TABLE 5. Comparison of Estimated Age Composition of Early Pacific Mackerel Catches by NORMSEP and by Otolith Readings. ' 1000 fish)

| Season | Otolith sample size | 0 | 1 | 2 | 3 | 4 | 5 | $6+$ | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1933-34 |  |  |  |  |  |  |  |  |  |
| Otoliths | 400 | 0 | 3746 | 15419 | 25754 | 18943 | 6711 | 3446 | 74119 |
| NORMSEP |  | 0 | 2517 | 5511 | 21843 | 18560 | 16969 | 8721 | 74120 |
| 1934-35 |  |  |  |  |  |  |  |  |  |
| Otoliths | 765 | 0 | 3369 | 36726 | 24504 | 28090 | 16675 | 6075 | 115438 |
| NORMSEP |  | 0 | 2199 | 35238 | 33004 | 21332 | 19086 | 4577 | 115436 |
| 1939-40 |  |  |  |  |  |  |  |  |  |
| Fitch (1951) | 1524 | 2960 | 25200 | 26540 | 35130 | 10570 | 5340 | 6100 | 111840 |
| NORMSEP |  | 6431 | 23621 | 19729 | 34603 | 16597 | 3858 | 7001 | 111940 |

landings by time period as do the otolith-based estimates (Fitch, $1951^{1}$ ). Moreover, no consistent bias in age structure is apparent in the NORM$S E P$ estimates except for a possible tendency to overestimate weak age groups which are surrounded by more numerous age groups, as in the estimate for age 3 in 1934-35. Due to the importance of the 1930's in the history of the Pacific mackerel fishery, and the desirability of obtaining an analysis of this period, the NORMSEP estimates of age composition will be used with the reservations necessary in interpreting analyses based on such unreliable data. The age compositions for 1933-34 and 1934-35 which were calculated from D. Fry's otolith readings are retained as being more reliable than the NORMSEP estimates. Catches by age and season are given in Table 6.
' The description of the weighting procedure in Fitch (1951) is partially in error. Age sampling was stratified by length category and, as Fitch states, the otoliths read do not represent a random sample. Age frequency was not calculated as shown in his Table 19. The actual procedure used was similar to the stratified sampling plan of ACECOM (Abramson. 1971), wherein the number of fish observed in each length stratum is taken into accoumt.
TABLE 6. Catches by Age and Season ( 1000 fish)

| Season | 0 | 1 | 2 | 3 | 4 | 5 | $6+$ | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1929-30* | 26 | 11469 | 20724 | 19204 | 4804 | 3574 | 4592 | 64396 |
| 1930-31** |  | 1224 | 6296 | 4252 | 1684 | 589 | 60 | 14105 |
| 1931-32** |  | 848 | 8851 | 5484 | 1158 | 667 | 512 | 17520 |
| 1932-33* |  | 130 | 2899 | 5259 | 1254 | 846 | 685 | 11073 |
| 1933-34 |  | 3746 | 15419 | 25854 | 18943 | 6711 | 3446 | 73669 |
| 1934-35 |  | 3369 | 36726 | 24504 | 28090 | 10675 | 6074 | 109438 |
| 1935-36** |  | 7621 | 8929 | 43255 | 44738 | 23577 | 6771 | 134891 |
| 1936-37* |  | 1705 | 15477 | 13198 | 25079 | 26669 | 6201 | 88329 |
| 1937-38** | 137 | 1273 | 2236 | 6931 | 13724 | 22451 | 10560 | 57322 |
| 1938-39* | 2058 | 11036 | 30473 | 15755 | 4108 | 10375 | 9805 | 83610 |
| 1939-40 | 3204 | 27274 | 28724 | 38021 | 11440 | 5779 | 6602 | 121044 |
| 1940-41 | 2408 | 21646 | 72164 | 26297 | 14107 | 1502 | 1722 | 115792 |
| 1941-42 | 432 | 13584 | 28732 | 27870 | 5562 | 1054 | 596 | 77830 |
| 1942-43 |  | 32193 | 10087 | 13916 | 5776 | 901 | 285 | 63158 |
| 1943-44 | 928 | 13840 | 60090 | 11279 | 7922 | 1202 | 438 | 95699 |
| 1944-45 |  | 17640 | 20295 | 36126 | 8217 | 1722 | 473 | 84473 |
| 1945-46 | 593 | 15247 | 11010 | 10937 | 10994 | 3548 | 1565 | 53894 |
| 1946-47 | 626 | 10429 | 28865 | 13271 | 5210 | 2564 | 2802 | 63767 |
| 1947-48 | 8759 | 1680 | 9734 | 13348 | 6205 | 2463 | 1892 | 44081 |
| 1948-49 | 1180 | 70410 | 3530 | 841 | 1229 | 477 | 325 | 77992 |
| 1949-50 | 153 | 24558 | 55441 | 4816 | 774 | 657 | 346 | 86745 |
| 1950-51 | 7 | 4659 | 23247 | 19134 | 1133 | 87 | 169 | 48436 |
| 1951-52 | 858 | 1766 | 4941 | 15479 | 12417 | 243 | 172 | 35876 |
| 1952-53 | 104 | 56 | 630 | 1555 | 11471 | 3333 | 40 | 17189 |
| 1953-54 | 18559 | 1025 | 720 | 884 | 244 | 557 | 593 | 22582 |
| 1954-55 | 852 | 60482 | 5881 | 314 | 107 | 0 | 59 | 67695 |
| 1955-56 | 7728 | 6497 | 38586 | 10980 | 372 | 27 | 232 | 64422 |
| 1956-57 | 30 | 70145 | 21252 | 20777 | 5167 | 88 | 0 | 117459 |
| 1957-58 | 1505 | 6764 | 33112 | 12308 | 8863 | 2500 | 1100 | 66152 |
| 1958-59 | 17304 | 1342 | 6217 | 11419 | 3671 | 1182 | 306 | 41441 |
| 1959-60 | 1595 | 58544 | 4341 | 1082 | 1323 | 432 | 143 | 67460 |


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## POPULATION BIOLOGY

## GROWTH

A very large amount of data is published on the age composition of the southern California catch of Pacific mackerel. Annual growth in length is also well documented. However, documentation is lacking on the seasonality of growth and on growth in weight generally. Individual weights were not recorded for the market samples until the mid 1960's. In addition published age-composition data represent a composite of information for the entire season.

Von Bertalanffy growth equations and length-weight relationships were calculated by Knaggs and Parrish (1973) for data from the 1958-1959 to 1969-70 seasons. They reported that there were no significant differences at the $1 \%$ level between their data and Fry's (1936b) data. They also reported little correlation between 29 years of estimates of recruit abundance and mean size at age $1(r=-0.208)$. However, it should be noted that a good comparison (i.e., weight at a given age) is lacking. In this instance mean size at age 1 is the mean length of fish sampled during the season (i.e. May 1-April 30) and this mean age may differ from year to year due to availability or seasonal variations in fishing pressure.

The growth estimates used in the present paper are from the von Bertalanffy growth equation and the length-weight relationship given by Knaggs and Parrish (1973). Both annual growth and weight at capture were used in simulation models (Table 7). Weight at the beginning of the season (May) was used to calculate spawning biomass and annual growth.

TABLE 7. Length ' and Weight ${ }^{2}$ By Age of Pacific Mackerel (From Knaggs and Parrish 1973)

| Age |  | $t$ | At beginning of season (Birthday) |  | At capture |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Length | Weight | Length | Weight |
| 12 | May |  | 0.5 | 252 mm . | 192 gms. |  |  |
|  | Oct. | 1.0 |  |  | 273 mm . | 25.3 gms . |
|  | May | 1.5 | 292 | 317 |  |  |
|  | Oct. | 2.0 |  |  | 308 | 382 |
| 3 | May | 2.5 | 323 | 448 |  |  |
|  | Oct. | 3.0 |  |  | 336 | 512 |
| 4 | May | 3.5 | 348 | 574 |  |  |
|  | Oct. | 4.0 |  |  | 358 | 633 |
| 5 | May | 4.5 | 367 | 689 |  |  |
|  | Oct. | 5.0 |  |  | 375 | 741 |
| 6 | May | 5.5 | 382 | 789 |  |  |
|  | Oct. | 6.0 |  |  | 388 | 834 |

Weight at capture (October) was used to calculate catch. Length at the first birthday (May), with the von Bertalanffy equation as fitted by Knaggs and Parrish (1973), is calculated with $t=0.5$ and the length of age 1 fish at capture is calculated with $t=1.0$. This correction is necessary due to the fact that the von Bertalanffy equation was calculated with the criteria for age 1 being all fish between the ages of 1 and 2. The von Bertalanffy estimate with $t=1.0$, therefore, is an estimate of length at an age of 1.5 years.

## REPRODUCTION

Age at maturity and percent spawning by age group were not well documented during the early fishery. According to Fry (1936b) "the yearling fish do not spawn whereas inost of the two-year-olds do." Fitch (1951) stated that most mackerel do not spawn until their third or fourth year (i.e., age 2 or 3). For the period of 1958-70 Knaggs and Parrish (1973) found that $22.5 \%, 65.7 \%, 75.1 \%, 84.7 \%, 84.2 \%$ and $87.0 \%$ of age group 1 through $6+$ females sampled during the period of April-August were mature or maturing.

The above figures represent minimum percentage maturity of female fish, as early spawners might have completed spawning when captured in August or late spawners might be immature when captured in May. Therefore, in the present work we have decided to assume that $100 \%$ of the fish of age 4 or older are mature. The percentages mature of ages 1 , 2 , and 3 were increased by the same proportion as ages $4+$ (i.e., 0.17). This results in percentages of $26 \%, 77 \%$, and $88 \%$ for ages 1,2 , and 3 females.

Males apparently mature at a slightly younger age than females (Klingbeil, Calif. Dept. Fish and Game, personal communication). However, only the proportion of female fish are considered in measuring spawning biomass, with the assumption that males spawn in the same proportion as females. The fact that egg and larva surveys are used to measure biomass is the primary reason for this assumption Such surveys are capable of measuring spawning products of female fish only. A second reason is that the true reproductive potential of a pelagic fish population is measured by that segment which produces eggs (i.e., females), given the condition that fertilization is efficient over a wide range of male to female abundance ratios.

The major inconsistency between the data taken in the early fishery, when biomass levels were high, and the late fishery, when biomass levels were low, is the percentage of age 1 fish that spawn. The Fry (1936b) and Fitch (1951) data were taken when biomass was high. The percentages mature reported by Knaggs and Parrish (1973) are average values taken over the period 1958-1959 to 1969-1970, when biomass varied from moderately high to very low levels. In an attempt to determine if the percentage of age 1 fish spawning depends on density, the original market samples usted by Knaggs and Parrish (1973) were analyzed to see if a pattern could be determined. Maturity stages were not recorded in market samples prior to $1958-1959$, and in individual samples these data were sometimes missing for several years thereafter. When analyzed by individual year the
numbers became so small that validity was questionable. However, during the period 1969-1971, when the spawning biomass was at extremely low levels and large numbers of age 1 fish were sampled, $50 \%$ of the age group 1 fish were mature or maturing.

The available information suggests that there is an inversely densitydependent relationship between population size and the percentage of age 1 fish that spawn, although the exact form of this relationship is difficult to demonstrate. It appears that the percentage of age 1 spawners can be approximated at three general biomass levels. An exponential curve fitted to these points gives the following relationship, which was used in the regressions to determine recruit-spawner functions and in all simulations. (Figure 2)

PS $=0.540 \mathrm{e}^{-0.00717 \text { TPOP }}$
where $\mathrm{PS}=$ proportion of age 1 fish spawning TPOP $=$ total population biomass in millions of pounds


TOTAL BIOMASS (IN MILLIONS OF POUNDS)
FIGURE 2. The relationship between fotal biomass and the proportion of age 1 spawners
There is a hypothesis other than density dependence to explain the increasing percentage of age 1 fish that spawn at low biomass levels. Fry (1936b) stated that a small proportion of fish in the southern Baja California stock spawned at age 1. It is possible that a small number of fish from the southern Baja California stock enter the California fishery. These fish could provide an increasing proportion of the mackerel available to the California fishery as the northern stock declined to the very low levels of the late 1960 's. Tagging studies neither confirm nor invalidate this alternate hypothesis, because fish south of central Baja California were not tagged during the major tagging work carried out by Fry and Roedel (1949) or in more recent work (Knaggs 1974).

The eggs and larvae of Pacific mackerel are pelagic. The eggs hatch approximately three days after fertilization, depending on temperature (Fry 1936a). Fry (1936b) found that most of the eggs were spawned in water less than 88 m deep and between 16.7 and 20.6 C ( 62 and $69^{\circ} \mathrm{F}$ ). Ahlstrom (1959) suggests that spawning occurs closer to the shore and closer to the surface in Pacific mackerel than in the other major pelagic species in the California Current region. Kramer (1969) reported that the abundance of Pacific mackerel eggs fell off sharply below 23 m . Estimates of fecundity in Pacific mackerel are based on relatively few individuals. MacGregor (1966) reported that the Pacific mackerel produces 304 eggs per gram of fish (based on counts for six specimens). MacGregor (1975) reported that 18 Pacific mackerel averaged 259 eggs per gram. He suggested that a lower estimate of fecundity per body weight was associated with first-time spawners in a number of species but he did not report that this occurs in Pacific mackerel.

Fry (1936a) found that Pacific mackerel eggs varied in size during the spawning season; eggs were larger in April-May than in June-July. The data on age at maturity reported by Knaggs and Parrish (1973) showed that spawning of older mackerel peaks in May while in age 2 it peaks in June and in age 1 it peaks in July. Bakun (1973) shows that peak upwelling in central Baja California occurs in May. This suggests that older fish produce larger eggs that are hatched during the period of peak upwelling in central Baja California and that the smaller eggs from younger fish hatch after the normal peak of upwelling. Thus the alteration of the age structure of the population by fishing could result in a reduction of average spawning success and an increase in the variance if upwelling is vital to larval survival. The larvae of younger fish could have a shorter period before starvation would occur. This could be caused by less caloric yolk reserves or a higher metabolic rate due to the higher temperatures they would encounter later in the season. Hempel (1965) suggests that the above considerations affect survival of Norwegian herring.

The distribution of Pacific mackerel larvae is considerably wider than that of the eggs. Principal concentrations are often well offshore and undoubtedly are heavily controlled by transport and convergence patterns. Most larvae have been taken off of central Baja California in the region near Punta Eugenia (Figure 3).

## SCHOOLING

Schooling behavior in the California Pacific mackerel stock is not well documented in the literature. Sette (1943), in discussing Atlantic mackerel (Scomber scombrus), reported that fish-of-ther-year school separately from the rest. Yearlings usually school separately but may join schools of adults, especially when the adults are predominantly 9 -year-olds. The adults, age $2+$, travel in mixed schools. Sette attributed the above schooling by age to the fact that the larger, older fish tend to have a higher cruising speed than smaller fish. The age composition of market samples of Pacific mackerel caught off of California suggests that this same pattern is also found in Pacific mackerel. Yearling Pacific mackerel are often found


FIGURE 3. Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960)
schooling with immature jack mackerel (Trachurus svmmetricus) which tend to have a lower cruising speed than adult Pacific mackerel. Early management policies favored by members of the canning industry reflected an awareness of this pattern, as they were largely concerned with limiting the catch of young-of-the-year and yearling fish. It therefore appears that size restrictions could be effective in preventing the capture of
young-of-the-year mackerel, and to a lesser extent yearlings. Restrictions at sizes or ages larger than this are not feasible in the purse-seine fishery due to mixed schooling.

## NATURAL MORTALITY RATE

As in most fishery analyses, the rate of natural mortality (M) will be assumed to be constant for lack of better information. The most direct measure of M for the Pacific mackerel was made by analysis of the number of tags returned from fish released in southern California waters (Fry and Roedel, 1949). Estimates of M ranging from 1.1 to 1.3 were obtained depending on method of analysis and assumptions of tagging mortality rates. These estimates are very high, corresponding to loss of 70 percent per year, and are inconsistent with age frequency in the catches particularly for the early years of the fishery when older fish were common. Fry and Roedel concluded that tagging experiments did not supply realistic values of natural mortality rates for the Pacific mackerel.

Another source of mortality rate information is length frequency data taken in the very early period of the fishery. Length frequencies were first taken in the 1929-30 season, the second season of significantly large landings (cf. Figure 1). Comparison of 1929-30 with 1930-31 length frequency (Figure 4) shows a more rapid decrease in abundance of larger fish in the latter season, suggesting an increase in total mortality. A bulge in the 1929-30 graph involving 36 to 41 cm fish suggests large recruitment in the mid 1920's and will cause an underestimate of the mortality rate. This bulge disappeared in the length frequency for the following 1930-31 season.

Beverton and Holt (1956) showed that the total mortality rate (Z) can be estimated from length frequency information if von Bertalanffy growth constants are available:

$$
Z=\left[K\left(L_{00}-\bar{L}\right)\right] /\left(\bar{L}-L^{1}\right]
$$

where $L^{1}$ is the smallest length fully represented (or lower cut-off point) and $\bar{L}$ is mean length of fish $L^{1}$ or longer. $K$ and $L_{o c}$ are the von Bertalanffy growth constants. Pacific mackerel appear to show different relative growth rates for different years, possibly an effect of varying population size (Knaggs and Parrish 1973). Von Bertalanffy growth constants were calculated from length and age data taken in 1933-34 and 1934-35, the closest available data to the time period under consideration (Table 5). Using the method of regressing annual growth increment on initial length (Figure 5), the X -intercept is an estimate of $\mathrm{L}_{00}$ and the slope is a function of $K$ (Gulland 1969). In order to avoid effects of uneven recruitment on the catch curve analysis, $L^{1}$ was increased the equivalent of a year's growth by the relationship

$$
\mathrm{L}_{t+1}=\mathrm{L}_{\infty}\left[1-\mathrm{e}^{-\mathrm{K}}\left(1-\left[\mathrm{L}_{t} / \mathrm{L}_{\infty}\right]\right)\right]
$$

which is derived from the von Bertalanffy growth equation. Thus we obtain total mortality rates for approximately the same cohort of fish in the two seasons. The Beverton and Holt equation gives a $Z$ of 0.317 for the 1929-30 catch curve, and a $Z$ of 0.424 for the $1930-31$ catch curve (Table
8). As discussed previously, these values are probably biased and represent low estimates; however, the values imply a natural mortality rate much lower than those obtained from the mark-recapture data. Since the Pacific mackerel had undergone only one full season of fishing in addition to the season underway in 1929-30, a natural mortality rate of 0.3 to 0.5 is consistent with these data.


FIGURE 4. Pacific mackerel comparison of length frequency for 1929-30 and 1930-31


FIGURE 5. Pacific mackerel von Bertalanffy growth curve parameter estimation. Data from D.H. Fry ofolith readings 1933-1934.

A final method of estimating the rate of natural mortality involves the $y$-intercept of the regression of total mortality rate upon effort. Since M is being estimated for use in cohort analysis, and the estimates of total mortality rate in this procedure are derived from cohort analysis, it may appear circular. Actually it is not circular, since in cohort analysis errors in $M$ result in counterbalancing errors in estimated $F . Z$ is relatively unaffected making an iterative solution appropriate.

Table 8. Catch Curve Estimates of Total Moriality Rates from Length Frequency and Von Bertalanffy Growth Curve ( $L \infty=404.6 \mathrm{~mm}, \mathrm{~K}=0.221$ ).

| Season | $n$ | $\bar{L}$ | $\bar{L}$ | $Z$ |
| :--- | :--- | :--- | :--- | :--- |
| $1929-30$ | 346 | 337.5 | 365.05 | $Z$ |
| $1930-31$ | 317 | 350.0 | 368.70 | 0.317 |

Direct effort estimates for Pacific mackerel are not available, but a relative effort measure can be obtained from the night-light survey data collected by the California Department of Fish and Game sea surveys in the fall of the years 1950 to 1961 (Mais 1974). An abundance index was calculated as the percent of night-light stations at which Pacific mackerel were observed (Table 9). The geographic area covered by the survey is Ensenada to Point Conception. This abundance index can be used to derive an effort index (f). If the abundance index (I) is related to true mean abundance ( $\overline{\mathrm{N}}$ ) by some constant c ,

$$
\overline{\mathrm{N}}=\mathrm{cI}
$$

and instantaneous fishing mortality ( F ) is related to catch and mean abundance by

$$
\mathrm{F}=(\mathrm{C} / \overline{\mathrm{N}})
$$

a measure of nominal effort ( $f$ ) which is proportional to $F$ is obtained by:

$$
\mathrm{f}=\mathrm{cF}=(\mathrm{C} / \mathrm{I})
$$

Estimates of $f$ obtained by this method, and estimates of $Z$ from a cohort analysis using $\mathrm{M}=0.5$ are given in Table 9. The regression of Z upon estimated f gives an M estimate of 0.95 , while the regression of f upon Z gives $\mathrm{M}=0.32$ (Figure 6). The variance of the effort estimate relative to the variance of the Z estimate is quite large, due to the crude method of estimation and small sample size, so the latter regression is to be favored (Ricker 1973). The Z-intercept estimate of 11 would therefore fall between 0.4 and 0.6 . Since $\mathrm{M}=0.5$ was used in the cohort analysis, this value of M is consistent with the data.

Table 9. Abundance Index, Effort Index and Tatal Martality Rate Estimates for Pacific Mackerel.

| Season | Night-light abundance index (\% occurrence) | $\begin{gathered} \text { Total } \\ \text { catch } \\ (1000 \mathrm{lb} .) \end{gathered}$ | Effort index (f) | Tot:I mortality rate $(1 /=0.5)$ |
| :---: | :---: | :---: | :---: | :---: |
| 1950-51 | 17.3 | 38497 | 2225 | 1.363 |
| 1951-52 | 8.8 | 34910 | 3967 | 1.604 |
| 1952-53 | 2.6 | 22692 | 8728 | 2.397 |
| 1953-54 | 0 | 11546 | - | 1.839 |
| 1954-55 | 23.4 | 40364 | 1725 | 0.729 |
| 1955-56 | 12.3 | 48800 | 3967 | 1.528 |
| 1956-57 | 15.2 | 81070 | 5334 | 1.046 |
| 1957-58 | 6.7 | 61027 | 9109 | 2.556 |
| 1958-59 | 3.9 | 26040 | 6677 | 1.554 |
| 1959-60 | 18.9 | 42552 | 2252 | 1276 |
| 1960-61 | 11.7 | 45805 | 3915 | 2.019 |
| 1961-62 | 7.2 | 57678 | 8011 | 1.636 |

A last source of information on probable values of M result.s from comparing relationships between population parameter values and rate of natural mortality in other species. Beverton (1963) shows the relationship of $M$ to the maximum age observed (Tmax) for a number of different species. The oldest Pacific mackerel which has been observed was 11 years of age (Fitch 1951) suggesting a probable range of M from 0.3 to 0.7 .

$$
\simeq-75860
$$



FIGURE 6. Estimation of $M$ by the relationship of $Z$ to $F$.
Another comparison can be made between the von Bertalanffy parameter K, and M, as shown in Beverton and Holt (1959). Values for K of 0.244 (Knaggs and Parrish 1973) for recent years, and of 0.221 for earlier years as estimated above, suggest an M of 0.4 to 0.6 when compared with similar values for other free-swimming large species of fish (Beverton and Holt 1959). Estimates of $\mathbf{M}$ from comparative studies such as these are of poor reliability, but do give support to the other estimates.

Comparision of estimates of the rate of natural mortality is obtained by various methods (Table 10), suggests that $M$ is probably in the range of
0.4 to 0.6 , with the most consistent single value being $\mathrm{M}=0.5$. This value will be used throughout the rest of the analysis.

Table 10. Estimates of Natural Martality Rate for Pacific Mackerel

| Natural mortality <br> rate estimate <br> $M$ | Source |
| :--- | :--- | :--- |$\quad$| Tagging (Fry and Roedel, 1949) |
| :--- |
| $1.1-1.3$ |
| $0.3-0.5$ |$\quad$| Early catch curves |
| :--- |
| 0.5 |

## COHORT ANALYSIS

## ESTIMATION OF FISHING MORTALITY RATES

Fishing mortality rates were estimated using the method of cohort analysis first developed by Murphy $(1965,1966)$ and generalized by Tomlinson (1970). A "backward" solution was chosen due to its properties of convergence: a wide range of fishing mortality rate estimates for the oldest or most recent age group gives a progressively narrower range of variation in estimates of $F$ for younger age groups or earlier seasons. A constant rate of natural mortality ( $M=0.5$ ) was assumed. All fish of age 4 and older were assumed to be fully recruited. This assumption was warranted by trial solutions using older ages at assumed full recruitment. Also, sample sizes of older fish are often very small and highly variable.

Two methods of determining seasonal estimates of F for fully recruited fish were investigated. The first method is similar to that used by Murphy (1966) for sardines. The cohort of fish consisting of those fish of age $4+$ is the same cohort as those fish age $5+$ in the succeeding season. In the same season, $4+$ and $5+$ cohorts are presumably fished at the same rate. as they are assumed to be fully recruited. Thus the fishing mortality rate for the age $5+$ fish can be used to estimate the fishing mortality rate for the age $4+$ fish of the preceding season by cohort analysis using the catch ratio of age $5+$ to age $4+$ fish. The mortality rate estimated for the age $4+$ fish can then be assigned to the age $5+$ fish in the same season as input to the next preceding season, and the backward solution of seasonal fishing mortality rates continues in stepwise fashion.

An alternative method was tried, which does not combine age groups of fish, but more fully utilizes the property that all fully recruited age groups are assumed to be equally exploited in a fishing season. The fishing mortality rates form a matrix with rows of year-classes (cohorts) and columns of ages, so that diagonals represent fishing seasons. An iterative procedure was used to obtain values of $F$ for all cells which minimize an overall weighted sum of squares of deviations with respect to the season means.

The first method considers seasons in pairwise fashion only, so that errors in fishing mortality rate estimates are passed on to the next season's estimate (with convergence reducing their magnitude). The second method connects several year-classes and seasons, with varying degrees of freedom due to the convergence property. Consider a single year-class for which trial fishing mortality rates have been determined by cohort analysis. $F$ for the youngest age group will vary little for a wide range of $F$ of the oldest group. Each age group is contributing to the sum of squares for its respective season, so the mean fishing mortality rate of the earliest
season tends to be anchored by the least variable $F$ of the youngest age group while F of the oldest age group is relatively free to assume a value which is most consistent with its season mean. Convergence of the backwards time series is still a basic property of the second method, although linkage involves every year-class which was fished in any season in which the year-class under consideration was fished, rather than the simple pairwise linkage of the first procedure. This linkage system gives the second method greater stability with respect to propagated errors, at a sacrifice of sample size. The respective advantages and disadvantages of the two methods require more extensive and quantitative examination than they have received here. In practice the two methods give very similar results, although the second method may vary in sensitivity over different portions of the time series, sensitivity goes undetected in the first method. Due to the unknown biases of the second method, and the general agreement with estimates made by the simpler first method the first method was used for this analysis.

No independent estimate of the fishing mortality rate ( $F$ ) for the recent portion of the time series is available, making it necessary to use a reasonable guess as a starting value. Alternative trial values of $0.5,1.0$ and 1.5 for 1969-70 were compared (Table 11), and convergence resulted in little difference for the 1966-67 season and earlier. The intermediate value, $\mathrm{F}=1.0$, is used as an arbitrary starting value for solution of the time series. For younger age groups, the starting value for 1967-70 was modified by arbitrary recruitment factors to give F (age 3 ) $=1.0, \mathrm{~F}$ (age 2 ) $=0.75$, F (age 1 ) $=0.50$, and F (age 0 ) $=0.25$, which were used to initiate cohort analysis of these year-classes. These estimates do not contribute to the general solution, and were made only to fill out the time series with estimates for recent seasons.

TABLE 11. Comparison of the Effect of Different Assumed Values of $F$ for the 1969-70 Season on the Time Series of Fishing Mortality Rate Estimates for Fully Recruited Fish.

| Season | Estimated fishing mortality rate |  |  |
| :--- | :--- | :--- | :--- |
| $1969-70$ | 0.5 | 1.0 | 1.5 |
| $1968-69$ | 0.547 | 0.781 | 0.906 |
| $1967-68$ | 0.390 | 0.481 | 0.519 |
| $1966-67$ | 1.651 | 1.800 | 1.847 |

The three trial solutions shown in Table 11 demonstrate a general rule in the behavior of cohort analysis: large values of F converge more rapidly than do small values of $F$. Use of cohort amalysis on simulated catch data shows that in the backward solution the rate of convergence (percent approach to true F per iteration, relative to the error in the preceding F estimate) increases as F increases, and is zero at $\mathrm{F}=0$ (Table 12). A forward solution will show similar rates of divergence, estimates of $\mathcal{F}$ will approach progressively either zero or infinity, leading to an unrealistic solution of the time series.

The cohort analysis solution of the time series of catches by age is given in Table 13. The catches themselves are given in Table 6. A cohort analysis

TABLE 12. Approximate Rates of Convergence * for Cohort Analysis, Backward Solution, $M=$ 0.5, as Defermined by Simulated Catches.

| $F$ | Rate of convergence |
| :---: | :---: |
| 0 | $0 \%$ |
| 0.1 | $11 \%$ |
| 0.2 | $19 \%$ |
| 0.3 | $26 \%$ |
| 0.5 | $39 \%$ |
| 1.0 | $65 \%$ |
| 1.5 | $78 \%$ |
| 2.0 | $85 \%$ |

*Approximate rate of convergence is $\left.100 \%\left(\mathrm{~F}_{\mathrm{i} \cdot \mathrm{i}}-\mathrm{F}_{\mathrm{i} \cdot \mathrm{i}}\right) / \mathrm{F}_{i} \cdot \mathrm{~F}_{\mathrm{i}}\right)$ when $\mathrm{F}_{\mathrm{i} \cdot \mathrm{i}}=\mathrm{F}_{\mathrm{i}}$, and $\mathrm{F}_{\mathrm{i}}$ is near F . Convergence becomes divergence in the forward solution.
of fishing mortality rates for the 1928-29 season was impossible due to lack of sampling. A rough guess of 0.2 was obtained by multiplying the $1929-30$ F by the ratio of total catches for the two seasons. Approximate fishing mortality rates for the younger age groups were obtained by applying approximately the same relative recruitment ratios as in 1929-30. Fishing mortality rate estimates before 1939 are unreliable due to the aforementioned problems in estimating age composition. The estimates for 1928 through 1932-33 are particularly poor due to the lack of convergence at low fishing mortality rates.

As there were two independent fisheries for the Pacific mackerel, it is useful to separate fishing mortality rates into purse seine and scoop fleet components. This separation is done by multiplying the total fishing mortality rate (age $4+$ ) by the ratio of the fishery segment catch to total catch:
$\mathrm{F}($ scoop $)=[\mathrm{C}($ scoop $) / \mathrm{C}($ total $)] \mathrm{F}($ total $)$
Scoop and striker catch were combined under the heading of "scoop" and purse-seine and "others" were combined under the heading of "purse seine" (Table 13). The "other" category amounts to a very small percentage of the catch. Catches by fishery segment were obtained from Roedel (1952) wherein values were given for 1939 through 1950, and estimates for the seasons before 1939 were presented graphically. More recent catches were compiled from source documents.

## POPULATION ESTIMATES

The fishing mortality rates in Table 13 are combined with the catches in Table 6 to give population sizes for age groups at the beginning of the fishing season (i.e., on the "birthday"). The annual exploitation rate (E) is given by

$$
E=(F / F+M)\left(1-e^{-(F+M)}\right)
$$

and initial population size is in numbers estimated by

$$
\mathrm{N}=\mathrm{C} / \mathrm{E}
$$

Population sizes in weight, or biomasses, are obtained by assigning the
tABLE 13. Fishing Mortality Rates By Season

| Season | Age |  |  |  |  | age $4+$ <br> Exploitation rate | Proportion catch by scoop | F purse seine \& other | Fscoop |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 1 | 2 | 3 |  |  |  |  |  |
| 1928-29 |  | 0 | (0.10) | (0.15) | (0.20) | (0.144) | - | (0.2) | - |
| 1929-311 | - | . 055 | . 162 | . 201 | . 330 | . 224 | - | . 330 | - |
| 1930-31 | 0 | . 003 | . 052 | . 066 | . 033 | . 026 | - | . 033 |  |
| 1931-32 | 0 | . 0022 | . 032 | . 080 | . 029 | . 022 |  | . 029 |  |
| 1932-33 | 0 | . 0002 | . 010 | . 032 | . 032 | . 025 | - | . 032 |  |
| 1933-34 | 0 | (0)7 | . 034 | . 159 | 214 | . 153 | 06 | 201 | . 013 |
| 1934-35 | 0 | . 017 | 120 | . 096 | . 366 | . 24.5 | 10 | . 331 | . 035 |
| 1933-36 | 0 | . 092 | . 079 | 282 | 357 | . 240 | . 04 | . 344 | . 013 |
| 1936-37 | 0 | . 016 | . 385 | 221 | 371 | . 248 | 06 | . 349 | . 022 |
| $1937-38$ $1934-34$ 198 | . 0101 | . 006 | . 13.35 | 425 | . 542 | . 337 | 13 | 472 | . 070 |
| $1933-39$ | . 005 | . 071 | . 253 | . 119 | . 715 | . 414 | 20 | . 574 | . 141 |
| 1939-4 (1) | . 110 | 110 | . 371 | 858 | 1.553 | . 655 | 59 | . 622 | . 911 |
| 1940-41 | .009 .001 | 132 | . 686 | 1.075 | 1.648 | . 678 | . 57 | . 711 | . 937 |
| 1941-42 | . 001 | . 091 | . 364 | . 969 | 1.115 | . 553 | ${ }_{6} 6$ | . 412 | . 703 |
| 1942-43 | 0 | . 105 | 125 | 431 | 825 | . 457 | 78 | . 181 | . 644 |
| 1943-44-45 | .005 0 | . 125 | . 411 | . 278 | . 694 | . 405 | ${ }_{71}$ | . 268 | . 426 |
| 1945-46 | . 011 | . 152 | . 233 | . 638 | . 4882 | . 307 | . 77 | . 113 | .369 .484 |
| 1946-47 | . 013 | . 379 | . 698 | . 717 | . 783 | .441 | . 52 | . 379 | 404 |
| 1947-48 | . 018 | . 061 | 1.166 | 1.387 | 1.532 | . 655 | 45 | . 835 | . 697 |
| 1948-49 | . 004 | . 275 | . 241 | . 392 | . 634 | . 379 | . 75 | . 160 | . 474 |
| 1949-30 | . 005 | . 166 | . 522 | . 911 | 1.223 | . 583 | . 57 | . 520 | .703 |
| 1950-51 | .00) | 298 | . 328 | . 495 | . 963 | . 471 | 43 | 488 | . 375 |
| 1951-52 | . 108 | 268 | 897 | 549 | 1.164 | . 570 | 16 | . 978 | 186 |
| $1952-53$ $1953-54$ | . 001 | . 012 | .200 | 1.348 | 1.897 | .719 | 03 | . 832 | . 065 |
| $1953-34$ $1954-55$ | . 049 | . 011 | 301 | 696 | 1.339 | . 612 | 24 | 1.013 | . 326 |
| $1954-55$ $1955-56$ | . 005 | 310 | . 110 | 292 | . 229 | . 163 | 49 | . 117 | 112 |
| $1955-56$ $1956-57$ | . 029 | . 071 | 479 | 435 | 1.028 | . 526 | 24 | . 780 | . 248 |
| $1956-57$ $1957-58$ | 001 | . 553 | . 498 | 768 | . 546 | . 338 | 11 | 487 | . 059 |
| $1957-58$ $1958-79$ | . 01019 | 232 | . 840 | . 929 | 1.556 | . 660 | . 25 | . 161 | 395 |
| 1958-39 | . 064 | . 028 | . 496 | 1.326 | 1.354 | . 616 | 44 | . 764 | .590) |




FIGURE 7. Total biomass of the California Current stock of Pacific mackerel (MacCall pers. comm.)
weights at age for May given in Table 7 to the populations estimated by the above equations. The resulting biomass estimates are given in Table 14. Total biomass (Figure 7) is estimated by summing the biomass of the individual age groups, not including age group 0 . Spawning biomass is estimated in similar fashion, except that age group contributions are modified by the percentage of females which are capable of spawning (Figure $2)$.

## RECRUITMENT AND SPAWNING SUCCESS

Recruit biomass ( R ), measured in weight at age 1 , is given in Table 14. Spawning success has been highly variable, and there appears to be little density-dependent effect even on a logarithmic scale, when population biomasses are in their normal historical size range (Figure 8). However it appears that recruitment strength is much less variable when spawning biomass $(\mathrm{P})$ is greater than 200 million pounds. All of the disastrously poor recruitments of 20 million pounds or less were produced by spawning biomasses less than 200 million pounds.

An index of spawning or reproductive success, as measured by $\ln$ (recruits/spawners) shows a somewhat cyclical pattern over time (Figure 9). The sequence of poor spawning successes that led to the collapse of the stock is remarkable both in its magnitude and its duration. Such a sequence of five consecutive spawning failures would have caused a drastic decline in abundance even in the absence of a fishery. However, harvest during and after the period undoubtedly retarded the subsequent recovery. Variability of spawning success during the period 1928 to 1945 was significantly ( $\mathrm{P}<0.01$ ) less than during later years (Table 15). Three hypotheses are suggested as possible explanations for the increase in variance. First, the computations are somewhat unreliable up to the 1939 season, and the method of estimating early age compositions may have artificially reduced the variability. Second, key environmental factors in spawning success may have actually been more variable in the later period. The environmental conditions which influence reproductive success from a spawning event will be termed the "spawning environment". The


FIGURE 8. Spawner-recruit relationship

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third and most interesting hypothesis is that the increase in variance is the result of decreased spawning biomass.


FIGURE 9. Time series of the natural tog of the observed recruit biomass per spawning biomass.
Overall spawning success is an average of all the results from individual spawning events in a given season. These events could be considered to be samples drawn from the total spawning environment, which extends through space and time. The true average spawning environment certainly changes from year to year, but presumably fluctuates about a mean set of conditions which reflect the long-term average. If we assume randomness of spawning behavior with respect to subsecuent conditions affecting larval survival, the hypothesis can be viewed as a basic statistical sampling problem. By treating mean biomass as an index of sample size, we can use the property that the standard error of the mean varies inversely with the square root of the sample size as an approximation. Thus, on the basis of population size, we would expect a relative increase in standard error of 1.64 (i.e. $\sqrt{286 / 106}$ ), whereas the actual increase was 1.89. The additional increase, if it is other than random error, could result from several causes. The temporal extent of spawning is largely dependent on the age structure of the population, and the mean age of the

TABLE 15. Comparison of Spawning Success for Two Periods of the Pacific Mackerel Fishery.

| Period | $1928-1945$ | $1946-1968$ |
| :--- | :---: | :---: |
| Number of years | 18 | 23 |
| Mean index of spawning success | -0.984 | -1.067 |
| Standard error* | 0.861 | 1.628 |
| Mean spawning biomass (million pounds) | 286 | 106 |
| Mean age of spawning biomass at beginning of season | 3.21 | 2.65 |

[^0]spawning biomass was lower for the latter period (Table 15). Also, the spawning environment is very contagiously distributed in space and time (Lasker, 1975), suggesting that small sample sizes would be highly variable. If the third hypothesis is correct, maintenance of a larger spawning biomass might have helped the stock survive the poor spawning successes of the 1960 's. Presumably, the recruitment failures would have been somewhat more moderate, and the larger surviving biomass would have aided recovery when better spawning successes returned in the late 1960's and 1970's.

## RECRUITMENT MODELS

## METHODS

The statistical procedures used in this report included extensive use of correlation and regression techniques. The Statistical Interactive Programming System (SIPS) developed and maintained by the Oregon State University Statistics Department (Guthrie, Avery, and Avery 1974) was used almost exclusively for the early analyses. Forward stepwise multiple regression as described by Draper and Smith (1966) was used for analysis including environmental variables. Later analyses included non-linerar regressions. These analyses used the Biomedical Computer Program BMDP3R (Dixon 1975). Several of the BMDP3R subroutines were altered for use on a CDC 6500 . The program was altered by the addition of the FORTRAN statements necessary to fit the functions used in the various recruitment models.

## Density-dependent recruitment functions

Spawner-recruit functions of several types were fitted to the estimates of recruit biomass (i.e., at age 1 ) and spawning biomass. The three principal density-dependent functions used were those used by Ricker (1975: 282), Beverton and Holt (1957: 49), and Cushing (1971). These three functions are shown in Figure 10. The major difference in the three functions is the amount of prerecruitment mortality associated with increasing population density (i.e., compensatory mortality). The Ricker function predicts that recruitment increases to a maximum at some moderate spawning biomass level and then decreases to low recruitment at a high


[^1]spawning biomass levels. The Beverton and Holt function predicts that recruitment increases to an asymptote as spawning biomass increases. The Cushing function predicts that recruitment continues to increase without bounds with increasing spawning biomass, however at a diminishing rate.

Clark (1974) has suggested that increased mortality may occur at low biomass levels in pelagic schooling fishes (i.e., depensatory mortality). This increase in mortality rate at low biomass levels would be caused by a decrease in the average school size, which would result in a reduction in the survival value of schooling. Two spawner-recruit functions were used to determine if Clark's hypothesis could be used to improve the spawner-recruit relationship in a stock that had suffered recruitment failure. These two spawner-recruit functions were made by including a depensatory term in the Ricker and Cushing spawner-recruit functions.

The five spawner-recruit functions were fitted with linear regressions, with $\log$ transformed variables, and nonlinear regressions. The equations for the five models and the regression variables used to fit the linear regressions are listed in Table 16. The $\mathrm{r}^{2}$ and F values for the transformed linear regressions were calculated by the SIPS program. These values for the linear and curvilinear models were calculated by a short FORTRAN program which calculates the total sum of squares, corrected for the mean, and the residual sum of squares for the regression models.

TABLE 16. Regression Variables for Spawner-Recruit Functions

| Name | Function | Linear regression variables |  |
| :---: | :---: | :---: | :---: |
|  |  | Dependent | Independent |
| Ricker | $\mathrm{R}=\mathrm{b}_{\mathbf{1}} \mathrm{Pe}^{-\mathrm{b}_{\mathbf{b}} \mathrm{P}}$ | $\ln (\mathrm{R} / \mathrm{P})$ | P |
| Cushing | $\mathrm{R}=\mathrm{b}_{1} \mathrm{P}^{\mathrm{b}_{1}}$ | $\ln (\mathrm{R})$ | $\ln (\mathrm{P})$ |
| Beverton and Holt | $\mathrm{R}=\left(\mathrm{P} /\left[\mathrm{b}_{1}+\mathrm{b}_{2} / \mathrm{P}\right]\right)$ | $\mathrm{P} / \mathrm{R}$ | P |
| Clark-Ricker | $\mathrm{R}=\mathrm{b}_{1} \mathrm{Pe}^{-\mathrm{b}_{2} P} \mathrm{e}^{-\mathrm{b}_{2} / P}$ | $\ln (\mathrm{R} / \mathrm{P})$ | P,1/P |
| Clark-Cushing | $\mathrm{R}=\mathrm{b}_{1} \mathrm{P}^{\mathrm{b}_{5}} \mathrm{e}^{-\mathrm{t}_{0} / \mathrm{P}}$ | $\ln (\mathbf{R})$ | $\ln (\mathrm{P}), 1 / \mathrm{P}$ |

> Where $$
\begin{array}{l}\mathbf{R}=\text { Hecruit biomass } \\ \mathbf{P}=\text { Parent biomass } \\ b_{1}=\text { Density independent coefficient } \\ b_{2}=\text { Compensatory, density dependent coefficient } \\ b_{3}=\text { Depensatory, density dependent coefficient }\end{array}
$$

## Environmental variables

The environmental data used in this study are available primarily as monthly means. Annual environmental factors, such as Bakun's (1973) upwelling indices or sea surface temperature at Scripps pier, therefore consisted of 12 individual variables. These variables are not completely independent. For example sea surface temperatures from adjacent months are obviously highly correlated. In fact seasonal patterns, in the association between themonthly means and recruitment, occurred in most of the environmental factors. The lack of independence between the
monthly means was not a necessary prerequisite in the development of recruitment models. The models were developed with stepwise regresssion, which does not require that all potential variables be completely independent.

The major spawning season for Pacific mackerel is May-July. The monthly means discussed above may cover too small a portion of the spawning season to test the associations between environmental conditions and recruitment. To assess the associations between longer term environmental conditions and recruitment, several 3-month combinations were made. The first combination was the mean value for the three main spawning months (May-July). On the hypothesis that conditions immediately prior to spawning should influence spawning, the second combination was the mean value for April-June. As previously noted there is a marked seasonal difference in the peak of maturity in Pacific mackerel of different ages. It was thought therefore that the age structure of the population would influence the recruitment response to environmental variables. For example a spawning population consisting primarily of age 1 fish, which have a maturity peak in July, would not be able to take advantage of favorable environmental conditions occurring in May. Therefore, linear combinations of the environmental variables from MayJuly and April-June were made. These linear combinations were prorated by Pacific mackerel age composition of an individual year. For example, if the age composition of the spawning biomass in a given year was $50 \%$ ages $3+, 20 \%$ age 2 , and $30 \%$ age 1 , the prorated variable was $50 \%$ of the May value, $20 \%$ of the June value, and $30 \%$ of the July variable. The same procedure was used for the prorated April-June variables.

The large number of environmental variables analyzed for this study necessitated that some pre-analysis be carried out before multiple regression models were developed. The pre-analysis was accomplished by calculating the correlation coefficient for the relationship between each environmental variable and recruitment. Three different correlations were made for each environmental variable. These three were the correlations with the recruit biomass (i.e., at age 1), the natural log of recruit biomass, and the natural $\log$ of the recruit biomass divided by the spawning biomass. Hereafter the above three will be referred to as $R, \ln (R)$, and $\ln (\mathrm{R} / \mathrm{P})$.

The choice of environmental variables to include as potential variables in recruitment functions for Pacific mackerel was largely dependent upon available long-term data. Unfortunately such data were not available on plankton populations. Data sources were limited therefore to physical oceanographic and meteorological data.

Environmental data analyzed can be grouped into three general categories based on the period of coverage. Category one includes land-based meteorological, sea level and sea surface temperature data. The period covered by these data includes the entire period of the data base of the population estimates (1928-1968). Data analyzed included monthly mean atmospheric pressure at San Diego, mean sea level difference between San Francisco and Hilo, Hawaii (Saur 1972), monthly mean sea surface temperature at Scripps pier, and the monthly mean sea level at La Jolla.

Sea level data were included as a potentially important variable because of the relationship between geostrophic flow and coastal sea levels. Reid and Mantyla (1976) have shown a close relationship between seasonal geostrophic flow and sea level elevations at La Jolla, California.

The second category included ship observation data. These data are available as monthly means by 5 degree blocks (i.e., Marsden Square quadrants). The data base starts in 1931. Data analyzed included wind speed, sea surface temperature, and cloud cover for Marsden Square quadrants 120 (2) and 84 (3) (Figure 11). All of the data for Marsden Squares and for sea level at La Jolla was provided by the Pacific Environ-


FIGURE 11. Marsden Square quadrants $\mathbf{1 2 0 ( 2 )}$ and $\mathbf{8 4 ( 3 ) \text { , and upwelling index locations }}$
mental Group of the National Marine Fisheries Service. Data on wind speed were included as it would be expected to be related to upwelling. Cloud cover could be important because it might be used as an index of insolation and it could also be related to upwelling.

The third category is composed of data from a series of mass transport calculations. The data were provided by Bakun (pers. comm.) and his calculations were made with the procedures described by Fofonoff (1960). Data analyzed included meridional total transport, meridional Ekman transport, divergence of Ekman transport [Bakun's (pers. comm.) offshore divergence indices], and Bakun's (1973) coastal upwelling indices (i.e., Ekman transport perpendicular to the coast). The transport calculations were based on a $3^{\circ}$ grid of monthly mean atmospheric pressure which was interpolated from pressure fields prepared by Fleet Numerical Weather Central, U.S. Navy. The data base starts in 1946. Analysis of the transport data included the calculations at three locations: $27^{\circ} \mathrm{N}, 30^{\circ} \mathrm{N}$ and $33^{\circ} \mathrm{N}$ (Figure 11). Nelson et al. (1976) have shown that Ekman transport, calculated by Bakun's (1973) methods, accounts for 84 percent of the variation from a Ricker spawner-recruit curve in Atlantic menhaden.

The four sets of transport data are actually indices of two processes. Bakun's (1973) upwelling indices and meridional Ekman transport are different angular components of wind-driven transport. The units of measure in these components are metric tons per second per 100 m . width. The second mechanism is wind stress curl, which is a measure of the rate of change of wind driven transport with respect to space. Sverdrup (1947) has shown that meridional total transport is proportional to wind stress curl. The divergence of Ekman transport, which is proportional to total meridional transport minus meridional Ekman transport, is dominated by total transport and is therefore essentially the same as wind stress curl. Units of the two measures of wind stress curl are given in terms of vertical velocity (millimeters per day, positive upwards) through the bottom of the Ekman layer.

## Environmental-dependent recruitment functions

Recruitment models incorporating both population and environmental variables were developed with stepwise multiple regression. The on-line statistical system used for stepwise multiple regressions (SIPS) is limited to 50 variables, so it was necessary to reduce the number of potential independent variables. The independent variables used were the previously discussed linear combinations of the spawning months and all other variables with a significant correlation ( $95 \%$ level) with the dependent variable.

In Pacific mackerel the environmental variables were more strongly correlated with recruitment than were the population variables. It was felt that the size of the parent stock must have underlying effects on recruitment as suggested by Clark (Clark and Marr 1955). The fact that recruitment is heavily dependent upon environmental factors does not negate the effects of parent stock size; it merely masks the effects. Therefore the multiple regression models developed included population variables. The
models were developed by adding the population variable to the regression model before the stepwise process was started (i.e., forcing in the population variable before any environmental variables were allowed to enter the regression). This had the effect of adding environmental variables that best describe recruitment given the fact that a population variable is included in the model. However, this is not to say that the multiple regression models describe variation from the density-dependent Ricker or Cushing models.

## DENSITY-DEPENDENT RECRUITMENT FUNCTIONS

Spawner-recruit functions were calculated with both linear and nonlinear regression procedures. The linear regression models were fitted with $\log$ transformed variables and will hereafter be referred to as transformed models. The exponentiated versions of the transformed models will be referred to as the linear models. Transformed models for the period of 1928-1968 were significant at the $1 \%$ level for the Cushing function but the Ricker and Beverton and Holt functions were not significant even at the $5 \%$ level (Table 17). None of the linear models is significant at the $5 \%$ level. The linear Cushing and Beverton and Holt models had a larger sum of squares than the total sum of squares corrected for the mean. This implies that the linear Cushing and Beverton and Holt models provide significantly worse estimates of recruitment than does mean recruitment.

The nonlinear (BMDP3R) Ricker and Cushing functions are both significant at the $99 \%$ level (Table 17). The addition of depensatory term to the Ricker and Cushing functions only slightly increased the coefficients of determination ( $r^{2}$ ); the Clark-Ricker function was significant at the $5 \%$ level (Table 17). The Clark-Ricker function converged to a positive coefficient and therefore this model contains two compensatory terms rather than a compensatory term and a depensatory term. The fact that the addition of depensatory terms did not improve the fits of the spawner-recruit functions does not necessarily imply that a depensatory i ecruitment factor does not exist in Pacific mackerel. The large observed v ariation in recruitment at low spawning biomass levels would have hin$d$ red detection of a depensatory factor and it is possible that depensation $w$ uld not occur until the spawning biomass reached extremely low levels.

The three Ricker models (Table 17) have very low density-independent corfficients. This suggests that the limiting equilibrium rate of exploitation will be quite low in comparison to other fisheries (Ricker 1975:286). The poor statistical fit of the Ricker model is apparent in the large variation in $\ln (\mathrm{R} / \mathrm{P})$ that occurred when the spawning biomass was less than 200 million pounds (Figure 12).

Fitted curves for the linear and nonlinear Ricker and Cushing functions are shown in Figure 13. The curves for the linear functions show considerable similarity in form at spawning biomass levels below 350 million pounds. The nonlinear, BMDP3R, Ricker and Cushing curves also show considerable similarity. It appears that at least for low and moderate spawning biomass levels the way the functions are fitted is more important than which function is used.
TABLE 17. Density-dependent Spawner-recruit Functions

| Name | Function | $R^{2}$ | $F$ | DF |
| :---: | :---: | :---: | :---: | :---: |
| Cushing transformed | $\ln (\mathrm{R})=2.0948+0.72888 \ln (\mathrm{P})$ | 0.297 | 16.49** | 1,39 |
| Cushing linear | $\mathrm{R}=8.1238 \mathrm{P}^{0.72888}$ | - | 7.78* | 1,39 |
| Cushing nonlinear | $\mathrm{R}=1069.9 \mathrm{P}^{0.36187}$ | 0.166 | $7.78 * *$ | 1,39 |
| Beverton and Holt transformed | $\mathbf{P} / \mathrm{R}=6.1961+0.0000030821 \mathrm{P}$ | 0.002 | 0.09 | 1,39 |
| Beverton and Holt linear | $\mathbf{R}=\mathbf{P} /(6.1961+0.0000030821 \mathbf{P})$ | - | - | 1,39 |
| Ricker transformed | $\ln (\mathrm{R} / \mathrm{P})=-0.67752-0.00000214 \mathrm{P}$ | 0.068 | 2.85 | 1,39 |
| Ricker linear | $\mathrm{R}=0.50787 \mathrm{Pe}^{\cdot 0.00000214 \mathrm{P}}$ | 0.057 | 2.31 | 1,39 |
| Ricker nonlinear | $\mathrm{R}=0.88093 \mathrm{Pe}^{-0.00000253 \mathrm{P}}$ | 0.236 | 12.06** | 1,39 |
| Clark-Cushing nonlinear | $\mathrm{R}=2435.4 \mathrm{P}^{0.29910} \mathrm{e}^{-7524.3 / \mathrm{P}}$ | 0.170 | 4.39* | 2,38 |
| Clark-Ricker nonlinear | $\mathrm{R}=0.85112 \mathrm{Pe}{ }^{-0.00000242 \mathrm{P}} \mathrm{e}^{350 \mathrm{l}^{\prime} \mathrm{P}}$ | 0.237 | 5.90** | 2.38 |

[^2]

SPAWNING BIOMASS
(in millions of pounds)

FIGURE 12. Natural logarithms and regression line of recruit biomass per spawning biomass plotted against spawning biomass

The Cushing and Ricker models above were transferred to spawner resultant-spawner models to show equilibrium points (Figure 14). This transfer was calculated by multiplying the calculated recruitment by a factor that determines the spawning biomass of a cohort that would occur when there was no fishing mortality. This factor (3.845) was calculated by the ISOE program (Appendix I). The resulting spawning biomass per unit weight of recruits calculated with this program assumed a constant (0.26) proportion of maturity of age 1 fish. With the assumption of densitydependent maturity of age 1 fish the spawn resultant spawner relationship would be somewhat more arched than shown in Figure 12 and the equilibrium points would be at a lower spawning biomass.


FIGURE 13. Ricker and Cushing spawner-recruit models fitted to Pacific mackerel population
data. (Values in millions of lbs.).

## ASSOCIATIONS BETWEEN RECRUITMENT AND ENVIRONMENTAL FACTORS

## Sea surface temperature

Off southern California, warm sea surface temperature during the spawning season was found to be associated with good recruitment in Pacific mackerel. This pattern was seen in the Marsden Square quadrant off southern Califormia, 120(2), and at Scripps pier (Figure 15). The sea surface temperature off Baja California, Marsden Square quadrant 84 (3), did not show this relationship (Figure 15). After the correlations were calculated it was found that the 84 (3) quadrant contained observations from the Gulf of California and this undoubtedly biased the data from this quadrant.

The generally expected relationship between sea surface temperature (SST) and the number of recruits per spawner is a dome-shaped curve (Ricker 1975:276). The number of recruits per spawner should rise to a maximum at some optimum temperature and then decline to lower levels


FIGURE 14. Ricker and Cushing spawner resultant-spawner models (values in millions of lbs)
as temperature continues to increase. The above pattern would be expected to occur in the center of the species' geographical range. The California stock of Pacific mackerel is on the northern, cold-water edge of the range of the species. The fact that upwelling is most intensive during the spawning season of Pacific mackerel also contributes to depressing SST. Therefore the dome-shaped relationship between SST and the number of recruits per spawner should not be expected to hold for the California stock of Pacific mackerel because the SST does not get high enough to depress recruitment. To approximate this relationship a quadratic multiple regression of $\ln (\mathrm{R} / \mathrm{P})$ vs. T and $\mathrm{T}^{2}$ was calculated (where $\mathrm{T}=$ prorated April-June sea surface temperature ( $\mathrm{C}^{\circ}$ ) in Marsden Square 120(2)). The first order value of temperature is the first variable to enter, with an $r^{2}$ of $0.2611\left(\mathrm{~F}=12.72^{* *}\right.$ with 36 df$)$. The entering of the second order term is not significant and the $r^{2}$ is only increased to (0.2613. The hypothesis that the relationship between $\ln (\mathrm{R} / \mathrm{P})$ and SST is quadratic must therefore be rejected for the range of SST observed in Marsden Square 120(2). The first order regression equation is significant at the $99 \%$ level.

$$
\ln (\mathrm{R} / \mathrm{P})=-13.527+.78815 \mathrm{~T}
$$

This model suggests that warm surface waters are positively associated with good spawning success; however, the relationship shown should only


FIGURE 15. Correlations of $\ln (R)$ with monthly environmental factors; A. SST in Marsden square 120(2), B. SST in Marsden square 84(3), C. SST at Scripps Pier, D. Sea level differences from Saur (1973), E. Sea level barometric pressure at San Diego, F. Sea level at La Jolla
be considered valid with Marsden Square 120 (2) sea surface temperatures between $14^{\circ}$ and $17.5^{\circ} \mathrm{C}$. It should be noted that only $26 \%$ of the variation in $\ln (R / P)$ is explained by these data.

## Sea level and atmospheric pressure

Monthly mean sea level at La Jolla, corrected for atmospheric pressure,
and Saur's (1972) sea level differences between San Francisco and Hilo, Hawaii show different correlation patterns with recruitment. There is a statistically significant negative correlation between recruitment in Pa cific mackerel and the sea level at La Jolla for the entire April-September spawning season, (Figure 15). Saur's sea level differences do not show a statistically significant correlation with recruitment during the spawning season but do show positive correlation during the late fall (Figure 15). Monthly means of barometric pressure at San Diego show little correlation with $\ln (\mathrm{R})$, (Figure 15).

## Wind speed and cloud cover

Wind speeds in both Marsden Squares show a constant negative correlation with $\ln (\mathrm{R})$, (Figure 16). Cloud cover appears to have little association with $\ln (R)$ and with the exception of one month the correlations are not significant at the $95 \%$ level (Figure 16).


FIGURE 16. Correlations of $\ln (R)$ with monthly environmental factors; A. Wind speed in Marsden square $120(2)$, B. Wind speed in Marsden square 84(3), C. Cloud cover in Marsden square 120(2), D. Cloud cover in Marsden square 84 (3).

## Ekman and total transport

Associations between $\ln (\mathrm{R})$ and transport data tended to show higher correlations than $\ln (R)$ and Marsden Square or shore-based data sets. Data from $30^{\circ} \mathrm{N}$ tended to be correlated considerably better with $\ln (R)$ than data from $33^{\circ} \mathrm{N}$ and slightly better than data from $27^{\circ} \mathrm{N}$. This is consistent with the observed center of larval distribution (Figure 3).

Bakun's (1973) upwelling indices at $30^{\circ} \mathrm{N}$, positive offshore, show spring and fall peaks in association with $\ln (\mathrm{R})$ (Figure 17). Meridional Ekman transport at $30^{\circ} \mathrm{N}$ shows to a lesser extent the same spring and fall peaks as Bakun's upwelling indices. Values for meridional Ekman transport were calculated with negative values southward, which accounts for the difference in the sign of the correlation coefficients between the upwelling indices and meridional Ekman transport. There is a positive correlation between $\ln (R)$ and the upwelling indices. This relationship is conceptually satisfying in that increased plankton production resulting from upwell-


## MONTH

FIGURE 17. Correlations of $\ln (R)$ with monthly environmental factors; A. Meridional Ekman transport at $30^{\circ} \mathrm{N}$; B. Meridional total transport at $30^{\circ} \mathrm{N}$; C. Bakun's (1973) upwelling indices af $30^{\circ} \mathrm{N}$; D. Divergence of Ekman transport af $30^{\circ} \mathrm{N}$.
ing should be beneficial to larval fishes. It is also noteworthy that the peak of spawning in Pacific mackerel is the same as the peak of upwelling off central Baja California (ie., May-June).

Meridional total transport shows significant, positive correlation with $\ln (\mathrm{R})$ during the end and after the spawning season (Figure 17). The divergence of Ekman transport shows essentially the same monthly correlation pattern as total meridional transport. Total meridional transport and the divergence of Ekman transport at $30^{\circ} \mathrm{N}$ (wind stress curl) are atypical for the California Current region in that the values are negative. Bakun and Nelson (in press) have shown that negative wind stress curl (convergence), which is characteristic of the offshore region, extends toward the coast in the region just north of Punta Eugenia. They point out that the patterns of negative and positive wind stress curl suggest separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Punta Eugenia (Figure 18). They also note that ship-drift data in the region of negative wind stress curl tend to confirm this hypothesis in that a poleward component is lacking during the fall when the relaxation of upwelling would favor surfacing of a coastal counter current.


FIGURE 18. Wind stress curl patterns off southern California and Baja California (Bakun and Nelson In Press)

## Linear combinations of spawning months

Several combinations and prorations of the spawning months resulted in larger correlation with recruitment $(\ln (\mathbf{R}))$ than did the individual months (Table 18). Some of this increased correlation may have been fortuitous. However, it is conceptually satisfying that environmental conditions over the entire spawning season are better correlated with recruitment than conditions occurring in any one month. We feel that it is noteworthy that the environmental variable found to have the highest correlation with recruitment is one with very strong biological implications. This variable, April-June upwelling indices at $30^{\circ} \mathrm{N}$ prorated by the age composition of the spawning biomass, had a correlation coefficient of 0.713 with $\ln (R)$. Over 50 percent of the variation in $\ln (R)$ is explained by this variable. The high correlation with this variable suggests that recruitment is increased if there is upwelling just prior to and during the early part of the spawning season. It also implies that changes in age structure, and therefore time of peak spawning, can alter the response to a given upwelling pattern. It should also be noted that prorating the May-July upwelling indices by the age composition reduced the correlation with $\ln (\mathrm{R})$ to 0.319 . The implications are that upwelling a month prior to peak spawning results in greatly increased reproductive success and that upwelling during peak spawning does not significantly increase reproductive success. The above is an agreement with field observations for the northern anchovy which suggest that storms and strong upwelling disperse chlorophyll maximum layers that provide forage necessary for survival of first-feeding anchovy larvae (Lasker 1975, 1978).

TABLE 18. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with $\ln (R)$

| Variable | $N$ | $\begin{gathered} \text { May-July } \\ \text { mean } \end{gathered}$ | Prorated ${ }^{1}$ May-July | April-June mean | Prorated ${ }^{1}$ April-June |
| :---: | :---: | :---: | :---: | :---: | :---: |
| SPIER | 41 | . 270 | .416** | . 276 | 255 |
| BARP | 41 | . 030 | $-.165$ | $-.007$ | --. 059 |
| SSTC | 38 | .434** | .432** | .432* | 392* |
| WINDC | 38 | -. $364 *$ | $-.380^{*}$ | $-.289$ | $-.306$ |
| SLLJ | 41 | -. $542^{* *}$ | -.391** | -.514** | - .392** |
| SLEV | 41 | $-.509^{* *}$ | --.348* | $-.509^{* *}$ | $-.366^{*}$ |
| UP | 23 | .458** | . 319 | .575** | .713** |
| ODI | 23 | .528** | .610** | .486* | .584** |
| SPIER - | -Sea surface temperature at La Jolla |  |  |  |  |
| BARP - | -Barometric pressure at San Diego |  |  |  |  |
| SSTC - | -_Sea surface temperature, Marsden Square quadrant 120(2) |  |  |  |  |
| WINDC - | -Wind speed, Marsden Square quadrant 120(2) |  |  |  |  |
| SLLJ - | -Uncorrected sea level height at La Jolla |  |  |  |  |
| SLEV - | -Sea level height at La Jolla corrected for atmospheric pressure |  |  |  |  |
| UP3 - | -Bakun's (1973) upwelling index at $30^{\circ} \mathrm{N}$ |  |  |  |  |
| ODI3 - | -Bakun's (pers comm.) offshore divergence index at 30 N (divergence of Ekrnan transport). |  |  |  |  |
| - | -Significant at 5\% level |  |  |  |  |
| ** | -Significant at the $1 \%$ level |  |  |  |  |
| 1 - | -Variables were prorated as described on page 27 |  |  |  |  |

## ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNCTIONS

Recruitment functions incorporating both density-dependent and envi-ronmental-dependent factors were developed with forward stepwise multiple regression procedures. This limited the possible recruitment models to functions that are linear or functions that can be transformed to linear functions. It was decided that the use of exponential environmental terms was the most promising as both the Ricker and Cushing spawner-recruit functions can be fitted with linear regression of log transformed terms. This approach has been recommended by Ricker (1975), who suggests that the expected effects of the physical environment are multiplicative rather than additive and therefore logarithms should be used in multiple regressions. Log transformed functions are fitted to the geometric mean rather than the arithmetic mean. When these functions are transformed back to the original form they are biased towards low values. To avoid this bias the parameters of the spawner-recruit functions developed with stepwise multiple regression were computed by regressing the functions with the BMDP3R nonlinear regression program. This program requires a FORTRAN subroutine, which principally consists of the individual functions and the partial derivatives of the parameters of the functions. The subroutine used for all nonlinear regressions is listed in Appendix III.

The stepwise multiple regression models were fitted, as previously described, with the density term assigned as a forced variable in the forward stepwise process. The density terms were $\ln (\mathbf{P})$ for the Cushing function and $P$ for the Ricker function. Entering environmental terms were accepted if their entering $F$ values were significant at the $95 \%$ level. The exception to this is that the number of variables accepted was limited by the number of observations in each case. Draper and Smith (1966:167) suggest that the fitted model should not have more than one variable for every 5 to 10 observations.

Models were developed over three different time periods. Models developed for the first time period (1931-1968) included the Ricker and Cushing based models fitted with the Marsden Square and shore-based data sets. A Ricker based model was developed for the same data set for the reduced period of 1931-1960. This model was used to determine if the population decline of the mid-1960's would be predicted with a model that was fitted to data that did not include this population decline. The third set of models included the Ricker and Cushing based models fitted with all environmental data sets (1946-1968)

It was decided to limit the multiple regression models fitted to the 1931-1968 data sets to four independent variables due to the number of observations (38). The four variables were the density term and three environmental terms. The model fitted to the 1931-1960 data sets was not fitted by stepwise multiple regression. This multiple regression model was used for comparative purposes and it was decided that it would include only the density and environmental variables that were in the comparable 1931-1968 model.

The models developed from the 1946-1968 data sets were limited to three independent variables, the density term and two environmental
terms due to the smaller number of observations (23). The stepwise multiple regression models based on the Ricker and Cushing functions did not always select the same environmental variables. For example in the 19311968 models the Cushing-based model selected the May-July mean sea surface temperature and the Ricker-based model selected the April-June prorated sea surface temperature (SSTC, Table 2). The two variables have very similar correlation coefficients with $\ln (R)$ and $r^{2}$ values were essentially the same in both the Cushing and Ricker based models. Due to the similarity of $\mathrm{r}^{2}$ values it was decided to incorporate the identical environmental variables in the Cushing and Ricker based models for simplicity.

To avoid confusion in later analysis with the environmental-dependent recruitment functions, the functions will hereafter be referred to by the following names: 1) The functions fitted to the 1931-1968 data sets will be called the Ricker sea level model and the Cushing sea level model. The name refers to the first environmental variable to enter the stepwise regressions; 2) The reduced Ricker sea level model will refer to the function fitted to the reduced 1931-1960 data set; 3) Functions fitted to the 1946-1968 data sets will be called the Ricker transport model and the Cushing transport model.
The five environmental-dependent spawner-recruit functions used in the report are listed in Table 19. The environmental variables that provide the best description of recruitment in Pacific mackerel from 1931-1968 are May-July mean sea level at La Jolla; prorated mean May, June, and July barometric pressure at San Diego; and mean April-June sea surface temperature in Marsden Square quadrant 120 (2). The Ricker and Cushing sea level models had very similar $r^{2}$ values, 0.587 and 0.597 , and the $F$ statistics for these models were approximately three times as large as the critical F value at the $99 \%$ significance level (Table 19). The reduced Ricker sea level model has an $r^{2}$ of 0.517 . Its $F$ statistic was considerably smaller than the other two sea level models but was still significant at the $99 \%$ level.

The Ricker and Cushing transport models include two environmental variables. Both of these variables describe surface transport. The first variable is the April, May and June offshore divergence indices at $30^{\circ} \mathrm{N}$ prorated by the age composition of the spawning biomass. The Ricker transport model has an $\mathrm{r}^{2}$ of 0.756 and a F statistic of 19.59 (Table 19). The corresponding statistics for the Cushing transport model are 0.676 and 13.31. The critical F statistic at the $99 \%$ level of significance is 5.01 .

The predicted recruitment with the Ricker and Cushing sea level models and the observed recruitment are shown in Figure 19A. The same data for the transport models are shown in Figure 19B. The sea level model provides a reasonable description of the general periodicity of recruitment but individual years are not well estimated. The transport model shows a close agreement with the observed recruitment. The only year that is markedly different in observed and predicted recruitment is 1961.

## FACTORS AFFECTING RECRUITMENT

The spawning biomass of Pacific mackerel undoubtedly establishes the limits on the possible size of an individual year class. Within these limits recruitment is heavily dependent upon physical environmental condi-


FIFURE 19. Observed and predicted recruitment of Pacific mackerel A. Ricker sea level model, B. Ricker transport model.

TABLE 19. Environmental-dependent Spawner-recruit Functions

tions. Interrelations with other species also play a role in determining recruitment (Hunter 1976). However, the direct relationship between the populations of other species and recruitment in Pacific mackerel is difficult to demonstrate with available data.

Over the period of 1928 to 1968 the estimated recruit biomass varied from 0.58 to 321 million pounds ( 260 to 145,603 metric tons). Recruitment success therefore varied by a factor of 560 . Density-dependent recruitment models account for a maximum of about 24 percent of the variation in recruitment. Recruitment models incorporating both density-dependent terms and environmental terms account for about 60 percent of the variation in recruitment from 1931-1968 and about 75 percent of the variation from 1946 to 1968. Year-classes in excess of 100 million pounds ( 45,000 metric tons) at age 1 , occurred in only 9 of the 41 years. In only one of these 9 years was the spawning biomass below 100 million pounds ( 57 million pounds). The spawning biomass exceeded 100 million pounds in 24 of the 41 years. This suggests that strong year-classes are most likely to be produced in years with good environmental conditions and a large spawning biomass. It also suggests that given a reasonably large spawning biomass the principal limiting factor in recruitment is not a density-dependent factor. When either a heavy fishery or a series of years with unfavorable environmental conditions occurs (and particularly when both occur together) the future spawning biomass is likely to fall to levels where even optimum environmental conditions cannot produce a strong year-class. In these situations the spawning biomass becomes the limiting factor. In the California Current stock the critical spawning biomass of Pacific mackerel appears to be around 20 to 30 million pounds. With this level of spawning biomass a strong year-class could occur only with the very best environmental conditions. At spawning biomass levels above this critical level recruitment will be progressively less influenced by the spawning biomass level. However, the pattern of variation of the annual environmental conditions appears to be the factor which has the greatest control over the Pacific mackerel population.

There has been much discussion of the role of the "critical period" in the determination of year-class strength. The term "critical period" has been used to cover what we feel are two distinct processes in larval survival of pelagic fishes. The first is the "critical period" in the usage of Hjort (1926), the period just after the yolk sac is absorbed. It is best characterized as time of first feeding. Density-dependence, within the cohort, is not likely to be of great importance to survival through first feeding or until the larvae are several weeks old and greatly increase their mobility. The total number and concentration of eggs in a single spawning spot will affect early survival within the individual spawning spot. During the early larval period mortality of larvae will be dependent primarily upon the following factors:

1) The amount and type of plankton in the immediate proximity of the spawning spot.
2) The concentration of planktonic predators in the vicinity of the spawning spot.
3) Predation by nekton.

The first two factors have undoubtedly contributed to selection for an optimum size and density of individual spawning spot. The larvae in this optimum spawning spot must be dense enough to satiate planktonic predators and sparse enough to insure that the density of planktonic food is sufficient to allow feeding and growth through the early, relatively non-mobile larval stages. Density-dependence in the survival of a cohort through this early feeding stage is likely to be a function of the combined biomass of the entire trophic level. If the biomass of small pelagic fishes is large in relation to the amount of plankton present prior to spawning the plankton concentration is likely to be too low to allow good larval survival and therefore a poor year-class will result. Cushing (1974) has suggested that density dependence within their trophic level is a major factor in the sardine-anchovy relationship in the California Current.

The above considerations have, in our opinion, selected for a reproductive pattern for Pacific mackerel (and other pelagic fishes in upwelling regions) in which the size of spawning schools is much smaller than the size of schools during the rest of the year. Little is known of the spawning behavior and spawning school size in mackerel; however, ripe fish are extremely rare in the commercial landings and purse seiner catches have traditionally been very small during the peak of the spawning period. Thus, it appears likely that optimum spawning school size is relatively small, at least too small to justify a purse seine set.

Lasker (1975-1978) has suggested that virtually all of the survival of first-feeding anchovy larvae is linked to relatively rare patches of suitablesized phytoplankters. He also observed that chlorophyll maximum layers that contain phytoplankters of suitable size for first-feeding anchovy larvae are likely to be completely dispersed by a single storm. This observation implies that survival through the first feeding could be heavily influenced by the periodicity of individual upwelling events. Closely spaced storms, while providing sufficient nutrients for rapid phytoplankton growth, may prevent the development of the dense concentrations of phytoplankters required for first-feeding larvae. Upwelling events followed by a week to 2 weeks of relatively calm weather may therefore be a requirement for good survival through first feeding. If the interval between upwelling events is too great, total production will be lowered and the survival of older larvae will be reduced.

The second mechanism affecting larval survival occurs during the latelarval and post-larval stages, when the fish are mobile enough to allow mixing between the survivors from different, more widely separated spawning spots. Mackerel in these developmental stages would be able to swim only relatively short distances and their distribution would still be heavily dependent on prevailing surface currents. During this period den-sity-dependent mortality could be grouped into the following categories:

1) Mortality dependent upon density within the cohort. Such mortality may be of two types.
a) Mortality resulting from competition for the same food source. This type of mortality could conceivably result in a recruitment function similar to the Ricker model where a very large biomass can result in poor recruitment.
b) Intraspecific predation of eggs and larvae spawned late in the
spawning season by the survivors from earlier spawning. This type of mortality would reduce the number of recruits-perspawner but is not likely to reduce total recruitment. Mortality of this type is likely to result in a recruitment function of the type used by Cushing (1971).
2) Mortality dependent upon density within the species (i.e., older cohorts).
3) Mortality dependent upon the biomass of the entire trophic level.

Because of their relatively large mouth, late-larval and post-larval mackerel probably feed on larger particle size food than the anchovy or sardine larvae. However, with present knowledge it is probably impossible to make a comparison between the food of these mackerel and pre-adult or adult mackerel. Pre-adult and adult anchovies and sardines undoubtedly feed on the same food organisms as post-larval mackerel. The amount and density of food available to late and post-larval mackerel is dependent on relationships between the production of plankton and the grazing of plankton by organisms at the same or lower trophic levels as the mackerel. It is difficult therefore to separate items 2 and 3 above.

Environmental-dependent mortality will be principally determined by primary production prior to and during the larval stages and upon surface transport of the fish during their relatively non-motile stages. Thus upwelling, divergence-convergence patterns, and geostrophic flow will heavily influence the proportion of prejuvenile fish that will contribute to the recruitment of Pacific mackerel in the California Current Region.

The use of the term environmental-dependent mortality does not necessarily imply that this mortality is either density independent or density dependent. For example mortality of larvae may be greater during a spawning season with reduced upwelling and the mechanism of this mortality may be density related. Conversely, transport of larvae out of the California Current area could be entirely density-independent. It should be emphasized that recruitment is an interplay between environmental factors and spawning stock size and therefore density-independent fluctuations and density-dependent relationships are not separate halves of the process.

The large environmentally related fluctuations in recruitment of Pacific mackerel suggest that the recovery of the stock is more likely to be related to environmental conditions than to the resiliency of a population that is under carrying capacity. The resiliency could be further reduced if a depensatory mortality factor becomes significant. Clark (1974) suggested that a depensatory factor could be associated with the collapses of the populations of pelagic schooling fishes. The mechanism suggested by Clark, increased mortality due to a reduction of the size of schools, is not likely to result in critical depensation because the Pacific mackerel subadults and adults commonly school with jack mackerel. A second mechanism, increased larval mortality due to suboptimum spawning school size, could result in critical depensation and long-term loss of the stock.

## COMPUTER SIMULATIONS

## SIMULATION MODELS

The computer simulation models used in this work were written in FORTRAN IV and were run on a CDC 6500 computer. Two simulation models were used. The simpler model (ISOE, Appendix I) is a yield-perrecruit model based on the yield equations described by Beverton and Holt (1957) and as revised by Ricker (1975). ISOE calcalates the relative yield from a cohort at various combinations of exploitation rate and age at recruitment to the fishery.

The ISOE program calculates yield matrices for 1000 weight units of recruits. The matrices are output with the exploitation rates (and instantaneous fishing mortality rates) on one axis and age at recruitment on the other axis. The program is run with user supplied increments of exploitation rate and the instantaneous fishing mortality rates are calculated with an iterative solution based on Newton's method. User supplied input includes the maximum age of the species, the proportion spawning by age group, the Bertalanffy growth equation constants, the length-weight equation constants, the minimum and maximum ages at recruitment, and the exploitation rates for which the simulation is run.

The second simulation model (QUOTAE, Appendix II) was developed to simulate the Pacific mackerel population under a quota system similar to the present California regulations governing the fishery. QUOTAE is a dynamic pool model and includes a spawner-recruit function. This model combines many of the ideas used by Walters (1969) and Allen (1973). QUOTAF calculates the mean yield over a period of years with various combinations of quota proportion and age at recruitment. The quota proportion is defined as a fraction of the stock above some minimum level. The minimum level in the case of the California Pacific mackerel regulations is the spawning biomass level at which a moratorium on commercial fishing comes into effect (i.e., 20 million pounds). In the case of salmon the minimum level might be the minimum escapement.

The program can be run with no minimum biomass level, with a minimum biomass level or with a lower biomass level and an upper biomass level. In the first option the quota proportions are identical to exploitation rates. The second option allows increments of the quota proportion above the minimum biomass level. The third option is patterned after the California regulations and also resembles the approach followed by Allen (1973). As used in the Pacific mackerel simulations the third option would have a lower biomass level of 20 million pounds, a lower quota proportion of 0.2 , an upper biomass level of 40 million pounds, and an upper quota
proportion that is varied to determine the yields under different quota proportions.

In fisheries where the estimates of recruit biomass are measured at essentially the same time as those of spawning biomass the spawner-recruit curve can be used as an excess production curve. This is the case in some salmon fisheries. In most fisheries this is not the case. Recruitment occurs at some intermediate age and each cohort is exploited over a period of years. Thus for most fisheries the shape of the excess production curve is influenced by both the exploitation rate and the age at recruitment. If environmental factors cause considerable variation from a spawner-recruit function the surplus production curve will also show considerable variation. The QUOTAE model can be used to evaluate the yields under the various surplus production curves resulting from different management policies. This includes policies based on equilibrium yield that use a density-dependent spawner-recruit function. It also allows assessment of yields under a recruitment function that includes both environmental and density-dependent factors. In the latter case the model can be either deterministic or stochastic.

Biological input to the model included growth and proportion spawning by age group, a recruitment function, and natural mortality. Annual growth and growth to capture were the growth proportions calculated with the ISOE program. These calculations were made with the Bertalanffy and length-weight equations presented by Knaggs and Parrish (1973). The proportion spawning by age group was the data discussed earlier and the proportion of age 1 spawners was density-dependent. The natural mortality and fishing mortalities were not age specific and an instantaneous natural mortality of $\mathbf{M}=0.5$ was used in all simulations. Spawner-recruit functions used in the simulations will be presented later and they included density-dependent functions and density-environmen-tal-dependent functions. In several of the environmental-dependent recruitment functions the response to the environmental variables is determined by the age structure of the spawning biomass.

The normal output of QUOTAE consists of yield matrices for the mean yield over the period of the simulation and the yield in the last year of the simulation. The yield in the last year of the simulation is used for equilibrium recruitment functions. Output options include the output of annual spawning biomass, total biomass, recruitment, and yield for each age at recruitment and upper quota proportion. Control card options include the following:

1) Alteration of the quota levels and proportions used to calculate the annual quota.
2) The quota can be based on either the spawning biomass, total biomass, or the combined biomass of one-year-olds and two-year-olds.
3) A percentage catch of undersized fish can be set.
4) The proportion of a year-class that spawns can be density-dependent.
5) The environmental variables used in the recruitment function can be weighed by the proportion of the biomass that spawns during different periods of time.
For specific details the reader is referred to Appendix II.

## YIELD-PER-RECRUIT MODEL

Yield-per-recruit isopleths were calculated an instantaneous natural mortality rate (M) of 0.5 . Von Bertalanffy growth data were the previously discussed coefficients from Knaggs and Parrish (1973). Our program used also calculates matrices of resultant spawning biomass per unit weight of recruits. A generalized version of the program is listed in Appendix I. The proportions of mature fish by age group used for these calculations were $0.26,0.77,0.88$, and 1.0 for age groups $1,2,3$, and $4+$. Maximum age was 11 (Fitch, 1952).

The maximum yield per unit weight of recruits is dependent upon the choice of natural mortality. The maximum in each case occurred with an age at recruitment of one or less and with $F=1.0$, the highest instantaneous fishing mortality rate used (Figure 20). The low age at recruitment for maximum yield is consistent with the species biomass curve with age (Figure 21). This curve shows that when there is no fishing mortality, biomass peaks when the fish are yearlings. Several workers (Walters 1969, Ricker 1975:241) have suggested that the best policy is to harvest each cohort close to the age when biomass loss through mortality balances biomass gain through growth, subject to the constraint that adequate reproduction is maintained.

A fishery operating at the high fishing rates and low age at recruitment necessary to achieve maximum yield-per-recruit in Pacific mackerel results in a situation that produces a minimum spawning biomass from a ton of recruits. Under this fishing strategy, spawning biomass per recruit is less than $1 / 4$ of that which occurs with no fishery (Figure 20B).

## EQUILIBRIUM YIELD SIMULATIONS WITH DENSITY-DEPENDENT RECRUITMENT

The QUOTAE model was run with several of the density-dependent recruitment functions previously described. The first series of simulations used the linear and nonlinear regression fits to the Ricker and Cushing spawner-recruit functions (Table 17). In these simulations the quota was based on the total biomass and the quota levels were set at zero. Therefore, in these simulations the model calculates the exploitation rates. The second series of simulations was run at various quota levels and the quota was based on the spawning biomass. This series utilized only the Ricker nonlinear regression function. This function was chosen because it has the highest predictive capability. All of the above simulations were run with the 1931 biomass as the starting population. The simulations were run with 5 age at recruitment levels and 20 exploitation rates. The simulations were run for 100 years and the equilibrium yield was taken to be the yield in the 100 th year. Simulations with all of the above models had stabilized by the 12 th to the 50 th year. Yields during the 90 th to 100 th year varied less than $0.001 \%$ with each of the above models.

Equilibrium yield isopleths for the Ricker and Cushing recruit-spawner models show the same similarity as previously described in the spawner-
A.


INSTANTANEOUS FISHING MORTALITY
B.


FIGURE 20. Isopleth model with $M=0.5$; $A$. Yield per unit weight of age 1 recruits; B. Resultant spawning biomass per unit weight of age 1 recruits.


FIGURE 21. Pacific mackerel biomass curve with no fishery and $\mathbf{M}=\mathbf{0 . 5}$.
recruit curves (Figure 22). The linear fits to the Ricker function and the Cushing function produce similar yield isopleths and the nonlinear fits also produce similar isopleths. The linear regressions with the Ricker and Cushing functions have a bias towards low estimates as they utilize log transformed variables. This bias is evident in the low equilibrium yields predicted by the isopleths calculated with the linear regression spawnerrecruit functions. Average observed yield from 1931 to 1968 was 49 million pounds ( 22,000 metric tons).

The recruitment functions fitted by linear regression predict that maximum yield will occur with an age at recruitment of above age 4 and at low exploitation rates. Maximum equilibrium yield with an age of recruitment of 1 is with exploitation rates of around 0.15 to 0.3 .

The recruitment functions fitted with nonlinear regressions predict that maximum equilibrium yield will occur with an age at recruitment of between 3 and 4 . At this age and with exploitation rates in excess of about 0.2 , the Ricker nonlinear function predicts equilibrium yields above 80


FIGURE 22. QUOTAE equilibrium yield isopleths with density-dependent spawener-recruit functions (Yield in millions of lbs)
million pounds; ( 36,000 metric tons) and the Cushing nonlinear function predicts yields above 60 to 70 million pounds ( 27,000 to 32,000 metric tons) . High exploitation rates show little reduction in yield at an age of recruitment of 3 to 4 . It should be noted that the Ricker functions predict that extinction will occur if the age at recruitment is 1 or lower and the exploitation rate exceeds 0.6 . It has been shown that during the population collapse of the late 1960's the exploitation rate on the Pacific mackerel exceeded 0.6 and the age at recruitment was less than age 1 (Parrish, 1974).

Equilibrium yield simulations with four different sets of quota levels show little difference in yields at upper quota proportions below 0.4 (Figure 23). When the upper quota proportions are above 0.5 and the age at recruitment is 1 or 2 the equilibrium yield is markedly depressed in the simulation with the quota levels set at zero (Figure 23A). The maximum
equilibrium yield with all four sets of quota levels occurs at an age of recruitment of around 4 and with an upper quota proportion of above 0.4.


FIGURE 23. QUOTAE equilibrium yield isopleths, at four different sets of quoto levels with the Ricker nonlinear model (Yield in millions of lbs, quota based on spawning biomass)

The present California regulations controlling the Pacific mackerel fishery consist of quota levels and lower quota proportion as in Figure 23B and an upper quota proportion of 0.3. The age at recruitment during most of the observed fishery was age 1 . This location in the yield isopleth is shown by the symbol $\mathbf{X}$. This series of simulations suggests that, if environmental factors are not considered, the quota levels and quota proportions in the California regulations are properly set from an equilibrium yield philosophy. The simulations suggest that the yields could be increased by enforcing a strict size limit. It would be impossible to achieve maximum equilibrium yield with the present purse-seine fishery but it could be
achieved by a return to the scoop fishery, which could technically be controlled to reduce greatly the catch of fish less than 3 years old.

## YIELD WITH ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNCTIONS

Two series of simulations were made with the QUOTAE program and environmental-dependent recruitment functions. The first series utilized the nonlinear Ricker sea level function (Table 19). These simulations started in 1931 with the observed 1931 biomass, by age group, and ran through 1968. The second series used the nonlinear Ricker transport recruitment function, the 1946 starting biomass, and ran through 1968.
The above simulations were run in a manner that differs from the way such simulations are normally run. In most fisheries models environmental variation in recruitment is considered to be a random process (Allen 1973, Walters 1975). Simulations are therefore usually run with a stochastic environmental term. The driving stochastic variable is usually picked from either a distribution with the same mean and variance as the observed environmental variation or from a distribution with a mean of zero and a variance the same as the observed variance from some recruitment function. Variation in recruitment of Pacific mackerel is markedly nonrandom; instead it shows an aperiodic cyclic pattern. This pattern can be seen in a time series of the natural $\log$ of the number of observed recruits per spawner (Figure 9). Because of the nonrandomness of recruitment it was decided that a more realistic assessment of the effects of alternative management policies would be obtained by using the observed environmental data to generate recruitment. For example, the simulations with the nonlinear Ricker transport function were run with the observed April, May and June mean values for the upwelling indices and offshore divergence indices at $30^{\circ} \mathrm{N}$.

The similarity of the yield isopleths in four simulations with the nonlinear Ricker sea level function and varying quota levels suggests that longterm yield is not very sensitive to alterations in the quota levels (Figure 24). Mean yield also appears to be independent of age at recruitment at upper quota proportions below 0.3. At upper quota proportions above about 0.4 mean yield is influenced by age at recruitment and maximum mean yield occurs at high upper quota proportions and an age at recruitment of about 3 years.

The 1946-1968 series of simulations made with the nonlinear Ricker transport recruitment function and the same quota levels as the previous series do not show that yield is greatly influenced by age at recruitment (Figure 25). When the quota levels are set at zero, mean yield is almost entirely dependent on the quota proportion. The exception to this is that when the quota proportions are above 0.3 the mean yield is less when age at recruitment exceeds age 3 . When the upper quota level is set at 80 million pounds ( 36,000 metric tons) the simulations suggest that mean yield is low, around 10 to 15 million pounds ( 4,500 to 6,800 metric tons) over the entire range of age at recruitment and the entire range of quota proportions.


FIGURE 24. QUOTAE mean yield isopleths (1931-1\%68), at different sets of quota levels, with the Ricker sea level model. (Yield in millions of lbs, quota based on spawning biomass)
The preceding simulations with the two environmental-dependent recruitment functions show considerable difference in mean yields. There are several reasons for this. First the recruitment functions were fitted to different time periods; the sea level function was fitted to data from 1931-1968 and the transport function included data from 1946-1968. The transport function was fitted to data with a much lower mean spawning biomass; and in addition, about half of the years from 1946-1968 were during the periods of the sharp population declines that occurred during the early 1950's and the mid 1960's. The simulations also differ in that the starting biomass for those with the sea level function used 1931 as a base while the transport simulations started with 1946. The 1931 biomass was about 4.7 times larger than that of 1946 ( 611 vs 131 million pounds, 277,000 vs 59,000 metric tons). This factor of course resulted in higher mean yields in the simulations which started with the 1931 biomass.


FIGURE 25. QUOTAE mean yield isopleths (1946-1968), at four different sets of quota levels, with the Ricker transport model (Yield in millions of lbs, quota based on spawning biomass)

## ANNUAL YIELD UNDER FOUR MANAGEMENT OPTIONS

To assess the similarity of yields under the different environment-dependent recruitment functions, simulations under four management options were run. These simulations had the same time periods (1946-1968) and were initialized with the observed 1946 biomass. A third environmen-tal-dependent recruitment function was included in this series of simulations. This recruitment function, the "reduced sea level model," was included to determine if the population decline of the late 1960's would have been predicted by a recruitment function that was fitted to a reduced data set that did not include the period of the population decline.
The major difference between the yield estimates with the densitydependent and environmental-dependent recruitment functions is the large variation in annual yield that occurs in the simulations run with the
environmental-dependent recruitment functions. Time series of yields in simulations with the density functions show a stable approach to equilibrium yield. Simulations (1946-1968) with the Ricker sea level functions and the Ricker transport function show considerable variation in anmaal yield under different management options. Figures 26 and 27 show simulations with the Ricker sea level, reduced Ricker sea level and Ricker trans-


FIGURE 26. QUOTAE simulations (1946-1968); A. Recruitment of age 1, no minimum quota level and a quata propartion of 0.7 ( $w$ in figs 21A and 22A) B. Present California Regulations recruitment at age 1 and an upper quota proportion of 0.3 ( $x$ in figs 21B and 22B)
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port recruit functions. Simulations for each recruitment function are shown with four different management options. The first option (Figure 26 A ) includes fishing rates that approximated those that occurred in the late 1960's. The other three options are based on the California regulations and have lower and upper quota levels of 20 and 40 million pounds (Figures $26 \mathrm{~B}, 27$ ).


FIGURE 27. QUOTAE simulations (1946-1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 ( $y$ in figs 218 and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 ( $z$ in figs $21 B$ and 22B)

The Ricker sea level and reduced Ricker sea level models show essentially the same yields within each option. Yields with the reduced Ricker sea level model are always slightly higher than those with the Ricker sea level model. The reduced model was fitted to data (1931-1960) with a slightly higher mean recruitment than the Ricker sea level model (19311968). The Ricker transport model shows considerably higher yields than the sea level models in the simulations with an age at recruitment of 1 and a quota proportion of 0.7 . Yields with the Ricker transport model under the three quota level options are considerably lower than yields with the sea level models and also much lower than yields with the Ricker transport model in the option with a quota proportion of 0.7 . The reason for the much higher predicted yields in the transport model with the 0.7 quota proportion is an apparent bias in the compensatory term in the Ricker function. This bias will be discussed later.

The simulations with the sea level models show considerably different yield patterns under the four management policies. For example, the yields in the simulations with an exploitation rate of 0.7 show a sharp decline from 1946 to 1954 (Figure 26A). Yields declined from about 70 million pounds to about 13 million pounds and then rose to about 35 million pounds in 1961 ( 32,000 to 5,900 to 16,000 metric tons). By comparison, the simulation with the present California regulations, which result in an exploitation rate below 0.3 , show yields of between $20-30$ million pounds ( $9,000-13,000$ metric tons) from 1946-1954 and a large increase in yields during the 1956-1966 period (Figure 27A). The heavy exploitation and resultant decrease in spawning biomass with the 0.7 quota proportion option decreased the large 1956-1966 increase in yields that is predicted by the simulations with the present California regulations. The simulations with age at recruitment of 4 (Figure 27B) show sharper variations in annual yield than with the other three options. This management option, which protects the spawning biomass, puts a very heavs exploitation rate on the 4 -year-olds. With this option almost the entire vield is 4 -ycar olds and therefore the annual yield is erratic breause it is dependent upon individual year classes.

The precipitous decline in the Pacific mackerel population in the late 1960's is evident in all of the simulations with envirommental-dependent recruitment functions. The decline went to lower spawning biomass levels in simulations with high exploitation rates; however, low spawning biomass also occurred in the late 1960's in simulations with no fishing mortality.

## DISCUSSION

## EVALUATION OF RECRUITMENT MODELS AND SIMULATIONS

The poor statistical fits of the density-dependent recruitment functions presented earlier (Table 17) suggests that these models are of limited use for management purposes. They could be used for long-term management purposes (i.e., to estimate long-term yields under a given exploitation rate) but should not be used for real time management. The recruitment models that include both density-dependent and environmontal-dependent components (Table 19) are considerably better than the densitydependent recruitment functions in predicting recruitment in a given year. Two important questions remain. How good are the environmental models? Are the variables in the models good indices of the real mechanisms that control recruitment.

The transport models have the best statistical fits; however, they are deficient in the sense that they were fitted to a shorter data series than the sea level models. This shorter series (1946-1968) did not include any years in which the spawning biomass was at the high levels that occurred prior to the peak of the fishery in 1936. Mean recruitment during the 1946-1968 period was considerably smaller than during the 1931-1968 period. The transport models therefore were fitted to a data series that is biased towards low recruitment. The computer simulations presented earlier show that the Ricker transport model predicts considerably smaller recruitment and yields tham the Ricker sea level models and the densitydependent Ricker and Cushing models. The low estimates are not caused by the environmental terms. The low recruitment estimates with the Ricker transport model are caused by the compensatory term of the Ricker model. The 1946-1968 and 1928-1968 linear fits to the Ricker spawnerrecruit model have very great differences in their density-dependent and compensatory terms.
$\begin{array}{ll}1946-1968 & \mathrm{R}=1.123 \mathrm{Pe} \\ 1928-1968 & \mathrm{R}=0.508 \mathrm{Pe}\end{array}$
The 1946-1968 model has a much stecper ascending curve and the compensatory term is important at much smaller spawning biomass levels. The 1946-1968 model predicts greater recruitment at low spawning biomass levels than does the 1928-1968 model. Thus the simulations with the Ricker transport model have greater yields than the Ricker sea level models when the exploitation rate is very high (ligure $26 B$ ) and smaller yields when the exploitation rate is moderate (Figures 26B, 27). The compensatory term (e ${ }^{\text {bp }}$, Table 16) for several spawning biomass levels is shown
below for the nonlinear Ricker, Ricker sea level and Ricker transport models.

Ricker Ricker sea level Ricker transport
Compensatory
Term (CT) $\quad e^{-0.00000253 P} \quad e^{-0.00000353 P} \quad e^{-0.0000377} P$
Spawning
biomass in
millions of
Pounds

| 20 | CT $=0.951$ | CT $=0.932$ | CT $=0.470$ |
| :--- | :--- | :--- | ---: |
| 50 | CT $=0.881$ | CT $=0.838$ | CT $=0.152$ |
| 100 | CT $=0.776$ | CT $=0.703$ | CT $=0.023$ |
| 200 | CT $=0.603$ | CT $=0.494$ | CT $=0.0005$ |
| 400 | CT $=0.363$ | CT $=0.244$ | CT $=0.0000003$ |
| 600 | CT $=0.219$ | CT $=0.121$ | CT $=0.00000000015$ |

The above data demonstrate a major difficulty in developing regression models to describe the spawner-recruit relationship in exploited populations. Such regression models are generally lacking in data at the high spawning biomass levels that typically occur before exploitation begins. The compensatory term of the Ricker transport model is a good example of the unrealistic, yet statistically valid, regression models that can result from regressions based on data sets which do not include a good representation of data from the entire range of population biomass.

Further work that would incorporate upwelling and offshore divergence indices back to 1928 is envisioned. Barometric pressure fields are available back into early 1900's. The use of these pressure fields to calculate upwelling and offshore divergence indices will soon be in progress and further refinement of the transport models is dependent on this longer data series.

We feel that the environmental variables in the transport model (Bakun's upwelling and wind stress curl indices) are more direct estimates of the mechanisms that regulate recruitment than are the variables in the sea level models. Upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current Region. Bakun and Nelson (In Press) have suggested that strong, negative wind stress curl (convergence) at $30^{\circ} \mathrm{N}$ would contribute to the separation of the surface waters north and south of the Punta Eugenia area. Weak, negative wind stress curl would be associated with an increase in the mixing between the two areas. Their hypothesis has several interesting features. It describes a physical boundary that explains the presence of the separate stocks of Pacific mackerel, sardine and anchovy that are found north and south of central Baja California. It also suggests that larvae from a wider geographical area could contribute to the California stock during periods of weak convergence at Punta Eugenia. A second hypothesis is that strong convergence at $30^{\circ} \mathrm{N}$ in the center of abundance of Pacific
mackerel could be inhibitory to survival of Pacific mackerel laryae. Wither downwelling or the formation of fronts conceivably could result in in creased larval mortality.

The sea level models do not have as good statistical fits as do the trams port models; however, they are fitted to data that include the entire range of observed spawning homass. The envirommental variables in the seat level model (sea level, barometric pressure and sea surface temperatume) are correlated with the real envirommental variables that control reand ment, but with the exception of sea surface temperature they are $11 \cdot a$ direct estimates of the real variables.

Sea level at La Jolla during the spawning season is negatively correlated with recruitment. Hicks and Crosby (1974) have shown long-tem in creases in sea level at La Jolla and San Diego. The trond in increasing see level could be camsed by land subsidence in the I a follat-San Diego arra or a wide range of oceanographic and atmospheric factors. It is possible that the negative correlation is affected by the opposing trends of increas ing sea level and decreasing population of Pacific mackerel that ocou over the 1928-1968 period. Of course, this trend would not account for the seasonal pattern of correlation coefficients.

The decadal differences in sea level between 1948 1957 and 1958 . 1999. at San Diego wore amalyed by Juang (1972). He mugested that gar. strophic flow provided the major contribution to the differenoes in soa level. Itigh correlations between geostrophic flow and sea lesel were also found during the Coastal Upwelling lixperiment (CW): increased sonth ward flow was associated with decreased soa level (Smith, 1974). It therefore appears that the correlation between 1 n ( $R$ ) and sealevel is a measum of the underlying relationship between recruitment in lacific mackerel and geostrophic tramsport. Increased geostrophice flow in the Cabifomia Current would be expected to increase the sontherly adsection of miti-ent- and plankton-rich water from the major upleding regions off of central and northern California. Therefore the survival and growth of larvae in the Southern California Bight and Baja ( $a \operatorname{lifomia}$ region shoukd be enhanced by increased geostrophic flow.

Barometric pressure is a measure of atmophenic circulation, and low barometric pressure at San Diego is associated with inereased winds in the southern end of the Califormia Current. Barometric pressure is therefore an index of upwelling in this region.

The positive correlation between sea surface temperature and recratment is expected. Warm SST should favor recratment in the Californiat Current stock of Pacific mackerel, because this stock is on the cold-water edge of its potential range. However, this correlation would seem to be in contradiction with the correlation between upwelling and recruitment. If increased upwelling occurs during the spawning season SST should be reduced. It is possible that $S S^{\prime}$ is influenced by the spacing of upwelling events, being lower if upwelling is morr continuous and higher if upwelling events are followed by periods of calm wather with ronsiderable isolation (a condition that should favor recruitment). Upwelling prior to the spawning season would also tend to decrease SST and possibly increase the number of planktonic predators. Large scale SST anomalies umelated
to upwelling in the northern Baja Califormia area could also increase SST' in this area.

Simulations with the density-dependent recruitment functions predict that at high exploitation rates equilibrium yield is quite sensitive to changes in the age at recruitment. Maximum yield with the nonlinear Ricker and Cushing spawner-recruit functions occurs at exploitation rates above 0.3 and at an age of recruitment of between 3 and 4 years of age. If the fishery were to be managed with the present California regulations, the Ricker function predicts that equilibrium yield would be about 67 million pounds (30,000 metric tons) per year ( $X$ in Figure 23B). The simulations suggest that equilibrim vield could be increased to over 95 million pounds ( 43,000 metric tons) if the upper quota proportion were increased to 0.5 and the age at recruitment increased to age IV ( $Z$ in Figure 23B). This large an increase in potential yield is not predicted by comparable simulations with the environmental-dependent recruitment functions. Simulations with the aca level spanner-recruit function predict that mean yield for the period of 1931-1968 would have been just over 51 million pounds 23,000 metric tons) if the present (alifomia regulations had been in effect over this period ( $X$ in Figure 24B). Observed yield for this period averaged 49 million pounds ( 22,000 metric tons). The above simulation predicts that mean yield would have increased to 69 million pounds ( 31,000 metric tons) if the quota proportion had been set at 0.5 and the age at recruitment had been IV ( $Z$ in Figure 24B). However, vields would fluctuate more. The highest age at recruitment that could be considered practical for the Pacific mackerel fishery is age 2. This is due to the mixed schooling of different age groups of mature Pacific mackerel. When the age at recruitment is set at age 2 the equilibrium yield with the Ricker $\$ 1$ odel is a maximum of 75 million pounds ( 34,000 metric tons) at an upper yuota proportion 0.4 (Y in Figure 23B). The Ricker sea level model predicts that the mean yield under this management (Y in Figure 24B) would have been 60 million pounds ( 27,000 metric tons).

The Ricker sea level model predicts that the mean annual yield over the period of 1946-1968 would have been 31 million pounds ( 14,000 metric tons) if the California regulations had been enacted in 1946. The observed mean yield over this period was 31 million pounds. Mean yield over this period with an age at recruitment of 2 and an upper quota proportion of 0.4 is predicted at 35 million pounds ( 16,000 metric tons). The corresponding predictions with the Ricker transport model (Figure 26) are 16 and 19 million pounds ( 7,200 and 8,600 metric tons)

It appears that the simulations with the Ricker sea level model are more realistic than those with the Ricker transport model. Yields with the environmental models are considerably lower than those predicted by the equilibrimm simulations with the density-dependent recruitment models. The yield-per-recruit simulations (ISOE) predict that maximum yields on an individual cohort occur at an age at recruitment of less than 1 and at high fishing mortality rates. Spawning biomass levels with this management policy are minimal and long term yield under this policy is low in both the equilibrium and environmental-dependent simulations with the QUOTAE program.

The predictive capability of recruitment in a given season is highest with the transport models. The Ricker transport model accounts for over $\mathbf{7 5 \%}$ of the variation in recruitment for the period of 1946-1968. It would be desirable to test the predictive capabilities of the various recruitment models with data from years outside of the perita fom which the monde were fitted. Unfortunately good quality population estmates an - not avail able for the period of 1970-1975. This lack of data 11 as caused by the moratorium on the commercial fishery. The motatorimm halted the wat ket sampling program from which age composition data were derived Estimates of the population size and recruitment for the 1970-1975 period therefore cannot be based on a cohort andysis. Available estimates on the recent spawning biomass are based on small scale taggings studics, and estimates of recruitment during the 1970-1975 period are not available: However, the environmental portion of the Ricker transport model predicts that from 1963 to 1975 there were no years in which the ens inommen tal conditions greatly favored recruitment. Moderately gond environmental conditions were predicted in 1971, 1972 and 1974.

## ALTERNATIVE MANAGEMENT PLANS

Pacific mackerel management policies that could be developed with this. several modeling approaches contained in this study vary considerably. Policies based on yield-per-recruit simulations would favor the very high exploitation rates and an age at recruitment of 1 or less that are necessary to achieve maximum yield per recruit. Equilibrimm yield simulations. based on the Cushing or Ricker spawner-recruit models suggest that near maximum sustained yield (MSY) would be achieved with a wide range of exploitation rates ( $\mathrm{E}=0.3$ to 0.6 ) and an age at recruitment of age 3 or 4. With a management policy based on a maximmit seld per reeruit philosophy equilibrium yield simulations based on the Ricker spawner recruit model predict that the stock would become extinct. Similar simulations with the Cushing spawner-recruit model predice that yields would be well below MSY.

Simulations with a wide range of quota options and the envirommental dependent recruitment models suggest that no mandement policy is likely to stabilize the yield at reasomably high levels. The best management policy therefore appears to be one that will reduce the pusibility of future population collapses and at the same time achieve a maximum long-term yield. That is a polics that will reduce the exploitation rato when the population level is low and increase the exploitation rate when the level is high.

Determination of the optimum management policy will require considerable economic analysis and is therefore beyond the soope of the present work. However, in the absence of such analyses we fere that the list of potentially optimum management policies can be reduced to three alternatives. These alternatives are maximum long-term yiold with an age at recruitment of 1,2 , or 3 . Maximum long-term yield is likely to be close to optimum yield because of a combination of biological and economic factors. The stock is a member of a multispecies wetfish fishery and it is of
secondary importance in this fishery. The stock is readily avalable to the fishery and the fiching fleet has demonstrated that it is capable of hamesting Pacific mackerel at rates in ceress of their reproduetive potential. The comomics of the fisher are primarily dependent upon relationships with the more abondant species in the fishery (i.e., presently anchovy). In addition the price for Pacifie mackerel has traditionally been higher than the price for the more abundat pecies in the fishery. Therefore, cononiics are mikely to be the limiting factor in the Pacific mackerel fishery and maximmon economic yeld maty approach maximum biological yied

The three alternative management policies (Table 20; are based on the quota proportions that resulted in the maximum predicted long-term vield with an age at recruitment of 1,2 and 3 . All three management policirs contain portions of the present Califorma regulation. Specificalls they maintan the present moratormm, or lower quota level, at 20 million pounds spawning biomass to ensure a viable sport fishery. They have a lowe quota proportion of 0.2 and an upper quota level of 40 million poumds to allow only a minor fishery when the spawning biomass is relalively small.

The suress in desoribang past recratment in Pacifie mackere with statistical fits to emirommental and population data does not prove that the factors found to be associated with recmitment are those that control recruitment. It is also pessible that these envirommental factors may not continue to be associated with recruitment in fature years. The tentative decision to accept the hypothesis that recrutment can be predicted with more accuracy if the associated envirommental factors are taken into consideration should only be made if the environmental factors make biological sense. We believe that a very strong case can be made that the

TABLE 20 Alfernative Management Options *

## Management Option 1. The present California regulations.

```
No minimum size restrictions
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.3
Predicted long-term yield
    50 million pounds per year
    22,600 metric tans per year
    $2,260,000 per year at $100 per short ton
Advantages
    Status Quo
    Least amount of regulation of the fishery
```


## Disadvantages

```
Long-term yield is the lowest of the 3 options
Age structure will be the most altered
```


fisherese of Mexicu and Cadifornia

## Management Option 2. Compromise option

Minimum size restriction to protect 1 year olds
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.5
Predicted long-term yield
64 million pounds per year
29,000 metric tons per year
$\$ 2,900,000$ per year at $\$ 100$ per short ton

## Advantages

Long-term yield is increased without precluding a purse-seine fishery

## Disadvantages

Size restriction will increase the fishing effort necessary to catch the quota Enforcement costs for minimum size limit.

## Management Option 3. Near MSY option

Minimum size restriction to protect 1 and 2 year olds
Quota levels of 20 and 40 million pounds
Lower quota proportion of 0.2
Upper quota proportion of 0.7
Predicted long-term yield
76 million pounds per year
34,500 metric tons per year
$\$ 3,450,000$ per year at $\$ 100$ per short ton

## Advantages <br> Largest long-term yield <br> Least altered age structure

Disadvantages
Annual yield is the most variable
Size restrictions will preclude a purse seine fishery
Enforcement costs will be the highest
environmental factors found to be associated with recruitment are in fact those that describe major components of the mechanisms that control that mortality of pelagic fish eggs and larvae in the California Current Region.

Management of the fish stocks in the California Current Region must recognize that changing environmental conditions will cause large variations in the recruitment of commercially important species of the California Current. If this factor is not recognized and incorporated in management policies, overfishing very likely will occur during a period of poor recruitment and the list of populations in the California Current that have suffered recruitment failure will include species other than the Pa cific sardine and the Pacific mackerel.

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# APPENDIX I．YIELD PER RECRUIT SIMULATION PRO－ GRAM． 

## FFOGRAF ISCE IINFLT，CLTPLI，PLACH）

C
CCNTROL CARO VAFIAELE CESCFIFIICA
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IST MINIMLY AEE AT RECEUIINENT
IET NAXIMUR AGE AT EECEUITMENT
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XMI M IHCFENEAT
NM HUNEER CF F STCEEEA
EIAR EXFLCIIAIICN FATE INCFEMEAT
NE MUMEER CF EXFLCITATICA RAIES TC EE FIN
LINF EERTALANFFY CCASIANT
K EERTALAAFFYCCASTANT
TO EERTALAAFFY CCNSTANT
－LENETH－WEIGHT CCNSTANT
E LENCTH－WEICHT CCASTANT
PSII FRCPCRTICA SPANAIAG BY AGE GFQUP
CALY INFLT FCR ACES IET TC 10 （10 1 AFE ASSUMEC 1．C）
COMMON M，IET，IET，EIAC，NE，FST（2才），FT（Z2），IS（Ew，EC），IY（EO， 50$)$
1，KARD
OIMENSION EC（2C，59），PS（51），G（51），CH（51），HT（51），hト（51），XL（51），
$1 \mathrm{XLH}(51)$ ，TCT（ C ），TITLE（20）
INTEGEFT
REAL M，LINF，K
READ 3CG．NRLNS，KAFC
399 FORNAT（2I2）
1 NFUNS＝ARUAS－1
READ 403，（TITEE（I），I＝1，そこう
4CO FORMAT（1JAB，／，1UA8）
PRINT 4E土，（TITLE（I），I＝1，（̌i）
401 FORMAT（1H1，／／，1X，13AB，／，1X，12A8）
READ $1 C C, I B E R T, M A X A, I 己 T, I E T, X M S, X M I, A M, E I A C, N E$
100 FCRMAT $\{413, \angle 厶 55.3,13, F 5.3, I 31$
IF（IRERT．NE．1）GC TC 2
REAO 101 ，LIAF，K，IC，A，
101 FORMAT（F1J．2，F10．E，F1E．O，F15．12，F1E．E） PRINT 1U2，LINF，K，TC，A， 3


 EOTO 4
ADO OTHER IAPUT CPYICA
2 CCNTINLE
FEAD 6EG，（WT（N），$A=1,1$, ）
EGE FCRMAT（1 JFE． 2 ）
REAO GEB，（PS（N），$A=1,1$ ？）
E68 FORMAT（ICFE．4）
DO 67」 $N=11,31$
E70 PS $(N)=1.0$
CO $671 \mathrm{~N}=1,14$
TEMP＝WT（N＋1）／WI（N）
E71 C（N）$=G H(N)=T E M F$
CC $672 \quad N=15, \mathrm{MA}$ YA $G H(N)=G(N)=T E M F$
ETE WT（N）＝HT（A－1）＊TEMF IF（IEERT．EG．O）GG TC 7

```
        GC TO 38
        400 5 I=1,51
        PS\I\=1.0
        READ 103,(PSII),I=IET,士こ:)
    103 FORMAT (1OFG.4)
        IA = MAXA+1
        00 6 A=IEI,IA
        XL(N) = LINF* (1-EXP(-K*N*K*TO))
        U=N+0.5
        XLH(N) = LINF* (1-EXF(-K*L + K*IC)\
        WT(N) = A*XL(A) **E
        WH(N)=A*XLF(A)**E
        GH(N)=WH(N)/HT(N)
        IF (N.ET.IET) G(N-1) = WI(N)/WI(N-1)
    & CONTINLE
        nCTE that the LNIIS afe depeneENt ufCN INfUT
    FFINT 2GD
    200 FORMAT (//,1X,*AGE LENETH WEIGHT GROW GRCWH*)
    00 8 N=I日T,MAXA
        PRINT 104,N,XL(N),WT(N),PS(N),G(N),EF(N)
    104 FORMAT (1X,I3,2FG.2,3F9.3)
    - CONTINUE
        M=XMS-XMI
        OC 26 MM=1,NM
        1CT(MM)=0
        M=M+XHI
        E=-EINC
        DO 24 J=1,NE
        E=E + EINC
        F=E $ N=0
        IFIE.EC.JI GO TO 12
    10 N=N+1 & IF(A.GT.EG) GC TC 90
    EV=EVAL(F)
    E1=EVAL(F-0.01) & E E= =EvfL(F+U.01)
    SLOPE=(E2-E1)/0.02
    DIFFE=EV-F
    F=F-UIFFE/SLCFE
    IF(AGS(OIFFE),GT.G.OCCOO1) GC TO 10
    12 FST(J)=F
    2=M+F
    0O 22 I=IRT,IET
    HS = C=C
    FOP=1040
    On 2J T=IET,MAXA
    IF(I.GT.IEI) EC TC 15
    LF(F.EC.O) TCT(MM)=ICT(MM)&PCF
    IF(F.EG.O) BC(MM,T)=FOP
    15 HS=HS + PCFFFS(T)
        IF (T.LT.I) GC IO 14
        H=2
        FF=F
        GC TO 15
    14 }\textrm{K}=\textrm{M
    FF=0
    1E C=POP*(1-EXP(-h))
    IF(FF.EG.C) GC TC 18
    C=D*(FF/Z)*(FIT) + C
    1& PCP=(PCP-[) G(T)
    20 CONTINUE
    IS(I,J) = HS
    IY(I;J)=C
    22 CONTINUE
    24 CCNIINLE
    PFINT 105,M
```


 CALL OUTISO(IY) PaINT 110, H
110 FCRMAT (//,31X, "SPAGNING EICHASS CVER LIFE CF CCHCRT N=*,FE.4, 1//**AGE**/*AT****REC.*)
CALL OUTISC(IS)
2E CONTINUE
FFINT 111
 1*AGE IASTAATAAFOUS NATURAL MCRTALITY*,//I
$M=X M S-X M I$
CO $28 \mathrm{~N}=1, \mathrm{NM}$
$M=M+X M I$
$28 \mathrm{FT}(\mathrm{N})=\mathrm{r}$
PRINT 112, (FT(N), N=1,NM)
11 ( FCRMAT (7), 2JFE.2)
$I Y R=I R T-1$
DC 30 I=IET, MAXA
LYK=IYF+1
PRINT 113, IYR, IEC(MR,II, KY=1,NM)
113 FORMAT $(1, X, 14$, EX, 2 JFE, $?$ )
30 CCNTINUE
DO 34 MM $=1$, NM
CO $32 \mathrm{I}=1 \mathrm{ET}, \mathrm{NaXA}$
$B C(M M, I)=E C(M M, I) / T C T(M M)$
3 E CCNTINLE
34 CCNTINUE
PRIAT 115
115 FCRMATI//,3IX, "PFCPCFTICA CF THE POFLLATICN EY MEIGHT F=0*, 1//,* AGE IASTANTANEOLS NATUQAL MORTALIIY*,//I
PRINT 112, (FT(A), $A=1, A M)$
$I Y R=I B T-1$
DC 36 I=IET, NAXA $I Y R=I Y G+1$
PRINT 116, IYR, ( $\theta C(M M, I), N+=1, N M)$
11€ FCRMAT(1X,I4, ¿X, टCFE.4)
3E CCNTINUE
IF (NRUAS.ET.D) EC IC 1
GOTO 999
38 PRINT 444
444 FCRMAT (//.* CFIICN NCT IASTALLEC:
90 FRINT 999
©98 FCRMAT (1/, * ITERATICNSFCF F EXCEEDED 50 *)
©gG STOP \$ END
FUNCTICN EVAL(F)
COMMON M \$ FEAL N
EVAL $=(1.0-E X F(-F-F)): F /(F+M)$
RETURN S ENO
SUBROUIINE CUIISCCJT

1,KARD
FEAL M
OIMENSION JT(50,50)
$N \mathrm{~N}=-1$
CO $200 \mathrm{~N}=1 \mathrm{ET}, \mathrm{IET}$
$\mathrm{N}=\mathrm{N}=\mathrm{N}+1$
$I=I E T-A N$
ZUO PFINT 2C1,I,(JT(I,J),J=1,NE)
201 FCRMAT $1 / 1,2 x, 12,2 x, 23161$
TEM=-EING
CO $202 N=1, N E$
ISM = IEM+EINC

```
    ZCE FT(N) = TEM
    FFIAT ZU3,(FT(A),N=1,NE)
    203 FCRMAT(//1,*E *,2OFE.3)
        FRIAT 204,(FST(N),N=1,NE)
    2O4 FORMAT(* F *,2OF6.3)
        FFINT द्\5
    ZOE FCRMAT(/,EX,*E = EXFLCITATICN RATS,F = INST. FISMING MCFT.RATE*S
        IF(KARC.EG.J) GO IC 210
        CC 2.16 I=IET,IET
    2CG PUNCH 207,(JT(I,J),J=1,NE)
    CC7 FCRMAT (1018,/,1018)
        PUNCH COB
    20& FCRMAT (/)
    Z10 RETURN & ENO
    TYPICAL IAPUT FCR ISCE
OOCACCIC ROCKFISH OATA FROR FHILLIPS(IGE4) CFG FISH BULL. 126
APFIL 14, :976 EF PAFFISH
    1 30 1 14.20G.050 3.023 20
        81z.97 .14784 -i.E43C .0C006j018860 J.0¢41
00CugogjuJj0 .1 .5 .8 1.0 1.0 1.0 1.0 1.0
CHILEPEPPER ROCKFISH OATA FFOM PHILLIFSIIGE4) CFGFISH GULL. }12
APKIL 14, 1976 FF FAFEISH
    116 1 10.300.0500 3.023 2n
```



## APPENDIX II. QUOTA SIMULATION PROGRAM.



```
    3,1,* NATURAL MORTALITY M=*,F4,2,1** SIMULATEO FOR *,I4,* YEARS*
    4,/,* STARTING POPULATION *,I4,//,* MODEL FARAMETERS BY AGE GROUP*
    5,%: AGE STARTIAG PRCFCRTION PROPORTICN PROPORTION
    GGRONTH*,1,* GROUP POPULATICN SPAWNING ANNUAL GRCWTH
    70 CAPTURE*)
    PRINT 104,(N,BPOP(N),PS(N),G(N),GH(N),N=IRT,MAXA)
    104 FORNAT(I2,F13.0,F12.3.F15.3,F18.3)
    105 FORMATI//,60H EXTINCTION CURVE FOR PS(1)=0.54*EXP(-.0000071709*TPO
    1PI J
        IF (ILOGI.EQ.1) PRIAT 105
        IFIIGSET-1)106,108,110
    106 PRINT 107
    107 FORHAT(//,* QUOTA BASED ON SPANNING EIOMASS*I
        GO TO 112
    108 PRINT 109
    109 FORMAT(//.* QUCTA BASED CN TGTAL BIOMASS*)
    GO TO 112
    110 PRINT 111
    111 FORMATI/I,* QuOTA gaSED ON THE bIOMASS OF agEI + AGEII*I
    112 PRINT 113,QAL,QA,OQL
    113 FORHAT (//,F LCHER OUOTA LEVEL =*,FB.O,/,F LOWER QUOTA PROPORTICN=
        1*,F6.3.%:* UPPER OUOTA LEVEL = *,F8.0)
        PRINT 114
    114 FORMAT (///,* RECRUITMENT MOOEL*,//,1X,
        1* RICKER BMDPJR TRANSPDRT MODEL*,I,
        PRINT 115,IET,IET,IRUN,ILCGI,IENV,IPRO,IOSET,RHAX,SLP,HAXA,OMIN,
    1QIMC,NQ
115 FORMATI//,* IBT=*,I4,/,* IET=*,I4,/,* IRUN=*,I4,/,*ILOGI=*,I4,/t
    1* IENV =*,I I , /,* IPRO=*,I4,I,* IQSET=*,I4,/,* RMAX=*,F8.0,1,
    2* SLP=*,F4.2.1,* MAXA=*,I4,/,* QHIN=*,F5.3,/,* QINC=*,F5.3./.
    3* NQ=*,I4)
        IF(KLM.GT.1) GO TO 119
        IFIIENV.GT.OI GO TO 150
        IF(IPRO.GT.0) GO TO 150
    116 CONTINUE
C
    BOOV STARTS HERE
    119 IF(NQ.EQ.1) GO TO 120
    GO TO 122
    120 IU=-9
    DO 121 N=18T,IET
    121 CALL MACQE
        CALL OUTM
        STOP
    122 IU=NQ $ QB=OMIN-QINC $ NL=IET-IBT+1
        DO 124 IQP=1,NQ
    QB=QB+QINC $ L=O
    00 123 J=I8T,IET
    L=L+1
    Call macQe
    MAT(L, IQB) = TYIELD(LI/NYRS
123 MA(L,IOB)=ACATCH
124 CALL OUTM
    PRINT 125,NYRS
1<5 FORMAT (1H1,//,20X,I4,* YEAR MEAN YIELD*)
    CALL OUTMAT(MAT)
    IT=ITO+NYRS-1
    PRINT 125,IT
126 FCRMAT (1H1,//,20X,*YIELO IN *,I4)
    CALL OUTMAT\MAI
    GO TO 199
150 IFIIENY.LT.1) GO TO 160
    OO 151 N=1,NYRJ
151 READ 152, (ENVIN,NN),NN=1,IENV)
152 FORMAT (6F8.2)
```

```
160 IF(IPRO.GT.0) GO TO 1EI
    GO TO 116
161 DO 162 N=1,NYRS
162 READ 163, (ENV(N,NN),NN=7,9)
163 FORMA T (35x,3F5.0)
    IF(IPRO.EQ.1) GO TO 11%
    00 164 N=1,NYRS
164 READ 165, FNY(N,NN},NN=10.121
165 FCRMAT (35 X +3F5.0)
    GO T0 116
199 CONTINUE
    STOP & ENO
    SubROUIINE MACGE
    COMHON
```



```
    1Q2,QA,QB,QAL,OEL,QPOP,SUBC,EG,SLP,MAXA,SUEPOM,I,J,POPCEST,.SMA.
    2REC,IBI,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IOSET.RMAX,GMIM,OINL,NG,
```



```
    4TREC(100),TSPOP(1JO),TYIELO(100),TTPOP(100),G{E, ,CH(E1):
```



```
    REAL M
```



```
    TSPOP(L) = TREC(L)=TYIELO(I)= TYPOFILS=0
    OO 503 H=IST,MAXA
500 POPA(N)=BPOP(N)
    00 516 I=1,NYRS
    SPOP=ACATCH=TPOP=O
    00501 N=18T,MAKA
    POPC(N)=POPA(N)FGH(N)
501 IPOP=\POP+POPA(N)
    IF(ILOGI.EG.1) CALL LORI
    OO 502 N二 IGT,MAXA
502 SPOP= SPOP+PO:A(N)*PS(N)
    CALL FLN
    IF (IOSEI-1)503,534,505
503 Q2=SPOP 3 GOTO 506
504 Q2=TPOP $GO TO 506
505 02=POPA(1) &POPA(2)
506 IF(Q2.LT.GAL) TO TO EOV
    GO TO 508
507 Z=M $ A=&.0-EXP(-T)
    DO 58 N=IBT,MAXA
    5B XMOKT(N) = POPA(N)*A
    G0 10 512
508 CALL QUNT
    E=CQ/QPOP
    F=FVAC(E,M)
    Z=F&M & A=1.0 - EXP(-T)
    DO 509 N=J.MAXA
    XMORT (N) = POPA(N)*A
509 ACATCH = ACATCH + XMCRICNIFIFIIIFGH{N}
    IF&J.GF.IEII GO rO 510
    G0 ro 512
510 E = SUBQ/SUPPOP
    F=FVAL(E,M)
    ZS=F +H D AS=1.0-EXP(-ZS)
    JT=J-1
    00 511 N=101, JI
    XMORT(N) = PCPA(N)*LS
511 ACATCH=AGATCH + KMORT(N) (F/7S) - SH(N)
S12 NT=MA KA+2
    DO 513 N=I日T,MAXA
    NT=NT-1
```

```
    5{3 POPA:NT:=(POPA(NT-1)-XMORI(NT-1)) * G(NT-1)
    POPA(MAXA) = POOA(MAXA) + POPAIMAXA+1)
    PODA(TBT)=REC
    TPPOP(L):TSPCP(L) + SPOP
    TREM(L) = TREC(L) + REC
    TYLE:C(L) = TYIYLO(L) + ACATCH
    TYPOE(L) = TYPCD(L) TPGP
    ASPOP(I,L) = SPOP
    \triangleRFC(I,I) = QEC
    APASL[:I,L: = ACAICH
    ATPOP(I,L) = TPOP
    IF(REC.ST.RMAX) GO TO 514
    GC in 5:5
    514 PRIOTT 5:5
    525 FORMAI (* REIFLITMENT GLEHUF OR FAILED*)
        Call ourm
        STop
    5:6 CNNTINUF
    517 RETUREN 5 ENO
        subroutine fun
        COMMON
    OTTIPNYRS. TPOP,PS(51),POPA(51),P(121,ENV(100,12),IMEAN(100,12),
    102, WA,GB,GAL,QEL,GPOP,SUBQ,CG,SLP,MAXA,SUBPDH,I,J,POPCIS1I,SPOP,
    ?REC,IBI,IET,IL,IRUN,ILOGI,IENV,IPRO,M,IQSET,RNAX,QMIN,QINC,NQ,
    3MAT(15,1ヶ),MA(10,26),30,E1,32,B4,ACATCH,XPORT(51),NENV,L,NL
        REぶ, M
        ZFIMPRO.FG.OF GO TO GEG
        P(1)=(PS(1)*POPA(1)) /SPOP
        #(2:=(PS(2:*POPG(2))/SPOP
        P(3)={PS(3)*YOFA(3) +POPA(4) +POPA(5) +POPA(6)I/SPOP
        PROA=P(3)*ENV(I,7)+P(2)*ENV(I,B) & P(1) FENV(I, g)
        IF(IPRO,EQ.2) PROB=P(3)*ENV(I,1J)+P(2)*ENY(I,11)+P(1)*ENV(I,12)
    666 COITIINUE
        REGRUITMENT MCCEL AFIER THIS CARD
        2* REC=0.97815*SPOP*EXP(-C.0U0037741*SPOP)*EXP(0.020787*PROA)
        3 *EXP(0.2039065*PROE) *1
        RETURN & END
        FUNCTION FVALIE,M)
C ITERATIVE SOLUTION FOR INST. FISHING MORT. GIVEN EXPLCITATION RATE
C AND INST. NATURAL MCRT.
        COMMON ITC, NYRS
        REAL M
        F=E % N=0
        IFIE.EO.O) GO TO 2
    1 N=N+1 $ IF(N.GI.50) GOTC 90
        F1=F-0.01 S F2=F+..01
        EV=(1.0-EXP(-F-M))*F( (F+M)
        E1=(1.0 - EXP(-F1-M))*F1/ (F1+M)
        E2=(1.0 - EXP(-F2-M))*F2) (F2+M)
        SLOPE= {E2-Ei| / i.0Z
        DIFFF= EY-E
        F=F - DIFFE, SLOPE
        LF(ABS (OIFFE).GT.U.GOGODI) GC TO 1
    2 FVAL=F
    RETURN
    90 PRINT 90G
    900 FORMAT(1/,* ITERATIONS FCR F EXCEEDED 50*)
    CO1 STOP % ENO
    Sut?OUfINE lOGI
C PACIFIC MACKEREL SUEROUTIAE
    COMMON
    OITO,NYRS, TPOP,PS(51),POPG(51),P(12),ENY(10G,12),IMEAM(100,12)
    PS(1)=.54*EXPI-.3UOOC72POO*TFOP)
    RETIJRN $ ENO
```

SUBROUTINE QUOT
COMMON
OITO,NYRS, TPOP,PS(51), POPA(51), P(12), ENV (100, 12), IMEAR(100, 12) y 1QZ, QA, QB, QAL, OBL, QPOP, SUQQ, CO, SLP, MAXA, SUBPOP, I, J, POPC(51), SPOP, 2REC, IBT,IET,IU,IRUN,ILOGI, IENV, IPRO, M, IGSET,RMAX, OMIN, QING,NG,
 REAL M
IF(Q2.GT. QBL) GO TO guo
QUO = QA* (Q2-QAL)
GO ro 901
900 QUO $=($ QRL-GAL)*GA * (O2-OEL)*CE
901 QPOP $=S U B Q=0.01$ \& $S U S P O P=0.1$
DO 902 IC $=J$, MAXA
902 QPOP = QPOP + POPC (IC)
IF(J.EQ.IBT) GC TO 904
$J J=J-1$
DO 903 IC=1, JJ
©O3 SUGPOP=SUGPOP + POPC(IC)
SUBQ $=$ SLPFQUO
QUO=RUO-SUBQ
IFIQUOAQPOP.GT.L.U GC TO 905
944 CQ=QUO 3 GO 10926
$905 \mathrm{CQ}=\mathrm{QPOP}$
G06 IFISUBG/SUBPOP.LT.0.51 5J TC 907
$X=0.5 *$ SUBPOP \& $\quad Y=5 U B Q-x$
SUBQ $=X \quad$ \& $\quad C G=G U D+Y$
907 RETURN $\$$ ENO
subroutine outm
COMMON
OITO,NYRS, IPOP, PS(51),PCPA(51), P(121, ENV(100,12) YNFAA (100, 12), LQ2, QA, QO, CAL, GBL, GPCF, SUYO,CQ, SLP,MAXA, SUEPOP, I, J,FOPCESIV,STOF, 2REC,IBT,IET,IU.IRUN,ILOGI,IENV,IPRO,M,IQSET, RMAX,OMIN,GINT,NC,
 4 TREC(100), TSPOP(1UO), IYIELD(1C3), TIPOPIIOO), GIEA: GH(5i), SAREC( 100,16 ), ASPOP(1EO,16), AYIELO(1GU,16),ATPOP:100,161, BPOP(E1)
REAL M
INTEGER ASPOP, AYIELO, AREC, ATFOP, TSPOP, TYIFLO, TREC, TTPOP
IF(REC.GT.RMAX) GO TO 636
IFPIRUN.EG.OI GO 10699
IOK=1
IF(QBL.LT.I.AND.IOSET.EQ.1) IOK=0
IFIIOK.EQ.1) PRINT GCU,QB
IF(IOK.NE.1) PRINT EDI,GE
600 FORMATI/I,TZ1, *ANNUAL SPANNING BICMASS, UPPER GUOTA PKOPORTION =* 1,F6.3)

CALL OUTP (ASPOP, ISPOP)
IFIIRUN.EQ.1) GO 10609
IFIIOK.EQ.11 PRINI 602, QB
IFIIOK.NE.11 PRINT 6C3,DE
EO2 FCRMAT (\%, $/ 21$, "ANNUAL YIELD, UPPER GUOTA PROPCRTICN =*, TE.3)
603 FORMAT (//, Y21,*ANNUAL YIELD. EXPLOITATIOA RATE =*,F6.3)
CALL OUTP (AYIELD,TYIELD:
IF(IOK.EG.1) PRINI EC4,OB
IF(IOK.NE.1) PRINT EG5,QS
604 FORMAT $/ / /, T 21$, FANNLAL TCTAL GICMASS, UPPER QUCTA PROFORIICN $=$ = 1,F6.3)
EU5 FCRMAT (//,T21,FANNLAL TOTAL BIOMASS, EXPLOITATION RATE =*, F6. 31
CALL OUTP (ATPOP,ITPOP)
606 CONTINUE
IFIIOK.EQ.1) PRINT EC7.QE
IFITOK.NE.1) PRINT 6OB.QA
607 FORMAT (//,T21,*ANNUAL RECRUITMENT, UPPER QUOTA PROPORTIOR - *
2,F6.3)

```
GO8 FORMAT 1//,T:I,*ANNUAL RECRUITMENT, EXPLOITATICA RATE =*,F6.3!
    CALL OUTP (AREC,TREC)
EOG PETIMNN 5 ENO
    SUBPOUTINE OUTP (IANN,ITOT)
    COMMON
    OI#G.NYRS, TPGP,PS(51),POPA(51),P(12), ENVI10G,12I,IMEAM(100,121,
    12E, IA, OR, QAL, QGL,OPCF,SUEQ,CG,SLP,MAXA, SUEPOP, I,N,POPCI51), SPOP,
    2RCG,IBI,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,GMIN,QINC,NQ,
    3MAT (16,:5I,MA{15,kE},20,31,Ez,34,ACATCH,XMORTP51),NENU,L,NL,
    4TREC(100%,ISPOP(1~0), TYIELO(1C0I,TTPOP(10.),G(E1),GH(51),
    SARF(\(100,16), ASPOP{100,16), AYIELD(1]:,16),AYPOF(100,1E), BPOP(51)
        REGG M
        MATEGEO ASPOP, AYIELD,AREC,ATPCP, ISPGF,TYIELI,TREC,TtPCP
        EIMENSION IAN:(IOJ.16),ITOT(10J)
    FQINT 700,(N,N=IBT,IET)
    700 FCQNATM///, T21,*AGE AT RECRUIIMENT*,/%* SEASCA*,1EI8!
        IS=ITO-1
        00 121 N=LPNORS
        IS=55+1
    701 PRENT 702,IS,(IANN(N,K),K=1,NL)
702 FORHAT (ix,l4,己x,i&I8)
    IFIIU.PE.-3' RETURN
```



```
    U3 ITOT(N) = ITOT(N)/NYPS
    RRINT :S -,ITOT(NI,N:IBT,IET)
    3O4 FORIGAT :* :4:AN *,IEI#I
        RETUNAN: &HO
        UYOCUTINE OUTHATIMTI
        COMmON
    OITO,NYPS, rPOD,PS(51),POPA(51).P(12),ENV(1CC,12),IMEAN(100,12),
    1O2,QA,OE,GAL,QEL,GPCP,SUPQ,CG,SLP,MAXA,SUBPOP,I,J,POPCR51:,SPOP,
    2HTE,IBT,IET,IU,IRUN,ILOGI,IEAV,IPQO,M,IOSET,RMEX,GMIN,QINC,NO,
```



```
    4TREC(10E), TSPOF(1.0),TYIELO(200),ITPOP(10C),G(Si),GH(51),
    SAREC(100, 16), ASPOP(100,10), AYIELO(16J,15), ATPOP(100,1EI,PPOP(51)
    FEA: M
    INTEGER ASPOP, AYIELC,AREC,AIFOP, TSPOC,TYIELD,TREC,TTPCF
    OIMENSION MT(16,16) ,ON(16)
    PRINT SOC
BLO FORHAT {* ASE*,/,* AT*,/,* REC.*!
    K=TET+2
    MO BO1 NJ:=1,NL
    k=k-1
C PINOH GARC OUTPUT FCR YIELG ISOPLETH PLOTS
    ICMCH 00&, IMT(K,N),N=1,NC)
    00& FURM4T (1013)
    su1 FRIHT Su? ,K,(MT(K,N),N=1,NG)
    802 FORMAT (/I,1K,I2,4X,16I8)
    PRINT QG3
60.3 FORMAT 1//.7X1
    Qv=QMIA-QINC
    00 8J4 N=1,N%
    ay:-2r+JINC
304 D\(%)-0y
    PRINT GG5,(QJ(N),N=2,N2)
805 FJRMAT (7X,16FR.?)
    1F(IOSFT.NE.1) GOTO 907
    IF{Q3L.LT.1.j) P=INT 80E
AGG FCRMAT(/, \32,*EXFLCITATICP FATE*I
    IF(Q9L.1.!.1.j) 50 TC 399
    8)/ polvi s]8
    8心S FORMAT(%,132,*gUOIA PROPORTICA*I
89% RFTURN I ENT
```

TYPICAL INPUT FOR QUOTAE


## APPENDIX III. UPDATE FOR CDC VERSION OF BMDP3R NONLINEAR REGRESSION.

*IC MAY25

- D P 3RJUL. 2
- 1 BMOP3R. 25

XMAY 25, 1976 PEG

- D BMDP3R.34
- I BMDP3R.33

CTOL $=1 . \cap E-8$

- D UNCOLA. 73
- I UNCOLA. 72
$x 50 H$ TOLERANCE FOR CONVERGLNCE ,Fi1.8/
* 0 P3PJUL. 24

EI P3RJUL. 23
1 F20.5)

- O RITEIT. 15
- I RITEIT. 14

3 OLJ FORMAT $\{2 \mathrm{X}, \mathrm{I} 4,7 \mathrm{X}, \mathrm{I} 4, \mathrm{~F} 21.6,1 \mathrm{X}, \mathrm{F} 18.7,5(1 \mathrm{X}, \mathrm{F} 14,91)$

- 0 REDEV. 13
- I REDEV. 17

3 LOO FORMAT(1X,I4,2X,A1,AB,1X,F14.6,1X,F14.6,2(2X,F13.6))

- 0 RITENO. 28
* I RITENO. 27

90 FCRMAT (2X,I4,7X,I4,F21.6,4X,6(1X,F14,6)

- 0 RITEND.48,RITEND. 53
- I RITEND.47

5EUO FORMATIHO, $2 \mathrm{X}, 7 \mathrm{H}$ CASE , 1 CMPREOICTED. 7 X , - 1OHSTD DEV OF,5X,RHOSSERVED/

- IuX,AB, $9 X, 1 J H P R E D$ VALUE,
- $5 X, A B, G X, A 3,4(7 X, A B)$ )

5803 FORMAT $11 X, I 4, A 2, F 13.6,2 X, F 15.5,2 X, F 13.6$, - 2X,F15,E,4(zX,F12.6))

* I RITENO. 96

IF(ISFUN.GT.5) GO IC 47

- D FUN. 10
- I FUN. 9

IFIISFUN.GE.. . AND. I SFUN.LE, 19)GO TO $(100,200,300,400,500,600,700$,


## *I FUN. 99

${ }_{c}^{C}$
C RICKER MODEL
$600 \mathrm{~F}=\mathrm{P}(1) * \times(1) * \operatorname{EXP}(P(2) * \times(1))$
$\operatorname{CF}(1)=X(1) * E X P(P(2) * X(1))$
DF(2) $=P(1) * X(1) * X(1) * E X P(P(2) * X(1))$
RETURN
C
CUSHING MOOEL
7UO $F=P(1) \times(1) \neq \mp(2)$
$D F(1)=x(1) *=p(2)$
DF(2)=P(1)*x(1)**P(2)*ALOG(x(1))
RETURN
C
CLARK-RICKER MCDEL
Bú $\mathrm{F}=\mathrm{P}(1) * \times(1) * E \times P(P(2) * \times(1)) * E X P(P(3) / X(1))$ $D F(1)=X(1) * E X P\{P(2) * X(1)\} * E X P(P(3) / \times(1)\}$ DF(2) $=P(1) * X(1) * X(1) * E X P(P(2) * X(1)) * E X P(P(3) / \times(1))$ $D F(3)=P(1) * X(1) * E X P(P(2) * X(1)) \cdot(1 / X(1)): E X F(F(3) / X(1))$ RETURN
$C$
$C$ GLARK-CUSHING MODEL
EiO $F=P(1)=X(1) *=P(2) * E X P(P(3) / X(1))$ DF(1) $=\mathrm{X}(1) * * P(2) * E X P(P(3) / X(11)$
$D F(2)=P(1) * X(1) * * P(2) * A L O G(X(1)) * E X P(P(3) / X(1)$ $O F(3)=P(1) * X(1) *+P(2) *(1) \times(1))$ EXP(P(3)/X(1)) RETURN

```
C
    CUSHING TRANSPORT MOCEL
    1000 F=P(1)*X(1)**P(2)*EXP{P(3)*X(2))*EXP(P(4)*X(3))
        DF(1)=X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
        OF(2)= P(1)*X(1)**P(2)*ALCG(X(1)) *EXP(P(3)*X(2)) *EXF(P(4)*X(3)}
        OF(3)=P(1)*X(1)**P(2)*X(2)*EXP(P(3)*X(2))*EXF(P(4)*X(3))
        OF(4)=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*X(3)*EXP(P(4)*X(3))
        RETURN
C
    C CUSHING SEA LEVEL MCDEL
    1100 F=P(1)*X(1)**P(2)*EXP(P(3)*X(2))
        1 *EXP(P(4)*X(3) * EXP{P(5)*X(4) )
            OF(1) = X(1)**P(2)*EXP(P(3)*X(2) )
        1 *EXP(P(4)*X(3))*EXP(P(5)*X(4))
            OF(2)=P(1)*X(1)**P(2)*ALOG(X(1))* EXP(P(3)*x(2))
        1 *EXP(P(4)*X(3)) F EXP(P(5)*X(4) )
            DF(3)=P(1)*X(1)**P(2) * X(2)*EXP(P(3)*X(2))
            *EXP(P(4)*X(3):*EXP(P(5)*X(4) '
            OF(4)=P(1)*X(1)**P(2)*EXP(P(3)*X(2))
        1**(3)*EXP(P(4)*x(3))*EXP(P(5)*X(4))
            JF(5)=P(1)*X(1)**P(2)*EXF(P(3)*X(2) )
        1 *EXP(P(4)* X(3))*X(4)*EXP(P(5)*X(4) )
            RETURN
C
    1200F=P(1) * EXP(D(2)*X(1))
            DF(1) = EXP(P(2)*x(1))
            DF(2)=P(1)*X(1)*EXP(F(2)*X(1))
            RETURN
C
    1300 F=P(1)*EXP(P(2)*X(1))*EXP(P(3)*X(2))*EXF(P(4)*X(3))
            DF(1)= EXP(P(2)*X(1))*EXP(P(3)*X(2))*EXF(P(4)*X(3))
            DF(2)=P(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)*X(2)) FEXP(P(4)*X(3))
            DF(3)=P(1)*EXP(P(2)*X(1))*X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
            DF(4) = P(1)*EXP(P(2)*X(1)) *EXP(P(3)*)(2))* X(3)*EXP(P(4)*X(3))
            RETURN
C
    1400F=P(1)*X(1)*EXP(P(2)* (11)
        1*EXP(P(3)*X(2))* EXO(P(4)* (3))
            DF(1) = X(1) = EXP(P(2)*X(1))
        1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
            DF(2)=P(1)* X(1)* X(1)*EXP(O(2)*X(11)
        1*EXP(P(3)*X(2))*EXP(P(4)*x(3))
            DF(3)=P(1) * X(1) * EXP(P(2)*x(1)) * X(2)
        1* EXP(P(3)*X(2))* EXP(P(4)*X(?))
            OF(4)=O(1)*X(1)*EXP{P(2)*X(1))* X(3)
        1*EXP{P(3)*X(2))* EXP(P(4)*X(3))
            RETURN
C
1500 F = P(1) * X(1) EXP(P(2)*X(1))
    1.EXP(P(3)*X(2)) EXP(P(4)=X(3)) EXP(P(5)=X(4))
            DF(1)= X(1)* EXP(P(2)*X(1))
        1:EXP(P(3)*X(2)) * EXP(P(4)*X(3))*EXP(P(5)*X(4))
        DF(2) = P(1) * X(1) * EXP(P(2)*X(1)) F X(1)
        1* * EXP(P(3)*X(2))* EXP(P(4)*X(3))*EXP(P(5)*X(4))
        DF(3)=P(1)*X(i) FXP(P(2)*X(1)) * X(?)
        1* EXP(P(3)*X(2))* EXP{P(4)*X(3)) F EXP(P(5)**(4))
        DF(4) = P(1) F X(1) * EXP(P(2)*X(1)) * X(3)
        1 * EXP(P(I)*X(2))*EXP(P(4)*X(3))*EXP(P(5)*X(4))
        DF(5)=P(1)*X(1):EXP(P(2)*X(1): *X(4)
        1* EXP(P(3)*X(2))* EXP(P(4)*X(3))*EXP(P(5)*)(4))
        RETURN
```

```
C
C GLARK-RICKER TRANSPCRT MCOEL
1600 F=P(1)*X(1) *EXP(P(2)*X(1)) E EXP(P(3)/X(1))
        1* EXP(P(4)*X(2)) E EXP(P(5)*X(3))
        OF(1)=X(1) *EXP{P(2)*X(1)} EXP(P(3)/X(1))
        1* EXP(P(4)*X(2): * EXP(P(5)*X(3))
        OF(2)=P(1)*X(1)*X(1) * EXP(P(2)*X(1)) E EXP(P(I)/X(1))
        1*EXP(P(4)*X(2)) * EXP(P(5)*X(3))
            OF(3)=P(1)*X(1)*EXP(P(2)*X(1))* (1.0/X(1)) * EXP(P(3)/XX(1))
            1* EXP{P(4)*X(2)) * EXPIP(5)*X(3))
            DF(4)=P(1)*X(1)*EXP{P(2)*X(11)*EXP(P(3)/X(11)
            1*X(2) *EXP(P(4)*X(21)*EXP(P(5)*X(3))
            DF(5)=P(1)*X(1) * EXP{P(2)*X(1)) E EXP(P(3)/X(1))
            1* EXP{P(4)*X(2))* X(3)* EXP(P(5)*X(3))
            RETURN
C
1700 RETURN
1800 RETURN
1900 RETURN
```

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[^0]:    * F statistic $=3.575 ; \mathrm{P}_{\left(\mathrm{F}_{22,17} 3.12\right)=0.01}$

[^1]:    FIGURE 10. Density-dependent spawner-recruit models; A. Ricker, B. Beverton and Holt, C. Cushing

[^2]:    $\mathrm{R}=$ Recruit biomass in thousands of pounds
    $\mathrm{P}==$ Parent biomass in thousands of pounds
    $*=$ Significant at $5 \%$ level
    $* *=$ Significant at the $1 \%$ level

