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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 M = 0.5, shows a fluctuating stock size with a maximum total biomass of 965 million pounds (438,000 MT) in 1933 and a minimum of 3.3 million pounds (1500 MT) in 1968. The number of recruits-per-spawner shows large fluctuations with considerable coherence between adjacent years. There was no marked downward trend in recruits-per-spawner 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 spawning 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 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 MT). With an age-at-recruitment of 1, maximum steady state yield (69 million pounds, 31,000 MT) occurs at an exploitation rate of 0.2. Maximum long-term yield with this fishing strategy, under the 1931–68 environmental conditions, would have been 45 million pounds (20,000 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 long-term 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 larval 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.

1. THE FISHERY

1.1. 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 (RA = 0.88), while the converse is not true; fish from southern California are much less available to the central California fishery (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 (Ensenada)

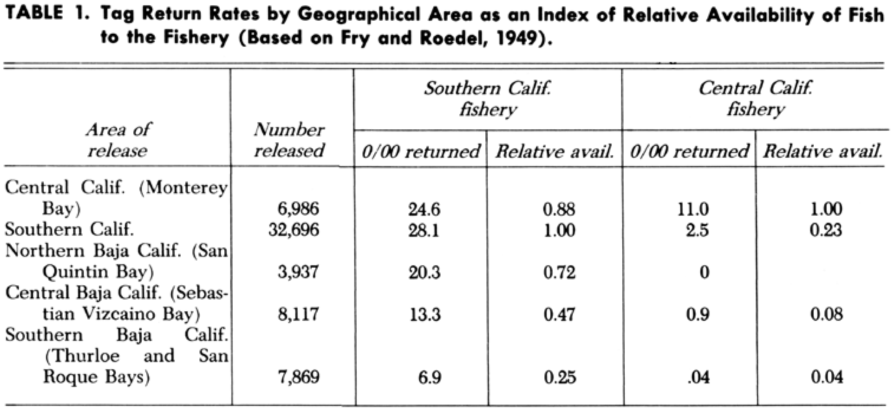

TABLE 1. Tag Return Rates by Geographical Area as an Index of Relative Availability of Fish to the Fishery (Based on Fry and Roedel, 1949).

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.	32,696	28.1	1.00	2.5	0.23
Northern Baja Calif. (San 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

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

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.

1.2. 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 1953–54 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 alternative 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

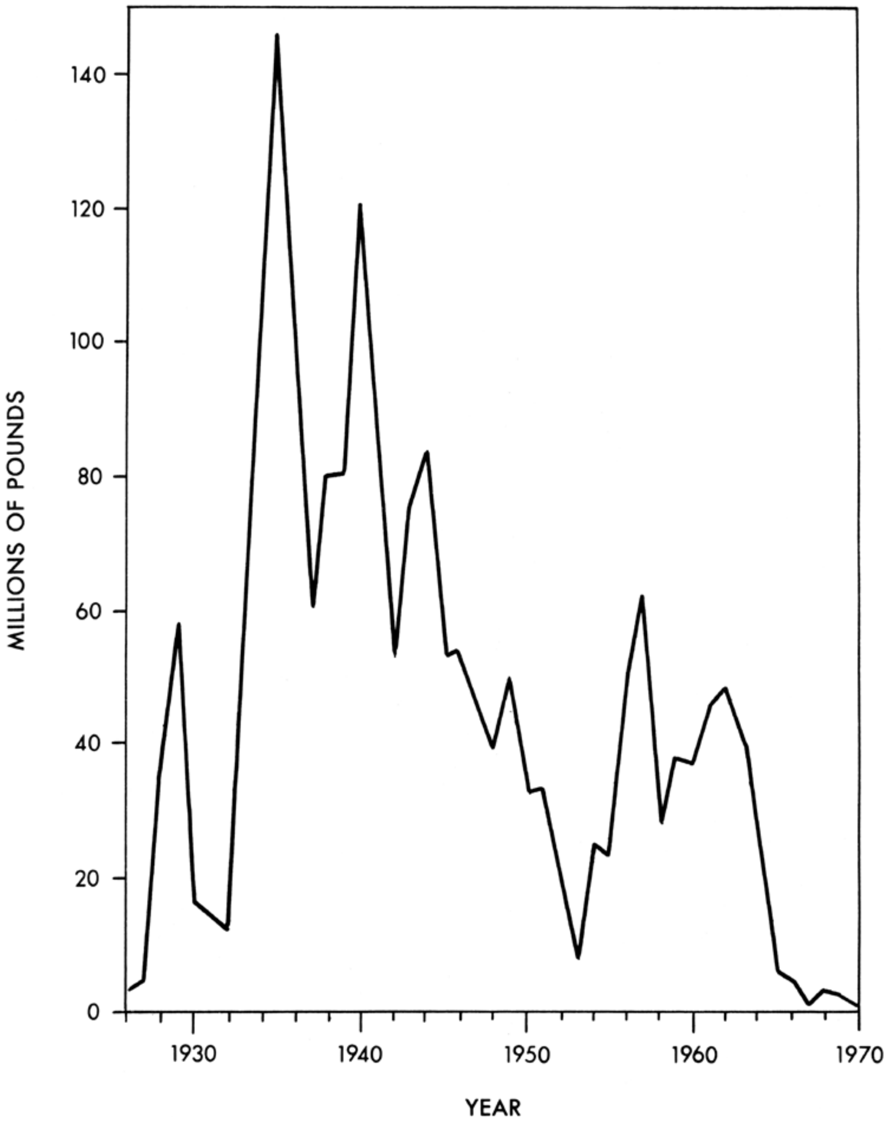

FIGURE 1. Pacific mackerel landings in California (1928–1970)

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).

1.3. 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 California 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 January 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.

1.4. 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 problems

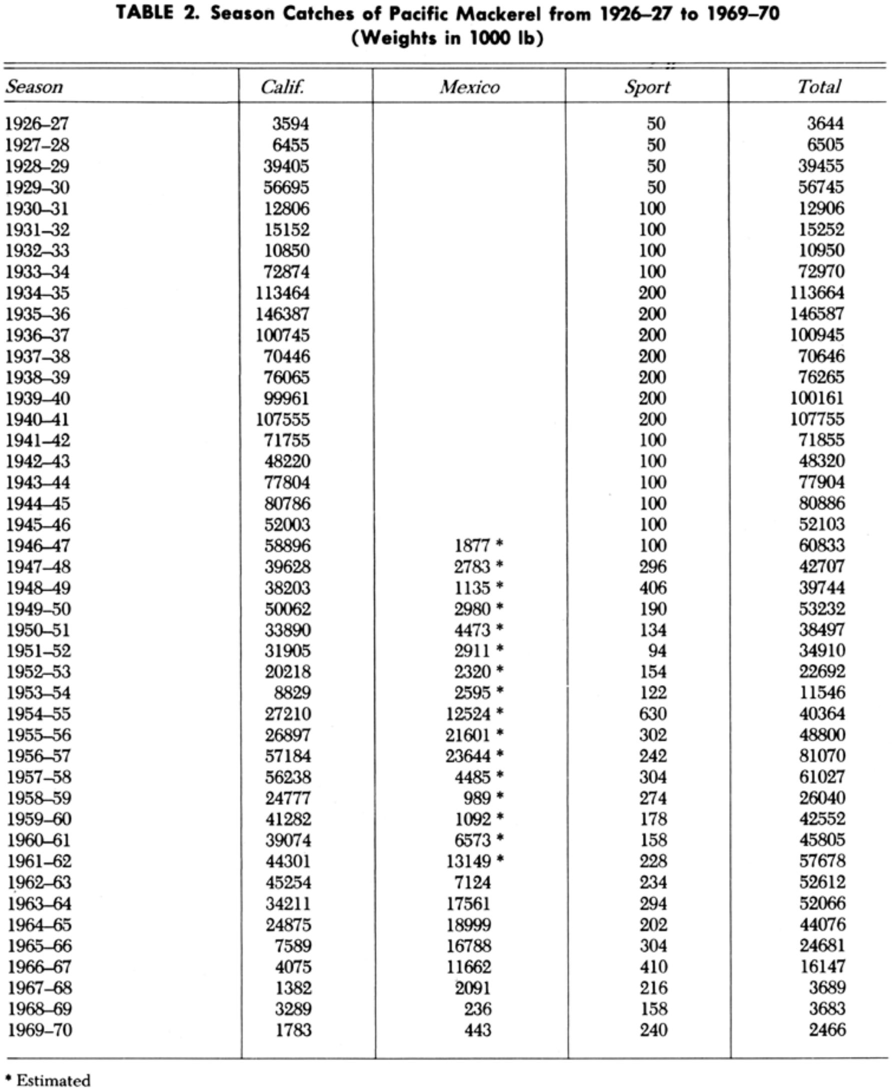

TABLE 2. Season Catches of Pacific Mackerel from 1926–27 to 1969–70
(Weights in 1000 lb)

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
1940–41	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	52066
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

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

1.5. 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 California 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).

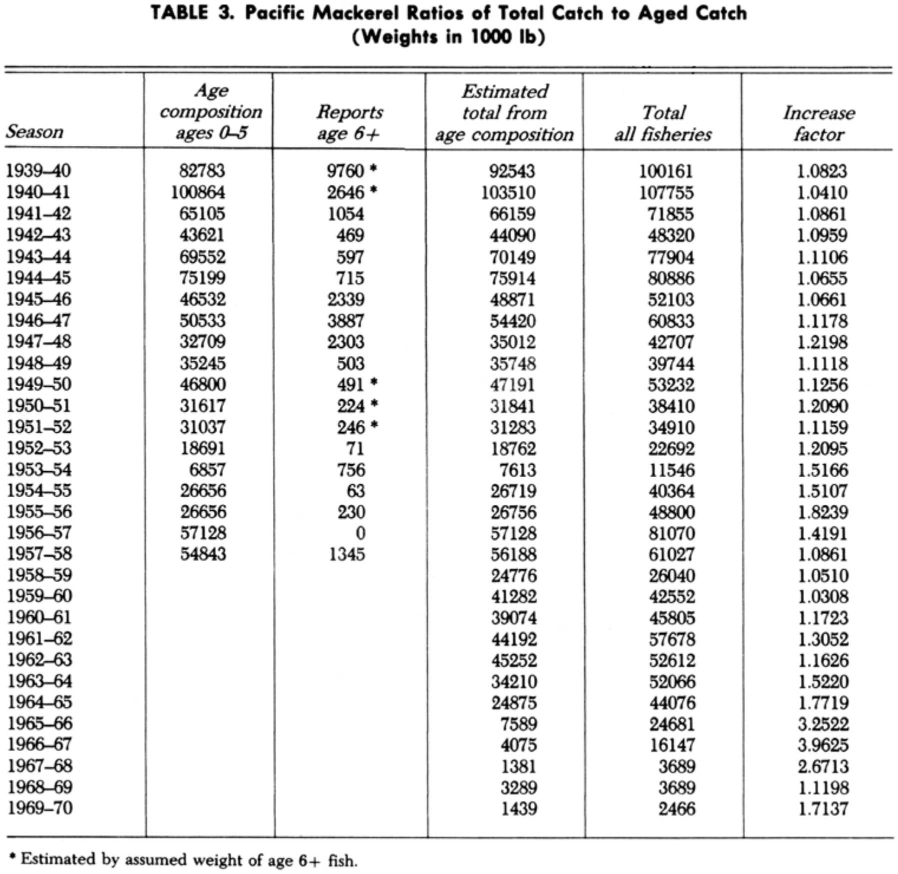

TABLE 3. Pacific Mackerel Ratios of Total Catch to Aged Catch (Weights in 1000 lb)

Season	*Age composition ages 0–5*	*Reports age 6+*	*Estimated total from age composition*	*Total all fisheries*	*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	1.1178
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.

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

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.

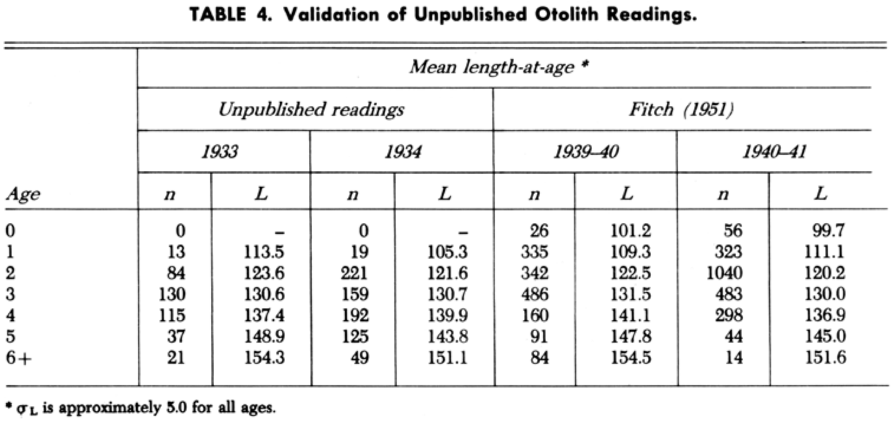

TABLE 4. Validation of Unpublished Otolith Readings.

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

* σ_L is approximately 5.0 for all ages.

TABLE ***4. Validation of Unpublished Otolith Readings.***

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

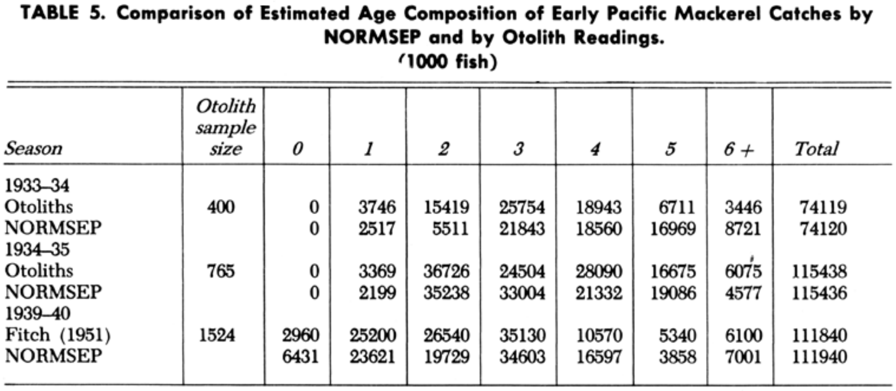

TABLE 5. Comparison of Estimated Age Composition of Early Pacific Mackerel Catches by NORMSEP and by Otolith Readings.
(1000 fish)

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

TABLE ***5. Comparison of Estimated Age Composition of Early Pacific Mackerel Catches by NORMSEP and by Otolith Readings. (1000 fish)*** landings by time period as do the otolith-based estimates (Fitch, 1951[1]). Moreover, no consistent bias in age structure is apparent in the *NORMSEP* 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.

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[1] 1 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 AGECOM (Abramson, 1971), wherein the number of fish observed in each length stratum is taken into account.

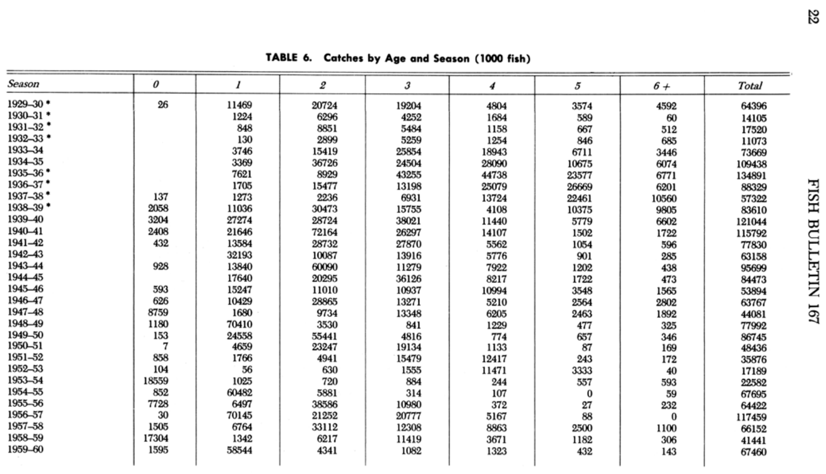


TABLE 6. Catches by Age and Season (1000 fish)

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	22461	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

TABLE ***6. Catches by Age and Season (1000 fish)***

1960–61	2928	20726	23316	9004	2354	487	302	59117
1961–62	23490	33441	17054	12158	2556	268	90	89057
1962–63	60	30235	13936	10056	3867	398	41	58593
1963–64	67	3840	22285	12945	7899	1071	137	48244
1964–65	140	7006	5410	10210	13527	1740	152	38195
1965–66	12976	1255	761	1688	5483	8612	1551	32326
1966–67	2627	7453	1438	1106	935	2512	1569	17640
1967–68	7656	363	254	270	158	85	134	17640
1968–69	7069	548	204	356	86	81	122	8920
1969–70	14	2641	470	74	84	81	14	3378

* Age composition estimated from length frequency. These data are unreliable.

TABLE 6—Cont'd.

2. POPULATION BIOLOGY

2.1. 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.

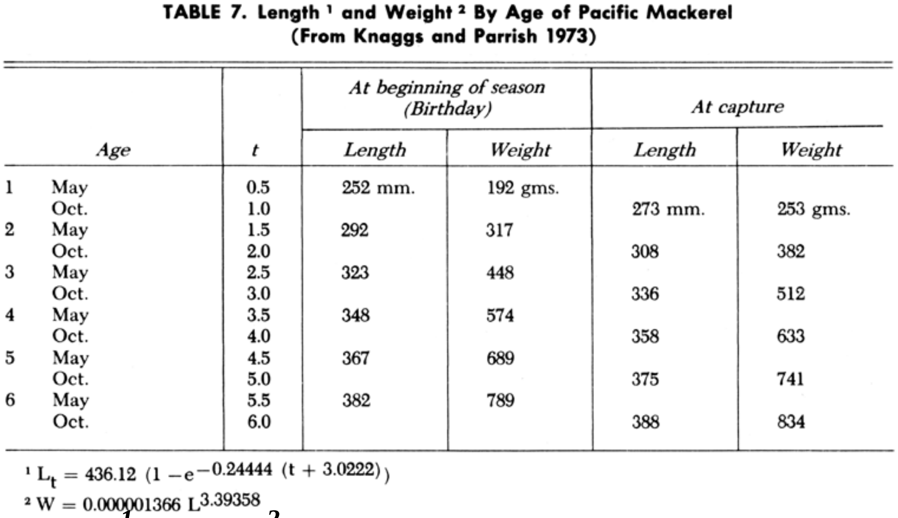


TABLE 7. Length[1] and Weight[2] By Age of Pacific Mackerel (From Knaggs and Parrish 1973)

Age		t	At beginning of season (Birthday)		At capture	
			Length	*Weight*	*Length*	*Weight*
1	May	0.5	252 mm.	192 gms.		
	Oct.	1.0			273 mm.	253 gms.
2	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

[1] $L_t = 436.12 \left(1 - e^{-0.24444 \, (t + 3.0222)}\right)$

[2] $W = 0.000001366 \, L^{3.39358}$

TABLE ***7. Length[1] and Weight[2] By Age of Pacific Mackerel (From Knaggs and Parrish 1973)***

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.

2.2. 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 most 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 used 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 density-dependent 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)

$PS = 0.540\, e^{-0.00717\, TPOP}$

where PS = proportion of age 1 fish spawning

TPOP = total population biomass in millions of pounds

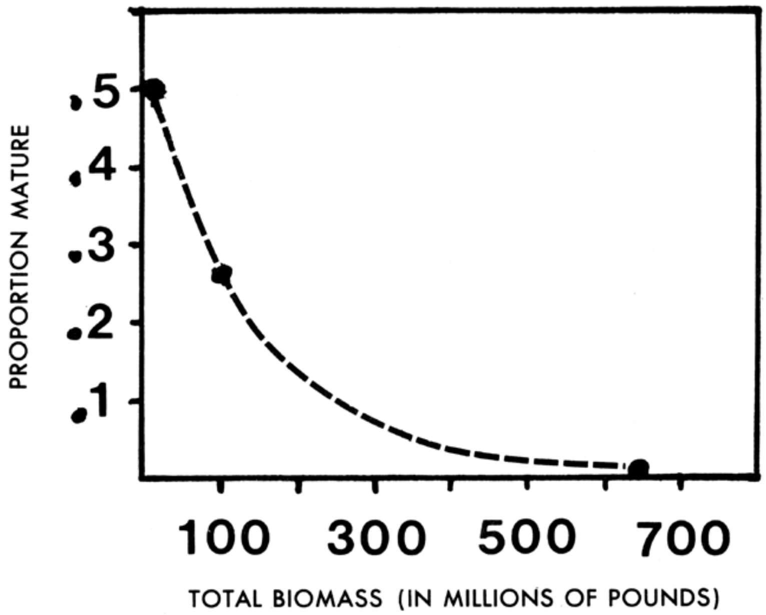


FIGURE 2. The relationship between total biomass and the proportion of age 1 spawners

FIGURE ***2. The relationship between total 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 20.6C (62 and 69°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).

2.3. 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-the-year school separately from the rest. Yearlings usually school separately but may join schools of adults, especially when the adults are predominantly 2-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

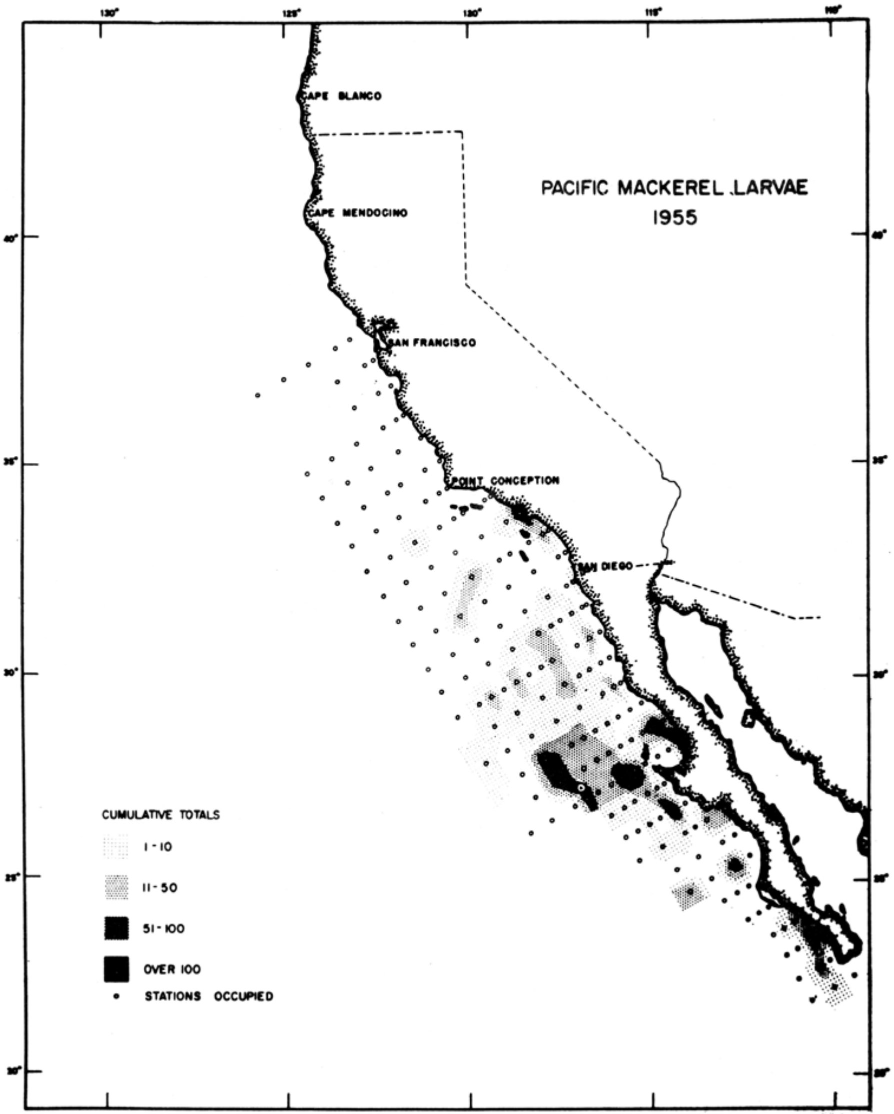


FIGURE 3. Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960)

FIGURE ***3. Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960)***

schooling with immature jack mackerel (Trachurus symmetricus) 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.

2.4. 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:

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

EQUATION

where L^1 is the smallest length fully represented (or lower cut-off point) and **L** is mean length of fish L^1 or longer. K and $L[_{oo}]$ 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 $L[_{oo}]$ 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 $L_{t+1} = L[_{oo}][1 - e^{-K} (1 - [L_t / L[_{oo}]])]$ 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.

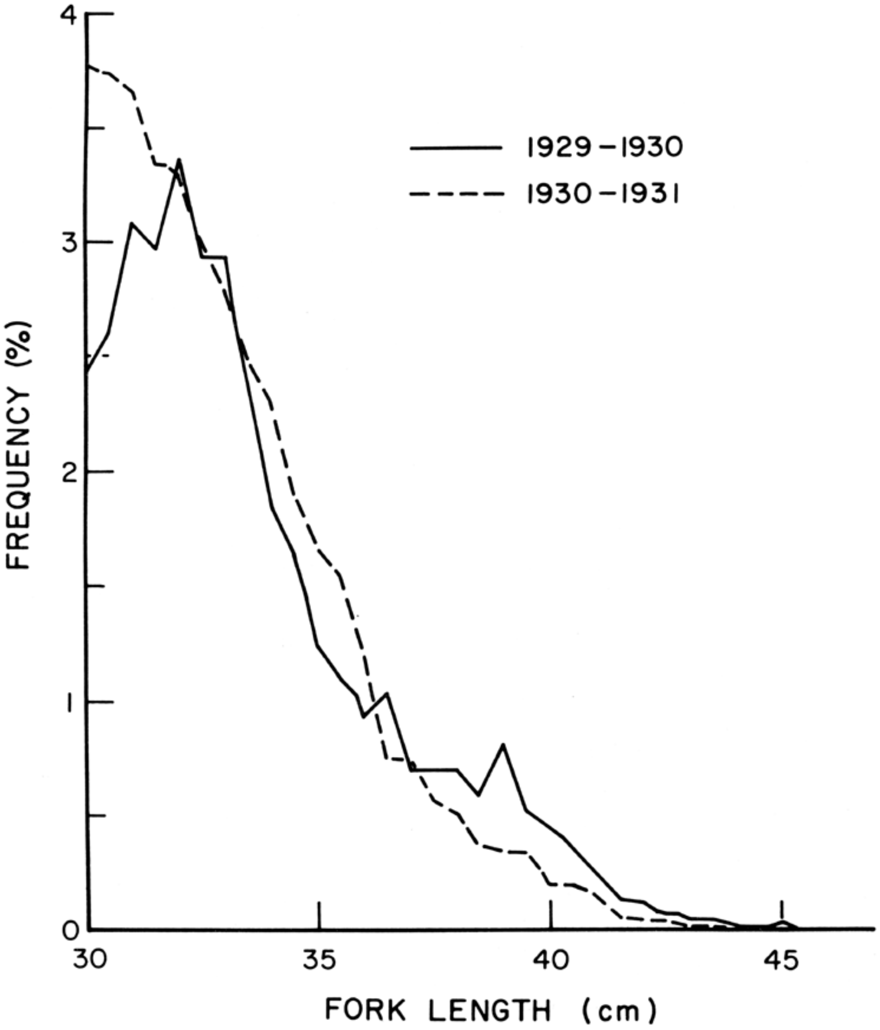


FIGURE 4. Pacific mackerel comparison of length frequency for 1929–30 and 1930–31

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

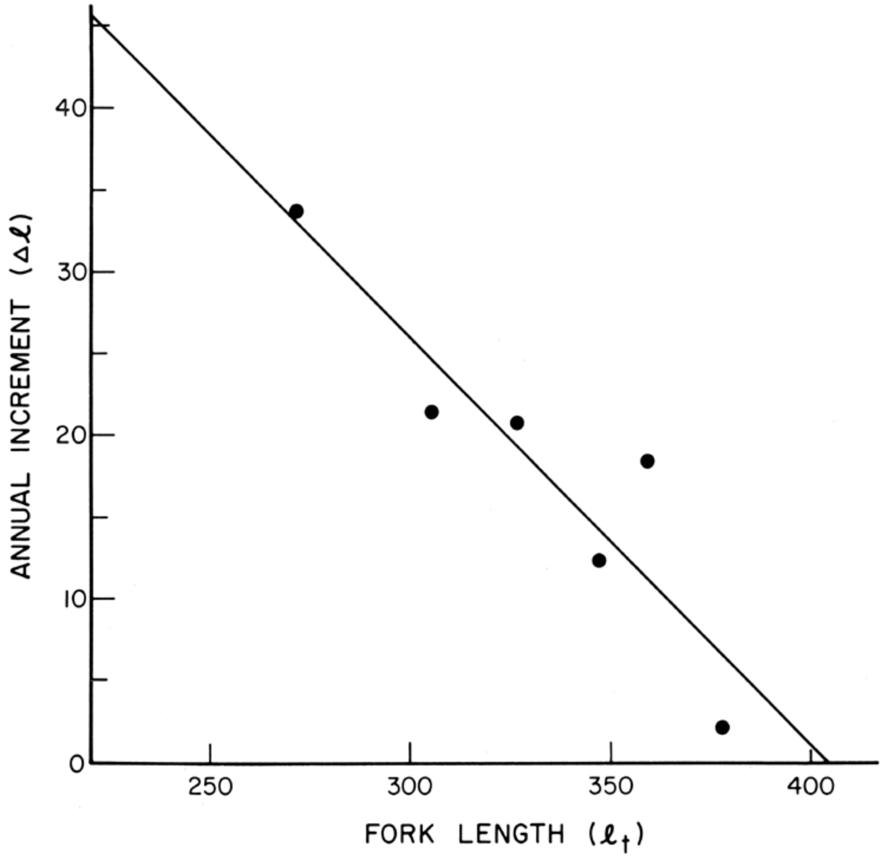


FIGURE 5. **Pacific mackerel von Bertalanffy growth curve parameter estimation. Data from D.H. Fry otolith readings 1933–1934.**

FIGURE ***5. Pacific mackerel von Bertalanffy growth curve parameter estimation. Data from D.H. Fry otolith 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.

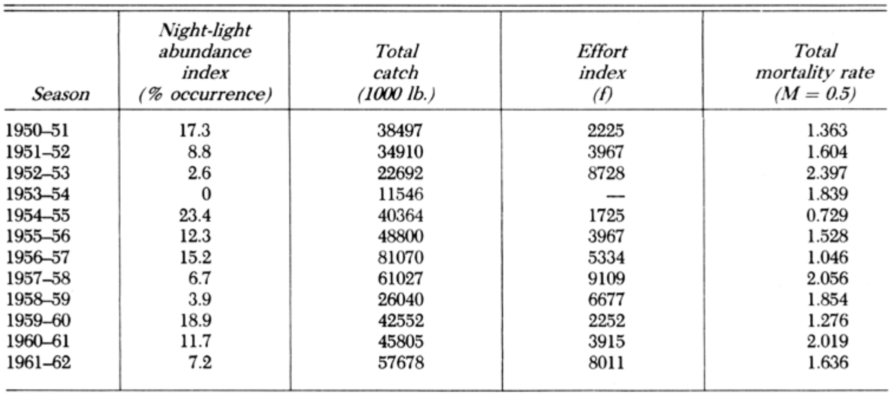
Table 8. Catch Curve Estimates of Total Mortality Rates from Length Frequency and Von Bertalanffy Growth Curve (L_∞ = 404.6 mm, K = 0.221).

Season	*n*	$\overline{L}$	$\overline{L}$	*Z*
1929–30	346	337.5	365.05	0.317
1930–31	317	350.0	368.70	0.424

Table ***8. Catch Curve Estimates of Total Mortality Rates from Length Frequency and Von Bertalanffy Growth Curve ([L8] = 404.6 mm, K = 0.221).***

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 (**N**) by some constant c, **N** = cI and instantaneous fishing mortality (F) is related to catch and mean abundance by F = (C/**N**) a measure of nominal effort (f) which is proportional to F is obtained by: f = cF = (C / I) Estimates of f obtained by this method, and estimates of Z from a cohort analysis using 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 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 M would therefore fall between 0.4 and 0.6. Since 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 Total Mortality Rate Estimates for Pacific Mackerel.



Season	*Night-light abundance index (% occurrence)*	*Total catch (1000 lb.)*	*Effort index (f)*	*Total mortality rate (M = 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	2.056
1958–59	3.9	26040	6677	1.854
1959–60	18.9	42552	2252	1.276
1960–61	11.7	45805	3915	2.019
1961–62	7.2	57678	8011	1.636

Table ***9. Abundance Index, Effort Index and Total Mortality Rate Estimates for Pacific Mackerel.***

A last source of information on probable values of M results 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.

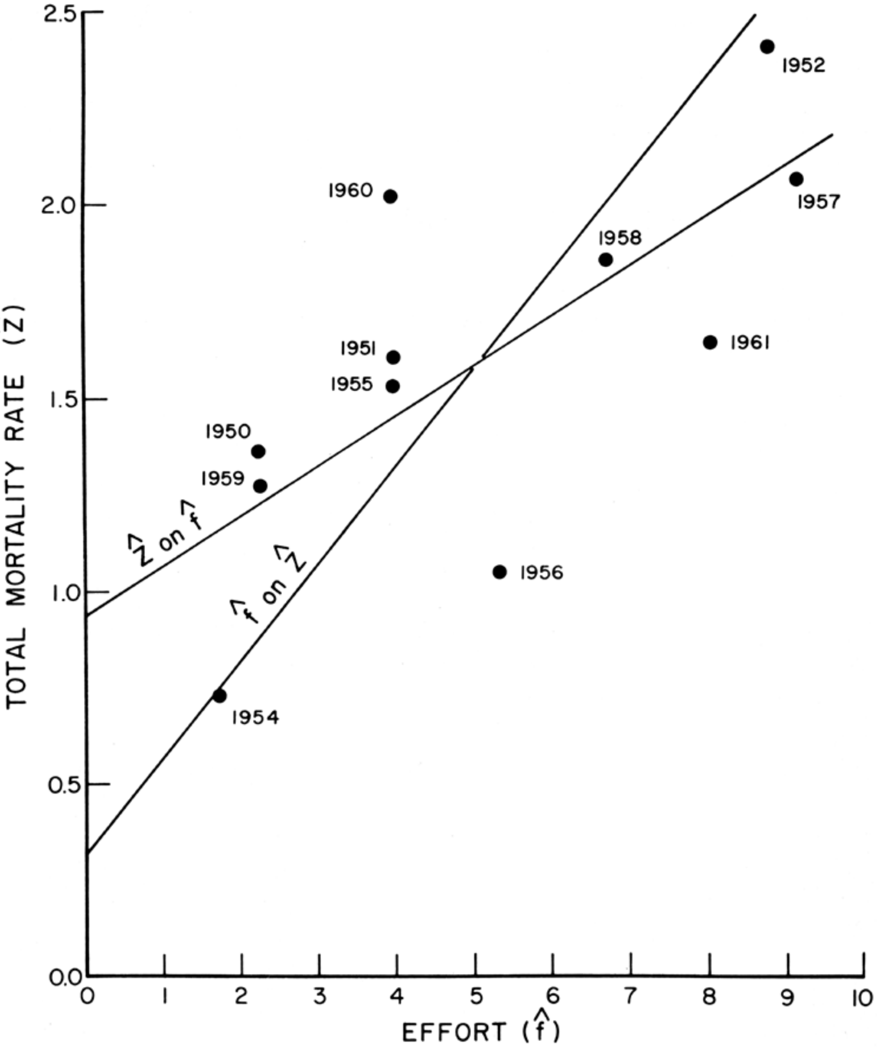


FIGURE 6. Estimation of M by the relationship of Z to F.

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 M from comparative studies such as these are of poor reliability, but do give support to the other estimates.

Comparison 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 M = 0.5. This value will be used throughout the rest of the analysis.

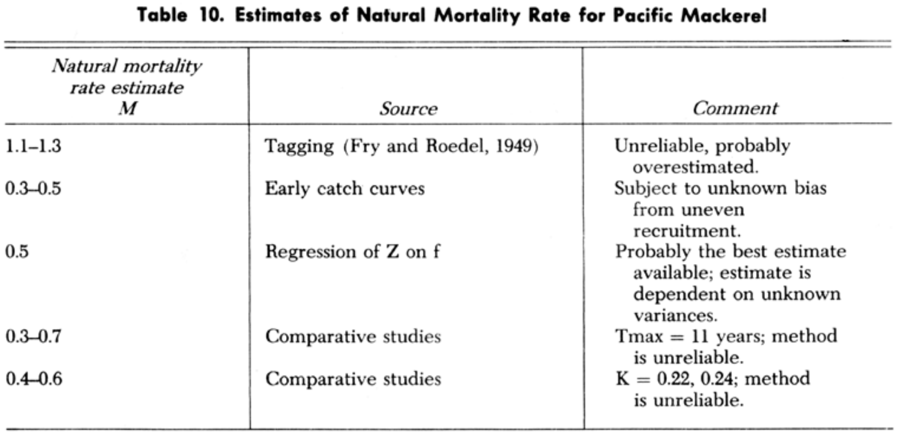


Table 10. Estimates of Natural Mortality Rate for Pacific Mackerel

Natural mortality rate estimate M	*Source*	*Comment*
1.1–1.3	Tagging (Fry and Roedel, 1949)	Unreliable, probably overestimated.
0.3–0.5	Early catch curves	Subject to unknown bias from uneven recruitment.
0.5	Regression of Z on f	Probably the best estimate available; estimate is dependent on unknown variances.
0.3–0.7	Comparative studies	Tmax = 11 years; method is unreliable.
0.4–0.6	Comparative studies	K = 0.22, 0.24; method is unreliable.

Table ***10. Estimates of Natural Mortality Rate for Pacific Mackerel***

3. COHORT ANALYSIS

3.1. 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, 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, 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 full 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

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.***

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 analysis 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 F = 0 (Table 12). A forward solution will show similar rates of divergence, estimates of 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

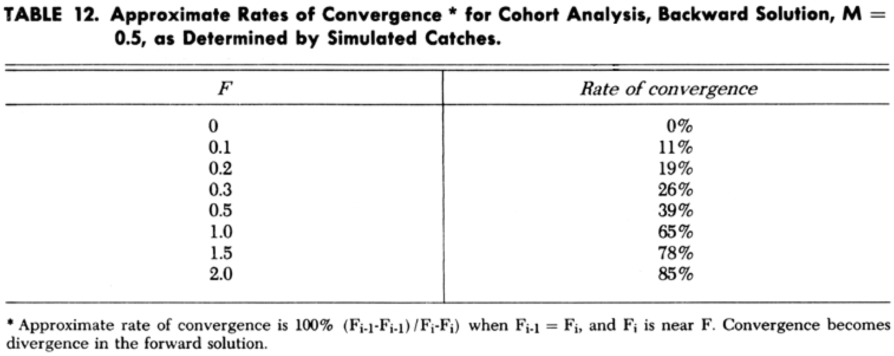


TABLE 12. Approximate Rates of Convergence * for Cohort Analysis, Backward Solution, M = 0.5, as Determined by Simulated Catches.

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 100% $(F_{i-1}\text{-}F_{i-1})/F_i\text{-}F_i)$ when $F_{i-1} = F_i$, and F_i is near F. Convergence becomes divergence in the forward solution.

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

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: F (scoop) = [C (scoop)/C (total)] 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.

3.2. 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 $E = (F/F + M)(1 - e^{-(F+M)})$, and initial population size is in numbers estimated by N = C/E.

Population sizes in weight, or biomasses, are obtained by assigning the

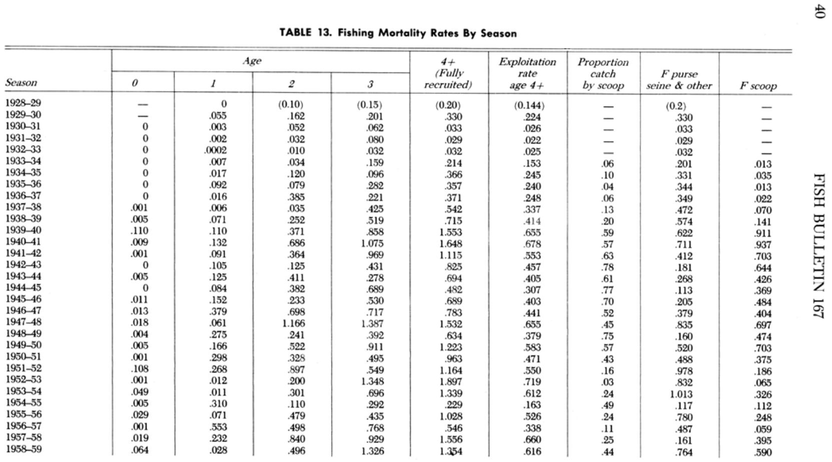


TABLE 13. Fishing Mortality Rates By Season

Season	*Age*				*4+ (Fully recruited)*	*Exploitation rate age 4+*	*Proportion catch by scoop*	*F purse seine & other*	*F scoop*
	0	*1*	*2*	*3*					
1928–29	—	0	(0.10)	(0.15)	(0.20)	(0.144)	—	(0.2)	—
1929–30	—	.055	.162	.201	.330	.224	—	.330	—
1930–31	0	.003	.052	.062	.033	.026	—	.033	—
1931–32	0	.002	.032	.080	.029	.022	—	.029	—
1932–33	0	.0002	.010	.032	.032	.025	—	.032	—
1933–34	0	.007	.034	.159	.214	.153	.06	.201	.013
1934–35	0	.017	.120	.096	.366	.245	.10	.331	.035
1935–36	0	.092	.079	.282	.357	.240	.04	.344	.013
1936–37	0	.016	.385	.221	.371	.248	.06	.349	.022
1937–38	.001	.006	.035	.425	.542	.337	.13	.472	.070
1938–39	.005	.071	.252	.519	.715	.414	.20	.574	.141
1939–40	.110	.110	.371	.858	1.553	.655	.59	.622	.911
1940–41	.009	.132	.686	1.075	1.648	.678	.57	.711	.937
1941–42	.001	.091	.364	.969	1.115	.553	.63	.412	.703
1942–43	0	.105	.125	.431	.825	.457	.78	.181	.644
1943–44	.005	.125	.411	.278	.694	.405	.61	.268	.426
1944–45	0	.084	.382	.689	.482	.307	.77	.113	.369
1945–46	.011	.152	.233	.530	.689	.403	.70	.205	.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
1949–50	.005	.166	.522	.911	1.223	.583	.57	.520	.703
1950–51	.001	.298	.328	.495	.963	.471	.43	.488	.375
1951–52	.108	.268	.897	.549	1.164	.550	.16	.978	.186
1952–53	.001	.012	.200	1.348	1.897	.719	.03	.832	.065
1953–54	.049	.011	.301	.696	1.339	.612	.24	1.013	.326
1954–55	.005	.310	.110	.292	.229	.163	.49	.117	.112
1955–56	.029	.071	.479	.435	1.028	.526	.24	.780	.248
1956–57	.001	.553	.498	.768	.546	.338	.11	.487	.059
1957–58	.019	.232	.840	.929	1.556	.660	.25	.161	.395
1958–59	.064	.028	.496	1.326	1.354	.616	.44	.764	.590

TABLE ***13. Fishing Mortality Rates By Season***

1959–60	.007	.449	.165	.206	.776	.438	.54	.361	.415
1960–61	.007	.158	.465	.902	1.519	.652	.04	1.461	.058
1961–62	.105	.146	.264	.702	1.136	.559	.05	.080	.056
1962–63	.002	.265	.114	.346	.760	.432	.01	.754	.006
1963–64	.003	.194	.456	.204	.748	.428	.02	.731	.017
1964–65	.017	.761	.667	.570	.487	.310	.01	.480	.007
1965–66	.620	.290	.234	.670	1.096	.547	.02	1.074	.022
1966–67	.937	1.539	.966	.952	1.800	.704	—	1.800	—
1967–68	1.180	.447	.244	.711	.481	.306	—	.481	—
1968–69	.494	.322	.727	.966	.781	.440	—	.781	—
1969–70	(.250)	(.500)	(.750)	(1.000)	(1.000)	(.518)	—	(1.000)	—

TABLE 13—Cont'd.

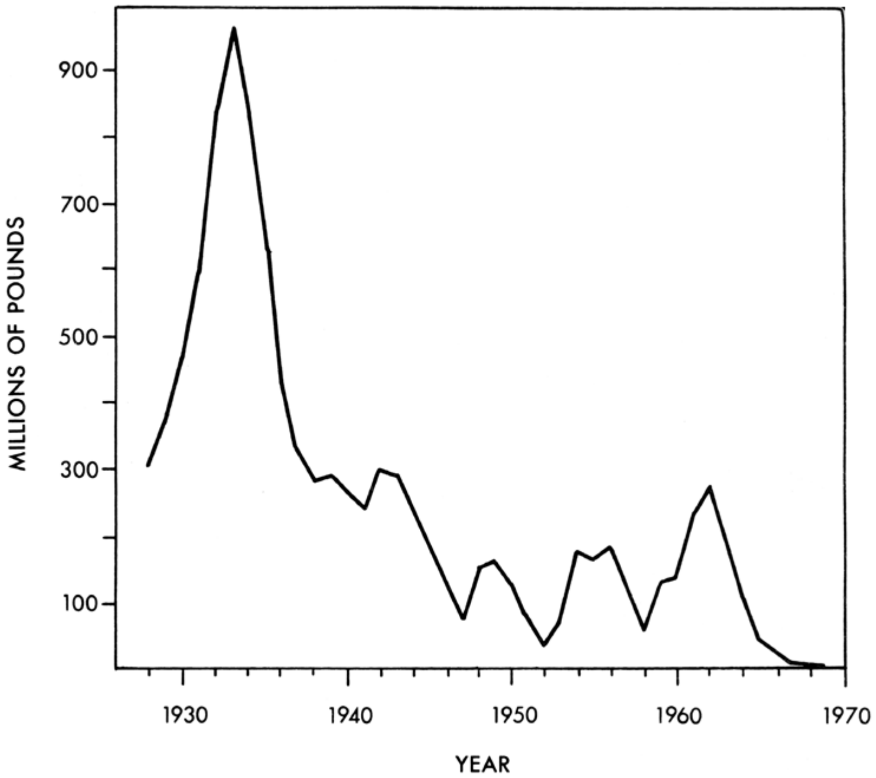


FIGURE 7. Total biomass of the California Current stock of Pacific mackerel (MacCall pers. comm.)

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).

3.3. 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 (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 ($P < 0.01$) 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

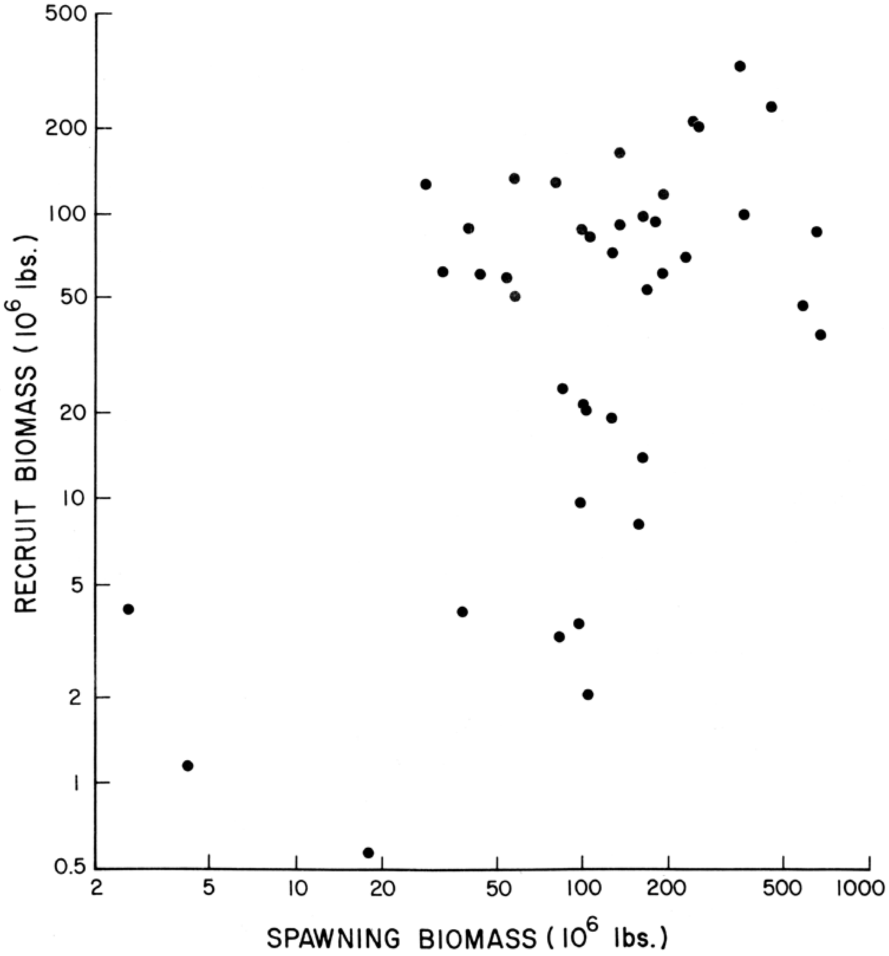


FIGURE 8. Spawner-recruit relationship

FIGURE ***8. Spawner-recruit relationship***

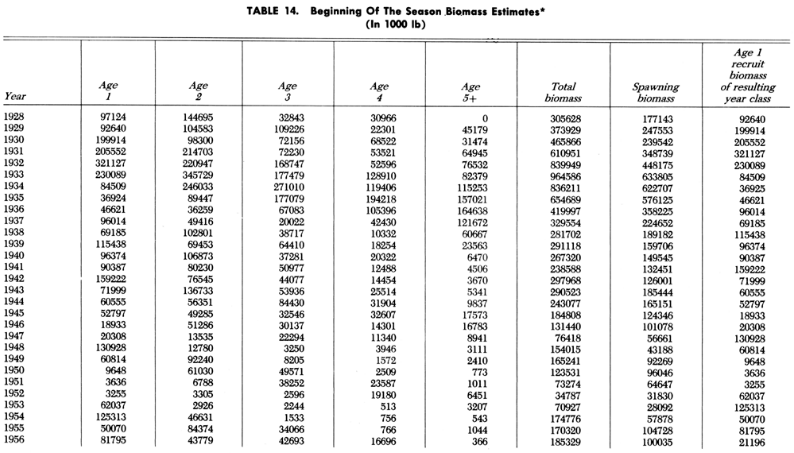


TABLE 14. Beginning Of The Season Biomass Estimates*
(In 1000 lb)

Year	Age 1	Age 2	Age 3	Age 4	Age 5+	Total biomass	Spawning biomass	Age 1 recruit biomass of resulting year class
1928	97124	144695	32843	30966	0	305628	177143	92640
1929	92640	104583	109226	22301	45179	373929	247553	199914
1930	199914	98300	72156	68522	31474	465866	239542	205552
1931	205552	214703	72230	53521	64945	610951	348739	321127
1932	321127	220947	168747	52596	76532	839949	448175	230089
1933	230089	345729	177479	128910	82379	964586	633805	84509
1934	84509	246033	271010	119406	115253	836211	622707	36925
1935	36924	89447	177079	194218	157021	654689	576125	46621
1936	46621	36259	67083	105396	164638	419997	358225	96014
1937	96014	49416	20022	42430	121672	329554	224652	69185
1938	69185	102801	38717	10332	60667	281702	189182	115438
1939	115438	69453	64410	18254	23563	291118	159706	96374
1940	96374	106873	37281	20322	6470	267320	149545	90387
1941	90387	80230	50977	12488	4506	238588	132451	159222
1942	159222	76545	44077	14454	3670	297968	126001	71999
1943	71999	136733	53936	25514	5341	290523	185444	60555
1944	60555	56351	84430	31904	9837	243077	165151	52797
1945	52797	49285	32546	32607	17573	184808	124346	18933
1946	18933	51286	30137	14301	16783	131440	101078	20308
1947	20308	13535	22294	11340	8941	76418	56661	130928
1948	130928	12780	3250	3946	3111	154015	43188	60814
1949	60814	92240	8205	1572	2410	165241	92269	9648
1950	9648	61030	49571	2509	773	123531	96046	3636
1951	3636	6788	38252	23587	1011	73274	64647	3255
1952	3255	3305	2596	19180	6451	34787	31830	62037
1953	62037	2926	2244	513	3207	70927	28092	125313
1954	125313	46631	1533	756	543	174776	57878	50070
1955	50070	84374	34066	766	1044	170320	104728	81795
1956	81795	43779	42693	16696	366	185329	100035	21196

TABLE ***14. Beginning of The Season Biomass Estimates (In 1000 lb)***

TABLE 14—Cont'd.

1957	21196	47760	23617	15188	6815	114576	84594	24184
1958	24184	11879	14738	5962	2778	59541	39377	88151
1959	88151	29150	7930	3830	2047	131108	53892	58799
1960	58799	58641	19054	4481	1800	142775	79608	126860
1961	126860	67164	29087	5352	892	229355	96783	86791
1962	86791	130399	45235	10976	1453	274854	159173	13744
1963	13744	61556	90361	22556	4122	192339	155462	8160
1964	8160	13588	30741	55323	9503	117315	104241	2044
1965	2044	3218	4129	11932	19188	40511	38057	4021
1966	4021	2177	2375	1719	10275	20567	17634	575
1967	575	1122	675	626	1727	4725	4111	1141
1968	1141	339	743	232	820	3275	2569	4075
1969	4075	194	140	210	280			

* Spawning biomass was calculated with the percentage of age 1 spawners as in Figure 14; 77%, 88%, and 100% of ages 2, 3, and 4 were considered mature. (Estimates before 1939 and after 1967 are unreliable).

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

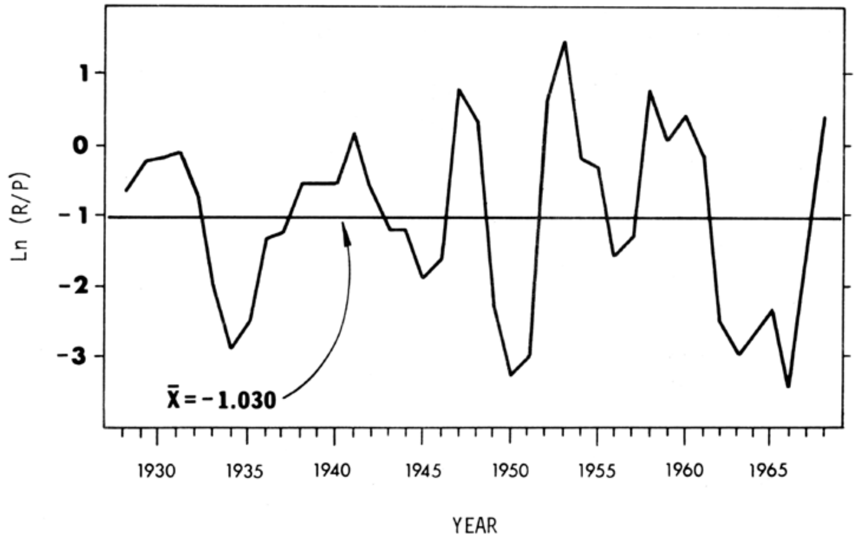


FIGURE 9. Time series of the natural log of the observed recruit biomass per spawning biomass.

FIGURE ***9. Time series of the natural log 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 subsequent 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. [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

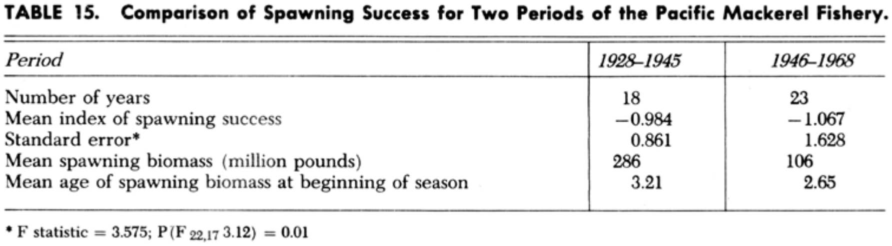


TABLE 15. Comparison of Spawning Success for Two Periods of the Pacific Mackerel Fishery.

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

* F statistic = 3.575; P(F $_{22,17}$ 3.12) = 0.01

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

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.

4. RECRUITMENT MODELS

4.1. 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.

4.1.1. 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

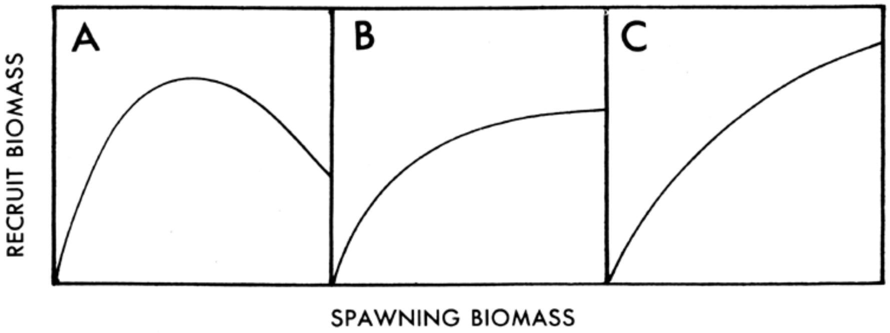


FIGURE 10. Density-dependent spawner-recruit models; A. Ricker, B. Beverton and Holt, C. Cushing

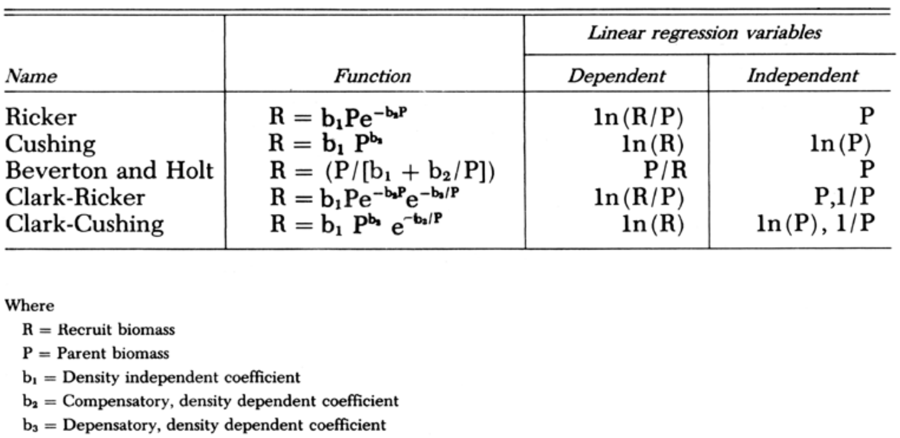
FIGURE ***10. Density-dependent spawner-recruit models; A. Ricker, B. Beverton and Holt, C. Cushing***

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 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	$R = b_1 P e^{-b_2 P}$	$\ln(R/P)$	P
Cushing	$R = b_1 P^{b_2}$	$\ln(R)$	$\ln(P)$
Beverton and Holt	$R = (P/[b_1 + b_2/P])$	P/R	P
Clark-Ricker	$R = b_1 P e^{-b_2 P} e^{-b_3/P}$	$\ln(R/P)$	$P, 1/P$
Clark-Cushing	$R = b_1 P^{b_2} e^{-b_3/P}$	$\ln(R)$	$\ln(P), 1/P$

Where
R = Recruit biomass
P = Parent biomass
b_1 = Density independent coefficient
b_2 = Compensatory, density dependent coefficient
b_3 = Depensatory, density dependent coefficient

TABLE ***16. Regression Variables for Spawner-Recruit Functions***

4.1.2. 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 the monthly 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 regression, 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 May–July 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 (R/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 Environmental

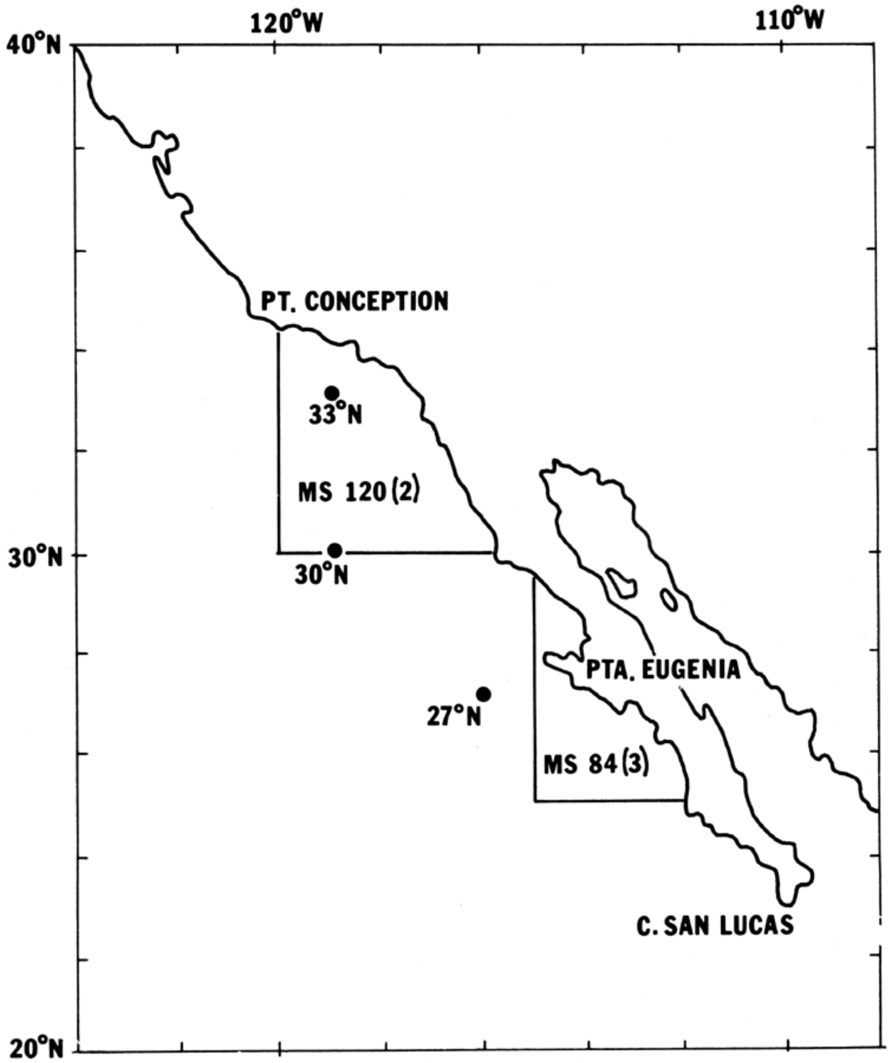


FIGURE 11. Marsden Square quadrants 120(2) and 84(3), and upwelling index locations

*FIGURE **11. Marsden Square quadrants 120(2) and 84(3), and upwelling index locations***

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° 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°N, 30°N and 33°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.

4.1.3. 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.

4.2. 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 a 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 recruitment factor does not exist in Pacific mackerel. The large observed variation in recruitment at low spawning biomass levels would have hindered detection of a depensatory factor and it is possible that depensation would not occur until the spawning biomass reached extremely low levels.

The three Ricker models (Table 17) have very low density-independent coefficients. 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 (R/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.

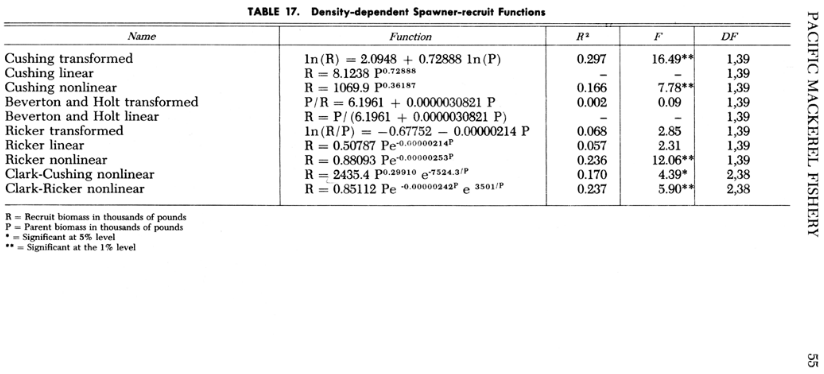


TABLE 17. Density-dependent Spawner-recruit Functions

Name	*Function*	*R^2*	*F*	*DF*
Cushing transformed	$\ln(R) = 2.0948 + 0.72888 \ln(P)$	0.297	16.49**	1,39
Cushing linear	$R = 8.1238\ P^{0.72888}$	–	–	1,39
Cushing nonlinear	$R = 1069.9\ P^{0.36187}$	0.166	7.78**	1,39
Beverton and Holt transformed	$P/R = 6.1961 + 0.0000030821\ P$	0.002	0.09	1,39
Beverton and Holt linear	$R = P/(6.1961 + 0.0000030821\ P)$	–	–	1,39
Ricker transformed	$\ln(R/P) = -0.67752 - 0.00000214\ P$	0.068	2.85	1,39
Ricker linear	$R = 0.50787\ Pe^{-0.00000214P}$	0.057	2.31	1,39
Ricker nonlinear	$R = 0.88093\ Pe^{-0.00000253P}$	0.236	12.06**	1,39
Clark-Cushing nonlinear	$R = 2435.4\ P^{0.29910}\ e^{-7524.3/P}$	0.170	4.39*	2,38
Clark-Ricker nonlinear	$R = 0.85112\ Pe^{-0.00000242P}\ e^{3501/P}$	0.237	5.90**	2,38

R = Recruit biomass in thousands of pounds
P = Parent biomass in thousands of pounds
* = Significant at 5% level
** = Significant at the 1% level

TABLE **17. Density-dependent Spawner-recruit Functions**

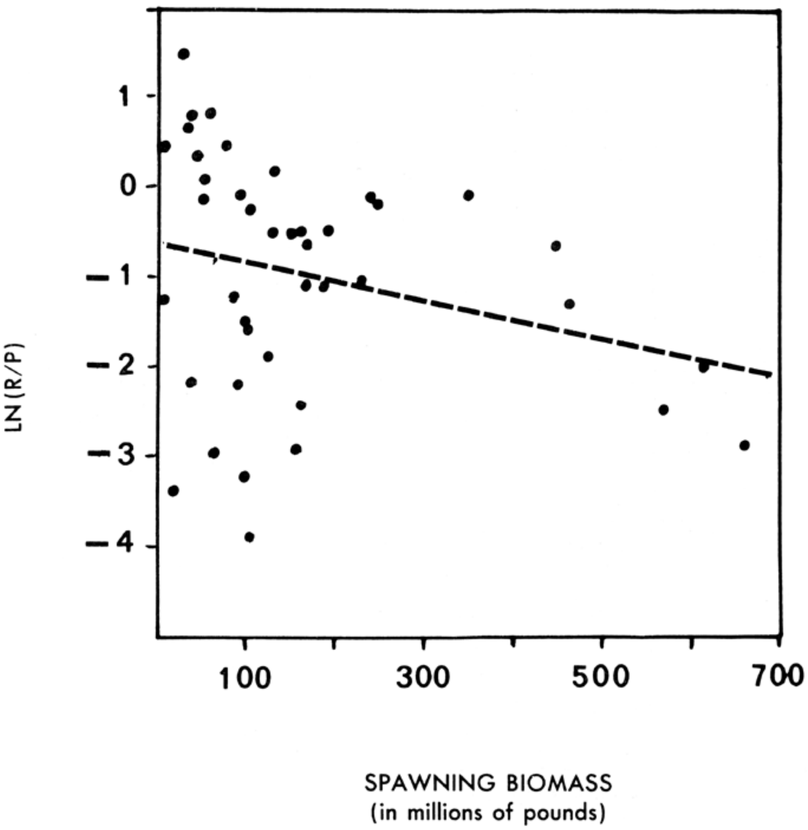


FIGURE 12. **Natural logarithms and regression line of recruit biomass per spawning biomass plotted against spawning biomass**

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 density-dependent 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.

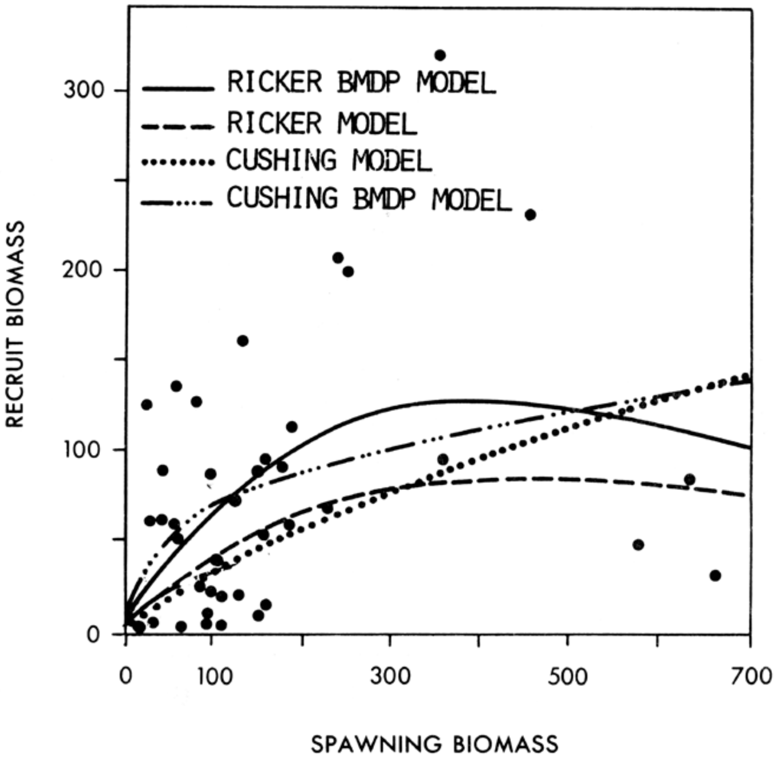


FIGURE 13. **Ricker and Cushing spawner-recruit models fitted to Pacific mackerel population data. (Values in millions of lbs.).**

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

4.3. ASSOCIATIONS BETWEEN RECRUITMENT AND ENVIRONMENTAL FACTORS

4.3.1. 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 California, 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

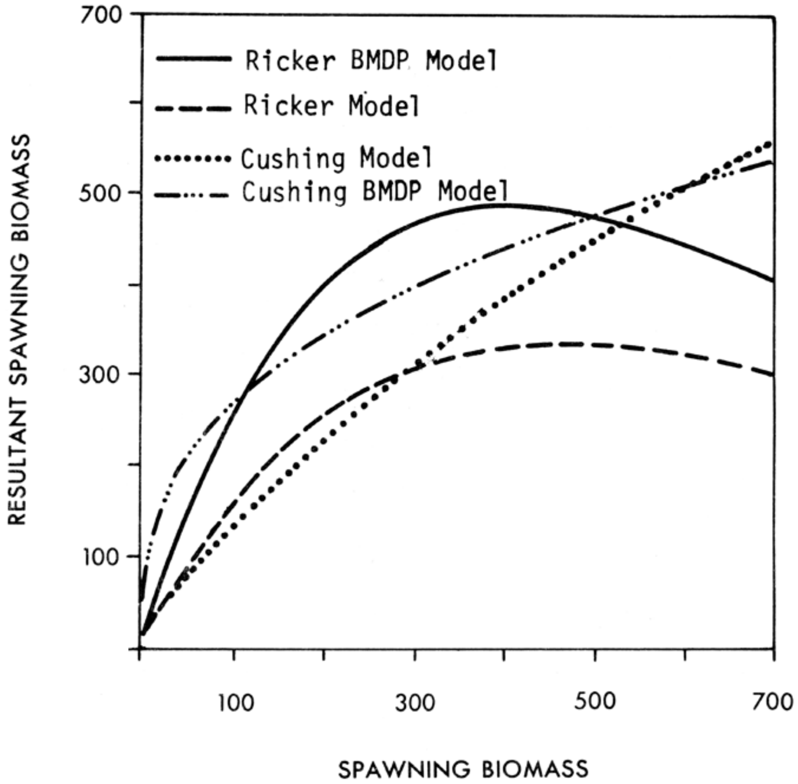


FIGURE 14. Ricker and Cushing spawner resultant-spawner models (values in millions of lbs)

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 (R/P) vs. T and T^2 was calculated (where T = prorated April–June sea surface temperature (C°) in Marsden Square 120(2)). The first order value of temperature is the first variable to enter, with an r^2 of 0.2611 (F = 12.72** 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 (R/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(R/P) = -13.527 + .78815 T

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

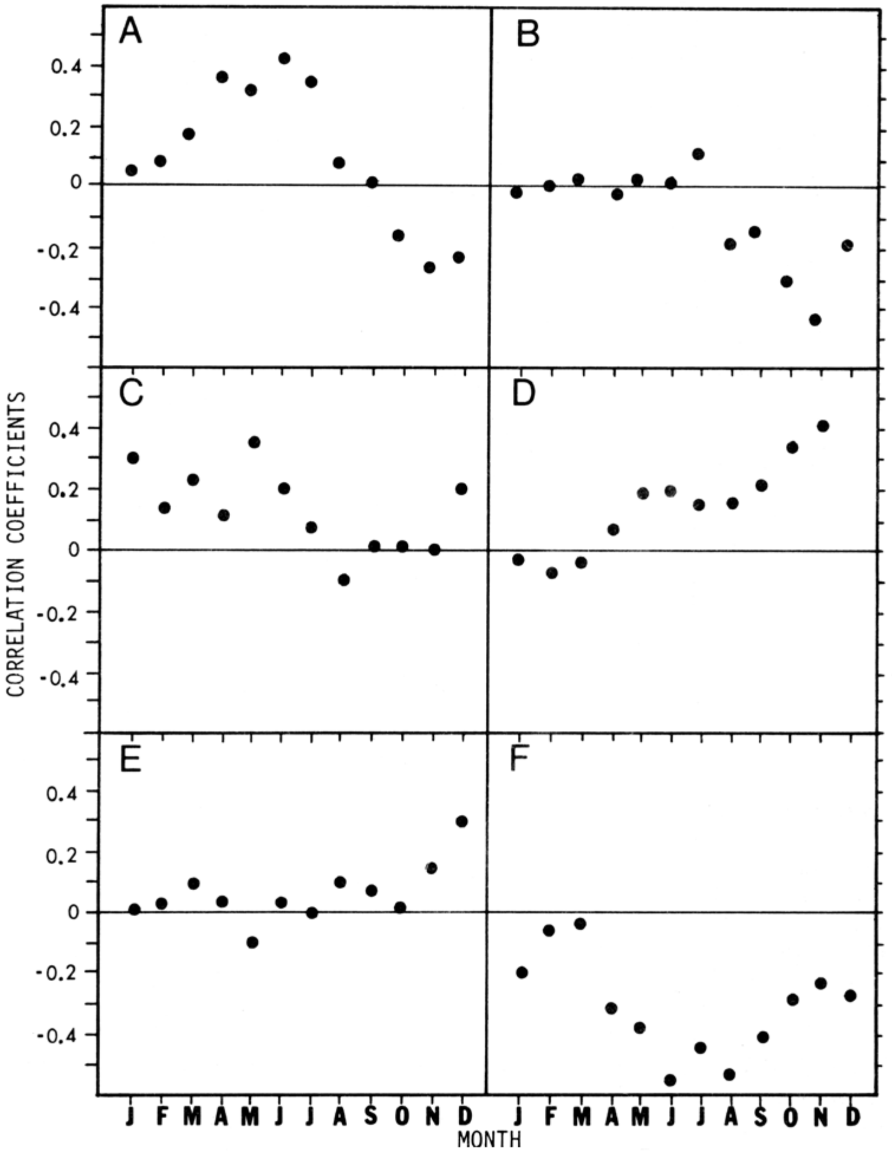


FIGURE 15. Correlations of ln(R) with monthly environmental factors; A. SST in Marsden square 120(2), B. SST in Marsden square 84(3), C. SST at Scripps Pier, D. Sea level differences from Saur (1973), E. Sea level barometric pressure at San Diego, F. Sea level at La Jolla

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° and 17.5°C. it should be noted that only 26% of the variation in ln(R/P) is explained by these data.

4.3.2. 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 Pacific 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(R), (Figure 15).

4.3.3. Wind speed and cloud cover

Wind speeds in both Marsden Squares show a constant negative correlation with ln(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).

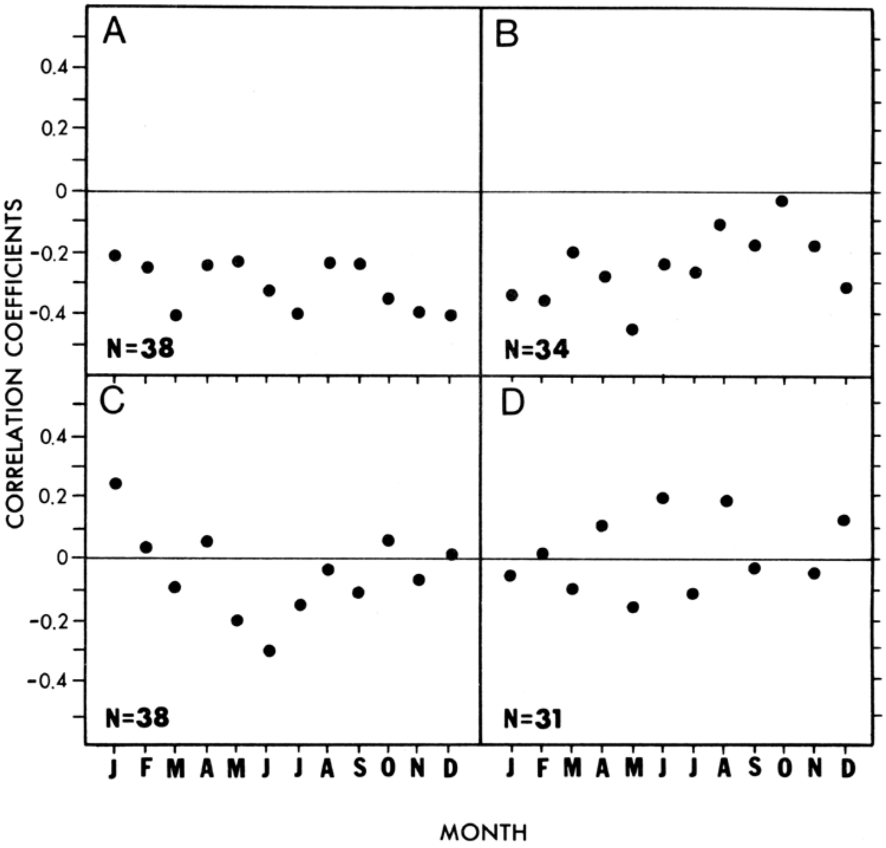


FIGURE 16. Correlations of ln(R) with monthly environmental factors; A. Wind speed in Marsden square 120(2), B. Wind speed in Marsden square 84(3), C. Cloud cover in Marsden square 120(2), D. Cloud cover in Marsden square 84(3).

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).***

4.3.4. Ekman and total transport

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

Bakun's (1973) upwelling indices at 30°N, positive offshore, show spring and fall peaks in association with ln(R) (Figure 17). Meridional Ekman transport at 30°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 upwelling

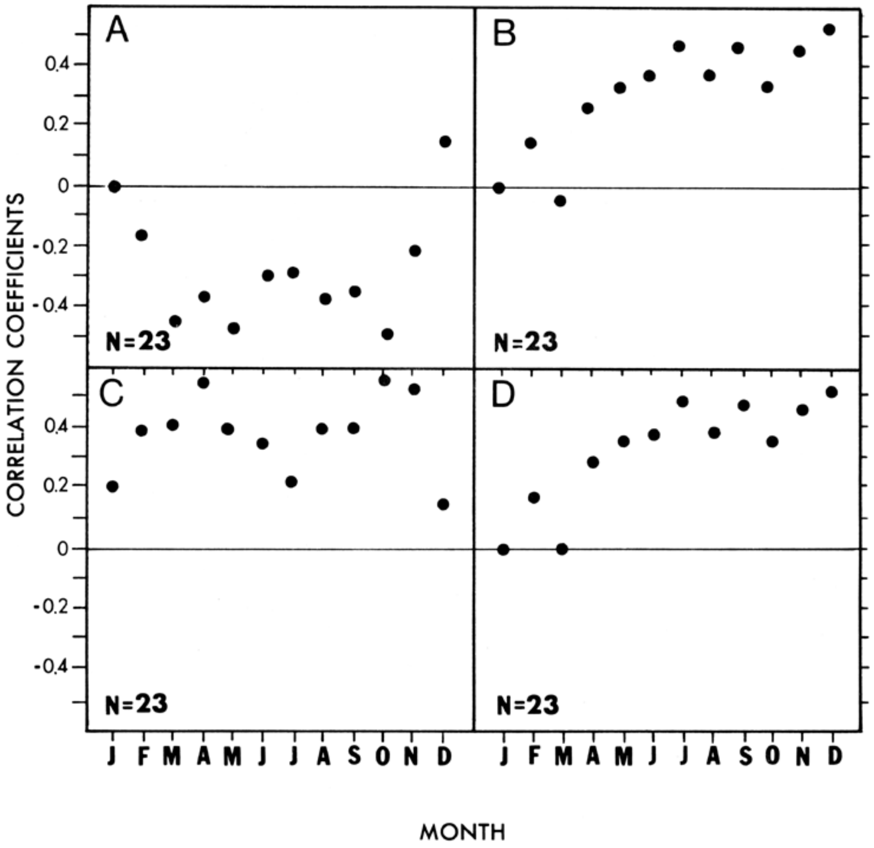


FIGURE 17. Correlations of ln(R) with monthly environmental factors; A. Meridional Ekman transport at 30°N; B. Meridional total transport at 30°N; C. Bakun's (1973) upwelling indices at 30°N; D. Divergence of Ekman transport at 30°N.

*FIGURE **17. Correlations of ln(R) with monthly environmental factors; A. Meridional Ekman transport at 30°N; B. Meridional total transport at 30°N; C. Bakun's (1973) upwelling indices at 30°N; D. Divergence of Ekman transport at 30°N.***

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 (i.e., May–June).

Meridional total transport shows significant, positive correlation with ln(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°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.

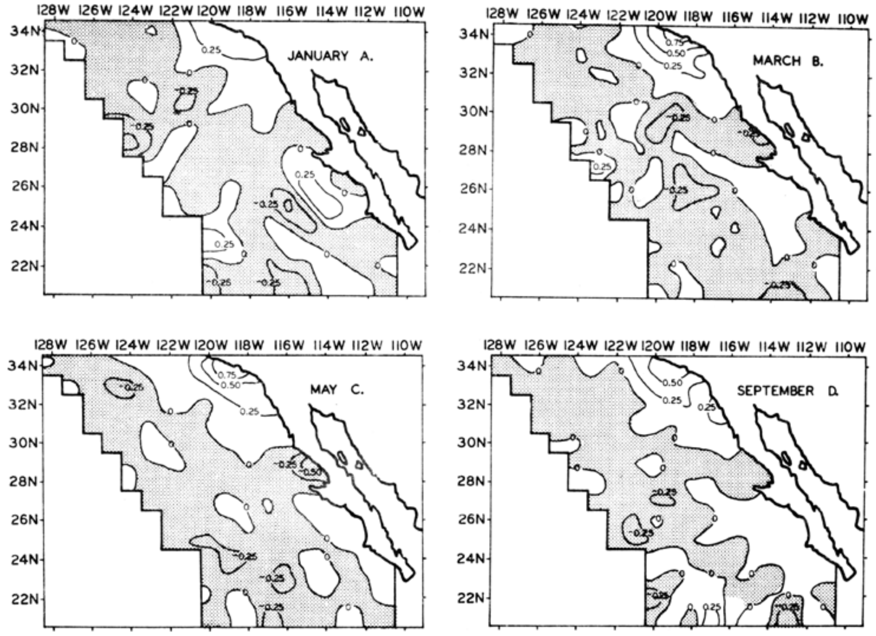


FIGURE 18. Wind stress curl patterns off southern California and Baja California (Bakun and Nelson In Press)

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

4.3.5. Linear combinations of spawning months

Several combinations and prorations of the spawning months resulted in larger correlation with recruitment (ln(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°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(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).

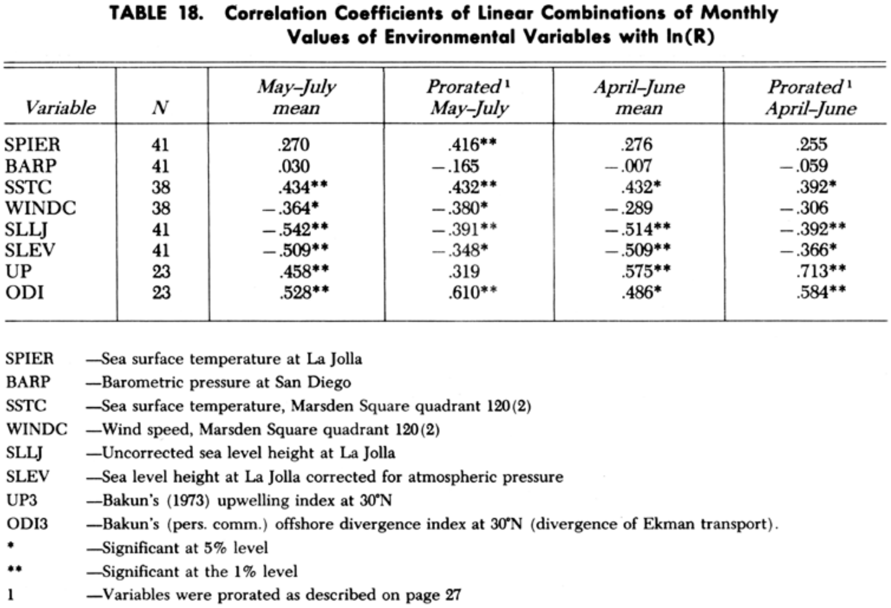


TABLE 18. Correlation Coefficients of Linear Combinations of Monthly Values of Environmental Variables with ln(R)

Variable	*N*	*May–July mean*	*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°N
ODI3 —Bakun's (pers. comm.) offshore divergence index at 30°N (divergence of Ekman transport).
* —Significant at 5% level
** —Significant at the 1% level
1 —Variables were prorated as described on page 27

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

4.4. ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNCTIONS

Recruitment functions incorporating both density-dependent and environmental-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(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 1931–1968 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 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°N prorated by the age composition of the spawning biomass. The Ricker transport model has an 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.

4.5. 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 conditions.

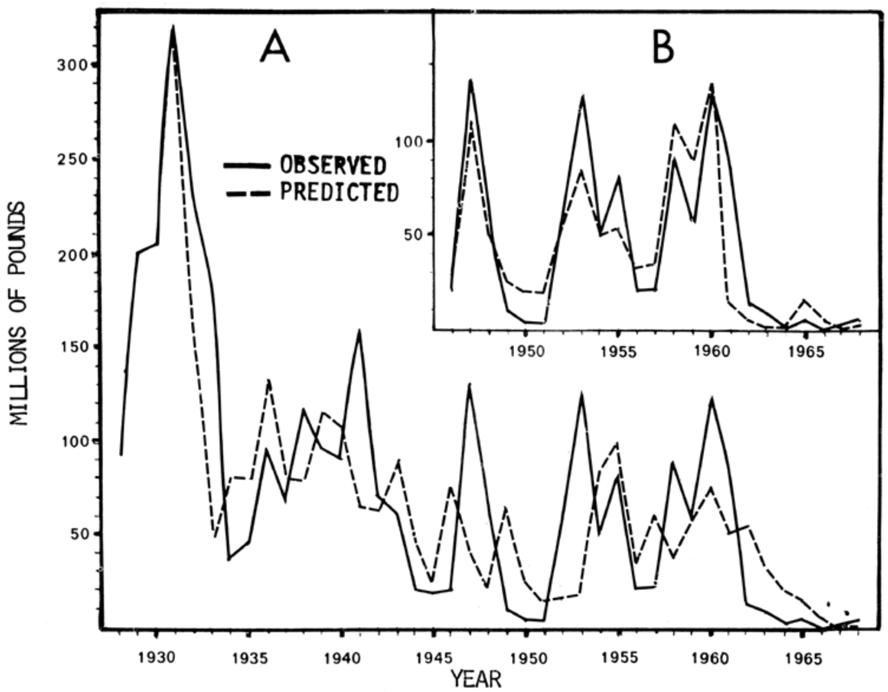
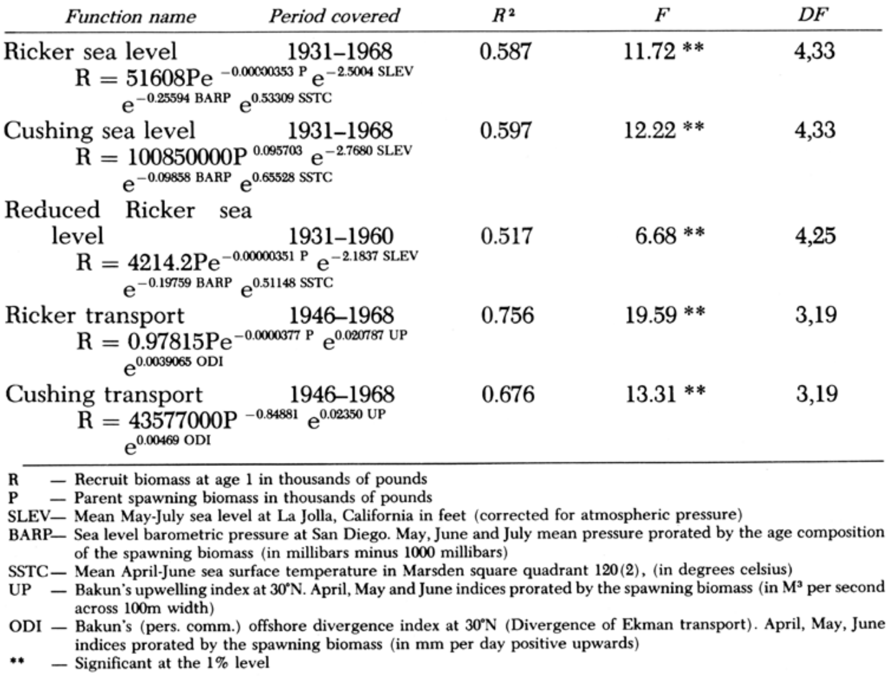


FIGURE 19. Observed and predicted recruitment of Pacific mackerel A. Ricker sea level model, B. Ricker transport model.

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

TABLE 19. Environmental-dependent Spawner-recruit Functions



Function name	*Period covered*	R^2	*F*	*DF*
Ricker sea level $R = 51608Pe^{-0.00000353\ P}\ e^{-2.5004\ SLEV}$ $e^{-0.25594\ BARP}\ e^{0.53309\ SSTC}$	1931–1968	0.587	11.72 **	4,33
Cushing sea level $R = 100850000P^{0.095703}\ e^{-2.7680\ SLEV}$ $e^{-0.09858\ BARP}\ e^{0.65528\ SSTC}$	1931–1968	0.597	12.22 **	4,33
Reduced Ricker sea level $R = 4214.2Pe^{-0.00000351\ P}\ e^{-2.1837\ SLEV}$ $e^{-0.19759\ BARP}\ e^{0.51148\ SSTC}$	1931–1960	0.517	6.68 **	4,25
Ricker transport $R = 0.97815Pe^{-0.0000377\ P}\ e^{0.020787\ UP}$ $e^{0.0039065\ ODI}$	1946–1968	0.756	19.59 **	3,19
Cushing transport $R = 43577000P^{-0.84881}\ e^{0.02350\ UP}$ $e^{0.00469\ ODI}$	1946–1968	0.676	13.31 **	3,19

R — Recruit biomass at age 1 in thousands of pounds
P — Parent spawning biomass in thousands of pounds
SLEV— Mean May-July sea level at La Jolla, California in feet (corrected for atmospheric pressure)
BARP— Sea level barometric pressure at San Diego. May, June and July mean pressure prorated by the age composition of the spawning biomass (in millibars minus 1000 millibars)
SSTC— Mean April-June sea surface temperature in Marsden square quadrant 120(2), (in degrees celsius)
UP — Bakun's upwelling index at 30°N. April, May and June indices prorated by the spawning biomass (in M^3 per second across 100m width)
ODI — Bakun's (pers. comm.) offshore divergence index at 30°N (Divergence of Ekman transport). April, May, June indices prorated by the spawning biomass (in mm per day positive upwards)
** — Significant at the 1% level

TABLE ***19. Environmental-dependent Spawner-recruit Functions***

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 suitable-sized 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 late-larval 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 density-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.

spawning season by the survivors from earlier spawning. This type of mortality would reduce the number of recruits-per-spawner 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.

5. COMPUTER SIMULATIONS

5.1. 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-per-recruit model based on the yield equations described by Beverton and Holt (1957) and as revised by Ricker (1975). ISOE calculates 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). QUOTAE 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 $M = 0.5$ was used in all simulations. Spawner-recruit functions used in the simulations will be presented later and they included density-dependent functions and density-environmental-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.

5.2. 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 ¼ of that which occurs with no fishery (Figure 20B).

5.3. 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 100th year. Simulations with all of the above models had stabilized by the 12th to the 50th year. Yields during the 90th to 100th 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-recruit

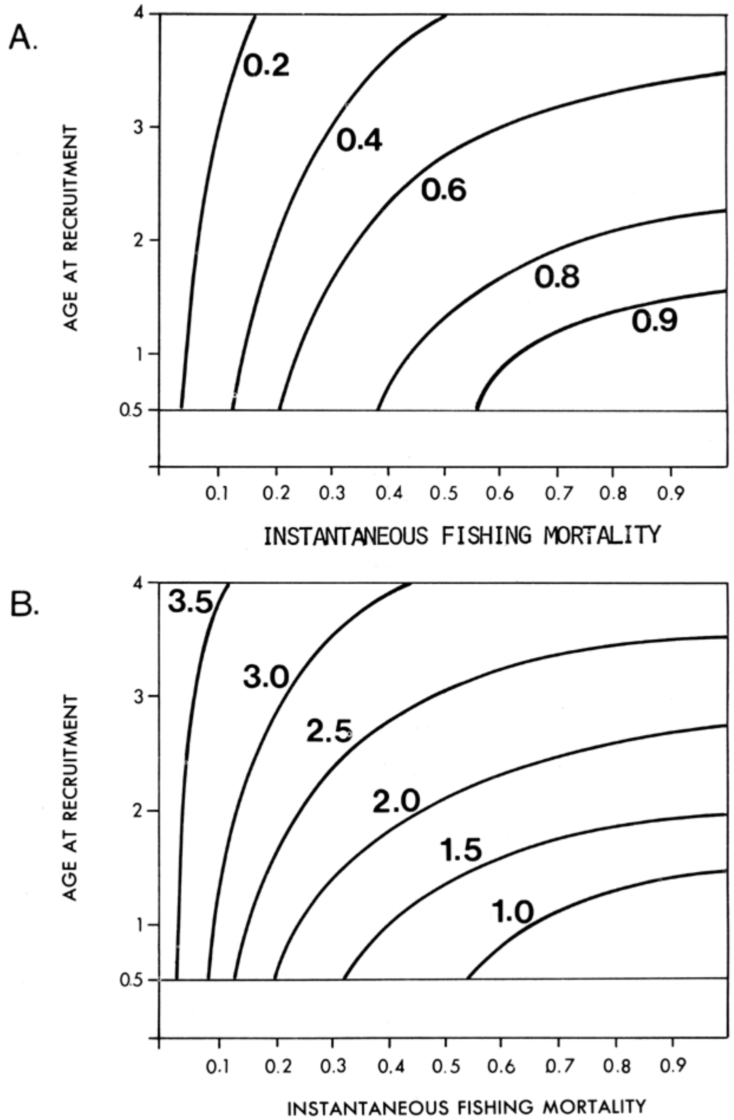


FIGURE 20. Isopleth model with M = 0.5; A. Yield per unit weight of age 1 recruits; B. Resultant spawning biomass per unit weight of age 1 recruits.

FIGURE ***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.***

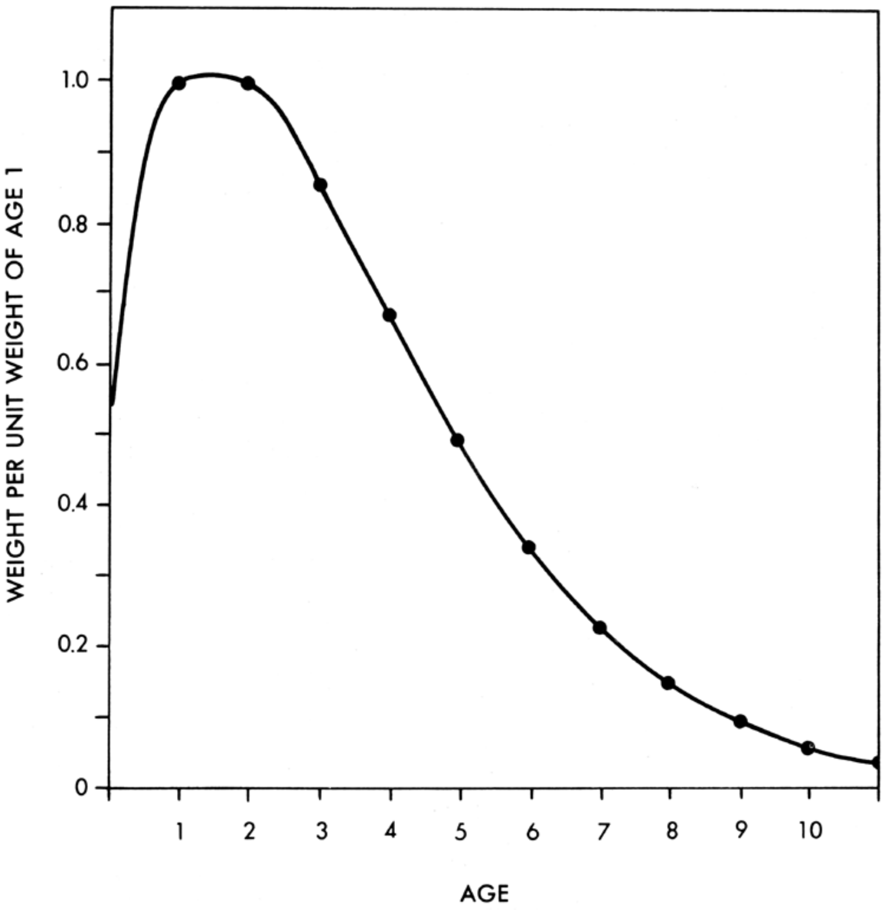


FIGURE 21. Pacific mackerel biomass curve with no fishery and M = 0.5.

*FIGURE **21. Pacific mackerel biomass curve with no fishery and M = 0.5.***

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 spawner-recruit 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

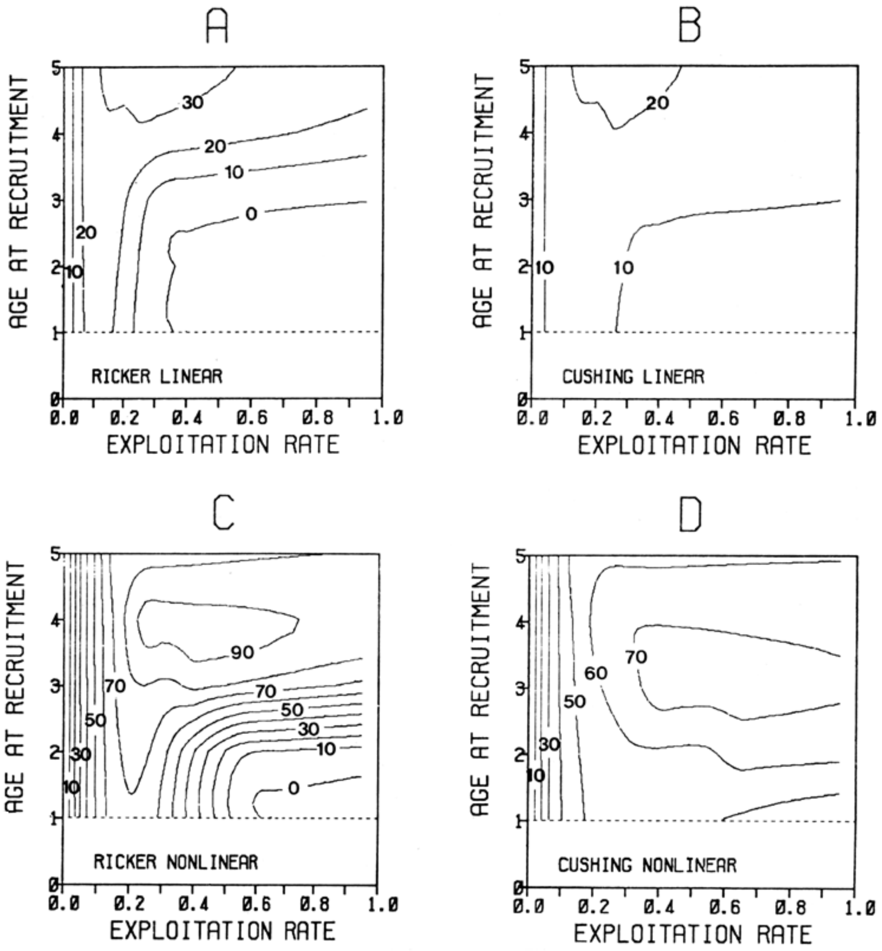


FIGURE 22. **QUOTAE equilibrium yield isopleths with density-dependent spawner-recruit functions (Yield in millions of lbs)**

*FIGURE **22. QUOTAE equilibrium yield isopleths with density-dependent spawner-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.

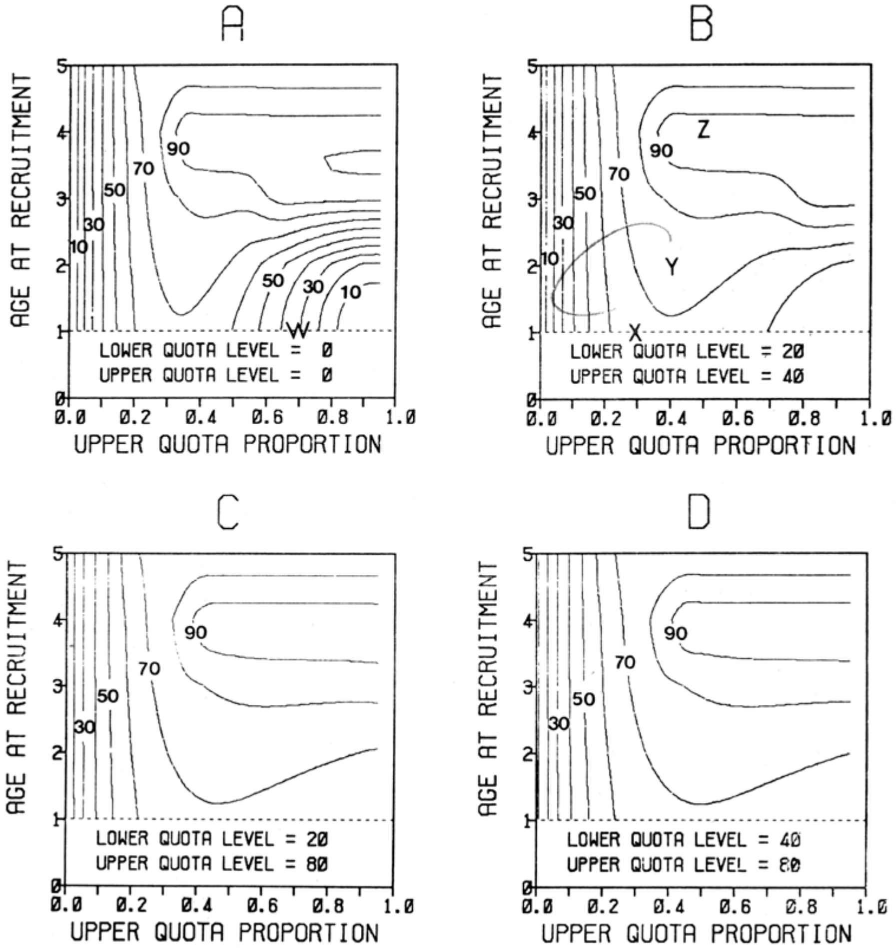


FIGURE 23. QUOTAE equilibrium yield isopleths, at four different sets of quota levels with the Ricker nonlinear model (Yield in millions of lbs, quota based on spawning biomass)

FIGURE ***23. QUOTAE equilibrium yield isopleths, at four different sets of quota 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 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.

5.4. 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°N.

The similarity of the yield isopleths in four simulations with the nonlinear Ricker sea level function and varying quota levels suggests that long-term 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.

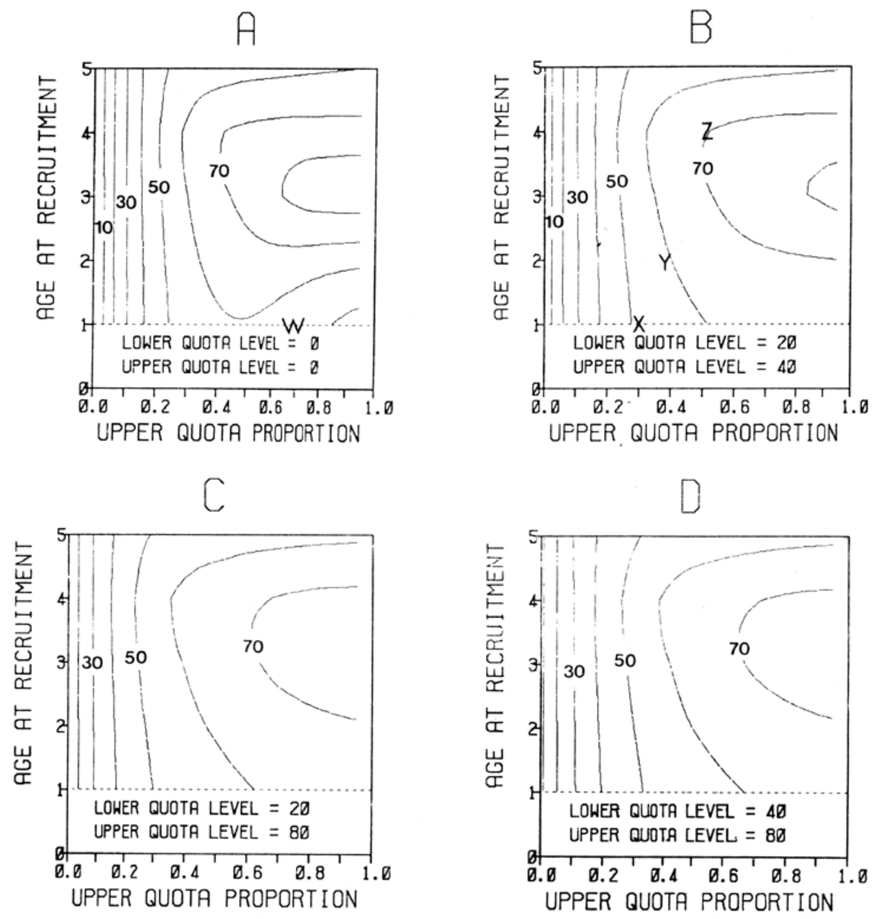


FIGURE 24. **QUOTAE mean yield isopleths (1931–1968), at different sets of quota levels, with the Ricker sea level model. (Yield in millions of lbs, quota based on spawning biomass)**

FIGURE ***24. QUOTAE mean yield isopleths (1931–1968), 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.

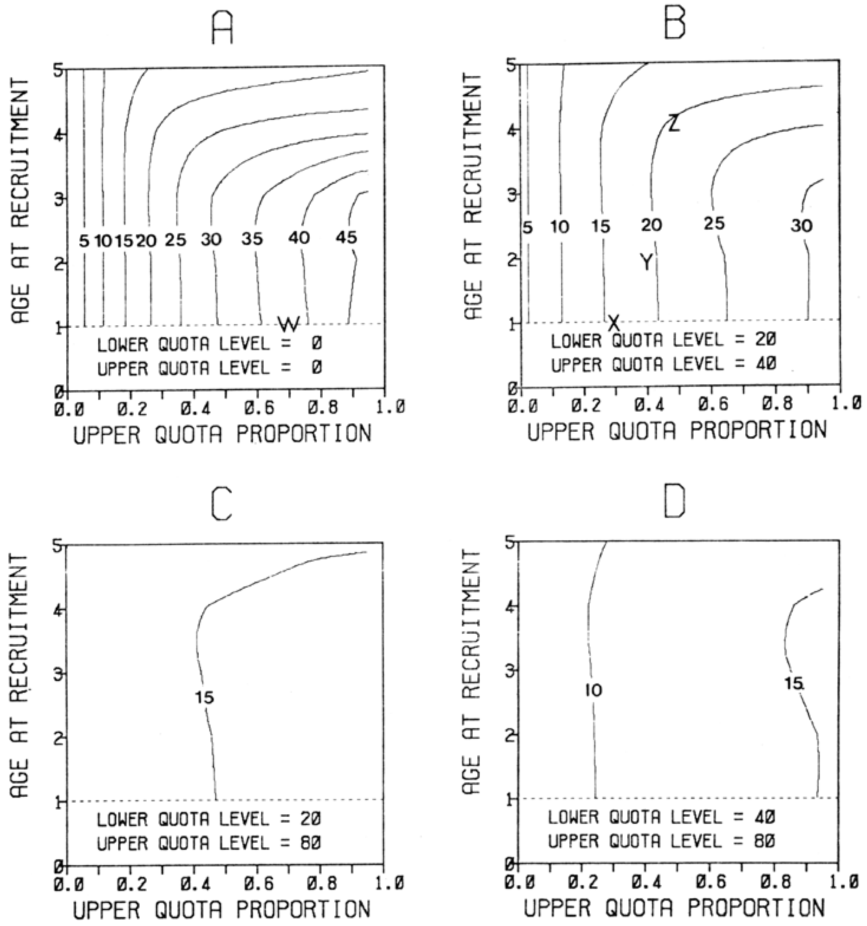


FIGURE 25. QUOTAE mean yield isopleths (1946–1968), at four different sets of quota levels, with the Ricker transport model (Yield in millions of lbs, quota based on spawning biomass)

*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)***

5.5. 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 environmental-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 density-dependent 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 annual yield under different management options. Figures 26 and 27 show simulations with the Ricker sea level, reduced Ricker sea level and Ricker transport

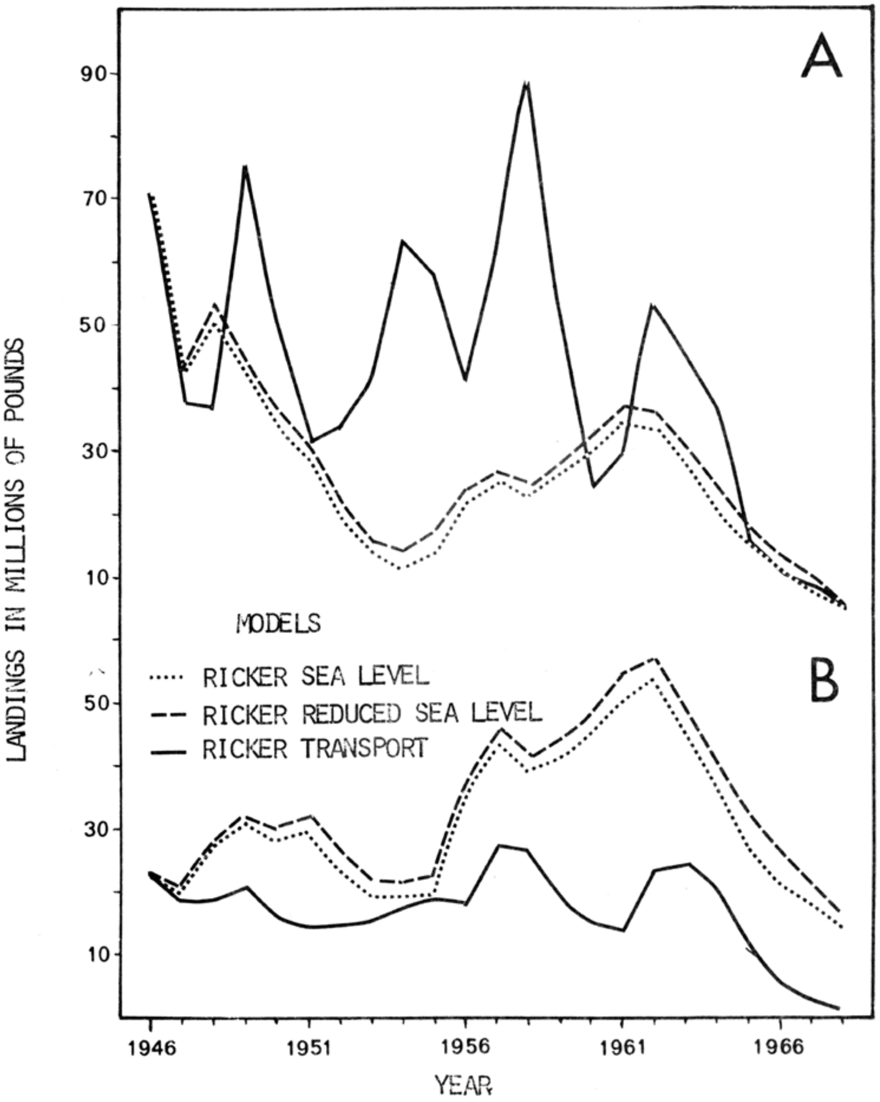


FIGURE 26. QUOTAE simulations (1946–1968); A. Recruitment at age 1, no minimum quota level and a quota proportion of 0.7 (w in figs 21A and 22A) B. Present California Regulations recruitment at age 1 and an upper quota proportion of 0.3 (x in figs 21B and 22B)

*FIGURE **26. QUOTAE simulations (1946–1968); A. Recruitment at age 1, no minimum quota level and a quota proportion 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)***

recruit functions. Simulations for each recruitment function are shown with four different management options. The first option (Figure 26A) 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 26B, 27).

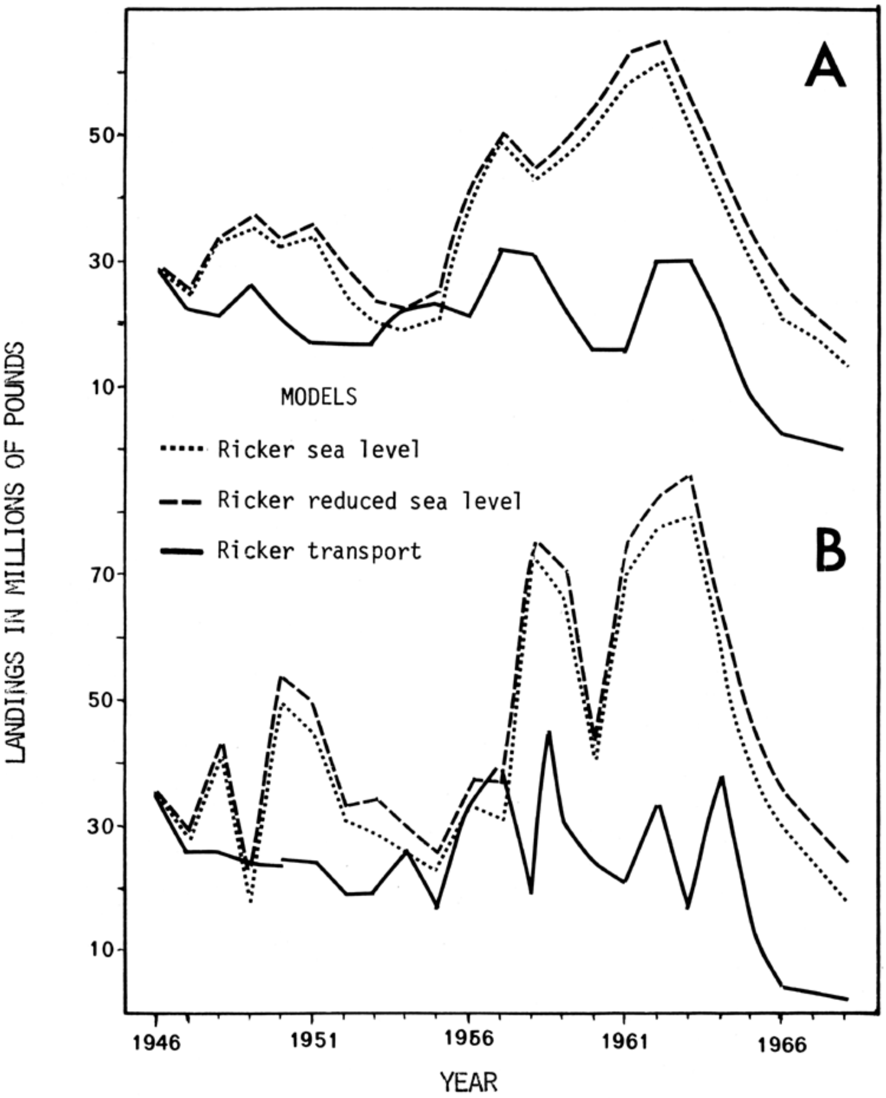


FIGURE 27. **QUOTAE simulations (1946–1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 (y in figs 21B and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 (z in figs 21B and 22B)**

FIGURE ***27. QUOTAE simulations (1946–1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 (y in figs 21B and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 (z in figs 21B 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 (1931–1968). 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 heavy exploitation rate on the 4-year-olds. With this option almost the entire yield is 4-year-olds and therefore the annual yield is erratic because 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 environmental-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.

6. DISCUSSION

6.1. 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 environmental-dependent components (Table 19) are considerably better than the density-dependent 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 than the Ricker sea level models and the density-dependent 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 spawner-recruit model have very great differences in their density-dependent and compensatory terms.

1946–1968 $R = 1.123Pe^{-0.0000169\,P}$

1928–1968 $R = 0.508Pe^{-0.00000214\,P}$

The 1946–1968 model has a much steeper 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 (Figure 26B) and smaller yields when the exploitation rate is moderate (Figures 26B, 27). The compensatory term (e^{-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)	$e^{-0.00000253 P}$	$e^{-0.00000353 P}$	$e^{-0.0000377 P}$
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°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°N in the center of abundance of Pacific mackerel could be inhibitory to survival of Pacific mackerel larvae. Either downwelling or the formation of fronts conceivably could result in increased larval mortality.

The sea level models do not have as good statistical fits as do the transport models; however, they are fitted to data that include the entire range of observed spawning biomass. The environmental variables in the sea level model (sea level, barometric pressure and sea surface temperature) are correlated with the real environmental variables that control recruitment, but with the exception of sea surface temperature they are not 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-term increases in sea level at La Jolla and San Diego. The trend in increasing sea level could be caused by land subsidence in the La Jolla-San Diego area or a wide range of oceanographic and atmospheric factors. It is possible that the negative correlation is affected by the opposing trends of increasing sea level and decreasing population of Pacific mackerel that occur 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 1958–1969, at San Diego were analyzed by Huang (1972). He suggested that geostrophic flow provided the major contribution to the differences in sea level. High correlations between geostrophic flow and sea level were also found during the Coastal Upwelling Experiment (CUE); increased southward flow was associated with decreased sea level (Smith, 1974). It therefore appears that the correlation between 1n (R) and sea level is a measure of the underlying relationship between recruitment in Pacific mackerel and geostrophic transport. Increased geostrophic flow in the California Current would be expected to increase the southerly advection of nutrient- and plankton-rich water from the major upwelling regions off of central and northern California. Therefore the survival and growth of larvae in the Southern California Bight and Baja California region should be enhanced by increased geostrophic flow.

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

The positive correlation between sea surface temperature and recruitment is expected. Warm SST should favor recruitment in the California 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 SST is influenced by the spacing of upwelling events, being lower if upwelling is more continuous and higher if upwelling events are followed by periods of calm weather with considerable 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 unrelated to upwelling in the northern Baja California 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 equilibrium yield 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 sea level spawner-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 California 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, yields 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 Model is a maximum of 75 million pounds (34,000 metric tons) at an upper quota 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 equilibrium 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 75% 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 period for which the models were fitted. Unfortunately good quality population estimates are not available for the period of 1970–1975. This lack of data was caused by the moratorium on the commercial fishery. The moratorium halted the market 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 analysis. Available estimates on the recent spawning biomass are based on small scale tagging studies, 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 environmental conditions greatly favored recruitment. Moderately good environmental conditions were predicted in 1971, 1972 and 1974.

6.2. ALTERNATIVE MANAGEMENT PLANS

Pacific mackerel management policies that could be developed with the 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. Equilibrium 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 ($E = 0.3$ to 0.6) and an age at recruitment of age 3 or 4. With a management policy based on a maximum yield per recruit 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 predict that yields would be well below MSY.

Simulations with a wide range of quota options and the environmental-dependent recruitment models suggest that no management policy is likely to stabilize the yield at reasonably high levels. The best management policy therefore appears to be one that will reduce the possibility of future population collapses and at the same time achieve a maximum long-term yield. That is a policy that will reduce the exploitation rate 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 scope of the present work. However, in the absence of such analyses we feel that the list of potentially optimum management policies can be reduced to three alternatives. These alternatives are maximum long-term yield 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 available to the fishery and the fishing fleet has demonstrated that it is capable of harvesting Pacific mackerel at rates in excess of their reproductive potential. The economics of the fishery are primarily dependent upon relationships with the more abundant species in the fishery (i.e., presently anchovy). In addition the price for Pacific mackerel has traditionally been higher than the price for the more abundant species in the fishery. Therefore, economics are unlikely to be the limiting factor in the Pacific mackerel fishery and maximum economic yield may approach maximum biological yield.

The three alternative management policies (Table 20) are based on the quota proportions that resulted in the maximum predicted long-term yield with an age at recruitment of 1, 2 and 3. All three management policies contain portions of the present California regulation. Specifically they maintain the present moratorium, or lower quota level, at 20 million pounds spawning biomass to ensure a viable sport fishery. They have a lower quota proportion of 0.2 and an upper quota level of 40 million pounds to allow only a minor fishery when the spawning biomass is relatively small.

The success in describing past recruitment in Pacific mackerel with statistical fits to environmental and population data does not prove that the factors found to be associated with recruitment are those that control recruitment. It is also possible that these environmental factors may not continue to be associated with recruitment in future years. The tentative decision to accept the hypothesis that recruitment can be predicted with more accuracy if the associated environmental 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 Alternative 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 tons 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 .

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[*] It should be noted that the alternative management options are for the total catch, including the sport and commercial fisheries of Mexico and California.

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
  - Largest long-term yield
  - 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 Pacific sardine and the Pacific mackerel.

7. REFERENCES

Aasen, Kenneth D. 1967. Review of the pelagic wet fisheries for the 1963–64, 1964–65, 1965–66 seasons. Mar. Res. Comm., Calif. Coop. Ocean. Fish. Invest., Rept., 11: 21–22.

Abramson, N. J. 1971. Computer programs for fish stock assessment. FAO (Food and Agric. Organ., U.N.) Fish. Tech. Pap., 101: 1–154.

Ahlstrom, E. H. 1954. Distribution and abundance of eggs and larvae populations of the Pacific sardine. U.S. Fish and Wildl. Ser., Fish. Bull., 93 (56): 83–140.

Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish and Wildl. Ser., Fish. Bull., 161 (60): 107–146.

Ahlstrom, Elbert H., J.L. Baxter, J.D. Isaacs, and P.M. Roedel. 1967. Report of the CalCOFI Committee. Mar. Res. Comm., Calif. Coop. Ocean. Fish. Invest., Rept., 11: 5–9.

Allen, K. Radway. 1973. The influence of random fluctuations in the stock-recruitment relationship on the economic return from salmon fisheries. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer, 164: 350–359.

Bakun, Andrew. 1973. Coastal upwelling indices, west coast of North America, 1946–71. U.S. NOAA Tech. Rept., NMFS, SSRF, 671: 1–103.

Bakun, Andrew. 1975. Daily and weekly upwelling indices, west coast of North America, 1967–73. U.S. NOAA Tech. Rept., NMFS, SSRF, 693: 1–114.

Bakun, Andrew, and Craig S. Nelson. In Press. Climatology of upwelling-related processes off Baja California. Paper presented at A Symposium on Fisheries Science, Auto. Univ. of Baja Calif., February 1975. Ms on file at Southwest Fisheries Center, La Jolla, Calif., 75p.

Beverton, R. J. H. 1963. Maturation, growth and mortality of clupeid one engraulid stocks in relation to fishing. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer, 154: 44–67.

Beverton, R. J. H., and S. J. Holt. 1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer, 140 (1): 67–83.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish., Fish. Invest., Ser. 2 (19): 533.

Beverton, R. J. H., and S. J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: Wolstenholme, G. E. W. and M. O'Connor. CIBA Foundation Colloquia on Ageing, Vol. 5, The Lifespan of Animals. J. and A. Churchill Ltd. London. 324p.

Blunt, C.E., and Richard H. Parrish. 1969. The Pacific mackerel fishery: A summary of biological knowledge and the current status of the resource. Calif. Dept. Fish and Game, MRO Ref., (69–7): 1–25.

California, State of, Marine Research Committee. 1952. Calif. Coop. Sardine Res. Prog., Prog. Rept., 1 January 1951 to 30 June 1952. Sacramento, State Printer. 51p.

Clark, Colin W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. Cons. Perm. Int. Explor. Mer, J., 36 (1): 7–14.

Clark, Frances N. and John C. Marr. 1955. Population dynamics of the Pacific sardine., p. 11–48. *In* California, State of, Marine Research Committee. 1955. Calif. Coop. Ocean. Fish. Invest., Prog. Rept., 1 July 1953–31 March 1955. Sacramento, State Printer.

Croker, Richard S. 1933. The California mackerel fishery. Calif. Div. Fish and Game, Fish Bull., 40: 1–149.

Croker, Richard S. 1938. Historical account of the Los Angeles mackerel fishery. Calif. Div. Fish and Game, Fish Bull., 52: 1–62.

Cushing, D. H. 1971. The dependence of recruitment on parent stock in different groups of fishes. Cons. Perm. Int. Explor. Mer, J., 33: 340–362.

Cushing, D. H. 1974. The possible density-dependence of larval mortality and adult mortality in fishes, p. 103–111. *In* J. H. S. Blaxter, The Early Life History of Fish. Springer-Verlag. New York.

Dixon, W. J. (ed.). 1975. BMDP Biomedical computer programs. Univ. of Calif. Press, Berkeley. 792p.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons Inc., New York. 407p.

Fitch, John E. 1951. Age composition of the southern California catch of Pacific mackerel 1939–40 through 1950–51. Calif. Dept. Fish and Game, Fish Bull., 83: 1–73.

Fitch, John E. 1952. The decline of the Pacific mackerel fishery. Calif. Fish and Game, 38(3): 381–389.

Fitch, John E. 1953a. Age composition of the southern California catch of Pacific mackerel for the 1951–52 season. Calif. Fish and Game, 39(1): 141–144.

Fitch, John E. 1953b. Age composition of the southern California catch of Pacific mackerel for the 1952–53 season. Calif. Fish and Game, 39(4): 553–558.

Fitch, John E. 1955. Age composition of the southern California catch of Pacific mackerel for the 1953–54 season. Calif. Fish and Game, 41(1): 107–112.

Fitch, John E. 1956. Age composition of the southern California catch of Pacific mackerel for the 1954–55 season. Calif. Fish and Game, 42(2): 143–148.

Fitch, John E. 1958. Age composition of the southern California catch of Pacific mackerel for the two seasons, 1955–56 and 1956–57, p. 19–26. *In* Calif. Dept. Fish and Game, Fish Bull., 106.

Fofonoff, N. P. 1960. Transport computations for the North Pacific Ocean—1958. Fish. Res. Board Can., Manuscr. Rept. Ser. (Oceanogr. Limnol.) 80: 1–81. (Processed).

Frey, Herbert W., and Eric H. Knaggs. 1973. Status of Pacific mackerel spawning population, 1973. Calif. Dept. Fish and Game. Mar. Res. Admin. Rept., (73–7): 1–16.

Fry, D. H., Jr. 1931. Mackerel, p. 35–37. *In* The commercial fish catch of California for the year 1929. Calif. Div. Fish and Game, Fish Bull., 30.

Fry, D. H., Jr. 1936a. A description of the eggs and larvae of the Pacific mackerel. Calif. Fish and Game, 22(1): 28–29.

Fry, D. H., Jr. 1936b. A preliminary summary of the life history of the Pacific mackerel. Calif. Fish and Game, 22(1):30–39.

Gulland, J.A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO (Food and Agri. Organ., U.N.) Man. Fish. Sci., 4: 1–154.

Guthrie, Donald, Carole Avery and Keith Avery. 1974. Statistical interactive programming system (SIPS). Dept. of Stat., Ore. State Univ., Tech. Rept., 36: 1–111. (Processed).

Hempel, Gotthilf. 1965. On the importance of larval survival for the population dynamics of marine food fish, *In* California, State of, Marine Research Committee. 1965. Calif. Coop. Ocean. Fish. Invest., Rept., 10.

Hicks, Steacy D. and James E. Crosby. 1974. Trends and variability of yearly mean sea level 1893–1972. U.S. NOAA Tech. Memo., NOS, 13: 1–14.

Hjort, J. 1926. Fluctuations in the year-classes of important food fishes. Cons. Perm. Int. Explor. Mer, J., 1: 5–38.

Huang, Joseph Chi Kan. 1972. Recent decadal variation in the California Current System. J. Phys. Oceanogr., 2(4): 382–390.

Hunter, John R. 1976. Report on a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. U.S. NOAA Tech. Rept., NMFS, CIRC, 395: 1–5.

Hyatt, H. 1960. Age composition of the southern California catch of Pacific mackerel, Pneumatophorus diego for the 1957–58 season. Calif. Fish and Game, 46(2): 183–188.

Jones, R., and W. B. Hall. 1973. A simulation model for studying the population dynamics of some fish species, p. 35–39. *In* M. S. Bartlett and R. W. Hiorns. The mathematical theory of the dynamics of biological populations. Academic Press. London and New York.

Klingbeil, R. A. 1976. Status of Pacific mackerel spawning population, 1976. Calif. Dept. Fish and Game, Mar. Res. Admin. Rep., (76–12: 1–22.

Klingbeil, R. A. 1977MS. Status of Pacific mackerel spawning population, 1977.

Knaggs, E. H. 1972. Southern California Pacific mackerel fishery and age composition of commercial landings during the 1968–69 and 1969–70 seasons. Calif. Fish and Game, 58(2): 116–120.

Knaggs, E. H. 1974. Status of Pacific mackerel spawning population, 1974. Calif. Dept. Fish and Game, Mar. Resour. Adm. Rep., (74–5): 1–10.

Knaggs, Eric H., and Richard H. Parrish. 1973. Maturation and growth of Pacific mackerel, Scomber japonicus Houttuyn. Calif. Fish and Game, 59(2): 114–120.

Knaggs, E. H. and J. S. Sunada. 1975. Status of Pacific mackerel spawning population, 1975. Calif. Dept. Fish and Game, Adm. Rept., (75–5): 1–12.

Kramer, David. 1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952–56. Fish. Bull., U.S., 60(174): 393–438.

Kramer, David. 1969. Synopsis of the biological data on the Pacific mackerel, Scomber japonicus Houttuyn (northeast Pacific). FAO (Food and Agri. Org., U.N., Fish. Synopsis, 40: 1–18.

Lasker, Reuben. 1965. The physiology of Pacific sardine embryos and larvae. Mar. Res. Comm., Calif. Coop. Ocean. Fish. Invest. Rept., 10: 96–101.

Lasker, Reuben. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S., 73(3): 453–462.

Lasker, Reuben. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 1973. In Press.

Longhurst, Alan R. 1969. Pelagic invertebrate resources of the California Current, p. 60–62. *In* California, State of, Marine Research Committee. 1969. Calif. Coop. Ocean. Fish. Invest., Rept., 13.

MacCall, Alec. 1973. The status of the Pacific mackerel resource and its management. Calif. Dept. Fish and Game, Mar. Res. Tech. Rept., 12: 1–13.

MacGregor, John S. 1966. Synopsis on the biology of the jack mackerel (Trachurus symmetricus) . U.S. Fish and Wildl. Serv., Spec. Sci. Rep., Fish., 526: 1–16.

MacGregor, John S. 1975. Estimation of fish biomass from egg and larvae surveys. Anchovy Workshop Meeting July 21–22, 1975. Contribution No. 3. Southwest Fisheries Center, National Marine Fisheries Service. (Processed).

Mais, K. F. 1974. Pelagic fish surveys in the California Current. Calif. Dept. Fish and Game, Fish Bull., 162: 1–79.

Messersmith, James D. 1969. A review of the California anchovy fishery and results of the 1965–66 and 1966–67 reduction seasons, p. 6–32. *In* Calif. Dept. Fish and Game, Fish Bull., 147.

Messersmith, James D., John L. Baxter, and Philip M. Roedel. 1969. The anchovy resources of the California Current Region off California and Baja California, p. 32–38. *In* California, State of, Marine Research Committee. 1969. Calif. Coop. Ocean. Fish. Invest., Rept., 13.

Murphy, G. I. 1965. A solution of the catch equation. Fish. Res. Board Can., J., 22: 191–202.

Murphy, G. I. 1966. Population biology of the Pacific sardine (Sardinops caerulea) . Proc. Calif. Acad. Sci., 34(1): 1–34.

Nelson, Craig S. 1976. Wind stress and wind stress curl over the California Current. M.S. Thesis Naval Postgraduate School, Monterey, Calif. 136p.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1976. Larval transport and year-class strength of Atlantic menhaden. Fish. Bull., U.S., 75(1): 23–41.

Parrish, Richard H. 1968. Current status of Pacific mackerel, p. 9–14. *In* Report on the 1968 CalCOFI Conference. John D. Isaacs, Chairman. Scripps Institution of Oceanography, La Jolla, California.

Parrish, Richard H. 1974. Exploitation and recruitment of Pacific mackerel, Scomber japonicus in the northeastern Pacific, p. 136–140. *In* California, State of, Marine Research Committee. 1974. Calif. Coop. Ocean. Fish. Invest., Rept., 17.

Parrish, Richard H. and E. H. Knaggs. 1971. Revision of the age composition of the southern California catch of Pacific mackerel for the 1958–59 through 1963–64 seasons. Calif. Fish and Game, 57(3): 182–201.

Parrish, Richard H. and E. H. Knaggs. 1972. The southern California Pacific mackerel fishery and age composition of the catch for the 1964–65 through 1967–68 seasons. Calif. Fish and Game, 58(1): 13–21.

Calif. marine sportfishing survey: Private boats, 1964; shoreline, 1965–66. Calif. Dept. Fish and Game, Fish Bull., 143: 1–42.

Pinkas, Leo, J. C. Thomas, and J. A. Hanson. 1967. Marine sportfishing survey of southern California piers and jetties, 1963. Calif. Fish and Game, 53(2): 88–104.

Radovich, J. 1961. Relationships of some marine organisms of the northeast Pacific to water temperatures particularly during 1957 through 1959. Calif. Dept. Fish and Game, Fish Bull., 112: 1–62.

Reid, Joseph L. and Arnold W. Mantyla. 1976. The effects of the Geostrophic flow upon coastal sea elevations in the northern North Pacific Ocean. Journal Geophys. Res., 81(18): 3100–3110.

Ricker, W. E. 1973. Linear regressions in fishery research. Fish. Res. Board Can., J. 30: 409–434.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull., 191: 1–382.

Roedel, Phil M. 1952. A review of the Pacific mackerel (Pneumatophorus diego) fishery of the Los Angeles region with specific reference to the years 1939–1951. Calif. Fish and Game, 38(2): 253–273.

Roedel, P. M. and D. C. Joseph. 1954. The Pacific mackerel fishery in the 1951–52 and 1952–53 seasons. Calif. Fish and Game, 40(1): 55–59.

Saur, J. F. T. 1972. Monthly sea level differences between the Hawaiian Islands and the California Coast. Fish. Bull., U.S., 70(3): 619–636.

Scofield, W. L. 1947. Drift and set line fishing gear in California. Calif. Div. Fish and Game, Fish Bull., 66: 1–38.

Scofield, W. L. 1951. Purse seines and other roundhaul nets in California. Calif. Dept. Fish and Game, Fish Bull., 81: 1–83.

Sette, Oscar E. 1943. Biology of the Atlantic mackerel (Scomber scombrus) of North America. Part II. Migrations and habits. U.S. Fish and Wildl. Ser., Fish. Bull., 51(49): 251–358.

Smith, Paul E., Elbert H. Ahlstrom. 1970. The saury as a latent resource of the California Current, p. 88–130. *In* California, State of, Marine Research Committee, 1970. Calif. Coop. Ocean. Fish. Invest., Rept., 14.

Smith, Robert L. 1974. A description of current, wind, and sea level variations during coastal upwelling off the Oregon coast, July-August 1972. J. Geophys. Res., 79(3): 435–443.

Sverdrup, H. U. 1947. Wind-driven currents in a baroclinic ocean; with application to the equatorial currents of the eastern Pacific. Pro. Nat. Acad. Sci., 33: 318–326.

Talbot, G. B. 1973. The California sardine-anchovy fisheries. Amer. Fish. Soc., Trans., 102(1): 178–187.

Tomlinson, P. K. 1970. A generalization of the Murphy catch equation. Fish. Res. Board Can., J., 27: 821–825.

Walters, Carl J. 1969. A generalized computer simulation model for fish population studies. Amer. Fish. Soc., Trans., 98(3): 505–512.

Walters, Carl J. 1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. Fish. Res. Board Can., J., 32(10): 1777–1784.

Young, Parke H. 1969. The California partyboat fishery 1947–1967. Calif. Dept. Fish and Game, Fish Bull., 145: 1–91.

APPENDICES

APPENDIX I. YIELD PER RECRUIT SIMULATION PROGRAM

```
     PROGRAM ISOE (INFUT, OUT-
     PUT, PUNCH)
C    YIELD PER RECRUIT MODEL       RH PARRISH MAY 10,1976
C    CONTROL CARD VARIABLE DE-
     SCRIPTION
C    NRUNS                         NUMBER OF RUNS TO BE MADE
C    KARD                          CARD OUTPUT KARD=1 NO CARD OUTPUT KARD=0
C    TITLE                         TITLE LIMITED TO 80 CARD COLUMNS
C    IBERT                         IBERT=1 IF BERTALANFFY GROWTH EQUATION IS USED
C    MAXA                          MAXIMUM ARE OF THE SPECIES
C    IBT                           MINIMUM AGE AT RECEUITMENT
C    IET                           MAXIMUM AGE AT RECEUITMENT
C    XMS                           STARTING INST. NATURAL MORTALITY RATE (M)
C    XMI                           M INCREMENT
C    NM                            NUMBER CF M S TO EE RUN
C    EINC                          EXPLOITATION RATE INCREMENT
C    NE                            NUMBER OF EXPLOITATION RATES TO BE RUN
C    LINF                          BERTALANFFY CONSTANT
C    K                             BERTALANFFY CONSTANT
C    TO                            BERTALANFFY CONSTANT
C    A                             LENGTH-WEIGHT CONSTANT
C    B                             LENGTH-WEIGHT CONSTANT
C    PS(I)                         PROPORTION SPAWNING BY AGE GROUP
C                                  ONLY INPUT FOR AGES IET TO 10 (10+ ARE ASSUMED 1.0)
C
      COMMON M, IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50) 1,KARD
      DIMENSION BC(20,50),PS(51),G(51),GH(51),WT(51),WH(51),XL(51), 1XLH(51),TOT(20),TITLE(20)
      INTEGER T
      REAL M,LINF,K
      READ 399, NRUNS, KARD
399   FORMAT (212)
1     NRUNS=NRUNS-1
      READ 400,(TITLE(I),I=1,20)
400   FORMAT(10A8,/,10A8)
      PRINT 401,(TITLE(I),I=1,20)
401   FORMAT (1H1,//,1X,10A8,/,1X,10A8)
      READ 100,IBERT,MAXA,IBT,IET,XMS,XMI,NM,EINC,NE
100   FORMAT (4I3,2F5.3,I3,F5.3,I3)
      IF (IBERT.NE.1) GO TC 2
      READ 101 , LINF,K,TC,A,B
101   FORMAT (F10.2,F10.6,F15.9,F15.12,F10.6)
      PRINT 102, LINF,K,TO,A,B
102   FORMAT (T5,*BERTALANFFY CONSTANTS*,/,T8,*L INFINITY =*,F10.2,/, 1T8,*K =*,F10.6,/,T8,*TC =*,F10.6,//,15,*LENGTH-WEIGHT CONSTANTS
      2*,/,T8,*A=*,F15.12,/,T8,*B=*,F10.6,/)
      GO TO 4
C     ADD OTHER INPUT OPTION
2     CONTINUE
      READ 666, (WT(N),N=1,15)
666   FORMAT (10F6.2)
      READ 668, (PS(N),N=1,10)
668   FORMAT (10F6.4)
      DO 670 N=11,51
670   PS(N)=1.0
      DO 671 N=1,14
      TEMP=WT(N+1) / WT(N)
671   G(N)=GH(N)=TEMP
      DO 672 N=15,MAXA
      GH(N)=G(N)=TEMP
672   WT(N)=WT(N-1)* TEMP
      IF (IBERT.EQ.0) GO TO 7
      GO TO 38
4     DO 5 I-1,51
5     PS(I)=1.0
      READ 103, (PS(I),I=IBT,10)
103   FORMAT(10F6.4)
      IA=MAXA+1
      DO 6 N=IET,IA
      XL(N) = LINF* (1-EXP(-K*N + K*TO))
      U = N + 0.5
      XLH(N) = LINF* (1-EXP(-K*U + K*TO))
      WT(N) = A*XL(N) **E
      WH(N) = A*XLH(N)**E
      GH(N) = WH(N)/WT(N)
      IF (N.GT.IBT) G(N-1) = WT(N)/WT(N-1)
6     CONTINUE
C     NOTE THAT THE LNITS ARE DEPENDENT UPON INFUT
7     PRINT 200
200   FORMAT (//,1X,*AGE LENGTH WEIGHT PS GROW GROWH*)
      DO 8 N=IBT,MAXA
      PRINT 104,N,XL(N),WT(N),PS(N),G(N),GH(N)
104   FORMAT (1X,I3,2F9.2,3F9.3)
8     CONTINUE
      M=XMS-XMI
```

```
      DO 26 MM=1,NM
      TOT(MM)=0
      M=M+XMI
      E=-EINC
      DO 24 J=1,NE
      E=E + EINC
      F=E $ N=0
      IF(E.EG.0) GO TO 12
10    N=N+1 $ IF(N.GT.50) GO TO 90
      EV=EVAL(F)
      E1=EVAL(F-0.01) $ E2=EVAL(F+0.01)
      SLOPE=(E2-E1) /0.02
      DIFFE=EV-E
      F=F-DIFFE/SLOFE
      IF(ABS(DIFFE).GT.0.000001) GO TO 10
12    FST(J)=F
      Z=M+F
      DO 22 I=IBT,IET
      HS = C = 0
      POP=1000
      DO 20 T=IBT,MAXA
      IF(I.GT.IBT) GO TO 15
      IF(F.EG.0) TOT(MM)=TOT(MM)+PCP
      IF(F.EG.0) BC(MM,T)=POP
15    HS=HS + POP*PS(T)
      IF (T.LT.I) GO TO 14
      W=Z
      FF=F
      GO TO 15
14    W=M
      FF=0
16    D=POP*(1-EXP(-W))
      IF(FF.EQ.0) GO TO 18
      C=D*(FF/Z)*GH(T) + O
18    POP=(PCP-D) * G(T)
20    CONTINUE
      IS(I,J) = HS
      IY(I,J) = C
22    CONTINUE
24    CONTINUE
      PRINT 105,M
105   FORMAT (//,31X,*YIELD PER METRIC TON OF RECRUITS M=*,F6.4,//, 1* AGE*,36X,*(IN KG.)*,/,* AT*,/,* REC.*)
      CALL OUTISO(IY)
      PRINT 110,M
110   FORMAT (//,31X,*SPAWNING BIOMASS OVER LIFE OF COHORT M=*,F6.4, 1//,* AGE*,/,* AT*,/,* REC.*)
      CALL OUTISO(IS)
26    CONTINUE
      PRINT 111
111   FORMAT (//,31X,*BIOMASS CURVES WITH NO FISHING MORTALITY*//,1X, 1*AGE INSTANTANEOUS NATURAL MORTALITY*,//)
      M=XMS-XMI
      DO 28 N=1,NM
      M=M+XMI
28    FT(N)=M
      PRINT 112,(FT(N),N=1,NM)
112   FORMAT (7X,20F6.2)
      IYR=IBT-1
      DO 30 I=IBT, MAXA
      IYR=IYR+1
      PRINT 113,IYR,(BC(MM,I),MM=1,NM)
113   FORMAT (1X,14,2X,20F6.0)
30    CONTINUE
      DO 34 MM=1,NM
      DO 32 I=IBT,MAXA
      BC(MM,I)=BC(MM,I)/TOT(MM)
32    CONTINUE
34    CONTINUE
      PRINT 115
115   FORMAT (//,31X,*PROPORTION OF THE POPULATION BY WEIGHT F=0*, 1//,* AGE INSTANTANEOUS NATURAL MORTALITY*,//)
      PRINT 112, (FT(N),N=1,NM)
      IYR=IBT-1
      DO 36 I=IBT,MAXA
      IYR=IYR+1
      PRINT 116, IYR, (BC(MM,I),MM=1,NM)
116   FORMAT (1X,I4,2X,20F6.4)
36    CONTINUE
      IF(NRUNS.GT.0) GO TO 1
      GO TO 999
38    PRINT 444
444   FORMAT (//,* OPTION NOT INSTALLED*)
90    PRINT 998
998   FORMAT(//,* ITERATIONS FOR F EXCEEDED 50 *)
999   STOP $ END
      FUNCTION EVAL(F)
      COMMON M $ REAL M
      EVAL=(1.0-EXP(-F-M)) * F/(F+M)
```

```
        RETURN $ END
        SUBROUTINE OUTISO(UT)
        COMMON M,IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50) 1,KARD
        REAL M
        DIMENSION JT(50,50)
        NN=-1
        DO 200 N=IBT,IET
        NN=NN+1
        I=IET-NN
200     PRINT 201,I,(JT(I,J),J=1,NE)
201     FORMAT (//,2X,I2,2X,20I6)
        TEM=-EINC
        DO 202 N=1,NE
        TEM = TEM+EINC
202     FT(N) = TEM
        PRINT 203,(FT(N),N=1,NE)
203     FORMAT (///,* E *,20F6.3)
        PRINT 204, (FST(N),N=1,NE)
204     FORMAT(* F *,20F6.3)
        PRINT 205
205     FORMAT(/,6X,*E = EXFLOITATION RATE, F = INST. FISHING MORT.RATE*)
        IF(KARD.EG.0) GO TO 210
        DO 206 I=IBT,IBT
206     PUNCH 207, (JT(I,J),J=1,NE)
207     FORMAT (10I8,/,10I8)
        PUNCH 208
208     FORMAT (/)
210     RETURN $ END
```

TYPICAL INPUT FOR ISOE

```
2 NUMBER OF RUNS
BOCACCIO ROCKFISH DATA FROM PHILLIPS(1964) OFG FISH BULL. 126
APRIL 14, 1976 RH PARRISH
1 30 1 10 .200 .050 3 .020 20
812.97 .14784 -0.6439 .000000012860 3.0941
000000000000 .1 .5 .8 1.0 1.0 1.0 1.0 1.0
CHILEPEPPER ROCKFISH DATA FROM PHILLIFS(1964) OFG FISH BULL. 126
APRIL 14, 1976 RH PARRISH
1 16 1 10 .300 .050 3 .020 20
552.67 .18204 -0.2283 .000000006260 3.2438
000000 .05 .3 .5 .8 1.0 1.0 1.0 1.0 1.0
```

APPENDIX II. QUOTA SIMULATION PROGRAM

```
     PROGRAM QUOTAE
     (INPUT,OUTPUT,PUNCH)
C    QUOTA SIMULATION MODEL RH
     PARRISH JUNE 15,1976
C    CONTROL CARD VARIABLE DE-
     SCRIPTIONS
C    ITO                           BEGINNING YEAR OF THE SIMULATION
C    NYRS                          NUMBER OF YEARS FOR THE SIMULATION
C    IBT                           MINIMUM AGE AT RECRUITMENT
C    IET                           MAXIMUM AGE AT RECRUITMENT
C    MAXA                          MAXIMUM AGE
C    IRUN                          CONTROL FOR OUTPUT
C                                  IRUN=0 OUTPUT IS LIMITED TO YIELD MATRICES
C                                  IRUN=1 OUTPUT IS ANNUAL SPAWNING BIOMASS + YIELD MATRICIES
C                                  IRUN=2 OUTPUT IS ANNUAL SPAWNING BIOMASS, YIELD, TOTAL
     BIOMASS AND RECRUIT BICMASS +
     YIELD MATRICIES
C    ILOGI                         ILOGI=0 FOR CONSTANT PS(1)
C                                  ILOGI=1 FOR DENSITY DEPENDENT PS(1)
C    IENV                          IENV= THE NUMBER OF ENVIRONMENTAL VARIABLES INPUT
     MAXIMUM NUMBER IS 6, FORMAT IS
     ON LINE 128
C                                  IENV=0 IF NC ENVIRONMENTAL VARIABLES ARE INPUT
C    IPRO                          IPRO=0, =1, =2 DEPENDING ON THE NO. CF PRORATED
     ENVIRONMENTAL VARIABLES,
     FORMAT IS ON LINES 133,137
C    IQSET                         SETS THE BIOMASS SEGMENT THAT THE QUOTA IS BASED ON
C                                  IQSET=0 QUOTA BASED ON SPAWNING BICMASS
C                                  IQSET=1 QUOTA BASED ON TOTAL EIOMASS
C                                  IQSET=2 QUOTA BASED ON AGE I + AGE II BIOMASS
C    RAMX                          MAXIMUM RECRUIT BIOMASS ALLOWED
C    QAL                           LOWER QUOTA LEVEL
C    QBL                           UPPER QUOTA LEVEL
C    M                             INSTANTANEOUS NATURAL MORTALITY RATE
C    SLP                           SUBLEGAL PROPORTION (SETS CATCH OF UNDERSIZED FISH)
C    QA                            LOWER QUOTA PROPORTION
C    QMIN                          MINIMUM UPPER QUOTA PROPORTION
C    QINC                          INCREMENT FOR UPPER QUOTA PROPORTION
C    NQ                            NUMBER OF QUOTA PROPORTIONS
C    BPOP(N)                       BEGINNING BIOMASS BY AGE GROUP
C    PS(N)                         PROPORTION SPAWNING BY AGE GROUP
C    G(N)                          PROPORTION ANNUAL GROWTH BY AGE GROUP
C    GH(N)                         PROPORTION GROWTH FOR HALF OF THE YEAR BY AGE GROUP
C                                  (IE AVERAGE GROWTH TO CAPTURE)
      COMMON 0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
      4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51), 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
      REAL M
      INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPCP
      READ 001,KL
001   FORMAT (12)
      DO 199 KLM=1,KL
      READ 100,ITO,NYRS,IET,IET,MAXA,IRUN,ILOGI,IENV,IPRO,IGSET, 1RMAX,QAL,GBL,M,SLP,QA,QMIN,QINC,NQ
100   FORMAT (10I4,/,3F 8.0,5F4.2,I4)
      IF (KLM.GT.1) GO TO 102
      READ 101,(BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
101   FORMAT (F6.0,3F6.4)
102   PRINT 103,M,NYRS,ITO
103   FORMAT (*1TWO STEP QUOTA SIMULATION MODEL FOR *, 1*PACIFIC MACKEREL RH PARRISH MAY 18, 1976* 1,/,* ALL FOP FIGURES INN THOUSANDS OF
      POUNDS* 3,/,* NATURAL MORTALITY M=*,F4.2,/,* SIMULATED FOR *,I4,* YEARS* 4,/,* STARTING POPULATION *,I4,//,* MODEL PARAMETERS BY AGE GROUP*
      5,/,* AGE STARTING PROPORTION PROPORTION PROPORTION 6GROWTH*,/,* GROUP POPULATION SPAWNING ANNUAL GROWTH T 7O CAPTURE*)
      PRINT 104,(N,BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
104   FORMAT (I2,F13.O,F12.3,F15.3,F18.3)
105   FORMAT(//,60H EXTINCTION CURVE FOR PS(1)=0.54*EXP(-.000071709*IPO 1P) )
      IF (ILOGI.EQ.1) PRINT 105
      IF(IQSET-1)106,108,110
106   PRINT 107
107   FORMAT(//,* QUOTA BASED ON SPAWNING BIOMASS*)
      GO TO 112
108   PRINT 109
109   FORMAT(//,* QUOTA BASED ON TOTAL BIOMASS*)
      GO TO 112
110   PRINT 111
111   FORMAT(//,* QUOTA BASED ON THE BIOMASS OF AGEI + AGEII*)
112   PRINT 113,QAL,QA,QBL
113   FORMAT (//,* LOWER QUOTA LEVEL =*,F8.0,/,* LOWER QUOTA PROPORTION= 1*,F6.3,/,* UPPER QUOTA LEVEL = *,F8.0)
      PRINT 114
114   FORMAT (//,* RECRUITMENT MODEL*,//,1X, 1* RICKER BMDP3R TRANSPORT MODEL*,/,
      PRINT 115,IBT,IET,IRUN,ILOGI,IENV,IPRO,IQSET,RMAX,SLP,MAXA,QMIN, 1QINC,NQ
115   FORMAT(//,* IBT=*,I4,/,* IET=*,I4,/,* IRUN=*,I4,/,* ILOGI=*,I4,/, 1* IENV=*,I4,/,* IPRO=*,I4,/,* IQSET=*,I4,/,* RMAX=*,F8.0,/, 2* SLP=*,F4.2,/,* MAXA=*,I4,/,*
      QMIN=*,F5.3,/,* QINC=*,F5.3,/, 3* NQ=*,I4)
      IF(KLM.GT.1) GO TO 119
      IF(IENV.GT.O) GO TO 150
      IF(IPRO.GT.O) GO TO 150
```

```
116   CONTINUE
C     BODY STARTS HERE
119   IF(NQ.EQ.1) GO TO 120
      GO TO 122
120   IU=-9
      DO 121 N=IBT, IET
121   CALL MACQE
      CALL OUTM
      STOP
122   IU=NQ $ QB=QMIN-QINC $ NL=IET-IBT+1
      DO 124 IQB=1,NQ
      QB=QB+QINC $ L=0
      DO 123 J=IBT,IET
      L=L+1
      CALL MACQE
      MAT(L,IQB)=TYIELD (L)/NYRS
123   MA(L,IQB)=ACATCH
124   CALL OUTM
      PRINT 125,NYRS
125   FORMAT (1H1,//,20X,I4,* YEAR MEAN YIELD*)
      CALL OUTMAT (MAT)
      IT=IT O+NYRS-1
      PRINT 126,IT
126   FORMAT (1H1,//,20X,*YIELD IN *,I4)
      CALL OUTMAT(MA)
      GO TO 199
150   IF(IENV.LT.1) GO TO 160
      DO 151 N=1,NYRS
151   READ 152, (ENV(N,NN),NN=1,IENV)
152   FORMAT (6F8.2)
160   IF(IPRO.GT.O) GO TO 161
      GO TO 116
161   DO 162 N=1,NYRS
162   READ 163, (ENV(N,NN),NN=7,9)
163   FORMAT (35X, 3F5.0)
      IF(IPRO.EQ.1) GO TO 116
      DO 164 N=1,NYRS
164   READ 165,(ENV(N,NN),NN=10,12)
165   FORMAT(35X,3F5.0)
      GO TO 116
199   CONTINUE
      STOP $ END
      SUBROUTINE MACQE
      COMMON 0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
      4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51), 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
      REAL M
      INTEGER ASPOF,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
      TSPOP(L) =TREC(L)=TYIELD(L)= TTPOP(L)=O
      DO 500 N=IBT,MAXA
500   POPA(N)=BPOP(N)
      DO 516 I=1,NYRS
      SPOP=ACAT CH=TPOP=O
      DO 501 N=IBT,MAXA
      POPC(N)=POPA (N)*GH(N)
501   TPOP=TPOP+POPA(N)
      IF(ILOGI.EQ.1) CALL LOGI
      DO 502 N=IBT,MAXA
502   SPOP=SPOP+POPA(N)*PS(N)
      CALL FUN
      IF (IQSET-1) 503,504,505
503   Q2=SPOP $ GO TO 506
504   Q2=TPOP $GO TO 506
505   Q2=POPA(1)+POPA(2)
506   IF(Q2.LT.GAL) GO TO 507
      GO TO 508
507   Z=M $ A=1.0-EXP (-Z)
      DO 58 N=IBT, MAXA
58    XMORT (N) = POPA(N)*A
      GO TO 512
508   CALL QUOT
      E=CQ/QPOP
      F=FVAL (E,M)
      Z=F+M $ A=1.0 -EXP(-Z)
      DO 509 N=J,MAXA
      XMORT (N) = POPA(N)*A
509   ACATCH = ACATCH + XMORT(N)*(F/Z)*GH(N)
      IF(J.GT.IBT) GO TO 510
      GO TO 512
510   E = SUBQ/SUBPOP
      F=FVAL(E,M)
      ZS=F +M $ AS=1.0 - EXP (-ZS)
      JT=J-1
      DO 511 N=IBT, JT
      XMORT (N) = POPA(N)*AS
```

```
511   ACATCH=ACATCH + XMORT(N) * (F/ZS) * GH(N)
512   NT=MAXA+2
      DO 513 N=IBT,MAXA
      NT=NT-1
513   POPA(NT)=(POPA(NT-1)-XMORT(NT-1)) * G(NT-1)
      POPA(MAXA) = POPA(MAXA) + POPA(MAXA+1)
      POPA(IBT)=REC
      TSPOP(L)=TSPOP(L) + SPOP
      TREC(L) = TREC(L) + REC
      TYIELD(L) = TYIELD(L) + ACATCH
      TTPOP(L) = TTPOP(L) + TPOP
      ASPOP(I,L) = SPOP
      AREC(I,L) = REC
      AYIELD(I,L) = ACATCH
      ATPOP(I,L) = TPOP
      IF(REC.GT.RMAX) GO TO 514
      GO TO 516
514   PRINT 515
515   FORMAT (* RECRUITMENT BLEWUP OR FAILED*)
      CALL OUTM
      STOP
516   CONTINUE
517   RETURN $ END
      SUBROUTINE FUN
      COMMON 0ITO,NYRS. TPOP,PS(51).POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M
      IF(IPRO.EQ.O) GO TO 666
      P(1)=(PS(1)*POPA(1)) /SPOP
      P(2)=(PS(2)*POPA(2))/SPOP
      P(3)=(PS(3)*POPA(3) +POPA(4) + POPA(5) +POPA(6))/SPOP
      PROA=P(3)*ENV(I,7)+P(2)*ENV(I,8) + P(1)*ENV(I, 9)
      IF(IPRO.EQ.2) PROB=P(3)*ENV(I,10)+P(2)*ENV(I,11)+P(1)*ENV(I, 12)
666   CONTINUE
C     RECRUITMENT MODEL AFTER THIS CARD 2* REC= 0.97815*SPOP*EXP(-0.000037741*SPOP)*EXP(0.020787*PROA) 3 *EXP(0.0039065*PROB) *)
      RETURN $ END
      FUNCTION FVAL (E,M)
C     ITERATIVE SOLUTION FOR INST. FISHING MORT. GIVEN EXPLOITATION RATE
C     AND INST. NATURAL MCRT.
      COMMON ITC, NYRS
      REAL M
      F=E $ N=0
      IF(E.EQ.O) GO TO 2
1     N=N+1 $ IF(N.GT.50) GO TO 90
      F1=F-0.01 $ F2=F+0.01
      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-E1) / 0.02
      DIFFE = EV-E
      F=F - DIFFE / SLOPE
      IF(ABS(DIFFE).GT.0.000001) GO TO 1
2     FVAL=F
      RETURN
90    PRINT 900
900   FORMAT (//,* ITERATIONS FOR F EXCEEDED 50*)
901   STOP $ END
      SUBROUTINE LOGI
C     PACIFIC MACKEREL SUBROUTINE
      COMMON 0ITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12)
      PS(1)=.54*EXP(-.0000071709*TPOP)
      RETURN $ END
      SUBROUTINE QUOT
      COMMON OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M
      IF(Q2.GT.QBL) GO TO 900
      QUO=QA*(Q2-QAL)
      GO TO 901
900   QUO=(QBL-QAL)*QA + (Q2-QBL)*GB
901   QPOP=SUBQ=0.01 $ SUBPOP=0.1
      DO 902 IC=J,MAXA
902   QPOP=QPOP+POPC(IC)
      IF(J.EQ.IBT) GO TO 904
      JJ=J-1
      DO 903 IC=1,JJ
903   SUBPOP=SUBPOP + POPC(IC)
      SUBQ=SLP*QUO
      QUO=QUO-SUBQ
      IF(QUO/QPOP.GT.1.0) GO TO 905
904   CQ=QUO $ GO TO 906
905   CQ=QPOP
906   IF(SUBQ/SUBPOP.LT.0.5) GO TO 907
      X=0.5*SUBPOP $ Y=SUBQ-X
      SUBQ=X $ CQ=QUO+Y
```

```
907  RETURN $ END
     SUBROUTINE OUTM
     COMMON OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPCP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
     4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51), 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
     REAL M
     INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
     IF(REC.GT.RMAX) GO TO 606
     IF(IRUN.EQ.0) GO TO 609
     IOK=1
     IF(QBL.LT.1.AND.IQSET.EQ.1) IOK=0
     IF(IOK.EQ.1) PRINT 600,QB
     IF(IOK.NE.1) PRINT 601,QB
600  FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, UPPER QUOTA PROPORTION =* 1,F6.3)
601  FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, EXPLOITATION RATE =*,F6.3)
     CALL OUTP (ASPOP,TSPOP)
     IF(IRUN.EQ.1) GO TO 609
     IF(IOK.EQ.1) PRINT 602,QB
     IF(IOK.NE.1) PRINT 603,QB
602  FORMAT (//,T21,*ANNUAL YIELD, UPPER QUOTA PROPORTION =*,F6.3)
603  FORMAT (//,T21,*ANNUAL YIELD, EXPLOITATION RATE =*,F6.3)
     CALL OUTP (AYIELD,TYIELD)
     IF(IOK.EQ.1) PRINT 604,QB
     IF(IOK.NE.1) PRINT 605,QB
604  FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, UPPER QUOTA PROPORTION =* 1,F6.3)
605  FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, EXPLOITATION RATE =*,F6.3)
     CALL OUTP (ATPOP,TTPOP)
606  CONTINUE
     IF(IOK.EQ.1) PRINT 607,QB
     IF(IOK.NE.1) PRINT 608,QB
607  FORMAT (//,T21,*ANNUAL RECRUITMENT, UPPER QUOTA PROPORTION =* 1,F6.3)
608  FORMAT (//,T21,*ANNUAL RECRUITMENT, EXPLOITATION RATE =*,F6.3)
     CALL OUTP (AREC,TREC)
609  RETURN $ END
     SUBROUTINE OUTP (IANN,ITOT)
     COMMON OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPCP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
     4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51), 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
     REAL M
     INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
     DIMENSION IANN(100,16),ITOT(100)
     PRINT 700,(N,N=IBT,IET)
700  FORMAT(///,T21,*AGE AT RECRUITMENT*,//,* SEASON*,16I8)
     IS=ITO-1
     DO 701 N=1,NYRS
     IS=IS+1
701  PRINT 702,IS,(IANN(N,K),K=1,NL)
702  FORMAT (1X,I4,2X,16I8)
     IF(IU.NE.-9) RETURN
     DO 703 N=IBT,IET
703  ITOT(N) = ITOT(N)/NYRS
     PRINT 704,(ITOT(N),N=IBT,IET)
704  FORMAT (* MEAN *,16I8)
     RETURN $ END
     SUBROUTINE OUTMAT(MT)
     COMMON OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12), 1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I.J,POPC(51),SPOP,
     2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ, 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
     4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51), 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
     REAL M
     INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
     DIMENSION MT(16,16) ,QQ(16)
     PRINT 800
800  FORMAT (* AGE*,/,* AT*,/,* REC.*)
     K=IET+1
     DO 801 NJ=1,NL
     K=K-1
C    PUNCH CARD OUTPUT FOR YIELD ISOPLETH PLOTS
     PUNCH 008,(MT(K,N),N=1,NQ)
008  FORMAT (10I8)
801  PRINT 802 ,K,(MT(K,N),N=1,NQ)
802  FORMAT (//,1X,I2,4X,16I8)
     PRINT 803
803  FORMAT (//,7X)
     QY=QMIN-QINC
     DO 804 N=1,NQ
     QY=QY+QINC
804  QQ(N)=QY
     PRINT 805,(QQ(N),N=1,NQ)
805  FORMAT (7X,16F8.2)
     IF(IQSET.NE.1) GO TO 807
     IF(QBL.LT.1.0) PRINT 806
806  FORMAT(/,T32,*EXPLOITATION RATE*)
     IF(QBL.LT.1.0) GO TO 899
807  PRINT 808
808  FORMAT(/,T32,*QUOTA PROPORTION*)
899  RETURN $ END
```

TYPICAL INPUT FOR QUOTAE

```
4 NUMBER OF RUNS
1946 30 1 5 6 2 1 0 2 0
900000. 20000. 40000. .50 .10 .20 .00 .05 10
18933 .00 1.649 1.316
51286 .77 1.508 1.207
30137 .88 1.282 1.143
143011.00 1.2 1.103
167831.00 1.146 1.076
01.00 1.109 1.057
30N 119W 1946          110   80    132   155   252   347   207   201   207   86    54    53
30N 119W 1947          110   60    111   191   114   176   243   152   102   95    70    61
30N 119W 1948          30    102   82    61    220   151   126   119   105   81    72    31
30N 119W 1949          63    121   90    150   158   160   113   155   123   91    84    53
30N 119W 1950          60    58    117   151   153   164   76    121   101   70    58    88
30N 119W 1951          112   85    115   91    204   207   157   120   155   128   73    49
30N 119W 1952          24    35    108   99    224   150   84    115   98    107   54    31
30N 119W 1953          56    125   158   183   218   235   143   191   154   139   128   113
30N 119W 1954          77    94    77    174   173   210   108   178   164   105   69    49
30N 119W 1955          81    68    99    226   265   299   202   173   242   173   111   61
30N 119W 1956          72    98    207   165   238   297   191   245   180   139   60    52
30N 119W 1957          20    56    165   184   190   274   202   170   167   122   93    71
30N 119W 1958          105   75    101   229   191   258   185   130   165   130   115   57
30N 119W 1959          99    33    168   149   231   304   195   139   151   153   64    27
30N 119W 1960          45    100   169   144   299   133   111   138   133   121   47    66
30N 119W 1961          33    157   168   164   210   158   94    124   70    66    47    53
30N 119W 1962          49    46    82    189   212   218   155   166   148   97    103   32
30N 119W 1963          9     63    87    115   150   163   182   131   93    71    63    41
30N 119W 1964          69    63    149   169   225   204   176   134   118   60    38    73
30N 119W 1965          44    54    50    39    185   142   95    74    59    58    1     27
30N 119W 1966          44    49    72    64    81    121   132   61    76    51    14    42
30N 119W 1967          29    65    56    73    163   130   126   156   71    91    13    58
30N 119W 1968          32    30    92    116   152   157   102   108   104   76    90    32
30N 119W 1969          8     45    136   185   227   194   219   202   173   134   7     70
30N 119W 1970          27    13    96    183   241   238   177   225   158   117   55    45
30N 119W 1971          82    164   166   232   241   265   196   147   170   142   139   82
30N 119W 1972          91    88    186   180   165   168   125   113   90    61    67    85
30N 119W 1973          64    7     178   192   155   178   137   149   121   90    93    97
30N 119W 1974          22    104   93    234   284   263   147   167   141   104   74    34
30N 119W 1975          50    62    127   174   187   197   192   194   180   146   134   58
30N 119W 1946 ODI      467   30    68    -201  -658  -578  -254  -69   -51   -51   88    34
30N 119W 1947 ODI      -78   48    -114  -140  -362  -303  -107  -274  -124  -46   232   104
30N 119W 1948 ODI      -75   68    -55   -270  -322  -338  -117  -100  -75   93    215   26
30N 119W 1949 ODI      182   125   -188  -167  -309  -105  -137  -56   50    78    184   87
30N 119W 1950 ODI      -76   -78   54    -206  -346  -356  -52   -120  -247  -141  3     -26
30N 119W 1951 ODI      -113  -36   84    -211  -449  -374  -162  -169  -266  12    -4    66
30N 119W 1952 ODI      -20   -68   -42   -55   -330  -278  -342  -134  -221  -152  -57   -17
30N 119W 1953 ODI      63    246   -255  -441  -439  -695  -362  -594  -532  -284  -121  166
30N 119W 1954 ODI      -31   -68   -166  -492  -455  -459  -195  -528  -118  -229  47    -75
30N 119W 1955 ODI      21    -36   -116  -370  -570  -657  -276  -119  -199  -230  108   -81
30N 119W 1956 ODI      23    -62   -26   -324  -532  -424  -402  -371  -137  -146  170   110
30N 119W 1957 ODI      -26   -181  -205  -393  -468  -363  -273  -205  -448  -213  -51   -19
30N 119W 1958 ODI      -123  -294  -397  -311  -834  -865  -608  -364  -183  -51   19    57
30N 119W 1959 ODI      -6    -89   -100  -405  -656  -671  -418  -407  -279  -38   57    61
30N 119W 1960 ODI      -54   -141  -245  -120  -409  -380  -230  -196  -57   -1    -4    76
30N 119W 1961 ODI      54    -59   -248  -112  -742  -652  -285  33    -40   58    -4    165
30N 119W 1962 ODI      173   -96   -125  -183  -592  -284  -786  -563  -308  -283  -88   13
30N 119W 1963 ODI      -20   -121  -336  -524  -619  -814  -875  -524  94    5     46    79
30N 119W 1964 ODI      102   36    -246  -818  -1960 -2005 -1432 -1165 -885  -483  -218  -468
30N 119W 1965 ODI      -251  -248  -412  -91   -421  -689  -817  -562  -481  -307  -66   -56
30N 119W 1966 ODI      23    -127  -255  -458  -798  -1953 -776  -568  -662  -301  -209  -127
30N 119W 1967 ODI      -100  -99   -539  -668  -1113 -1255 -1002 -870  -712  -462  -148  145
30N 119W 1968 ODI      -161  -223  -399  -473  -1180 -1082 -677  -778  -643  -540  -269  -86
30N 119W 1969 ODI      -117  -363  -540  -657  -1044 -1071 -954  -821  -848  -711  -143  -240
30N 119W 1970 ODI      -197  -168  -357  -513  -801  -810  -561  -680  -429  -457  -249  -165
30N 119W 1971 ODI      43    20    -374  -471  -549  -859  -800  -422  -544  -63   -206  -125
30N 119W 1972 ODI      97    -326  -434  -627  -651  -801  -687  -458  -408  -154  96    76
30N 119W 1973 ODI      -6    -23   -299  -461  -892  -924  -770  -652  -726  -338  -359  63
30N 119W 1974 ODI      -22   18    -338  -591  -969  -903  -590  -907  -555  -385  3     151
30N 119W 1975 ODI      189   -204  -332  -503  -909  -1223 -741  -832  -535  -379  46    71
1946 30 1 5 6 2 1 0 2 0
900000. 20000. 40000. .50 .10 .20 .50 .05 10
1946 30 1 5 6 2 1 0 2 0
```

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900000. 0. 0. .50 .10 .20 .50 .05 10
1946 30 1 5 6 2 1 0 2 0
900000. 0. 0. .50 .10 .20 .00 .05 10
```

APPENDIX III. UPDATE FOR CDC VERSION OF BMDP3R NONLINEAR REGRESSION

```
*ID MAY25
    *D P3RJUL.2
    *I BMDP3R.25 XMAY 25, 1976 PEG
    *D BMDP3R.34
    *I BMDP3R.33 CTOL=1.0E-8
    *D UNCOLA.73
    *I UNCOLA.72 X 50H TOLERANCE FOR CONVERGENCE ,F11.8/
    *D P3RJUL.24
    *I P3RJUL.23 1 F20.5)
    *D RITEIT.15
    *I RITEIT.14 3000 FORMAT (2X,I4,7X,I4,F21.6,1X,F18.7,5(1X,F14.9))
    *D REDEV.18
    *I REDEV.17 3000 FORMAT(1X,I4,2X,A1,AB,1X,F14.6,1X,F14.6,2(2X,F13.6))
    *D RITEND.28
    *I RITEND.27 900 FORMAT (2X,I4,7X,I4,F21.6,4X,6(1X,F14.6))
    *D RITEND.48,RITEND.53
    *I RITEND.47 5600 FORMAT(1H0,2X,7H CASE ,10HPREDICTED ,7X, * 10HSTD DEV
OF,5X,8HOBSERVED/ * 10X,A8,9X,10HPRED VALUE, * 5X,A8,9X,A8,4(7X,A8))
    5800 FORMAT(1X,I4,A2,F13.6,2X,F15.5,2X,F13.6, * 2X,F15.6,4(2X,F13.6))
    *I RITEND.96 IF(ISFUN.GT.5) GO TO 47
    *D FUN.10
    *I FUN.9 IF(ISFUN.GE.1.AND.ISFUN.LE.19)GO TO (100,200,300,400,500,600,700,
*800,900,1000,1100,1200,1300,1400,1500,1600,1700,1800,1900),ISFUN
    *I FUN.99
C
C   RICKER MODEL
600 F=P(1)*X(1)*EXP(P(2)*X(1))
    DF(1)=X(1)*EXP(P(2)*X(1))
    DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))
    RETURN
C
C   CUSHING MODEL
700 F=P(1)*X(1)**P(2)
    DF(1)=X(1)**P(2)
    DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))
    RETURN
C
C   CLARK-RICKER MODEL
800 F=P(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
    DF(1)=X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
    DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
    DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) *(1/X(1)) * EXP(P(3)/X(1) )
    RETURN
C
C   CLARK-CUSHING MODEL
900 F=P(1)*X(1)**P(2)*EXP(P(3)/X(1))
    DF(1)=X(1)**P(2)*EXP(P(3)/X(1))
    DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))*EXP(P(3)/X(1))
    DF(3)=P(1)*X(1)**P(2) *(1/X(1)) * EXP(P(3)/X(1))
    RETURN
C
C   CUSHING TRANSPORT MODEL
100 F=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
0
    DF(1)=X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
    DF(2) = P(1)*X(1)**P(2)*ALCG(X(1)) *EXP(P(3)*X(2)) *EXP(P(4)*X(3))
    DF(3) = P(1)*X(1)**P(2) *X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
    DF(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 MODEL
110 F= P(1)*X(1)**P(2) * EXP( P(3)*X(2) ) 1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
0
    DF(1) = X(1)**P(2) * EXP( P(3)*X(2) ) 1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
    DF(2) = P(1)*X(1)**P(2)*ALOG(X(1)) * EXP( P(3)*X(2) ) 1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
    DF(3) = P(1)*X(1)**P(2) * X(2)*EXP( P(3)*X(2) ) 1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
    DF(4) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) ) 1 *X(3)*EXP( P(4)*X(3) ) * EXP( P(5)*X(4) )
    DF(5) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) ) 1 *EXP( P(4)*X(3) ) * X(4)*EXP( P(5)*X(4) )
    RETURN
C
```

```
C    EXPONENTIAL MODEL
C
120 F = P(1) * EXP( P(2)*X(1))
0
     DF(1) = EXP( P(2)*X(1) )
     DF(2) = P(1) * X(1) * EXP(P(2)*X(1))
     RETURN
C
C    RECRUIT PER SPAWNER TRANSPORT MODEL
C
130 F = P(1) * EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
0
     DF(1) = EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
     DF(2) = P(1)*X(1)*EXP(P(2)*X(1)) *EXP(P(3)*X(2)) *EXP(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)*X(2)) * X(3)*EXP(P(4)*X(3))
     RETURN
C
C    RICKER TRANSPORT MODEL
C
140 F = P(1)*X(1)*EXP(P(2)*X(1)) 1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
0
     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(P(2)*X(1)) 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(3))
     DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3) 1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
     RETURN
C
C    RICKER SEA LEVEL MODEL
C
150 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))
0
     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)) * X(1) 1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
     DF(3) = P(1) * X(1) * EXP(P(2)*X(1)) * X(2) 1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
     DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3) 1 * EXP(P(3)*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)*X(4))
     RETURN
C
C    CLARK-RICKER TRANSPORT MODEL
C
160 F=P(1)*X(1) *EXP(P(2)*X(1)) * EXP(P(3)/X(1)) 1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
0
     DF(1) = X(1) *EXP(P(2)*X(1)) * EXP(P(3)/X(1)) 1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
     DF(2) = P(1)*X(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1)) 1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
     DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) * (1.0/X(1)) * EXP(P(3)/X(1)) 1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
     DF(4)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1)) 1*X(2) * EXP(P(4)*X(2)) * EXP(P(5)*X(3))
     DF(5)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1)) 1* EXP(P(4)*X(2)) * X(3) * EXP(P(5)*X(3))
     RETURN
C
170 RETURN
0
180 RETURN
0
190 RETURN
0
```