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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-perspawner shows large fluctuations with considerable coherence between adjacent years. There was no marked downward trend in recruits-perspawner over the 1928–1968 period. Density-dependent spawner-recruit models accounted for a maximum of 24 percent of the observed variation in recruitment. Multiple regression models, including both population and environmental variables, were fitted to the data available for two time periods; 1931-68 and 1946-68. The 1931-68 model accounted for 59 percent of the variation in recruitment; increased recruitment was associated with increased sea surface temperature, reduced sea level and reduced atmospheric pressure during the 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 vield 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 longterm yield with this fishing strategy, under the 1931–68 environmental conditions, would have been 45 million pounds (20,000 MT).

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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.

THE FISHERY

STOCK DEFINITION

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

A tagging study (Frv 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 (Ense-

Area of	Number	Southern Calif. fishery			Central Calif. fishery		
Area of release	released	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. (Sebas-				{			
tian 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		
-		1	1				

TABLE	۱.	Tag Return Rates by Geographical Area as an Index of Relative Availability of Fish
		to the Fishery (Based on Fry and Roedel, 1949).

nada) and Southern California areas when samples for individual regions were combined and compared by analysis of covariance. Roedel concluded that there was probably little mixing between these areas. As Roedel (1952) admits, these conclusions are not compatible with information from tagging studies.

Two reasons for this inconsistency can be postulated. First, as Roedel (1952) showed, even schools from the southern California area showed significant statistical differences, suggesting that populations tend to be much more heterogeneous than are individual schools. Such a condition is consistent with a north-south migration wherein schools retain their identity. Also, the presence of significant statistical difference between schools within geographic regions makes it difficult to interpret differences between geographic regions from combined samples. The second sources of possible inconsistency relates to the season in which sampling was done. If migration of Pacific mackerel follows a pattern of northward movement in early summer and southward movement in late fall, the samples on which measurements were made tend to be biased against migratory members of the population. Most of the southern California samples were taken in the winter and spring when migrants would be at the southern end of their range, and Sebastian Vizcaino Bay samples were taken in the fall when migrants would be north. Roedel's samples suggest a clinal variation in relative head length, and apparent discontinuities possibly would be smoothed if sampling were distributed over the entire vear.

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

HISTORY OF THE FISHERY

The development and subsequent decline of the Pacific mackerel fishery has been well documented in the literature. Croker (1933) discussed the early history of the fishery including fishing areas and the development of mackerel canning in California. Descriptions of the fishery during and after its peak include those by Croker (1933, 1938), Roedel (1952), Fitch (1952), and Roedel and Joseph (1954). The fishing gear used in the fishery was principally round-haul gear, primarily purse seine, and scoop gear (Fry 1931; Croker 1933; and Scofield 1947, 1951). More recent reviews of the fishery include Blunt and Parrish (1969), Kramer (1969), and Mac-Call (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 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)

were relatively unavailable in southern California from January through May, and then increased in availability until late fall. Purse seiners accounted for most of the catch up to September when the sardine season began. A few scoop boats would fish all year, supplying fresh fish markets, which preferred scoop-caught fish to purse seined fish as they sustained less injury. The main scoop fishing season was in the fall, from August through December. In the declining years of the fishery catches became sporadic, losing any definitive seasonal pattern. The sport landings of Pacific mackerel have been of relatively minor importance in the total marine sport landings. Young (1969) ranked them as the eleventh most important species in the southern California partyboat fishery. The mean catch from 1947–1967 was 127,921 fish. Only trace amounts of Pacific mackerel occur in the northern California partyboat catch.

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

MANAGEMENT OF THE FISHERY

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

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

In response to continuing requests to enact moratoriums on Pacific mackerel and to halt the bait fishery on sardine, the California Legislature requested the California Department of Fish and Game to arrange meetings with Mexican scientists to determine the exact status of the resource (MacCall 1973). In the fall of 1972 cooperative research was undertaken. However, the continued decline of Pacific mackerel off California and the increasing fishing mortality, which had by then become very heavy even

on age 0 Pacific mackerel, encouraged the California Legislature to enact a unilateral moratorium on the commercial fishery for Pacific mackerel. This moratorium allowed an 18% tolerance for Pacific mackerel in mixed loads.

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

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

Fishery complications arose in 1977, and further legislation has complicated the management of the Pacific mackerel. The southern 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.

CATCHES

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

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	1	200	113664
1935-36	146387		200	146587
1936-37	100745		200	100945
193738	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
194748	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
195556	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
196061	39074	6573 *	158	45805
1961-62	44301	13149 *	228	57678
196263	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
196869	3289	236	158	3683
1969-70	1783	443	240	2466

TABLE	2.	Season	Catches	of Pacific	Mackerel	from	1926-27 t	o 1969-	-70
			(Weights i	n 1000 lb))			

Estimated

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

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

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

AGE COMPOSITION

Age composition of the California commercial landings since 1939 have been published (Fitch, 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Parrish and Knaggs, 1971, 1972; Knaggs, 1972). Mexican commercial landings, the sport catch, and late reports from the 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

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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	Mackerei	Ratios	of Total	Catch to	Aged	Catch
		(Wei	ghts 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	1.1173
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
196061			39074	45805	1.1723
1961-62			44192	57678	1.3052
1962-63			45252	52612	1.1626
196364	1		34210	52066	1.5220
196465			24875	44076	1.7719
196566			7589	24681	3.2522
196667			4075	16147	3.9625
196768			1381	3689	2.6713
196869			3289	3689	1.1198
1969-70			1439	2466	1.7137

• Estimated by assumed weight of age 6+ fish.

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

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		Mean length-at-age *											
		Unpublishe	ed reading	Fitch (1951)									
	1933		1934		1939-40		1940-41						
Age	n	L	n	L	n	L	п	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					

TABLE 4. Validation of Unpublished Otolith Readings.

• σ_L is approximately 5.0 for all ages.

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

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

Season	Otolith sample size	о	1	2	3	4	5	6 +	Total
193334									
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 1939-40		0	2199	35238	33004	21332	19086	4577	115436
Fitch (1951)	1524	2960	25200	26540	35130	10570	5340	6100	111840
NORMSEP		6431	23621	19729	34603	16597	3858	7001	111940

landings by time period as do the otolith-based estimates (Fitch, 1951¹). Moreover, no consistent bias in age structure is apparent in the NORM-SEP 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 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.

	0	1	2	ŝ	4	S	6 +	Total
	26	11469	20724	19204	4804	3574	4592	64396
		1224	6296	4252	1684	589	96	14105
		848	8851	5484	1158	667	512	17520
	_	130	2899	5259	1254	846	685	11073
		3746	15419	25854	18943	6711	3446	13669
	_	3369	36726	24504	28090	10675	6074	109438
		7621	8929	43255	44738	23577	6771	134891
	_	1705	15477	13198	25079	26669	6201	88329
_	137	1273	2236	6931	13724	22451	10560	57322
	2058	11036	30473	15755	4108	10375	9805	83610
	3204	27274	28724	38021	11440	5779	6602	121044
	2408	21646	72164	26297	14107	1502	1722	115792
	432	13584	28732	27870	5562	1054	296	77830
	-	32193	10087	13916	5776	106	285	63158
	928	13840	06009	11279	7922	1202	438	95699
		17640	20295	36126	8217	1722	473	84473
	593	15247	11010	10937	10994	3548	1565	53894
	626	10429	28865	13271	5210	2564	2802	63767
	8759	1680	9734	13348	6205	2463	1892	44081
	1180	70410	3530	841	1229	477	325	77992
	153	24558	55441	4816	774	657	346	86745
	7	4659	23247	19134	1133	87	169	48436
	828 858	1766	4941	15479	12417	243	172	35876
	5	56	630	1555	11471	3333	40	17189
	18559	1025	720	884	244	557	593	22582
	852	60482	5881	314	107	0	59	67695
	7728	6497	38586	10980	372	27	232	64422
	ଚ	70145	21252	20777	5167	8	0	117459
	1505	6764	33112	12308	8863	2500	1100	66152
	17304	1342	6217	11419	3671	1182	306	41441
	1595	58544	4341	1082	1323	432	143	67460
	-							

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

		-	-	-		10.		20112
1060 61	9008	90796	23316	9004	2354	48/	302	11160
10-00-11	10 m					020	8	80057
1001 60	03400	33441	17054	12158	0007	202	R	0000
20-1061	00507				1000	100	14	58503
1069 63	60	30235	13936	10056	1005	060	F	0000
00-70ET	3				1000	1071	137	48244
1967 64	67	3840	22285	12945	669/	1001	101	
		1001		01001	12507	1740	152	38195
1064 65	140	000/	0410	10210	17001	24.1		
	0100.		761	1699	5483	8612	1551	32320
150-150 1	129/0	0071	101	1 CONT				01021
	1000		0071	1106	035	9319	1569	1/040
1999-996	707/	(CF)	1430	1111				17040
	CHUT	150	05.4	010	158	22	134	1/040
196768	000/		102	710	2	3		0000
	1000	140	200	336	86	81	122	02.62
FG	600/		5		3		2	0200
000 10	-	9641	470		2	81	14	0100
1202-10	F1	1607	-					
							T	
		1						
* Age composition estimated fi	om length freque	ncy. These data are	unreliable.					
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POPULATION BIOLOGY

GROWTH

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

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

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

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

			At beginnin (Birth	ng of season hday)	At ca	pture
	Age	t	Length	Weight	Length	Weight
	May	0.5	252 mm.	192 gms.		
	Oct.	1.0		Ŭ	273 mm.	253 gms
2	May	1.5	292	317		
	Oct.	2.0			308	382
	Мау	2.5	323	448		
	Oct.	3.0			336	512
	May	3.5	348	574		
	Oct.	4.0			358	633
•	May	4.5	367	689		
	Oct.	5.0			375	741
	May	5.5	382	789		
	Oct.	6.0			388	834

 $^{1}L_{t} = 436.12 (1 - e^{-0.24444} (t + 3.0222))$

 $^{2}W = 0.000001366 L^{3.39358}$

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

REPRODUCTION

Age at maturity and percent spawning by age group were not well documented during the early fishery. According to Fry (1936b) "the yearling fish do not spawn whereas 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 densitydependent relationship between population size and the percentage of age 1 fish that spawn, although the exact form of this relationship is difficult to demonstrate. It appears that the percentage of age 1 spawners can be approximated at three general biomass levels. An exponential curve fitted to these points gives the following relationship, which was used in the regressions to determine recruit-spawner functions and in all simulations. (Figure 2)

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

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).

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 PACIFIC MACKEREL FISHERY



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.

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:

 $\mathbf{Z} = [\mathbf{K}(\mathbf{L}_{oo} - \overline{\mathbf{L}})] / (\overline{\mathbf{L}} - \mathbf{L}^{1}]$

where L^{1} is the smallest length fully represented (or lower cut-off point) and \overline{L} is mean length of fish L^{1} or longer. K and L_{00} 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_{00} and the slope is a function of K (Gulland 1969). In order to avoid effects of uneven recruitment on the catch curve analysis, L^{1} was increased the equivalent of a year's growth by the relationship

 $L_{t+1} = L_{oo}[1 - e^{-K}(1 - [L_t/L_{oo}])]$

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 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	Ē	Ī	Z
1929-30	346	337.5	365.05	0.317
1930-31	317	350.0	368.70	0.424

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

 $\overline{N} = cI$

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
195354	0	11546	_	1.839
1954-55	23.4	40364	1725	0.729
195556	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
196061	11.7	45805	3915	2.019
1961-62	7.2	57678	8011	1.636

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.

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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.

Comparision of estimates of the rate of natural mortality is obtained by various methods (Table 10), suggests that M is probably in the range of

0.4 to 0.6, with the most consistent single value being M = 0.5. This value will be used throughout the rest of the analysis.

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
COHORT ANALYSIS

ESTIMATION OF FISHING MORTALITY RATES

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

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

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

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

No independent estimate of the fishing mortality rate (F) for the recent portion of the time series is available, making it necessary to use a reasonable guess as a starting value. Alternative trial values of 0.5, 1.0 and 1.5 for 1969–70 were compared (Table 11), and convergence resulted in little difference for the 1966–67 season and earlier. The intermediate value, 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 fill out the time series with estimates for recent seasons.

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

 Recruited Fish.
 Recruited Fish.
 Recruited Fish.

Season	Estir	Estimated fishing mortality rate							
1969-70	0.5	1.0	1.5						
1968-69	0.547	0.781	0.906						
196768	0.390	0.481	0.519						
196667	1.651	1.800	1.847						

The three trial solutions shown in Table 11 demonstrate a general rule in the behavior of cohort analysis: large-values of F converge more rapidly than do small values of F. Use of cohort 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

0%
11%
19%
26%
39%
65%
78%
85%

 TABLE 12. Approximate Rates of Convergence * for Cohort Analysis, Backward Solution, M =

 0.5, as Determined by Simulated Catches.

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

of fishing mortality rates for the 1928–29 season was impossible due to lack of sampling. A rough guess of 0.2 was obtained by multiplying the 1929–30 F by the ratio of total catches for the two seasons. Approximate fishing mortality rates for the younger age groups were obtained by applying approximately the same relative recruitment ratios as in 1929–30. Fishing mortality rate estimates before 1939 are unreliable due to the aforementioned problems in estimating age composition. The estimates for 1928 through 1932–33 are particularly poor due to the lack of convergence at low fishing mortality rates.

As there were two independent fisheries for the Pacific mackerel, it is useful to separate fishing mortality rates into purse seine and scoop fleet components. This separation is done by multiplying the total fishing mortality rate (age 4+) by the ratio of the fishery segment catch to total catch:

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.

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

 $E = (F/F \! + \! M) \ (1 - e^{\cdot (F + M)}),$

and initial population size is in numbers estimated by

N = C/E.

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

	F scoop		I		ļ	I	013	.035	.013	.022	020	.141	116	937	.703	.644	.426	369	484	404	697	.474	.703	.375	.186	.065	.326	.112	.248	.059	.395	.590
	F purse seine & other	(0.2)	330	033	660	032	201	331	344	.349	472	.574	.622	1112	.412	.181	268	.113	205	.379	.835	.160	.520	.488	.978	.832	1.013	.117	.780	487	.161	.764
Proportion	catch by scoop	1	ł	I	1	i	98	10	6	90	.13	20	59	.57	63	.78	19	11.	.70	.52	45	.75	.57	.43	.16	03	24	.49	24	II.	.25	44
Exploitation	rate age 4+	(0.144)	994	026	022	025	153	245	240	.248	.337	414	655	678	.553	.457	405	.307	.403	441	.655	379	.583	.471	055.	.719	.612	.163	.526	.338	.660	.616
++ ++	(Fully recruited)	(0.20)	330	033	029	.032	214	.366	357	371	.542	.715	1.553	1.648	1.115	.825	.694	.482	689.	.783	1.532	.634	1.223	.963	1.164	1.897	1.339	.229	1.028	.546	1.556	1.354
	3	(0.15)	201	062	.080	032	.159	960	.282	.221	.425	519	858	1.075	696	431	278	689.	.530	717.	1.387	.392	116.	.495	.349	1.348	9690	292	.435	.768	.929	1.326
e,	5	(0.10)	162	.052	.032	010	.034	.120	620.	.385	.035	.252	.371	.686	.364	.125	411	.382	.233	869.	1.166	.241	522	.328	768.	.200	301	.110	479	.498	.840	.496
<u>4</u> .	I	0	055	.003	.002	.0002	200.	-017	.092	.016	900	120	.110	.132	160	.105	.125	.084	.152	.379	.061	.275	.166	298	268	.012	110	310	120.	.353	232	.028
	0		1	0	0	0	0	0	•	•	100	.005	.110	600	100	0	002	0	110	.013	.018	004	.005	100.	.108	10 0	049	.005	.029	100	019	.064
	Season	1928-29	1929-30	1930-31	1931–32	1932-33	1933-34	1934-35	1935-36	1936-37	1937-38	1938-39	1939-40	1940-41	1941-12	1942-43	1943-44	1944-45	1945-46	1946-47	1947-48	1948-49	1949-50	1950-51	1951-52	1952-53	1953-54	1954-55	1955-56	1956-57	195758	1958-59

TABLE 13. Fishing Mortality Rates By Season

FISH BULLÈTIN 167

415 058 056 007 007 007
25 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
.438 .652 .559 .432 .432 .310 .310 .310 .547 .547 .547 .547 .518)
206 902 702 346 570 670 111 111 111 1000 6
165 465 264 114 114 264 234 234 234 234 234 234 234 234 234 23
. 449 146 146 146 146 1539 1539 1539 1539 1539 1539 1539 1539
.007 .007 .002 .003 .003 .003 .017 .037 1.180 .1.180 .1.180 .1.180
1959-60 1961-62 1961-62 1962-63 1962-63 1966-67 1966-67 1966-57 1966-77 1969-70 1969-70



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

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

RECRUITMENT AND SPAWNING SUCCESS

Recruit biomass (R), measured in weight at age 1, is given in Table 14. Spawning success has been highly variable, and there appears to be little density-dependent effect even on a logarithmic scale, when population biomasses are in their normal historical size range (Figure 8). However it appears that recruitment strength is much less variable when spawning biomass (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.

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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

Age I recruit biomass of resulting year class	09640	10001	905550	391197	230089	84509	36925	46621	96014	69185	115438	96374	90387	159222	66612	60555	52797	18933	20308	130928	60814	9648	3636	3255	62037	195313	50070	81705	21196
Spawning biomass	177143	247553	239549	348739	448175	633805	622707	576125	358225	224652	189182	159706	149545	132451	126001	185444	165151	124346	101078	56661	43188	92269	96046	64647	31830	28092	57878	104798	100035
Total biomass	305628	373929	465866	610951	839949	964586	836211	654689	419997	329554	281702	291118	267320	238588	297968	290523	243077	184808	131440	76418	154015	165241	123531	73274	34787	70927	174776	170320	185329
Age 5+	0	45179	31474	64945	76532	82379	115253	157021	164638	121672	60667	23563	6470	4506	3670	5341	9837	17573	16783	8941	3111	2410	773	1011	6451	3207	543	1044	366
Age 4	30966	22301	68522	53521	52596	128910	119406	194218	105396	42430	10332	18254	20322	12488	14454	25514	31904	32607	14301	11340	3946	1572	2509	23587	19180	513	736	766	16696
Age 3	32843	109226	72156	72230	168747	177479	271010	6/0//1	6/083	20022	38717	64410	37281	20977	44077	53936	04430	32546	3013/	64777	0025	0720	49571	38252	2596	2244	1533	34066	42693
Age 2	144695	104583	98300	214703	220947	345729	240033	19940	60706	49415	10201	100000	1005/3	00230	(0040)	1.00/3.5	10001	49/200	01200	10700	00040	01010	05010	2020	cons	0767	46631	84374	43779
Age 1	97124	92040	199914	20002	321127	230009	80040	1099F	17004	90014 50105	1154700	064011	F1006	150000	772601	60222	59707	16170	20208	130498	60814	0FAD	2636	1000	10000	10020	£15C21	0/000	C6/19 1
Year	1928	1020	1930	1000	1932	1034	1935	1936	1037	1038	1020	1940	1941	1049	1943	1944	1945	1946	1947	1948	1949	1950	1051	1050	1953	1054	1904	0221	0061

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

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FISH BULLETIN 167

PACIFIC MACKEREL FISHERY

24184 11879 14738 5962 2778 59541 39377 88151 88151 29150 7930 3830 2047 11879 14738 5962 5778 58799 58641 19054 4481 1800 142775 79608 58799 58791 130064 4481 1800 142775 79608 126860 58791 130399 45255 8922 2293555 96783 86791 15744 61556 90361 22556 4122 192339 15744 8160 1774 61556 90361 225556 4122 192339 157442 8160 2044 3218 4129 117315 104241 2044 2044 204 3218 4129 11922 192339 155462 8160 204 3218 4129 11922 192339 15744 2044 204 3218 4129 11922 192339 15742 4021 204 2177 2275 19188 40511 38057 4021 575 11122 675 626 1772 20567 17634 575 1141 3339 743 2205 2205 20567 176441 201 575 11122 675 626 1772 40511 30077 575 1141 3339 743 2202 2205 22050 2769 4075 <th>24184$11879$$14738$$5962$$2778$$59541$$39377$$88151$$88151$$29150$$14738$$5962$$2778$$59541$$39377$$88151$$88151$$29150$$7930$$3830$$2047$$131108$$53392$$58799$$88791$$19800$$142775$$79008$$1925800$$13744$$130399$$45235$$10976$$142775$$79008$$15749$$8791$$130399$$45235$$10976$$142775$$79008$$13744$$8791$$130399$$45235$$10976$$142775$$29973$$86791$$8794$$133039$$45235$$10976$$142775$$29933$$86791$$8794$$133039$$45235$$10976$$142775$$29933$$86791$$8714$$130399$$45235$$10976$$14222$$1992339$$86791$$8714$$133039$$45235$$10976$$14277$$7364$$2944$$8160$$13744$$1122$$117315$$104241$$2044$$8160$$13727$$4122$$1992339$$417315$$104241$$2044$$8160$$2375$$1719$$10226$$177315$$104241$$2044$$875$$1122$$1712$$275$$205671$$17634$$575$$4021$$1122$$1727$$4725$$2176$$32056$$40751$$1141$$339$$743$$2375$$22509$$4075$$1141$</th> <th>24184 11879 14738 5962 2778 59541 39377 88151 26181 29150 7930 3830 2047 131108 53822 58151 58799 58641 19054 4481 1800 14775 79608 15589 58640 19054 53830 5382 5382 5382 58799 58791 19054 5481 1900 14715 79608 15589 15860 67164 290367 5382 5382 58791 15744 13744 61556 90361 1422 192339 159173 159173 15744 1374 61556 90361 15756 11222 7453 159173 15744 1374 13288 30741 55323 19923 15742 2044 1374 1328 17735 11221 7453 13057 4021 2044 3218 4122 192667 17515 104241</th> <th></th> <th></th> <th></th> <th></th>	24184 11879 14738 5962 2778 59541 39377 88151 88151 29150 14738 5962 2778 59541 39377 88151 88151 29150 7930 3830 2047 131108 53392 58799 88791 19800 142775 79008 1925800 13744 130399 45235 10976 142775 79008 15749 8791 130399 45235 10976 142775 79008 13744 8791 130399 45235 10976 142775 29973 86791 8794 133039 45235 10976 142775 29933 86791 8794 133039 45235 10976 142775 29933 86791 8714 130399 45235 10976 14222 1992339 86791 8714 133039 45235 10976 14277 7364 2944 8160 13744 1122 117315 104241 2044 8160 13727 4122 1992339 417315 104241 2044 8160 2375 1719 10226 177315 104241 2044 875 1122 1712 275 205671 17634 575 4021 1122 1727 4725 2176 32056 40751 1141 339 743 2375 22509 4075 1141	24184 11879 14738 5962 2778 59541 39377 88151 26181 29150 7930 3830 2047 131108 53822 58151 58799 58641 19054 4481 1800 14775 79608 15589 58640 19054 53830 5382 5382 5382 58799 58791 19054 5481 1900 14715 79608 15589 15860 67164 290367 5382 5382 58791 15744 13744 61556 90361 1422 192339 159173 159173 15744 1374 61556 90361 15756 11222 7453 159173 15744 1374 13288 30741 55323 19923 15742 2044 1374 1328 17735 11221 7453 13057 4021 2044 3218 4122 192667 17515 104241				
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5579 55641 19054 4481 1800 142775 79606 1226960 55790 57164 29087 5352 4481 1800 142775 79606 1226960 126860 67164 29087 5352 892 229355 96783 86791 86791 130399 45235 10676 1453 229355 96783 86791 86791 130399 45235 10676 1453 229355 96783 86791 8160 13536 93031 225355 4122 192339 155462 8160 8160 13588 30741 55332 9563 17335 104241 2044 204 3218 4129 11932 19138 40511 38057 4021 575 1122 675 1793 12636 3275 27669 4021 575 1141 339 743 23275 20567 4111 4021	5579958411905444811800 142775 79608126860126860586411905444811800 142775 796081268601268605579153528892229355967838679113640130399452351097614532293355967838679113744615569036122355641221923391554628160137443328830741553529503117312104241204420432184129119321918840511380574021402121772375191884051138057402111413397432375102752056711764575575112267562617274725214111413397432375230523053275256940751141339743210230230250407557511226756261727402752569407511413397432102302302569407511413397432102302504075114133974321023025040751141339743210230250407511413397432102302504075114133974321023	55799 58641 19064 4481 1800 142775 79608 126860 86791 120399 55641 19076 4481 1800 142775 79608 126860 86791 130399 67164 29087 5335 9225355 95783 96783 86791 86791 130399 677164 230361 225555 4123 12744 13744 8160 135566 90361 225555 4122 192339 156471 38671 13744 8160 13556 90361 1255462 9103 36571 13744 8160 13538 4129 11932 19138 40511 30677 4021 375 2177 2375 17193 10275 20567 4111 1141 1141 339 775 20567 17634 575 4075 2305 2305 2569 3275 2656 4071 1141 134	2047	131108	53892	58799
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575 1122 675 626 1727 4725 4111 1141 1141 339 743 232 820 3275 2569 4075 4075 194 140 210 280 3275 2569 4075	575 1122 675 626 1727 4725 4111 1141 575 1122 675 626 1727 4725 4111 1141 1141 339 743 232 820 3275 2569 4075 4075 194 140 210 280 280 3275 2569 4075	575 1122 675 626 1727 4725 4111 1141 575 1122 675 626 1727 4725 4111 1141 1141 329 743 232 820 3275 2569 4075 4075 194 140 210 280 3275 2569 4075 wux 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	10275	20567	17634	575
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4075 194 140 210 280	4075 194 140 210 280	4075 194 140 210 280 4075 194 and after 1967 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	820	3275	2569	4075
		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	280			
	was calculated with the percentage of age 1 spawners as in Figure 14: 77% , 88%, and 100		8	280 % of ages 2, 3, and 4	280 % of ages 2, 3, and 4 were considered ma	280 % of ages 2, 3, and 4 were considered mature. (Estimates before

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.

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. $\sqrt{286/106}$), whereas the actual increase was 1.89. The additional increase, if it is other than random error, could result from several causes. The temporal extent of spawning is largely dependent on the age structure of the population, and the mean age of the

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

Period	1928-1945	19461968
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

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

RECRUITMENT MODELS

METHODS

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

Density-dependent recruitment functions

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



SPAWNING BIOMASS

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 r² 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.

IABLE IO. Regression variables for spawner-Recruit Functio	TABLE	16. Regressic	n Variables	for S	pawner-Recruit	Functions
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		Linear regression variables					
Name	Function	Dependent	Independent				
Ricker	$\mathbf{R} = \mathbf{b}_{1} \mathbf{P} \mathbf{e}^{-\mathbf{b}_{1} \mathbf{P}}$	$\ln(R/P)$	Р				
Cushing	$\mathbf{R} = \mathbf{b}_{\mathbf{i}} \mathbf{P}^{\mathbf{a}_{\mathbf{i}}}$	$\ln(\mathbf{R})$	$\ln(\mathbf{P})$				
Beverton and Holt	$R = (P/[b_1 + b_2/P])$	P/R	Р				
Clark-Ricker	$\mathbf{R} = \mathbf{b}_{1} \mathbf{P} \mathbf{e}^{-\mathbf{b}_{1}\mathbf{P}} \mathbf{e}^{-\mathbf{b}_{1}/\mathbf{P}}$	$\ln(\mathbf{R}/\mathbf{P})$	P,1/P				
Clark-Cushing	$R = b_1 \ P^{b_1} \ e^{-b_1/P}$	$\ln(\mathbf{R})$	$\ln(P), 1/P$				

Where

R = Recruit biomass

P = Parent biomass

 $b_1 = Density$ independent coefficient

 $b_2 = Compensatory$, density dependent coefficient

 $b_a = Depensatory$, density dependent coefficient

Environmental variables

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

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



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

mental Group of the National Marine Fisheries Service. Data on wind speed were included as it would be expected to be related to upwelling. Cloud cover could be important because it might be used as an index of insolation and it could also be related to upwelling.

The third category is composed of data from a series of mass transport calculations. The data were provided by Bakun (pers. comm.) and his calculations were made with the procedures described by Fofonoff (1960). Data analyzed included meridional total transport, meridional Ekman transport, divergence of Ekman transport [Bakun's (pers. comm.) offshore divergence indices], and Bakun's (1973) coastal upwelling indices (i.e., Ekman transport perpendicular to the coast). The transport calculations were based on a 3° 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.

Environmental-dependent recruitment functions

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

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

DENSITY-DEPENDENT RECRUITMENT FUNCTIONS

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

The nonlinear (BMDP3R) Ricker and Cushing functions are both significant at the 99% level (Table 17). The addition of 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 a ecruitment factor does not exist in Pacific mackerel. The large observed v triation in recruitment at low spawning biomass levels would have hind ared detection of a depensatory factor and it is possible that depensation w ould 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.

Name	Function	R ²	F	DF
Cushing transformed	$\ln(R) = 2.0948 + 0.72888 \ln(P)$	0.297	16.49**	1,39
Cushing times	R = 8 1938 P0.72888	1	1	1,39
	D = 1000 0 D0.36187	0 166	7 78**	1.39
Cushing nonlinear	u = 100000000000000000000000000000000000	0.000		06 1
Reverton and Holt transformed	P/R = 6.1961 + 0.000030821 P	0.002	60.0	1,03
Bouerton and Holt linear	R = P/(6.1961 + 0.000030821 P)	1	1	1,39
	$1_{11}/R/D$ = 0.67759 = 0.00000914 P	0.068	2.85	1.39
Kicker transformed	$T = \frac{1}{2} $			00 1
Ricker linear	$R = 0.50787 Pe^{-0.00000214r}$	0.057	2.31	1,JY
	$\mathbf{R} = 0 \ 28002 \ \mathbf{D}_{\alpha} \ 0.0000253^{\mathrm{P}}$	0.236	12.06^{**}	1.39
Kicker noninear			*00	0,00
Clark-Cushing nonlinear	$R = 2435.4 P^{0.29910} e^{7524.57}$	0.170	4.09	2,00
	$D \cap OE110 D_{\sim} -0.00000242P_{\sim} 3501/P$	0 937	**00 5	2.38
Clark-Ricker nonlinear	$\mathbf{u} = 0.00112$ I \mathbf{c}		5	
$\mathbf{B} = \mathbf{B}_{constrict}$ biomass in themsends of nonuds				
$P = P_{arent}$ biomass in thousands of pounds				
 Significant at 5% level 				
•• = Significant at the 1% level				

TABLE 17. Density-dependent Spawner-recruit Functions

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SPAWNING BIOMASS (in millions of pounds)

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

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



SPAWNING BIOMASS

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

ASSOCIATIONS BETWEEN RECRUITMENT AND ENVIRONMENTAL FACTORS

Sea surface temperature

Off southern California, warm sea surface temperature during the spawning season was found to be associated with good recruitment in Pacific mackerel. This pattern was seen in the Marsden Square quadrant off southern 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



SPAWNING BIOMASS

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 T² was calculated (where T = prorated April-June sea surface temperature (\mathbb{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 r² 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 1n(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.

Sea level and atmospheric pressure

Monthly mean sea level at La Jolla, corrected for atmospheric pressure,

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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).

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 1n(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).

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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 upwell-



MONTH

FIGURE 17. Correlations of 1n(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.

ing should be beneficial to larval fishes. It is also noteworthy that the peak of spawning in Pacific mackerel is the same as the peak of upwelling off central Baja California (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)

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 In(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
SLLI	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)

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

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 r² 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 r² 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 r² of 0.756 and a F statistic of 19.59 (Table 19). The corresponding statistics for the Cushing transport model are 0.676 and 13.31. The critical F statistic at the 99% level of significance is 5.01.

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

FACTORS AFFECTING RECRUITMENT

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

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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	R²	F	DF
Ricker sea level $R = 51608Pe^{-0.25594 \text{ BARP}}$	1931–1968 0.00090353 P e-2.5004 SLEV e ^{0.53309} SSTC	0.587	11.72 **	4,33
Cushing sea level $\begin{split} R &= 100850000 \\ e^{-0.09858\ \text{BARP}} \end{split}$	1931–1968 P ^{0.095703} e ^{-2.7680} SLEV e ^{0.65528} SSTC	0.597	12.22 **	4,33
Reduced Ricker s	ea			
$R = 4214.2Pe^{-1}$ $e^{-0.19759 \text{ BARF}}$	1931–1960 0.00000351 F e ~ 2.1837 SLEV e e 0.51148 SSTC	0.517	6.68 **	4,25
Ricker transport R = 0.97815Pe $e^{0.0039065 \text{ ODI}}$	19461968 0.0000377 P e ^{0.020787} UP	0.756	19.59 **	3,19
Cushing transport R = 43577000F $e^{0.00469 \text{ ODI}}$	1946–1968 -0.84881 e ^{0.02350 UP}	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)

SLE, v— Mean May-July sea level at La Jolia, California in teet (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 M³ per second across 100m width)
 OPI — It is to fight a different in the protection of the spawning biomass (in M³ 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

...

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

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

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

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

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

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

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

The second mechanism affecting larval survival occurs during the latelarval and post-larval stages, when the fish are mobile enough to allow mixing between the survivors from different, more widely separated spawning spots. Mackerel in these developmental stages would be able to swim only relatively short distances and their distribution would still be heavily dependent on prevailing surface currents. During this period 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.
 - b) Intraspecific predation of eggs and larvae spawned late in the

spawning season by the survivors from earlier spawning. This type of mortality would reduce the number of recruits-perspawner but is not likely to reduce total recruitment. Mortality of this type is likely to result in a recruitment function of the type used by Cushing (1971).

2) Mortality dependent upon density within the species (i.e., older cohorts).

3) Mortality dependent upon the biomass of the entire trophic level.

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

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

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

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

COMPUTER SIMULATIONS

SIMULATION MODELS

The computer simulation models used in this work were written in FORTRAN IV and were run on a CDC 6500 computer. Two simulation models were used. The simpler model (ISOE, Appendix I) is a yield-perrecruit model based on the yield equations described by Beverton and Holt (1957) and as revised by Ricker (1975). ISOE 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.
YIELD-PER-RECRUIT MODEL

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

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

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

EQUILIBRIUM YIELD SIMULATIONS WITH DENSITY-DEPENDENT RE-CRUITMENT

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-







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

recruit curves (Figure 22). The linear fits to the Ricker function and the Cushing function produce similar yield isopleths and the nonlinear fits also produce similar isopleths. The linear regressions with the Ricker and Cushing functions have a bias towards low estimates as they utilize log transformed variables. This bias is evident in the low equilibrium yields predicted by the isopleths calculated with the linear regression 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)

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)

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.

YIELD WITH ENVIRONMENTAL-DEPENDENT RECRUITMENT FUNC-TIONS

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 longterm yield is not very sensitive to alterations in the quota levels (Figure 24). Mean yield also appears to be independent of age at recruitment at upper quota proportions below 0.3. At upper quota proportions above about 0.4 mean yield is influenced by age at recruitment and maximum mean yield occurs at high upper quota proportions and an age at recruitment of about 3 years.

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

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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 Ibs, quota based on spawning biomass)

ANNUAL YIELD UNDER FOUR MANAGEMENT OPTIONS

To assess the similarity of yields under the different environment-dependent recruitment functions, simulations under four management options were run. These simulations had the same time periods (1946–1968) and were initialized with the observed 1946 biomass. A third 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 densitydependent and environmental-dependent recruitment functions is the large variation in annual yield that occurs in the simulations run with the environmental-dependent recruitment functions. Time series of yields in simulations with the density functions show a stable approach to equilibrium yield. Simulations (1946-1968) with the Ricker sea level functions and the Ricker transport function show considerable variation in annual yield under different management options. Figures 26 and 27 show simulations with the Ricker sea level, reduced Ricker sea level and Ricker trans-



FIGURE 26. QUOTAE simulations (1946–1968); A. Recruitment 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)

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port 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)

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 vield 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 vear 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.

DISCUSSION

EVALUATION OF RECRUITMENT MODELS AND SIMULATIONS

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

The transport models have the best statistical fits; however, they are deficient in the sense that they were fitted to a shorter data series than the sea level models. This shorter series (1946-1968) did not include any years in which the spawning biomass was at the high levels that occurred prior to the peak of the fishery in 1936. Mean recruitment during the 1946–1968 period was considerably smaller than during the 1931–1968 period. The transport models therefore were fitted to a data series that is biased towards low recruitment. The computer simulations presented earlier show that the Ricker transport model predicts considerably smaller recruitment and yields than the Ricker sea level models and the densitydependent Ricker and Cushing models. The low estimates are not caused by the environmental terms. The low recruitment estimates with the **Ricker** transport model are caused by the compensatory term of the Ricker model. The 1946–1968 and 1928–1968 linear fits to the Ricker spawnerrecruit model have very great differences in their density-dependent and compensatory terms.

1946-1968	F	= 1.123 Pe	0.000169 P
1928–1968	Ē	l = 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

	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 = 0.0000000015

below for the nonlinear Ricker, Ricker sea level and Ricker transport models.

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 in creased 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 recruit ment, but with the exception of sea surface temperature they are next 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 sealevel 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 vield would be about 67 million pounds (30,000 metric tons) per year (X in Figure 23B). The simulations suggest that equilibrium vield could be increased to over 95 million pounds (43,000 metric tons) if the upper quota proportion were increased to 0.5 and the age at recruitment increased to age IV (Z in Figure 23B). This large an increase in potential yield is not predicted by comparable simulations with the environmental-dependent recruitment functions. Simulations with the 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 man ket sampling program from which age composition data were derived. Estimates of the population size and recruitment for the 1970-1975 period therefore cannot be based on a cohort 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 environmen-Moderately tal conditions greatly favored recruitment. onnel environmental conditions were predicted in 1971, 1972 and 1974.

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 environmentaldependent 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

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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

It should be noted that the alternative management options are for the total eatch, 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.

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PACIFIC MACKEREL FISHERY

APPENDIX I. YIELD PER RECRUIT SIMULATION PRO-GRAM.

FROGRAF ISCE (INFLT, CLTPLT, PLNCH)

C CONTROL CARD VARIABLE DESCRIPTION C NRUNS NUMBER OF RUNS TO BE MADE C KARD CARE CLIPLI KAFDEI NO CARE CLI C IITLE TITLE LIMITED TO 85 CAPD COLUM C IBERT IEERTEI IF BERTALANFFY GROWTH C MAXA MAXIMUM ARE OF THE SPECIES C IBT MINIMUM AGE AT RECEUITMENT C IET MAXIMUM AGE AT RECEUITMENT C XMS STARTING INST. NATURAL MORTALI C XMS STARTING INST. NATURAL MORTALI C XMS STARTING TO FE RUN C EINC EXFLCITATION RATE INCREMENT C NM NUMEER OF TS TO FE RUN C LINF BERTALANFFY CONSTANT C NE NUMBER OF EXFLCITATION RATES T C LINF BERTALANFFY CONSTANT C A LENGTH-WEIGHT CONSTANT C A LENGTH-WEIGHT CONSTANT C A LENGTH-WEIGHT CONSTANT C PS(I) FROPORTION SPANING BY AGE GRO C COMMON M,IET,IET,EINC,NE,FST(20),FT(20),I 1,KARO DIMENSION EC(20,50),PS(51),G(51),GH(51),M 1XLH(51),TCT(20),TITLE(20) INTEGER T REAL M,LINF,K READ 359, NRUNS,KARC 399 FORMAT (212)	TFUT K/FE=C MAS EQUATION IS USEC ITY FATE (M) TO BE FUN (10+ AFE ASSUMED 1.C) IS(5.,5C),IY(50,50) (T(51),NH(51),XL(51),
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460 FORMAT (13A8, /, 10A8)	
PRINT 401, (TITLE(1), 1=1, 20)	
401 FURNAL(10197791X913659791X913407 DEAD 470 TOEDT HAVA TOT TET VMS VVI.LM ET	
400 ECONAT 2613-266 3.13.65 3.131	
TE (TRERT.NE.1) 60 TC 2	
READ 101 . LINE.K.TC.A.B	
101 FORMAT (F10.2, F10.6, F15.9, F15.12, F10.6)	
PRINT 102, LINF,K,TC,A,3	
162 FORMAT (T5,*BERTALANFFY CONSTANTS*,/,T9,*	*L INFINITY =*,F10.2,/,
1T8,*K =*,F10.6,/,T8,*TC =*,F11.6,//,T5,*L	ENGTH-WEIGHT CONSTANTS
2*,/,T8,*A=*,F15.12,/,T8,*E=*,F10.6,/)	
C CUNTINUE READ REAL (MT(N), N=1, 15)	
666 FCRNAT (13F6.2)	
READ 668, (PS(N),N≈1,13)	
E68 FORMAT (10F6.4)	
D0 67] N=11,51	
E70 PS(N) = 1.0	
00 671 N=1,14	
TEMP=WT(N+1) / WT(N)	
11 U(N)=UM(N)=UM(N)=UM(N) DD 672 N=15.8844	
6H(N)=6(N)=TEMP	
672 WT(N) = WT(N-1) + TEMP	
IF (IBERT.EG.S) GC TC 7	

```
GC TO 38
              4 00 5 I=1,51
5 PS(I)=1.0
       READ 103, (PS(I), I= IET, 10)
103 FORMAT(10F6.4)
                      IA=MAXA+1
                       \begin{array}{l} 1 & -1 & -1 \\ 0 & 0 & 0 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -1 \\ 0 & -1 & -
                     U = N + U.5
XLH(N) = LINF* (1-EXP(-K*L + K*TC))
MT(N) = A*XL(N) **E
WH(N) = A*XLF(N)**E
GH(N) = WH(N)/WT(N)
                      IF (N.GT.IBT) G(N-1) = WT(N)/WT(N-1)
              E CONTINUE
             NOTE THAT THE UNITS ARE DEPENDENT UPON INFUT 7 PRINT 200
С
                                                                                                                                                                                                             GROW
                                                                                                                                                                                                                                           GRCWH*)
       208 FORMAT (//,1X, #AGE LENGTH
                                                                                                                                   WEIGHT
                                                                                                                                                                                   ₽S.
                     DO & N=IBT.MAXA
                      PRINT 104, N, XL (N) . WT (N), PS (N), G (N), CH (N)
       104 FORMAT (1X,13,2F9.2,3F9.3)
               8 CONTINUE
                      H=XMS-XMI
                      DC 26 PM=1.NP
                      TCT(MM)=D
                      H=N+XHI
                      E=-EINC
                     D0 24 J=1,NE
E=E + EINC
F=E $ N=
                                                        N = 0
                      IF(E.EG.3) GO TO 12
                                                          IF(N.GT.50) GC TC 90
          10 N=N+1 8
                      EV=EVAL(F)
                      E1=EVAL(F+0.01) $ E2=EVAL(F+0.01)
                       SLOPE= (E2-E1) /0.02
                      DIFFE=EV-E
                      F=F+DIFFE/SLCFE
                      IF(A8S(DIFFE).GT.G.GCCCOU1) GC TO 10
          12 FST(J)=F
                      Z=M+F
                     DO 22 I=I0T,IET
HS = C = C
                      FOP=1040
                      00 20 T=IET,MAXA
                       IF(I.GT.IET) GC TC 15
          IF(F.EC.0) TCT(MP)=TCT(MP)+PCP
IF(F.EG.0) BC(MM,T)=FOP
15 HS=HS + PCP*FS(T)
                      IF (T.LT.I) GC TO 14
                      W=Z
                      FF=F
                      GC TO 15
           14 W=M
                     FF=0
          1E C=POP*(1-ExP(-+))
                     IF(FF.EG.C) GC TC 18
G=D*(FF/Z)*CF(T) + C
          18 PCP=(PCP-C) * G(T)
           20 CONTINUE
          IS(I,J) = HS
IY(I,J) = C
22 CONTINUE
          24 CONTINUE
                     PRINT 105,M
```

98

```
1.5 FORMAT (//,31X,*VIELC PER METRIC TON OF RECRUITS #=*,F6.4,//.
     1* AGE*,36X,*(IN KG.)*,/,* AT*,/,* REC.*)
      CALL OUTISO(IY)
      PRINT 110.P
 110 FORMAT (//,31X,*SPANNING EICMASS OVER LIFE OF COMORT #=*,F6.4.
1//,* AGE*,/,* AT*,/,* REC.*)
١
      CALL OUTISC(IS)
   26 CONTINUE
      FRINT 111
  111 FORMAT (//, 31X, *BICMASS CLEVES WITH NO FISHING PORTALITY*//, 1X,
     1*AGE
                    INSTANTANEOUS NATURAL MCRTALITY*,//)
      M=XMS=XMI
      00 28 N=1,NM
      M=M+XMI
   28 FT(N)=#
  PRINT 112, (FT(N), N=1, NM)
112 FCRMAT (7×,20FE.2)
      IYR=IBT-1
      DC 30 I=IET,MAXA
      LYK=IVR+1
      PRINT 113, IVR, (BC (MP, I), MP=1, NM)
  113 FORMAT (1,X, 14, 2X, 20F6.0)
   30 CONTINUE
      00 34 MM=1.NM
00 32 I=IET.MAXA
      BC (MM, I) = EC (MM, I) / TCT (MM)
   32 CONTINUE
   34 CONTINUE
      PRINT 115
  115 FCRHAT(//,31X, PRCPCFTICN OF THE POPULATION BY WEIGHT F=0*,
                          INSTANTANEOUS NATURAL PORTALITY*,//)
     1//,* AGE
      PRINT 112, (FT(N), N=1, NM)
       IVR=IBT-1
      DC 36 I=IET,MAXA
      IYR=IYR+1
      PRINT 116, IYR, (8C (MM, I), NF=1, NM)
  116 FCRMAT(1X, 14, 2X, 26FE.4)
   36 CONTINUE
      IF (NRUNS.GT.0) GC TC 1
   GO TO 999
38 PRINT 444
  444 FORMAT (//,* OFTICN NOT INSTALLED*)
   90 PRINT 998
  198 FORMAT(//,* ITERATIONS FOR F EXCEEDED 50 *)
  999 STOP $ END
       FUNCTION EVAL(F)
      COMMON M $ REAL P
EVAL=(1.0-EXP(-F-M)) * F/(F+P)
       RETURN $ END
      SUBROUTINE CUTISC(JT)
Common M, Iet, Iet, Einc, NE, FST (27), FT (20), IS(50, 50), IY(50, 50)
     1,KARD
       REAL M
       DIMENSION JT(50,53)
       NN=-1
       CO 200 N=101,101
       NN=NN+1
       I=IET-NN
  200 PRINT 261, I, (JT(I,J), J=1, NE)
201 FCRMAT (//,2X, 12, 2X, 2316)
       TEN=-EINC
       CO 202 N=1,NE
TEM = TEM+EINC
```

99

FISH BULLETIN 167

202 FT(N) = TEM PFINT 203,(FT(N),N=1,NE) 203 FCRMAT(///,* E *,20F6.3) PFINT 204,(FST(N),N=1,NE) 204 FORMAT(* F *,20F6.3) FFINT 205 205 FORMAT(/,6X,*E = EXFLUITATION RATE, F = INST. FISHING MORT.RATE*) IF(KARC.EG.J) GO TO 210 T31+181=1 012 00 206 PUNCH 207, (JT(I,J), J=1,NE) 207 FCRMAT (1018,/,1018) PUNCH 208 208 FORMAT (/) 210 RETURN \$ END TYPICAL INPUT FOR ISCE

100

.

APPENDIX II. QUOTA SIMULATION PROGRAM.

PROGRAM QUOTAE (INPUT, OUTPUT, PUNCH)

C	QUOTA SIM	ULATION MODEL	RH	H PARRISH JUNE 15,1976
C	CONTROL C	ARD VARIABLE DES	CRI	IPTICNS
C	ITO	BEGINNING YEAR O	F TI	THE SIMULATION
Ċ	NYRS	NUMBER OF YEARS	FOR	R THE SIMULATION
Ğ	181	MINIMUM AGE AT R	ECR	RUITMENT
č	IET	MAXIMUM AGE AT R	ECRI	RUITMENT
Č	MAXA	MAXIMUM AGE		
Ĉ	IRUN	CONTROL FOR CUTP	UT	
С		IRUN=0 CUTPUT	IS	S LIMITED TO VIELD MATRICES
C		IRUN=1 CUTPUT	15	S ANNUAL SPAWNING BICMASS + YIELD MATRICIES
С		IRUN=2 CUTPUT	IS	S ANNUAL SPAWNING BIOMASS, VIELD, TOTAL
С		BICMAS	S AI	AND RECRUIT BICHASS + VIELD MATRICIES
Ç	IL OG I	ILOGI=) FOR CONS	TAN	NT PS(1)
C		ILOGI=1 FOR CENS	ITY	Y DEPENDENT PS(1)
C	IENV	IENV= THE NUMBER	OF	F ENVIRONMENTAL VARIABLES INPUT
C		MAXIMUP NU	MBEI	ER IS 6, FURMAT IS UN LINE 128
C	1800	IENV=0 IF NC EN	VIR	RUNMENTAL VARIABLES ARE INPUT
Š	IPRU	1PR0=0, =1, =2	UEPI	PENDING UN INE NUI OF PRORATED
с С	TOSET	ENVIRUNMENTAL	VAR	RIABLES, FURMAL IS UN LINES ISSAISC Chent that the obota is gased on
č	I QGE I	TOSET-D DUDTA	0.0	ASED ON SPANNING RICHASS
č			84	ASED ON TOTAL FLOMASS
č			PA	ASED ON AGE I + AGE II BIOMASS
č	RMAX	MAXIMUM RECRUIT	910	OMASS ALLOWED
Ċ	QAL	LOWER QUOTA LEVE	ι	
Ċ	GBL	UPPER QUOTA LEVE	Ē	
C	M	INSTANTANECUS NA	TUR	RAL MORTALITY RATE
C	SLP	SUBLEGAL PROPORT	ION	N (SETS CATCH OF UNCERSIZED FISH)
С	QA	LOWER QUCTA PROP	ORT	TICN
С	GMIN	MINIMUM UPPER OU	OTA	A PROPORTION
С	GINC	INCREMENT FOR UP	PER	R QUOTA PROPORTION
С	NQ	NUMBER OF QUOTA	PRO	CPORTIONS
C	BPOP (N)	BEGINNING BIOMAS	Se	BY AGE GROUP
C	PS(N)	PROPORTION SPAWN	ING	G BY AGE GROUP
C	GEND	PROPERTION ANNUA	L 6	GROWTH BY AGE GROUP
5	GHINI	PROPORTION GROWT	H F	FUR HALF UF THE TEAR BY AGE GROUP
U	COMMON	I IL AVERAGE GRO		H TU CAPTUREI
	DILLOUNDE.	TPOP. 05(51). POR		51), 0(12), ENV(100, 12), THEAN(100, 12),
	102.04.09	0.01.081.0805.518	0.0	CO.SID.WAYA.SHEDOD.T. 1.DODT/511.SDOD.
	2850-181-1	FT. TU. TRUN. TI OGI	- TF	ENV. TPRO. H. TOSET .RMAX.OMIN.OTNC.NO.
	3MAT(16.16).MA(16.16).B0.B	1.0	H2.84.ACATCH.XMORT (51).NENV.L.NL.
	4 TREC (1 00)	.TSPOP(140).TYIE	LOC	(10)).TTPOP(100).G(51).GH(51).
	5 AREC(100,	16),ASPOP(100,16),A	AVIELD(100,16),ATPOF(100,16),8POP(51)
	REAL M			
	INTEGER A	SPOP, AYIELD, AREC	, AT	TPOP, TSPOP, TYIELD, TREC, TTPCP
	READ 001,	, KL		
	001 FORMAT(I2	2)		
	DO 199 KL	M=1,KL		
	READ 100,	IIO,NYRS,IET,IET	• MA	AXA,IKUN,ILUGI,IENV,IPRO,IGSET,
	1RHAX+QAL,	- 686 - Mastra GA - GM 1 - CTA - 7 26 - 0 56 4	N + G	LING, NU TAN
	TEANIN CT	LU149793584U93544 [.1] 68 TO 463	C 9 L	T.4.1
	READ 101-	(8POP(N)_PS(N)_0	(N)).GH(N).N=TRT.MAXA)
	101 FORMAT (F	6.0.3F6.4)		· · · · · · · · · · · · · · · · · · ·
	102 PRINT 103	S.M.NYRS, ITO		
	163 FORMAT	(+1THO STEP QUO	TA	SIMULATION NODEL FOR *,
	1*PACIFIC	MACKEREL PH PA	RRI	ISH MAY 18, 1976#
	I,/,* ALL	FOP FIGURES IN T	HOU	USANDS OF POUNEST

```
3,/,* NATURAL MORTALITY M=*,F4.2,/,* SIMULATED FOR *,I4,* YEARS*
4,/,* STARTING POPULATION *,I4,//,* MODEL FARAMETERS BY AGE GROUP*
5,/,* AGE STARTING PROPORTION PROPORTION PROPORTION
                                                                         PROPORTION
   6GROWTH*,/,* GROUP
                             POPULATION
                                               SPAWNING
                                                              ANNUAL GROWTH
                                                                                      T
    70 CAPTURE #)
PRINT 104, (N, BPOP(N), PS(N), G(N), GH(N), N=IBT, MAXA)
104 FORMAT(12, F13.0, F12.3, F15.3, F18.3)
105 FORMAT(//,60H EXTINCTION CURVE FOR PS(1)=0.54*EXP(-.00000071709*TP0
   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 BHOP3R TRANSPORT MODEL *,/
     PRINT 115, IBT, IET, IRUN, ILCGI, IENV, IPRO, IQSET, RMAX, SLP, MAXA, QMIN,
   1QINC,NG
115 FORMAT(//,* IBT=*,I4,/,* IET=*,I4,/,* IRUN=*,I4,/,* ILOGI=*,I4,/,
   1* IENV=*, 14,/,* IPRO=*, 14,/,* IQSET=*, 14,/,* RPAX=*, F8.0,/,
2* SLP=*,F4.2,/,* MAXA=*,I4,/,* QHIN=*,F5.3,/,* QINC=*,F5.3,/,
    3* NQ=+,14)
     IF(KLM.GT.1) GO TO 119
     IF(IENV.GT.0) GO TO 150
     IF(IPR0.GT.0) GO TO 150
                                                                                   .
116 CONTINUE
     BODY STARTS HERE
119 IF(NQ.EQ.1) GO TO 120
     GO TO 122
120 IU=-9
     DO 121 N=IBT,IET
121 CALL MACRE
CALL OUTH
     STOP
122 IU=NQ $ QB=QNIN-QINC $ NL=IET-IBT+1
D0 124 IQE=1,NQ
QB=QB+QINC $ L=D
     00 123 J= I8T, IET
     L=L+1
     CALL MACQE
     MAT(L, IQB) = TYIELD(L)/NYRS
123 MA(L, IQB) = ACATCH
124 CALL OUTH
PRINT 125,NYRS
125 FORMAT (1H1,//,20X,I4,* YEAR MEAN YIELD*)
     CALL OUTHAT (MAT)
     IT=IT0+NYRS+1
PRINT 125,IT
126 FCRMAT (1H1,//,20X, TYIELD IN T,I4)
     CALL OUTHATEMAN
     GO TO 199
150 IF(IENV.LT.1) GO TO 160
    00 151 N=1,NYRS
151 READ 152, (ENV(N, NN), NN=1, IENV)
152 FORMAT (6F8.2)
```

```
102
```

С

```
160 IF(IPR0.GT.0) GO TO 161
GO TO 116
161 DO 162 N=1,NYRS
162 READ 163, (ENV(N,NN),NN=7,9)
163 FORMAT(35×,3F5.0)
     IF(IPR0.EQ.1) GO TO 115
    00 164 N=1.NYRS
164 READ 165, (ENV(N, NN) , NN= 10, 12)
165 FORMAT (35 X . 3F5 .0)
     GO TO 116
199 CONTINUE
    STOP $ END
     SUBROUTINE MACGE
     COMMON
   OITO,NYRS, TPOP,PS(511,POPA(511,P(12),ENV(190,12),IMEARAIO0,104,
   1Q2, QA, QB, QAL, QEL, QPOP, SUBC, CG, SLP, MAXA, SUBPOP, I, J, POPC (51), SPOF.
   2REC, IBT, IET, IU, IRUN, ILOGI, IENV, IPRO, N, IQSET, RHAX, GHIN, QINC, NG,
   3NAT(16,16), MA(16,16), DU, B1, B2, B4, ACATCH, XNORE(51), NENY, La Ne.
   4TREC(100), TSPOP(100), TYIELD(100), TTPOP(100), G(51), GH(51),
   5AREC(100,16),ASPOP(1. ...16),AYTELD(190,16),ATPOP(100,16),800P(51)
     REAL M
     INTEGER ASPOF, AVIELD, AREC, ATFOR, TSPOP, TVIFLD, TREC, TTPOP
     TSPOP(L) =TREC(L)=TYIELD(L)= TTPOP(L)=0
     DO 500 N=IBT.MAXA
500 POPA(N)=BPOP(N)
    DO 516 I=1,NYRS
SPOP=ACATCH=TPOP=0
     00 501 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 3 GO TO 506
504 Q2=TPOP $GO TO 506
505 Q2=POPA(1)+POPA(2)
506 IF(Q2.LT.GAL) GO TO F07
    GO TO 508
507 Z=M $ A=1.0-EXP(-Z)
    DO 58 N=IBT, MAXA
 58 XHORT (N) = POPA(N)*A
    GO TO 512
508 CALL QUOT
     E=CQ/QPOP
     F=FVAL(E,M)
Z=F+M $ A=1.0 -EXP(-7)
D0 509 N=J+MAXA
XMORT(N) = POPA(N)*A
509 ACATCH = ACATCH + XMORT(N)*(F/Z)*GH(N)
     IF(J.GT.IBT) GO TO 518
     GO TO 512
510 E = SUBO/SUBPOP
     F=FVAL(E,M)
     ZS=F +M & AS=1.0 - EXP(-ZS)
     JT = J-1
     00 511 N=IBI,JT
     XMORT(N) = POPA(N)*AS
511 ACATCH=ACATCH + XMORT(N) . (F/ZS) . GH(N)
512 NT=MAX4+2
     DO 513 N=IBT.MAXA
     NT=NT-1
```

```
513 POPALNT) = (POPA(NT-1) - XMORT(NT-1)) * G(NT-1)
       POPA(MAXA) = POPA(MAXA) + POPA(MAXA+1)
       POPA(TAT)=REC
       TSPOP(L)=TSPOP(L) + SPOP
       TREC(L) = TREC(L) + REC

TYIELP(L) = TYIELD(L) + ACATCH

TTPOP(L) = TTPOP(L) + TPOP
       ASPOP(I,L) = SPOP
       AREC(I,L) = REC
       AVILEDTIAL) = AGATCH
       ATPOP(I.L) = TPOP
       IF (REC.GT.RMAX) GO TO 514
  GC TO 516
514 PRINT 515
  515 FORMAT (* REGRUITMENT BLENUF OR FAILED*)
       CALL OUTH
       STOP
  516 CONTINUE
  S17 RETURN 3 END
       SUBROUTINE FUN
       COMMON
      OTTO, NYRS. TPOP, PS(51). POPA(51), P(12), ENV(100, 12), INEAN(100, 12),
      1Q2,QA,QB,GAL,QEL,QPOP,SUBG,CG,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
2REC,IBT,IET,IU,IPUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
      3MAT (16,15), MA(10,16), 30, 61, 82, 84, ACATCH, XNORT (51), NENV, L, NL
       REAL M
       IF(IPRO.EG.0) 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(1,7)+P(2)*ENV(1,8) + P(1)*ENV(1,9)
       IF(IPR0.EQ.2) PROB=P(3)*ENV(I,1J)+P(2)*ENV(I,11)+P(1)*ENV(I,12)
  666 CONTINUE
C
       RECRUITMENT MODEL AFTER THIS CARD
      2* REG= 0.97815*SPOP*EXP(-0.000037741*SPOP)+EXP(0.020787*PROA)
      3 *EXP(0.0039065*PROB) *)
       RETURN 3 END
       FUNCTION FVAL(E,M)
       ITERATIVE SOLUTION FOR INST. FISHING MORT. GIVEN EXPLOITATION RATE
С
       AND INST. NATURAL HERT.
       COMMON ITC, NYRS
       REAL M
       F=E 3 N=0
       IF(E.E0.0) GO TO 2
     1 N=N+1 S IF(N.GT.50) GO TC 90
F1=F-0.01 S F2=F+0.01
                     8 F2=F+0.01
       EV=(1.0 - EXP(-F-N)) + F/ (F+M)
E1=(1.0 - EXP(-F1-M)) + F1/ (F1+M)
       E2=(1.0 - EXP(-F2-H))* F2/ (F2+H)
       SLOPE= (E2-E1) / 0.02
       DIFFE = EV-E
       F=F - DIFFE / SLOPE
       IF (ABS (DIFFE).GT.S.GOGOGI) GC TO 1
     2 FVAL=F
       RETURN
   90 PRINT 900
  900 FORMAT(//,* ITERATIONS FOR F EXCEEDED 50*)
  901 STOP $ END
       SUGROUTINE LOGI
С
       PACIFIC MACKEREL SUBROUTINE
       COMMON
     OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12)
PS(1)=.54*EXP(-.8000071709*TPOP)
       RETURN $ END
```

104

```
SUBBOUTINE QUOT
    COMMON
   01TO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
1Q2,QA,QB,QAL,OBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
   2REC, 18T, 1ET, 1U, IRUN, ILOGI, IENV, IPRO, M, IQSET, RMAX, QMIN, QINC, NG,
3MAT (16, 16), MA (16, 16), E0, B1, E2, B4, ACATCH, XMORT (51), NENV+L, NL
    REAL M
    IF(Q2.GT.Q8L) GO TO 900
    QUO=QA=(Q2-QAL)
    GO TO 901
900 QUO=(Q8L-CAL)+CA + (02-08L)+CB
901 QPOP=SUBQ=0.01 $ SUBPOP=0.1
    D0 902 IC= J. MAXA
90 2 QPOP=QPOP+POPC(IC)
    IF(J.EQ.IBT) GC TO 904
     1.1=.1-1
DO 903 IC=1+JJ
903 SUBPOP=SUBPOP + POPC(IC)
    SUBQ=SLP+QU0
    000=000-5080
    IF(QU0/QP0P.GT.1.3) GC TO 905
944 CQ=QUO 3 GO TO 906
905 CQ=QPOP
906 IF(SU80/SU8POP.LT.0.5) 50 TC 907
    X=0.5*SUBPOP $ Y=SUBQ-X
SUBQ=X $ CC=QUO+Y
907 RETURN
              $ ENO
     SUBROUTINE OUTM
    COMMON
   OITO,NYRS, [POP,PS(51),POPA(51),P(12),ENV(100,12), INEAN(100,12),
   1Q2, QA, QB, CAL, GBL, GPCP, SUBO, CO, SLP, MAXA, SUEPOP, I, J. FOPC(51), SPOF,
   2REC, IBT, IET, IU, IRUN, ILOGI, IENV, IPRO, M, IQSET, RMAX, QMIN, QINC, NO,
   3MAT (16,16), MA (16,16), 30, 81, 82, 84, ACATCH, XMORT 151), NEHV, L. NL,
   4TREC(100), TSPOP(100), TYIELD(100), TTPOP(100), G(51), GH(51),
   5AREC(100,16),ASPOP(100,16),AYTELD(100,16),ATPOP(100,16),BPOP(51)
    REAL M
     INTEGER ASPOP, AVIELD, AREC, ATFOP, TSPOP, TVIFLD, TREC, TTPOP
     IF(REC.GT.RMAX) GO TO 606
    IF(IRUN.EG.0) GO TO 609
     IOK=1
     IF(QBL.LT.1.AND.IQSET.EQ.1) IOK=0
    IF(IOK.EQ.1) PRINT 660,08
IF(IOK.NE.1) PRINT 601,08
600 FORMAT(//,T21, *ANNUAL SPANNING BICMASS, UPPER GUOTA PROPORTION =*
   1.F6.3)
601 FORMAT (//, T21, *ANNUAL SPANNING BIGMASS, EXPLOITATION RATE =*, F6.31
CALL OUTP (ASPOP, TSPOP)
     IF(IRUN.EQ.1) G0 TO 609
    IF(IOK.EQ.1) PRINT 602.08
IF(IOK.NE.1) PRINT 603.98
ED2 FORMAT (//,T21,*ANNUAL YIELD, UPPER GUOTA PROPERTION =*,F6.3)
603 FORMAT (//,T21,*ANNUAL YIELD, EXPLOITATION RATE =*,F6.3)
     CALL OUTP (AYIELD, TYIELD)
     IF(IOK.EQ.1) PRINT 604.08
IF(IOK.NE.1) PRINT 605.09
604 FORMAT (//,T21,*ANNLAL TOTAL BIOMASS, UPPER QUCTA PROFORTION =*
   1,F6.3)
605 FCRMAT (//.T21.*ANNUAL TOTAL BIOHASS, EXPLOITATION RATE =*.F6.31
CALL OUTP (ATPOP.TTPOP)
606 CONTINUE
     IF(IOK.EQ.1) PRINT 607.08
     IF(TOK.NE.1) PRINT 608,08
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 5 END
       SUBROUTINE OUTP (IANN, ITOT)
       COMMON
     0110.NYRS, TPOP, PS(51), POPA(51), P(12), ENV(100,12), IMEAN(100,12),
     192, QA, QB, QAL, QBL, QPCP, SUBS, CG, SLP, MAXA, SUBPOP, I, J, POPC(51), SPOP, 2REC, IBT, IET, IU, IRUN, ILOGI, IENV, IPRO, M, IQSET, RMAX, GMIN, QINC, NQ,
      3NAT (16,16), NA(16,16), 20,31,82,34, ACATCH, XMORT (51), NENV, L, NL,
     4TREC(100) . TSPOP(100) . TVIELD(100) . TTPOP(100) . G(51) . GH(51) .
     SAREG(100,16), ASPOP(100,16), AYIELD(100,16), ATPOP(100,16), BPOP(51)
       REAL M
       INTEGER ASPOP, AVIELD, AREC, ATPOP, TSPOP, TYIELD, TREC, TTPCP
       DIMENSION TANN(100,16), ITOT(100)
       PRINT 700, (N, N=IBT, IET)
  700 FORMAT(///,T21,*AGE AT RECRUITMENT*,//,* SEASCN*,1618)
       IS=I10-1
       00 701 N=1.NYRS
       IS=IS+1
  701 PRINT 702, IS, (IANN(N,K), K=1, NL)
  702 FORMAT (1X,14,2X,1618)
       IFILU.NE.-91 RETURN
       00 763 N=181,1ET
  203 ITOT(N) = ITOT(N)/NYRS
  PRINT 254,(ITOT(N),N=IBT,IET)
204 FORHAT (* MEAN *,1EIB)
RETURN 3 END
       CURROUTINE OUTHATIMT)
       COMMON
     OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
102,QA,QB,QAL,QBL,QPCP,SUB0,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
     2MEC, 181, IET, IU, IRUN, ILOGI, IENV, IPRO, M, IQSET, RMAX, GMIN, QINC, NQ,
     3HAT(16,16),MA(16,16),3C,31,82,84,ACATCH,XMORT(51),NEN%,L,NL,
4TREC(10C),TSPOF(1,0),TYIELO(10C),TTPOP(10C),G(51),GH(51),
     5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16), POP(51)
       REAL M
       PRINT 803
860 FORMAT (* AGE*,/,* AT*,/,* REC.*)
       K=IET+1
       00 801 NJ≈1.NL
       K≠K+1
       PUNCH CARE OUTPUT FCR YIELD ISOPLETH PLOTS
67
       PUNCH 008, (MT (K, N), N=1, NG)
  DD8 FORMAT (1018)
  801 FRINT 802 .K. (MT(K,N),N=1,NG)
802 FORMAT (77,1X,12,4X,1618)
PRINT 803
  503 FORMAT (//,7X)
       QY=QHIN+QINC
       DO 804 N=1.NO
       QY=QY+DINC
  804 091N) = 0Y
       PRINT 805, (Q1(N), N=1, NG)
  805 FORMAT (7X,16F8.2)
       IF(IQSET.NE.1) GO TO 807
       IF(Q3L.LT.1.J) PRINT 806
  AG6 FORMAT(/, T32, *EXPLOITATION RATE*)
       IF(Q9L.LT.1.3) SO TO 899
  807 PPINE 808
  858 FORMAT(/, 132, "GUGIA PROPORTICN")
899 RETURN 5 END
```

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106
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TYPICAL INPUT FOR QUOTAE

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4	NUMBER	OF RU	INS									
1946 33 1 5	62	1	0 6	2 0								
906000.20500.	40035.	.53 .1	LE •20	0.00	• 65	10						
	1.316											
30137 .89 1.282	1.163											
143011.00 1.2	1.133											
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	6J	111	191	114	176	243	152	102	95	72	61
30N 119W 1945	30	102	82	61	220	151	126	119	105	81	72	31
30N 119W 1949 30N 119W 1957	50 60	121	117	150	153	164	113	125	123	91	84 58	53
1100 1951	112	85	115	91	234	207	157	120	155	128	73	4 Q
30N 119H 1952	24	35	138	çĝ	224	156	64	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	216	138	178	164	195	6 9	49
30N 119W 1955	81	68	99	226	265	299	202	173	242	173	111	61
JUN 119W 1956	72	98	207	165	238	297	191	245	180	139	60	52
30K 119W 1957	1.05	70	101	229	190	258	185	130	165	130	115	57
30N 119W 1959	99	33	168	149	231	304	195	139	151	153	ĒĹ	27
3JN 119W 1960	45	103	169	144	299	133	111	138	133	121	47	66
30N 119W 1961	33	157	168	164	210	158	Ģ4	124	70	66	47	53
30N 119W 1962	49	46	82	189	212	21.8	155	156	146	97	103	32
JJN 1198 1953 Jan 4408 1966	9 60	63	37	115	150	163	172	131	93	/1 60	63	41
33N 119W 1965	65	54		39	185	142	66	76	59	58		27
30N 119W 1966	44	49	72	64	81	121	132	51	76	51	14	42
3JN 1198 1967	29	65	56	73	1ó3	130	126	15E	71	91	13	58
30N 119W 1968	32	30	92	116	152	157	102	128	104	76	90	32
30N 119W 1969	8	45	136	185	227	194	219	202	173	134	.7	70
30N 119W 1973	21	13	96	183	241	238	177	225	158	117	55	45
33N 119W 1971 Ran 119W 1972	91	104	100	1 8 0	241	168	125	117	170	142	139	85
30N 119W 1973	54	7	178	192	155	178	137	149	121	90	93	97
30N 119H 1974	22	134	93	234	284	263	147	167	141	104	74	34
39N 119H 1975	50	62	127	174	187	197	192	194	180	146	134	58
30N 119H 1946 0DI	467	30	68	-201	-558	-578	-254	-69	-51	-51	88	34
30N 119W 1947 0DI	-78	48	-114	-140	- 362	-303	-107	-274	-124	-46	237	194
30N 119H 1946 001 30N 119H 1946 001	12	125	-188	-270	-309	-105	-117	-10.5	- 75	93 78	184	87
30N 119W 195J OLI	-76	-78	54	-206	- 346	- 35 6	-52	-120	-247	-141	3	-26
36N 119W 1951 ODI	-113	-36	84	-211	-449	- 37 4	-162	-169	-266	12	-4	66
30N 119W 1952 0DI	-20	-68	-42	- 55	-330	-278	-342	-134	-221	-152	-57	-17
3JN 119W 1953 ODI	63	246	-255	-441	-439	-695	- JE 2	-594	-532	-284	-121	166
30N 119W 1954 001	- 31	- 6 3	-105	-492		-459	-195	-528	-118	-229	47	-/5
30N 119W 1956 001	23	-50	-110	-370	- 570	-426	-210	-371	-137	-230	170	110
30N 119W 1957 OGI	-26	-181	-265	-393	-468	-363	-273	-215	-448	-213	-51	-19
30N 119W 1958 001	-123	-294	-397	-311	- 334	-865	-628	-364	-183	-51	19	57
30N 119W 1959 ODI	-6	-93	-100	-405	-656	-671	-418	-407	-273	- 38	57	61
30N 119W 1960 0DI	-54	-141	-245	-120	-4.9	-38u	-230	-196	-57	-1	-4	76
SUN 1198 1961 ODI	54	-59	-245	-112	-742	-152	-285	-567	-40	-283	-4	165
30N 119W 19E3 OFT	-20	-121	-33F	-524	-619	-814	-875	-524		د <u>د</u> د ج	-58	79
30N 119W 1964 ODI	102	36	-246	-818	-1960-	2005	-1432-	1165	-885	-483	-218	-468
3GN 119W 1965 ODI	-251	-248	-412	-91	-421	-689	-817	-562	-4 81	-307	-66	-56
30N 119W 1966 00I	23	-127	-255	-458	-798-	-1-53	-776	-568	-662	-301	-209	-127
30N 119W 1967 ODI	-100	-99	-539	-603-	-1113-	1255-	1002	-673	-712	-462	-145	145
300 1190 1965 001 300 1190 1965 001	-101	-225	-544	-47 5-	-115U-	-1674	-5//	- 6 7 6	-045	-241	- 209	- 7 C - 24 D
30N 119W 1970 001	-197	-168	-357	-513	-811	-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 OCI	97	-326	-434	-627	-651	-801	-687	-458	-438	-154	96	76
30N 119W 1973 00I	-6	-23	-299	-461	- 192	-924	-773	-652	-726	-338	-359	63
JUN 1198 1974 001	-22	18	-338	-591	- 969	-903	-590	-907	-555	-385	3	151
1946 30 1 5	6 2	-204	- 3 3 Z	2 0	-919.	- * * * * *	-/41	-032	-939	-313	-0	· 1
900000. 20000.	40020.	.50 .1	10.20	.53	.05	10						
1946 30 1 5	6 2	1	0 2	2 0								
900000. 3.	, ⁹ ,	•5] •:	10.20	.53	.05	10						
1946 30 1 5	6 2 a	1	10 10 10 20	2 0	.0=	4 A						
	U •			ل ال ه د	• 117	1 U						

FISH BULLETIN 167

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

```
TIC MAY25
+D P 3R JUL.2
*I BNDP3R.25
    XMAY 25, 1976 PEG
TD BHDP3R.34
*I BMDP3R.33
     CTOL= 1.0E -8
+D UNCOLA.73
#I UNCOLA.72
            TOLERANCE FOR CONVERGENCE
    X 50H
                                                               .F11.8/
*0 P3RJUL.24
*I P3RJUL.23
            F20.5)
     1
#D RITEIT.15
*I RITEIT.14
3000 FORMAT(2X,14,7X,14,F21.6,1X,F18.7,5(1X,F14,9))
*D REDEV.18
*I REDEV.17
3600 FORMAT(1X, 14, 2X, A1, A8, 1X, F14.6, 1X, F14.6, 2(2X, F13.6))
#0 RITEND.28
*I RITEND.27
  900 FORMAT (2X, 14,7X, 14, F21.6, 4X, 6(1X, F14.6))
*D RITEND.48,RITEND.53
*I RITEND.47
5600 FORMAT(1H0,2X,7H CASE ,10HPREDICTED ,7X,
     10HSTO DEV OF,5X, HOBSERVED/
     1uX, A8, 9X, 13 HPRED VALUE,
     .
        5X, A8, 9X, A3, 4(7X, A8))
 5800 FORMAT (1X, 14, A2, F13.6, 2X, F15.5, 2X, F13.6,
        2X,F15.6,4(2X,F13.6))
     .
*I RITEND.96
     IF(ISFUN.GT.5) GO TC 47
+0 FUN.10
*I FUN.9
      IF(ISFUN.GE.1.AND.ISFUN.LE.19)G0 T0 (103,200,300,400,500,600,700,
     *800,960,1000,1100,1200,1300,1400,1500,1600,1700,1800,1900),ISFUN
*I FUN.99
С
С
      RICKER MODEL
  600 F=P(1)*X(1)*EXP(P(2)*X(1))
      OF(1) = X(1) * EXP(P(2) * X(1))
      DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))
      RETURN
С
С
      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
С
C
      CLARK-RICKER MODEL
  800 F=P(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
      OF(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(F(3)/X(1))
      RETURN
C
С
      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))
      OF(3)=P(1)*X(1)**P(2) *(1/X(1)) * EXP(P(3)/X(1))
      RETURN
```

108
```
С
            CUSHING TRANSPORT MODEL
 1000 F=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
          OF(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 MCDEL
 1100 F= P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
             *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
        1
          DF(1) = X(1)**P(2) * EXP( P(3)*X(2) )

+ EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
         1
          DF(2) = P(1)*X(1)**P(2)*ALOG(X(1)) * EXP( P(3)*X(2) )
          . *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) )
        1
          DF(4) = P(1) * X(1) * P(2) * EXP(P(3) * X(2))
          *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) )
         1
          RETHEN
С
          EXPONENTIAL MOCEL
С
С
  1200 F = P(1) + EXP(P(2)+X(1))
          DF(1) = EXP( P(2)*X(1) )
          DF(2) = P(1) * X(1) * EXP(F(2)*X(1))
          RETURN
С
3
         RECRUIT PER SPANNER TRANSPORT MODEL
C
  1300 F = P(1) + EXP(P(2) + X(1)) + EXP(P(3) + X(2)) + EXP(P(4) + X(3))
                             EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
          DF(1) =
          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
Ċ
           RICKER TRANSPORT MODEL
С
  1400 F = P(1)*X(1)*EXP(P(2)*X(1))
         1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
          DF(1) = X(1) * EXP(P(2) * X(1))
        DF(1) = \chi(1) * EXP(P(2)*\chi(1))
1 * EXP(P(3)*\chi(2)) * EXP(P(4)*\chi(3))
DF(2) = P(1) * \chi(1) * \chi(1) * EXP(P(2)*\chi(1))
1 * EXP(P(3)*\chi(2)) * EXP(P(2)*\chi(1)) * \chi(2)
1 * EXP(P(3)*\chi(2)) * EXP(P(2)*\chi(1)) * \chi(2)
1 * EXP(P(3)*\chi(2)) * EXP(P(2)*\chi(1)) * \chi(3)
DF(4) = P(1) * \chi(1) * EXP(P(2)*\chi(1)) * \chi(3)
1 * EXP(P(3)*\chi(2)) * EXP(P(4)*\chi(3))
DF(4) = P(1) * \chi(2) * EXP(P(4)*\chi(3))
DF(4) = P(3)*\chi(2) * EXP(P(4)*\chi(3))
          RETURN
С
          RICKER SEA LEVEL MODEL
С
С
 1500 F = P(1) * X(1) * EXP(P(2)*X(1))

1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))

DF(1) = X(1) * EXP(P(2)*X(1))
        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)
4 * EXP(P(3)*X(2) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
         1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
          RFTURN
```

```
C

C CLARK-RICKER TRANSPORT MODEL

C

1600 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))

OF(1) = X(1) *EXP(P(2)*X(1)) * EXP(P(3)/X(1))

1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))

OF(3) = 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))

OF(3) = 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))

OF(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))

OF(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))

OF(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

1700 RETURN

1000 RETURN
```

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