DENSITY DEPENDENCE OF CATCHABILITY COEFFICIENT IN THE CALIFORNIA PACIFIC SARDINE, *SARDINOPS SAGAX CAERULEA,* PURSE SEINE FISHERY

ALEC D. MacCALL

California Department of Fish and Game
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The California Pacific sardine fishery is examined for the period 1932 to 1950 to determine if the catchability coefficient, based on available measures of fishing effort, varied as a function of population size. Previous estimates of sardine fishery parameters indicate such a density dependence. New estimates of instantaneous fishing mortality rates and mean population sizes were calculated. Annual mean boat tonnages for the fleet were calculated and show a growth in mean effective vessel capacity from about 60 tons in early 1930's to 120 tons in 1946. To account for changes in efficiency of the fleet due to increases in vessel size, fishing effort in boat-months was converted to effort in ton-months. Two catch per unit effort indices of abundance, one unstratified by geographical area and one stratified into northern and southern segments of the fishery, gave very similar results. Estimates of the catchability coefficient for the sardine fishery were found to be inversely related to population abundance, N, and fit the power function $q = \alpha N^\beta$, with $\beta = -0.611$ for the period 1937–1944 when the fishery was least restricted and gear improvements were minimal.

INTRODUCTION

John Radovich (1973) recently hypothesized that the California fishery for the Pacific sardine experienced an increase in catchability coefficient as biomass decreased. This increase was presumably the result of the combined effects of behavior of the fish, which tended to maintain contagiously distributed schools of fishable size despite decreased total biomass, and nonrandom characteristics of the local purse seine fleet which was highly mobile, informed, and efficient. Similar relationships are suspected in other purse seine fisheries, particularly the northwest Atlantic menhaden fishery (Schaaf and Huntsman, 1972). Gulland (1964) voices serious doubts over the usefulness of most measures of effort in purse seine fisheries, and Ostvedt (1964) shows for the Norwegian winter herring fishery that purse seine catch per unit effort (CPUE) is considerably less sensitive than gill net CPUE to changes in herring abundance. Pope and Garrod (1975) have shown the catchability coefficient to be inversely related to stock size in three northwest Atlantic cod

fisheries, including two independent trawl fisheries and the Portuguese dory fishery. A model of purse seine catch and effort developed by Paloheimo and Dickie (1964) predicted a catchability coefficient inversely related to stock abundance resulting in constant CPUE.

Murphy (1966) calculated catchability coefficients and population sizes of Pacific sardines based on a cohort analysis of commercial catches. A plot of catchability coefficients against biomass estimates (Figure 1) shows a distinct rise in catchability coefficient as biomass decreases. This interpretation requires further investigation. There is a strong serial relationship in the increase in catchability which may have been related to the entry of progressively larger vessels into the sardine fleet (Clark, 1939). Clark's (1956) effort, on which Murphy's estimates are based is measured in boat-months, and is insensitive to this change in mean hold capacity. Marr (1950) shows that fishing power of sardine vessels in Oregon and Washington was highly correlated with boat length. A similar relationship is likely to hold for California vessels. If effort units are recalculated for the California sardine fleet, a recalculation of Murphy's (1966) fishing mortality rate estimates, which were based on Clark's CPUE, is desirable. Moreover, the recalculation can take the form of Tomlinson's (1970) generalization of the method, which estimates fishing mortality rates directly from catches.

This investigation was pursued with the purpose of determining if a correlation existed between the catchability coefficient and abundance of Pacific sardines. Since the sardine can no longer support a large fishery in California, the specific problem is of little direct relevance though it may be used as a model for other fisheries. Exploitation of other species by purse seine gear is increasing in California as well as in many other areas, and elucidation of the behavior and dynamics of purse seine fisheries in general may be of value to their management.

METHODS

Data used in this study are restricted to the fishing seasons between 1932 (1932–33) and 1950 (Table 1). The 1932 season is the earliest for which estimates of effort and fishing mortality rates are available. Clark (1939) felt that this was the earliest season for which
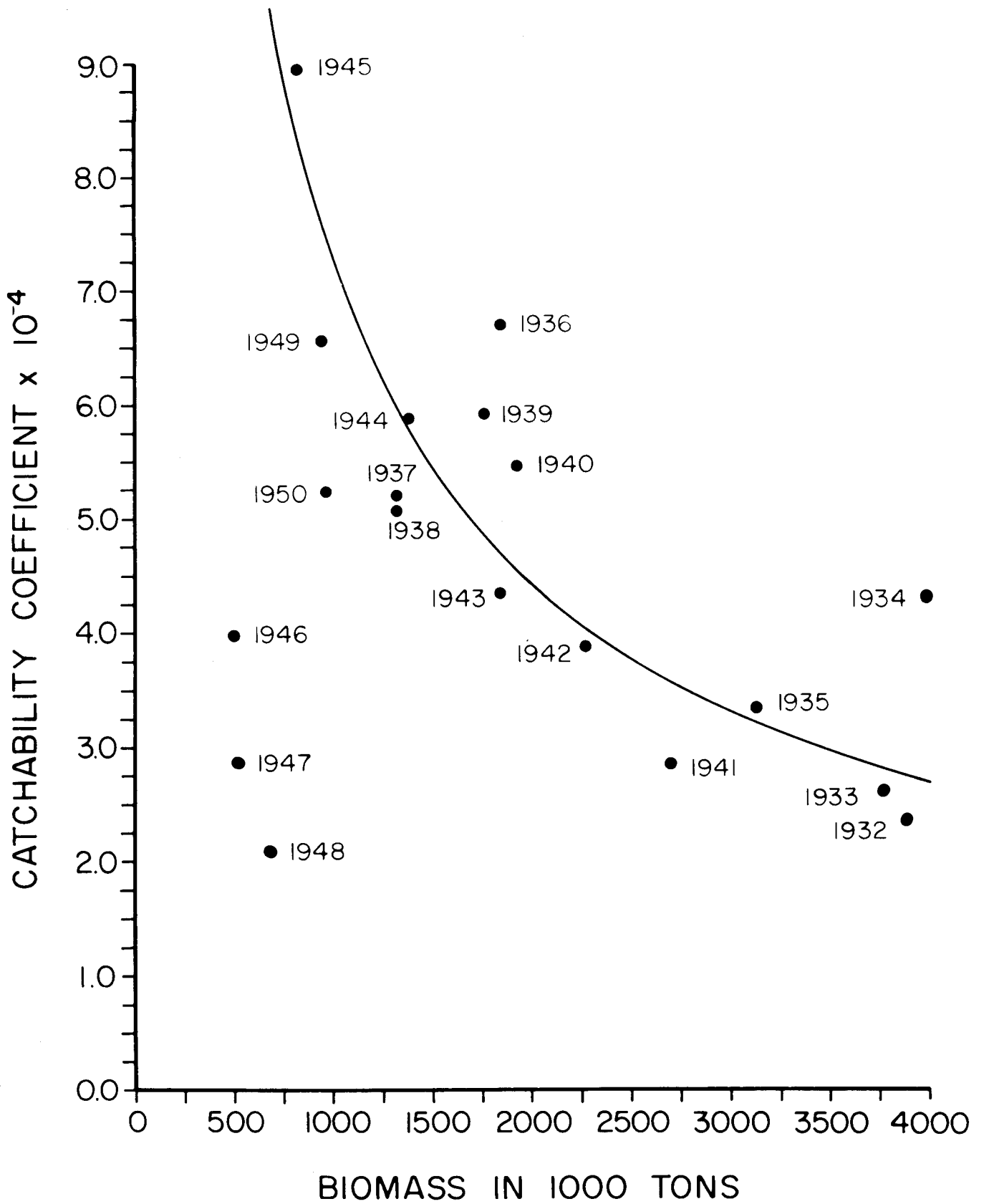
FIGURE 1.   Catchability coefficient as a function of population size (data from Murphy, 1966, Tables 11 and 15).

cannery limits on deliveries ceased to be a major factor in reducing fishing power. Starting in 1951, Murphy (1966) increased his estimate of natural mortality rate from M = 0.4 to M = 0.8, making it difficult to compare fishing mortality rates with the earlier period. Moreover, gear developments in the late 1940's and early 1950's undoubtedly changed the

fishing power of sardine vessels. Use of radio, depth finders, and aerial scouting was well established by the early 1950's (Knaggs, 1972). Presumably, the period 1932–50 was relatively free from increases in fishing power due to innovation and gear development.

TABLE 1

Pacific Sardine Fishery Parameters

Year	Fishing mortality rate F_1 (Murphy, 1966)	Recalculated fishing mortality rate F_2	Effort f_1 boat-months (Clark and Daugherty, 1952)	Number of boats examined	Mean boat tonnage	Effort f_2 ton-months	Catchability $q = F_2/f_2$ (10^{-6})	Mean fished population age 2+ (10^6)
1932–33	0.105	0.10	448.1	80	59.66	26734	3.74	17033
1933	0.156	0.15	600.2	80	57.91	34758	4.32	14242
1934	0.307	0.31	716.6	115	57.86	41462	7.48	12254
1935	0.292	0.28	876.1	145	51.27	44918	6.23	13326
1936	0.825	0.69	1236.9	163	71.18	88043	7.84	7115
1937	0.707	0.65	1366.4	178	80.39	109840	5.92	5491
1938	0.708	0.60	1399.0	178	86.98	121680	4.93	6794
1939	0.775	0.55	1314.4	213	89.89	118150	4.66	7233
1940	0.613	0.55	1124.5	176	90.79	102090	5.39	6251
1941	0.370	0.36	1304.0	199	94.10	122710	2.93	15504
1942	0.390	0.35	1010.3	143	95.90	96890	3.61	11654
1943	0.485	0.49	1121.7	151	96.92	108720	4.51	7224
1944	0.765	0.74	1304.8	151	104.71	136630	5.42	5003
1945	1.170	1.03	1314.7	170	115.92	152400	6.76	2666
1946	0.589	0.52	1485.0	182	121.05	179760	2.89	2270
1947	0.389	0.39	1358.4	224	72.51	98500	3.96	1900
1948	0.192	0.23	921.0	248	65.74	54160	4.25	5085
1949	0.619	0.60	946.8	280	58.25	44810	13.39	4292
1950	0.796	0.796	1526.8	287	54.19	103830	7.67	3277

Density-Dependent Catchability

The model proposed to describe the density-dependent variability of the catchability coefficient is:

$$q = \alpha N^\beta \qquad (1)$$

where: q is catchability coefficient,

N is mean population size or abundance, and

α and β are constants.

This power function allows the catchability coefficient to increase or decrease as abundance varies, depending on the sign of β.

Given

$$C = qfN$$

where: C is catch in numbers and

f is nominal effort, then

$$q = (C/f)N^{-1} \qquad (2)$$

and setting equations (1) and (2) equal, we obtain

$$(C/f)N^{-1} = \alpha N^\beta \text{ or}$$
$$C/f = \alpha N^{\beta+1} \qquad (3)$$

This indicates that if $\beta = 0$, $\alpha = q$ and CPUE is a perfect index of abundance. However, if $\beta = -1$, $\alpha = C/f$, and CPUE is a constant which is entirely useless as an index of abundance. This is the case predicted by Paloheimo and Dickie (1964). For values of β other than 0 or -1, CPUE bears a curvilinear relationship to abundance and may be of use as an abundance index after appropriate correction; but for values of β near -1, information

content of CPUE indices is greatly reduced and they must be used with caution.

Values of β can be obtained from fitting a production model to catch and effort data by a procedure developed by Fox (National Marine Fisheries Service, MS) or by directly calculating q from fishing mortality rates (F) and effort, and regressing these values on abundance estimates after log transformation. Since both variables are subject to an unknown measurement error, the best regression line was obtained by calculating the geometric mean of individual slopes obtained by Y on X, and X on Y linear regressions (Ricker, 1973). Fox obtains a β of -0.3 for the Pacific sardine fishery for 1932 to 1954, while the regression method gives a β of -0.608 for 1932 to 1950 based on Murphy's (1966) estimates; however, deletion of the 1946–48 outliers (a justification is given later) increases the statistical significance greatly and the estimate of β becomes -0.724 (Table 2). Statistical variability and bias is poorly known for either method, making comparison of β values difficult. A well known statistical problem arises in the regression method: regression of a variate Y/X on Z/Y (in this case F/f on C/F) may give a seemingly significant correlation despite X, Y and Z being entirely random, due to Y appearing in the numerator of the first term and in the denominator of the second. The degree to which this biases the results of the regression method is unknown in this case, but it is assumed to be minor.

The regression method will be assumed to give the best estimate of β for the purposes of this investigation. It is important to note that in this case β is near the critical value of -1 where CPUE is constant regardless of abundance.

TABLE 2

Regression Estimates of Density-Dependent Catchability Parameters for Pacific Sardine

Source	n	α	β	r
Murphy (1966) data*				
1932–1950	19	2.501	−0.608	−0.215
1932–45, 1949–50	16	16.05	−0.724	−0.826
Recalculation†				
Unstratified				
1932–45, 1949–50	16	16.78	−0.656	−0.605
1932–36	5	4.911	−0.610	−0.979
1937–44	8	78080	−1.005	−0.795
Stratified				
1932–45, 1949–50	16	77.48	−0.719	−0.695
1937–44	8	1029	−0.841	−0.896

* Effort in boat-months, population size in tons age 2+ at beginning of season.
† Effort in ton-months, population size in mean number age 2+ during season.

Estimation of Fishing Mortality and Population Size

Estimates of fishing mortality rates were recalculated from Murphy's (1966) catches by the cohort analysis method described by Tomlinson (1970). Fish were assumed to be fully recruited at age 3, and catch ratios (C_{4+}/C_{3+}) were used to obtain exploitation rates in a backward solution starting with $F_{1950} = 0.796$ which is identical to Murphy's F_{1950}. An M of 0.4 was assumed. Recalculated fishing mortality rates (Table 1) correspond clearly to those obtained by Murphy (Figure 2), with large discrepancies only for the series 1936 to 1940, and for 1945 and 1946. Errors in F are propagated from season to season in cohort analysis, but with a tendency for those errors to be reduced at each iteration in the backward solution (Tomlinson 1970).

Use of mean population sizes should reflect the average abundance of fish observed over the course of the fishing season better than would the initial population sizes at the beginning of the season. Annual mean available population sizes (Table 1) were obtained from F estimates by the relationship:

$$N' = C_t/F \qquad (4)$$

where: N' is mean available population, and

C$_t$ is total annual catch of all age groups.

N' will be used for quantity N in equation (1), since it can be interpreted as the size of that population necessary to give the observed catch if all individuals are fully recruited. This could be interpreted as the population fully available to the fishery.

Effort Adjustment for Vessel Size

The possible influence of increases in fishing power resulting from increasing effective hold capacity of the average boat used by Clark and Daugherty (1952) was removed by converting effort to ton-months. Estimated sardine carrying capacity of boats was derived from an empirical relationship relating skipper's estimates of carrying capacity to registered gross tonnage for 27 vessels active in the present San Pedro wetfish purse seine fleet. (Data supplied by Knaggs, California Department of Fish and Game, pers. comm.). The relationship

$$T = 1.003G + 1.349 \times 10^{-7}G^4$$

where: T is estimated sardine carrying capacity (short tons), and

G is registered gross tonnage

appears to fit the observations (Figure 3) quite well ($r = 0.997$), and should be valid for estimating approximate carrying capacity of boats within the general range of observed gross tonnages. Of 451 boats for which estimates were made, 41 exceeded 126 gross tons, and of those only 11 exceeded 150 gross tons.

Mean sardine capacity of the average boat in the fleet was calculated for each season as average estimated vessel capacity weighted by boat activity measured in months fished (Table 1). Average tonnages show a distinct rise from the mid 1930's to the mid 1940's (Figure 4). From 1932 through 1936 and 1945 through 1948, canneries are known to have imposed limits on the size of deliveries, thereby reducing the effective boat tonnage. For the latter period, a boat was assigned the limiting value of tonnage for ports and months in which limits were imposed if boat tonnage exceeded the limit. Clark (1939) gives some information on limits in effect from 1932 through 1936. The information is insufficient to calculate effective boat tonnages as above, but allows an estimate for each season to be made by a weighted mean based on boat activity:

$$\overline{T}_{est.} = \frac{\Sigma B_i (f_{lim}\overline{T}_{lim} + (1 - f_{lim})\overline{T}_{tot})}{\Sigma B_i} \qquad (5)$$

where: $\overline{T}_{est}$ is estimated effective tonnage for season,

B$_i$ is number of boats operating respectively in Monterey fall and winter and San Pedro fall and winter fisheries (Clark, 1939, Tables 3 and 4),

f$_{lim}$ is the fraction of time limits were in effect (Clark, 1939, Table 1),

$\overline{T}_{lim}$ is average effective boat tonnage under the influence of limits. Boats with carrying capacities larger than the mean limit for the season (Clark, 1939, Table 1) were assigned the mean limit as their effective tonnage, and

$\overline{T}_{tot}$ is average effective boat tonnage in the absence of limits.

This assumes the size distribution of vessels in the Monterey and San Pedro fall and winter subdivisions was equal, since more specific information is lacking.

Effort in ton-months was calculated by multiplying Clark and Daugherty's (1952, Table 6) all-California
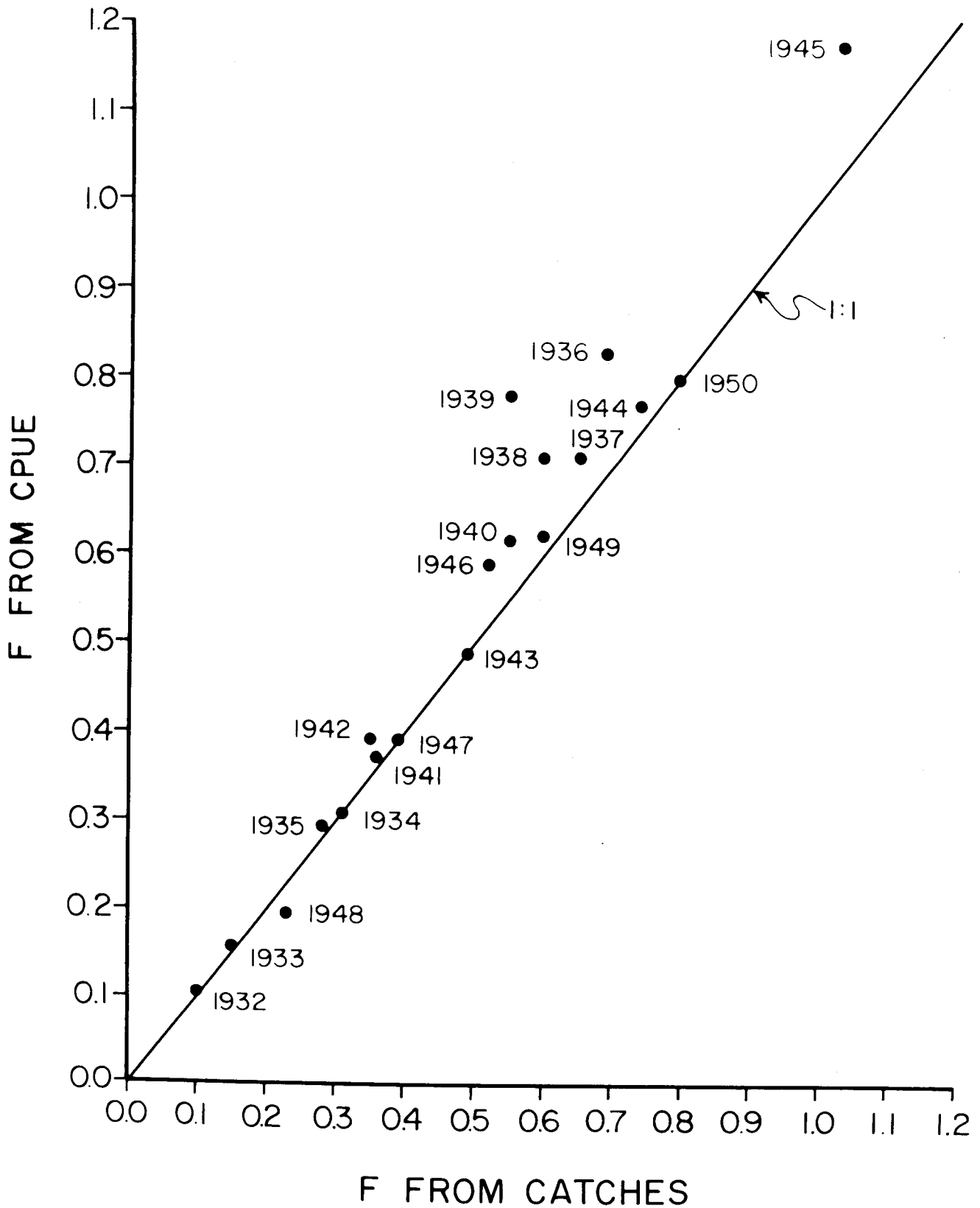
FIGURE 2.   Comparison of instantaneous fishing mortality rates for fishing seasons estimated by cohort analysis of sardine CPUE values (Murphy, 1966) and by cohort analysis of catches in numbers.
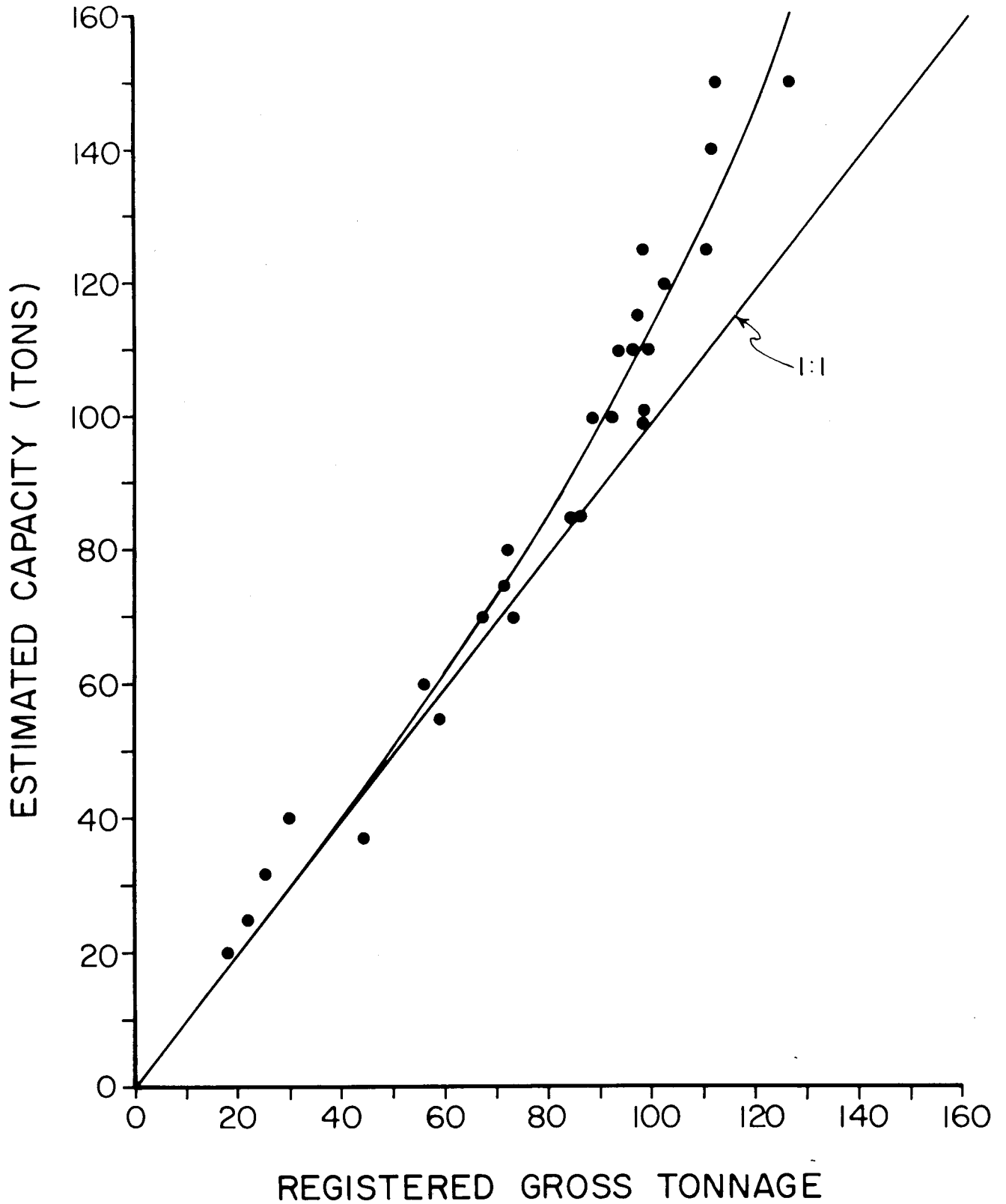
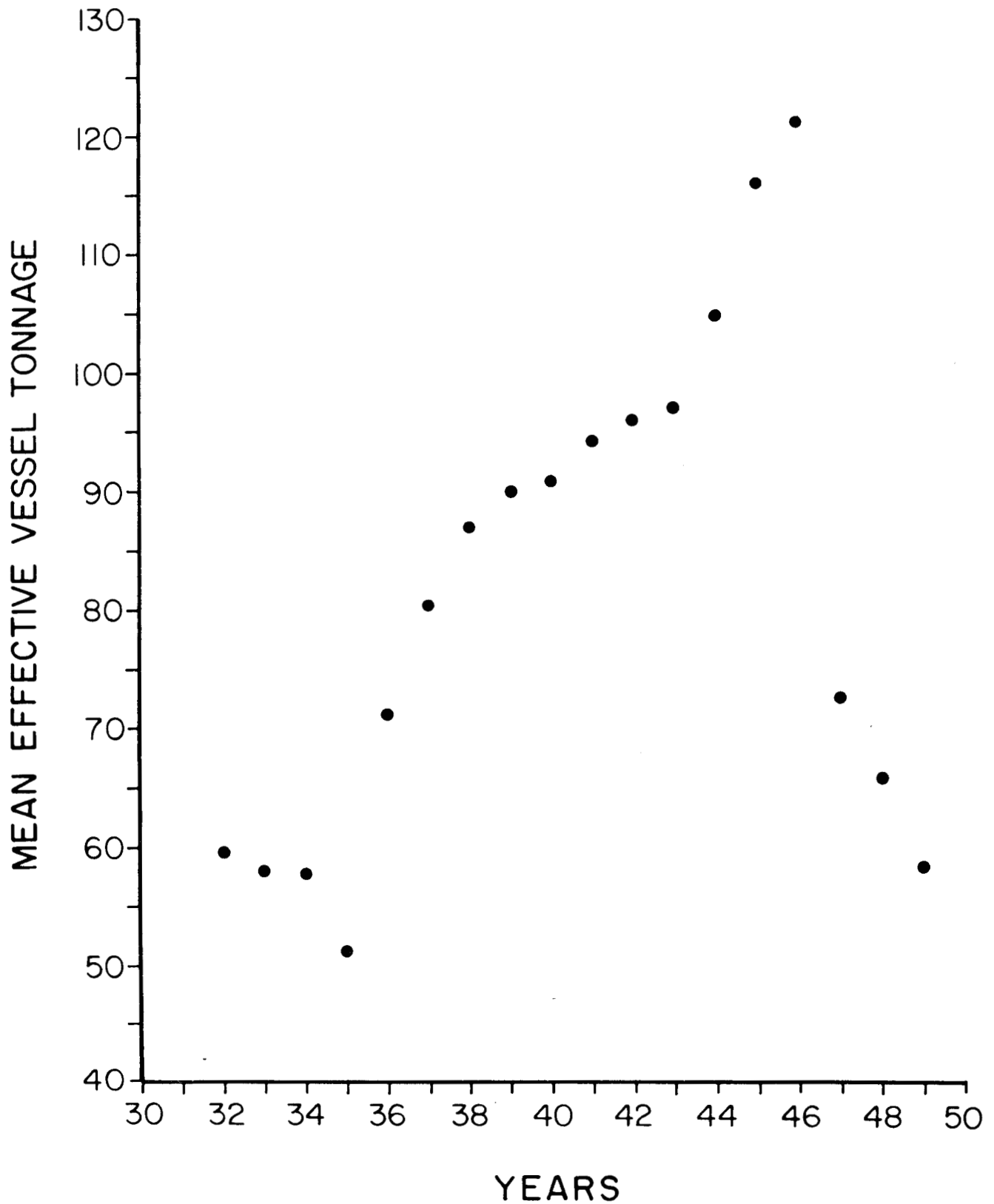FIGURE 3.   Relationship of estimated vessel carrying capacity of sardines to registered gross tonnage.

FIGURE 4. Mean effective sardine carrying capacity of vessels.

effort in boat-months by mean boat carrying capacity in tons. For seasons 1946–48, Clark's correction for limits was removed before multiplying by effective mean tonnage. In 1945, Clark's worksheets indicate a correction for limits, but values for the limits themselves are not available. Clark's corrected effort was retained, and was multiplied by unadjusted mean boat tonnage.

The effort points for 1946, 1947, and 1948 are anomalous in that Clark relaxed her effort criteria due to low abundance of sardines, and thus tended to overestimate effort. Daugherty (California Department of Fish and Game, MS) states: "For boats fishing at Monterey or San Francisco, one delivery in a dark was assumed to be evidence that a boat was fishing the whole dark" and "this year [1947–48], also, due to the large amounts of jack mackerel and Pacific mackerel that were caught, deliveries of those fishes were considered along with sardine deliveries in determining whether a boat was fishing at least 2 weeks out of the dark. This resulted in many boats being included which would not otherwise have been, there being a number of cases in which a boat made no sardine deliveries but its mackerel deliveries showed it to be actively fishing." A "dark" is a period of new moon, when fishing, which is done at night, is most actively pursued. Similar changes in criteria hold for 1946–47 and 1948–49. This change in criteria was an attempt to overcome a basic deficiency in the raw effort data: boat activity resulting in no catch went unreported, since the evidence for boat activity was landings receipts. Original criteria were resumed for 1949–50 and 1950–51.

Handbooks on methods for assessing fish stocks (Ricker, 1958; Gulland, 1969) recommend stratifying CPUE by geographic areas and adding the individual CPUE values, weighting each as the size of its sub-area. This method helps account for changes in distribution of the stock which may result from changes in population size. As a simple attempt at stratification, Monterey and San Pedro area CPUE values given by Clark and Daugherty (1952) were treated as separate area strata (Table 3). Areas were obtained from the catch distributions given by Pinkas (1951). Those reporting blocks wherein catch exceeded 100 tons were counted, giving an area of 74 blocks for Monterey and 111 blocks for San Pedro, with Point Conception as the arbitrary dividing line.

RESULTS

Recalculated catchability coefficients and mean population sizes (Table 1) were plotted (Figure 5), and an increase in catchability with reduced population size is clearly indicated. Howbeit, there remain problems in interpreting the time series. Data points for the late 1940's are subject to considerable question, as discussed earlier. Observations for 1949 and 1950 could be subject to

influences of the boom in gear development and fish detection methods which was in progress by the early 1950's. The 1945 point must be suspected to be affected by limits on cannery deliveries. The 1946–48 points are based on altered standards for determining effort, and are not comparable with points for other years; yet, judging by the catchability coefficients for those years, Clark's "relaxed" criteria may have led to a better measurement of effort (more constant q) than did her standard criteria.

Catchability coefficients based on the two-area stratified CPUE (Table 3) were plotted against mean population size (Figure 6) for comparison with unstratified CPUE. The two plots are very similar, indicating that this simple stratification does little to

TABLE 3

Catchability Coefficients for Two-Area Stratified CPUE

	Catch per unit effort			
	San Pedro	Monterey	Mean*	Catchability coefficient
Year	10⁶ fish/boat-month		10^5 fish/ ton-month	10^{-6}/ ton-month
1932	3.53	3.78	6.08	3.57
1933	4.88	3.70	7.61	5.34
1934	5.59	6.14	10.04	8.19
1935	4.21	4.49	8.43	6.33
1936	2.97	4.86	5.23	7.36
1937	2.20	2.54	2.91	5.29
1938	3.42	4.76	4.55	6.69
1939	2.56	4.46	3.69	5.11
1940	4.05	3.95	4.42	7.07
1941	3.42	5.27	4.42	2.85
1942	4.52	3.88	4.45	3.82
1943	2.58	3.98	3.24	4.48
1944	3.70	3.69	3.53	7.06
1945	3.33	1.91	2.38	8.94
1946	2.19	0.46	1.24	5.45
1947	0.96	0.32	0.97	5.11
1948	2.11	1.38	2.77	5.44
1949	3.75	3.22	6.07	14.15
1950	2.38	0.56	3.05	9.30

* San Pedro weight = 111, Monterey weight = 74.

improve the CPUE index.

Catchability coefficients for the period 1932–1935 are anomalous for both measures of CPUE, with the 1936 value also appearing as an outlier in the unstratified case. There is no definite explanation for this series of anomalous points, however, some possibilities may be suggested. The economic conditions of the early 1930's may have allowed only the most efficient boats to remain operating. Alternatively, the correction for the effect of cannery limits on mean boat carrying capacity may result in underestimated nominal effort, particularly with respect to landings at offshore reduction ships, which were probably unaffected by such limits. Mean uncorrected tonnages for the 1932 through 1936 seasons are 66.15, 66.09, 65.14, 65.57 and 72.53 tons respectively. Division of catchability coefficients by the uncorrected/corrected tonnage ratio results in a slight downward shift of the five points, however, they remain as distinct outliers. A
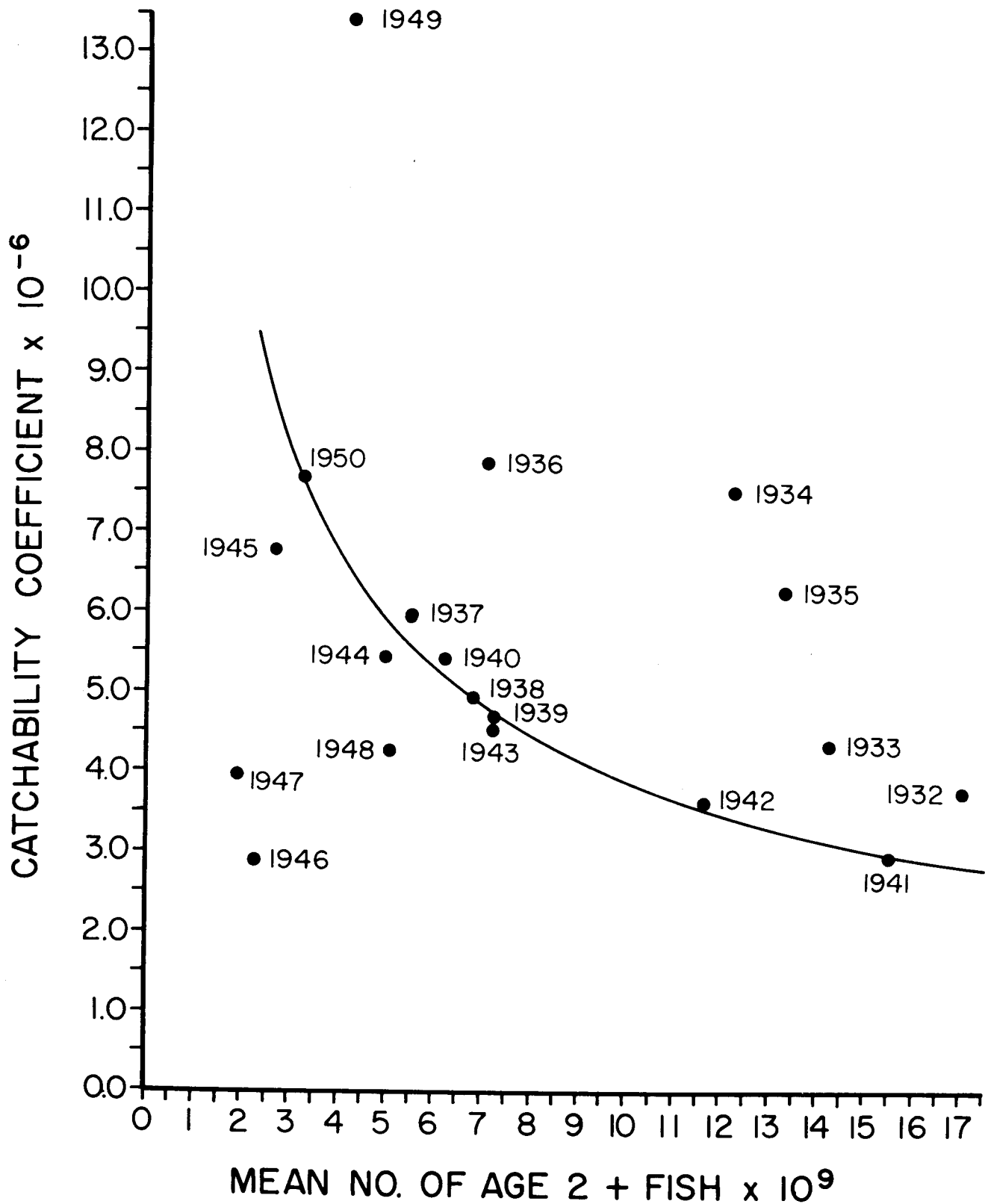
FIGURE 5.   The relationship of catchability coefficient to mean population size for unstratified CPUE.
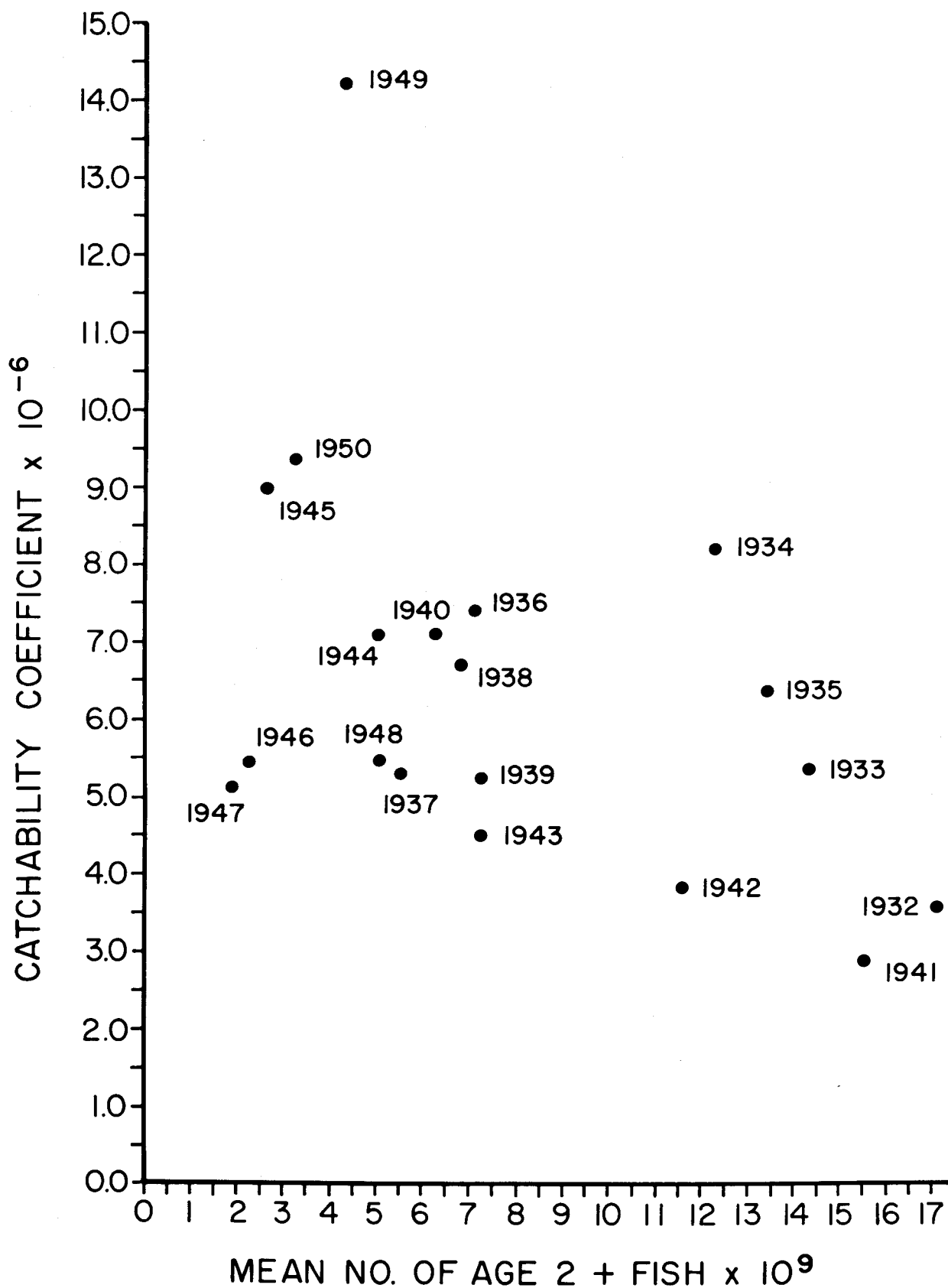
FIGURE 6.   The relationship of catchability coefficient to mean population size for two-area stratified CPUE.
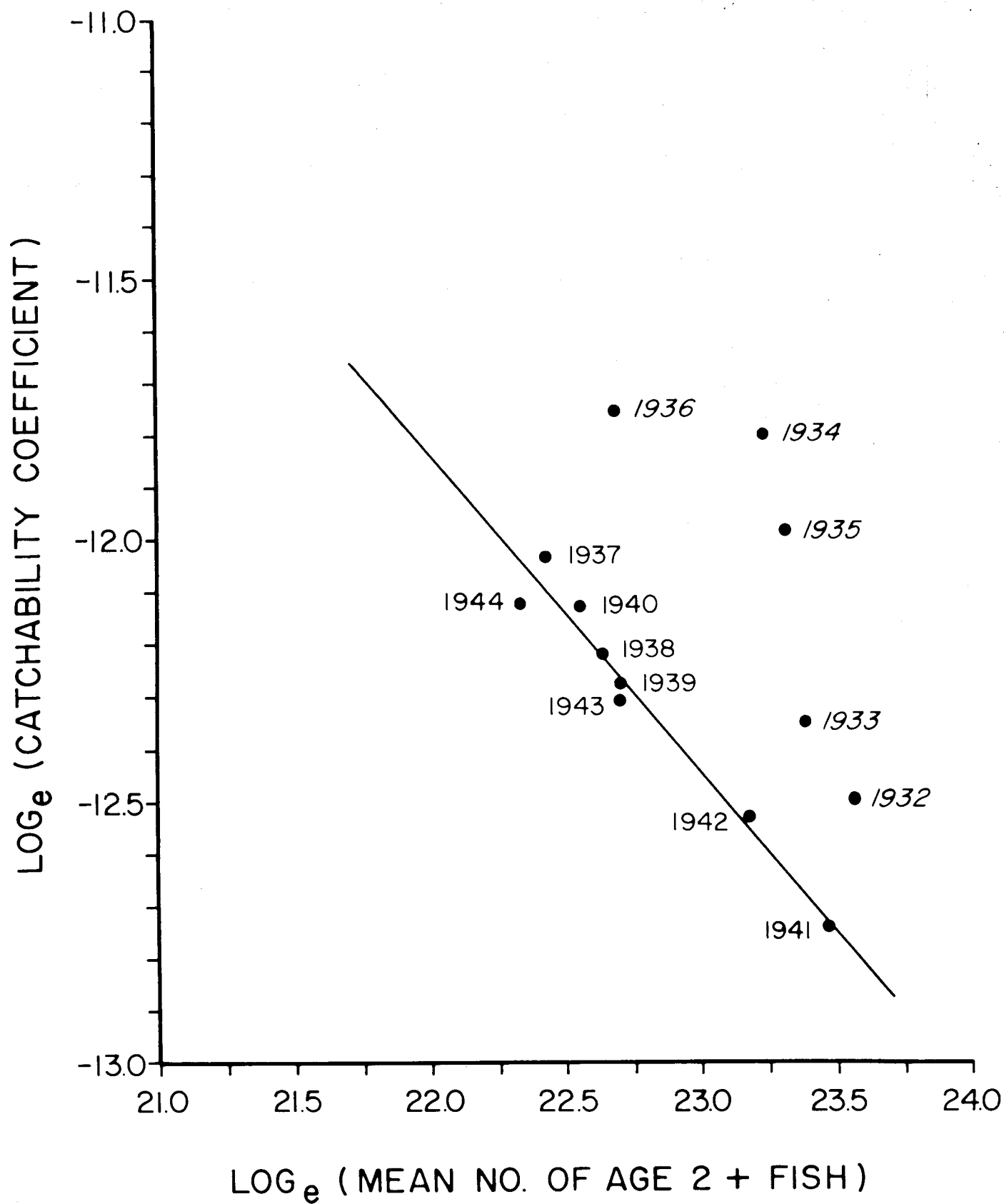
FIGURE 7.   Regression of catchability coefficient on mean population size after logarithmic transformations. (Years in italics not included in regression).

likely explanation for these outliers is overestimation of F and consequent underestimation of mean population size, although this cannot be verified and must remain a hypothesis.

Most other factors would suggest that catchability coefficients should have increased during the 1930s. Scofield (1951) describes several trends in gear development during this period. Radiotelephones were first tried in 1935 and by 1937 were fairly common in San Francisco and San Pedro. During the period 1930 to 1940 ringnets were replacing lampara nets (presumably because the fishermen felt they were more efficient), and the changeover from pulling nets by hand to use of power also was taking place. It is difficult to quantify the effects of these innovations, but the catchability coefficient for the early period is probably dominated by the combined effects of small boat tonnage and cannery limits. Gulland (1964) states " . . . small boats fishing for shoaling fish (e.g., sprats) may catch, in one successful haul, as many fish as they can conveniently carry. The catch per haul or per voyage is likely to be constant over a fair range of stock abundance . . ." suggesting a β value of -1. While a regression based on five points is of limited value, the β of -1.005 obtained from the 1932–36 unstratified CPUE (Table 2) supports the above contention, although the 1936 season was minimally affected by limits, which appeared only in the fall Monterey fishery.

Processing capacity of canneries increased by the mid-1930's so that limits were no longer necessary. This, combined with an influx of new large vessels from a resumption of boat building, resulted in a freely expanding fishery. In the absence of restrictions (except for fishing season), boats were able to operate at full capacity and the catchability coefficient was determined primarily by biological factors, particularly fish distribution and behavior. Catchability coefficients for the period 1937–44 show a highly significant density dependence $(F = 130.8^{**})$. The value of $\beta = -0.611$ (stratified case, $\beta = -0.841$) for this period furnishes clear evidence for a density dependent catchability coefficient and nonlinear CPUE. The evidence is strengthened by the fact that population size increased from 1937 to 1941 and subsequently decreased, with catchability coefficients maintaining the relationship over the complete cycle.

After 1944 conditions in the fishery changed, making comparison difficult. Limits of 30 tons per delivery were placed on small fish landed in Monterey. In 1946 and 1947 a lack of fish in central California resulted in a relocation of the fleet to southern California, where further delivery limits were imposed due to lack of sufficient processing facilities. Criteria for defining effort were changed, as described in a previous section. In the late 1940's aerial scouting began to be used in the fishery, and many of the less efficient vessels disappeared from the fleet, further biasing the apparent catchability coefficient. Analysis of the time series was not attempted for these later seasons.

An "overall" value of β was estimated from the entire time series with the 1946–48 data deleted using a GM regression (Richer, 1973) of log-transformed variables (Table 2). Since the periods 1932–35 and 1937–44 show separate and distinct trends (Figure 7), and values from the late 1940s are of questionable comparability due to changes in gear and methods, the "overall" value of $\beta = -0.670$ (stratified case, $\beta = -0.719$) may be useful as a general description of the trends in q over the entire time period, but fails to describe the detailed behavior of the fishery.

DISCUSSION

The assumption of constant catchability has been widespread in quantitative fisheries analysis, although it has been recognized as a weak point, particularly when CPUE is not stratified by geographic subareas, and when applied to the analysis of CPUE from purse seine fisheries in particular. This study presents further evidence that such a catchability coefficient may be a variable, and that it may be possible to describe its behavior as a function of fish abundance. Moreover, a simple attempt at stratification by large geographic areas yields no improvement in the CPUE index, giving further reason to reject the a priori assumption that geographical stratification of CPUE results in a reasonably constant catchability coefficient or valid index of abundance. A simple power function (Equation 1) appears to fit the observations well, has a parameter (β) of density dependence which is easily determined, has a simple interpretation, and has desirable mathematical properties for incorporation into more complex fisheries models (e.g., Fox, MS). If the power function proves to be a useful model for other fisheries and measures of effort, it may become possible to assume a value for β based on comparable fisheries rather than assume $\beta = 0$ as is presently done. For example, an assumed β of -0.5 would be equivalent to the assumption that the square of CPUE is a good index of relative abundance.

The assumption of constant catchability coefficient should be seriously considered before applying many of the standard quantitative methods used in fisheries analysis. A range of solutions can be obtained by incorporating maximum and minimum likely values for β; or the importance of assumptions of value for β can be determined by sensitivity analysis or simulation. Determination of natural mortality rate by regression of total mortality rate on effort is affected by changes in catchability coefficient (Garrod, 1964). The DeLury or Leslie method can be seriously affected by changes in q (Braaten, 1969). Fox (National Marine Fisheries
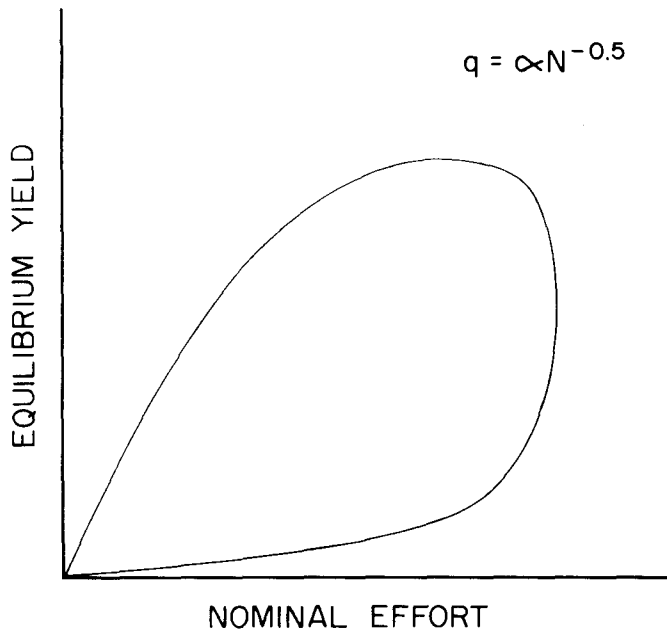
$$q = \propto N^{-0.5}$$

FIGURE 8. Production model behavior when $\beta = -0.5$ (after Fox, 1974 MS).

Service, MS) has shown that the shapes of equilibrium yield curves obtained from surplus production models are profoundly affected by values of β (Figure 8). As β approaches a value of -1, the level of nominal effort necessay to achieve maximum sustained yield approaches a critical point at which the fishery collapses, as seems to have happened in the case of the Pacific sardine. Unfortunately, production model estimation of β is difficult if effort has never approached the critical level.

The effectiveness of some forms of fishery management may be affected by violation of the assumption of a constant catchability coefficient. Pope and Garrod (1975) examine some of the implications of variable catchability coefficients on catch quotas and effort quotas for fishery management. Validity of limited entry or control of effort as a management tool is often based on the assumption of non-negative β. When $\beta = 0$, a unit of effort will generate a proportional rate of fishing mortality independently of population size. With $\beta > 0$, a unit of effort will generate a decreasing rate of fishing mortality as abundance decreases and limited entry may lead to an ideal buffering against overexploitation. On the other hand, when $\beta < 0$, a condition of instability results, due to fishing mortality becoming more intense as population declines (Radovich, 1973). In such a case, maximum nominal fishing effort must be kept below the critical level and a better measure of effort must be found, or inefficiencies must be imposed on fishing. Most management regulations applied to open fisheries,

such as catch quotas, gear restrictions, fishing seasons, and area closures fall under this latter category.

ACKNOWLEDGEMENTS

REFERENCES

Braaten, D. O. 1969. Robustness of the DeLury population estimator. Canada, Fish. Res. Bd., J., 26: 339–355.

Clark, F. N. 1939. Measures of the abundance of the sardine, Sardinops caerulea, in California waters. Calif. Div. Fish and Game, Fish. Bull., (53): 1–45.

Clark, F. N., and A. E. Daugherty. 1952. Average lunar month catch by California sardine fishermen, 1949–50 and 1950–51. Calif. Fish and Game, Fish. Bull., 38(1): 85–97.

Garrod, D. J. 1964. Effective fishing effort and the catchability coefficient q. Rapp. Cons. Explor. Mer., 155: 66–70.

Gulland, J. A. 1964. Catch per unit effort as a measure of abundance. Rapp. Cons. Explor. Mer., 155: 8–14.

——. 1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO, Manuals Fish. Sci. 4, 154 p.

Knaggs, E. H. 1972. San Pedro wetfish fleets: Major purse-seine gear changes, 1952–72. Commer. Fish. Rev., 34(5): 11–32.

Marr, J. C. 1950. Apparent abundance of the pilchard (Sardinops caerulea) off Oregon and Washington, 1935–43, as measured by the catch per boat. U.S. Fish. Wildl. Serv., Fish. Bull., 51(52): 385–394.

Murphy, G. I. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc. Calif. Acad. Sci., 4th Ser., 34: 1–84.

Ostvedt, O. J. 1964. Comparison between catch per unit effort in the Norwegian gill-net and purse-seine fishery for herring. Rapp. Cons. Explor. Mer., 155: 90–93.

Paloheimo, J. E., and L. M. Dickie. 1964. Abundance and fishing success. Rapp. Cons. Explor. Mer., 155: 152–163.

Pinkas, L. 1951. Yield per area of the California sardine fishing grounds, 1937–1949. Calif. Dept. Fish and Game, Fish. Bull., (80): 9–14.

Pope, J. G., and D. J. Garrod. 1975. Sources of error in catch and effort quota regulations with particular reference to variations in the catchability coefficient. ICNAF Res. Bull., 11: 17–30.

Radovich, J. 1973. A challenge of accepted concepts involving catch per unit of effort data. Proc. Annu. Meet. Calif.-Nevada Chapter Am. Fish. Soc., Feb. 3, 1973, 6 p.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Canada, Fish. Res. Bd. Bull., (119): 1–300.

——. 1973. Linear regressions in fishery research. Canada, Fish. Res. Bd. J., 30: 409–434.

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

Schaaf, W. E., and G. R. Huntsman. 1972. Effects of fishing on the Atlantic menhaden stock: 1955–1969. Trans. Am. Fish. Soc., 101: 290–297.

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

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