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SOUTHWEST FISHERIES CENTER

P.O. BOX 271
LA JOLLA, CA 92038

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ESTIMATING CURRENT RATES OF
INCREASE AND SURVIVAL RATES
FROM REPRODUCTIVE DATA FOR
DOLPHIN POPULATIONS IN THE
EASTERN TROPICAL PACIFIC

by

Tom Polacheck

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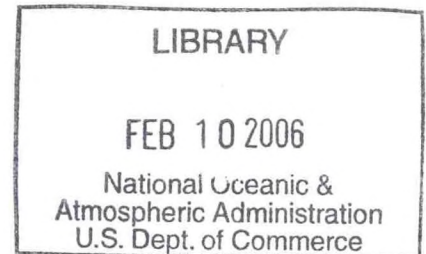


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ESTIMATING CURRENT RATES OF INCREASE AND
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POPULATIONS IN THE EASTERN TROPICAL PACIFIC

Tom Polacheck
Southwest Fisheries Center
National Marine Fisheries Service, NOAA
La Jolla, California 92038
and
Department of Biology
University of Oregon
Eugene, Oregon 97403

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National Marine Fisheries Service, NOAA
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Eugene, Oregon 97403

INTRODUCTION

Dolphins are killed incidentally in the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific. Samples of the animals killed have been collected in order to estimate the vital rates of the various dolphin stocks which are affected. Numerous estimates of the reproductive rates for various stocks have been based on these samples (Perrin, et al., 1976, 1977a, b; Perrin and Henderson, 1979¹; Henderson, et al., 1979²) but, at present, no estimates of survival rates are available. The age structure of a population is often used to provide estimates of survival (Seber, 1973), but the age structure of these samples of dolphins is not presently known. The purpose of this report is to point out that the reproductive structure (i.e. the proportion of individuals in different reproductive conditions) may contain implicit information on the age structure of a population and thus provide information on survival rates. The method used in this report has three parameters:

1. the age of maturity
2. the fecundity rate
3. the proportion of mature females.

The method also assumes that adult survival and fecundity rates are constant, juvenile survival rates are constant, and that the population sampled has a stable age distribution. Modifications of these assumptions are possible. Given these assumptions and the above three parameters, the implied

¹Perrin, W. F. and J. R. Henderson. 1979. Growth and reproductive rates in two populations of spinner dolphins, (*Stenella longirostris*) with different histories of exploitation. Southwest Fisheries Center, Admin. Rep. No. LJ-79-29.

²Henderson, J., W. F. Perrin and R. B. Miller. 1979. Gross annual production in dolphin populations (*Stenella* spp) in the eastern tropical Pacific, 1973-1978. NMFS-SWFC, SOPS/79/33.

juvenile survival rate can be determined as a function of the adult survival rate. This relationship provides a range of values for the survival rates, only a portion of which are likely to be biologically reasonable. Any combination of juvenile and adult survival rates, yields an associated estimate of the current net rate of increase, so that the method also provides a range of estimates of the current rate of increase.

For this report, this technique is applied to the large body of reproductive data available on the dolphin stocks in the eastern tropical Pacific, and survival rates are calculated for the three stocks for which estimates of all three parameters are available. In addition, some generalized results are presented to provide a method of assessing the sensitivity of the results to the parameter values used.

METHODS

The method of analysis used in this paper is based on solving for the stable age distribution (or eigenvector) of a modified Leslie projection matrix. The modification is to include a survival rate value in the lower right hand corner. The basic matrix used is of the form

$$\tilde{M}_1 = \begin{pmatrix} 0 & 0 & \cdot & \cdot & \cdot & & & F_A \\ S_1 & 0 & \cdot & \cdot & \cdot & & & 0 \\ 0 & S_2 & \cdot & \cdot & \cdot & & & 0 \\ & \cdot & & & & & \cdot & \\ & \cdot & & & & & \cdot & \\ & \cdot & & & & & \cdot & \\ 0 & 0 & \cdot & \cdot & \cdot & S_{M-1} & 0 & 0 \\ 0 & 0 & \cdot & \cdot & \cdot & 0 & S_M & S_A \end{pmatrix}$$

where F_A = the adult fecundity rate or the number of daughters born per adult female per year

M = the age of maturity

S_i = for $i = 1$ to M is a constant and equals the juvenile survival rate (S_j)

S_A = the adult survival rate

The use of S_A in the lower right hand corner greatly reduces the size of the projection matrix by assuming that survival rates past a certain age are constant. It is well-known that the age distribution of a population projected ahead according to the above matrix will converge to a stable age distribution. Thus, given F_A , M and the proportion of females which are mature, for any value of S_A there is a unique value for S_j such that for the stable age vector the proportion mature equals a specified value (or expressed in terms of the dominant eigenvector for the above matrix, the ratio of the $M+1$ element divided by the sum of all the elements must equal the specified value). In the present paper, solutions for S_j as a function of S_A are presented for the above matrix.

In addition to the solution for the above matrix (which is referred to as version I), solutions for three other versions of the projection matrix are considered in order to provide an indication of the sensitivity of the results to some of the basic assumptions. These three additional versions plus version I are all specific cases of the following general matrix:

$$\tilde{M}_2 = \begin{pmatrix} \partial_1 F_A & \partial_2 F_A & \cdot & \cdot & \cdot & \partial_N F_A \\ S_1 & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & S_2 & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & \cdot & \cdot & S_{N-1} & G \end{pmatrix}$$

where F_A , M , S_j are defined above and

$$\partial_i = \begin{cases} 1 & M < i \leq N \\ 0 & i \leq M \end{cases}$$

$$S_i = \begin{cases} S_j & i = 1, \dots, \alpha \\ S_A & i > \alpha \end{cases}$$

G = Survival past age N

α = Last age with juvenile survival rate

N = the number of columns or rows in the matrix

and α , G and N are version specific (see Table 1).

In version II, juvenile and adult survival rates differ only during the first year of life. Thus, $\alpha = 1$ or S_j equals S_A for $i > 2$. Version III gives animals a maximum life span of 30 years in order to explore the effects of senescence. Expanding the dimensions of the matrix to 30×30 , and setting the lower righthand corner of the matrix equal to zero accomplishes this. Version IV is the same as version III except the maximum age is set at 50.

Table 1 summarizes the difference in the parameterization of \tilde{M}_2 for the four versions of the matrix considered in this paper. For each version of \tilde{M}_2 , values for S_j as a function of S_A are presented. F_A , S_A , G , M , and N generate a matrix \tilde{M}_2 which allows iterative solution for S_j such that $u = \hat{u}$. This is equivalent to the expression below:

$$\{ S_j | F_A, S_A, G, M, N \} \text{ such that } u = \hat{u} \quad (1)$$

where

\hat{u} = estimated proportion mature in a population

u = the proportion mature assuming a stable age distribution given the projection matrix \tilde{M}_2 , that is

$$u = \frac{\sum_{i=M+1}^N V_i}{\sum_{i=1}^N V_i}$$

where V_i are the elements of the eigenvector of \tilde{M}_2 .

Note that given a solution for S_j in expression 1, all the elements of \tilde{M}_2 are determined. Thus the method provides an estimate of the dominant eigenvalue (λ) of the matrix, which is the current growth rate of the population.

Survival estimates using this method are considered for the northern offshore spotted population of Stenella attenuata and the eastern spinner and northern whitebelly spinner populations of Stenella longirostris. One-half the estimated pregnancy rates is used as an estimate of fecundity. The estimated proportion of mature females and the pregnancy rates are based on the pooled data base collected from 1973 to 1978 for each of the three stocks. Both method I and method II estimates of pregnancy rates are considered (see Henderson, et al., 1979²). The estimated ages of maturity are based on Perrin, et al. (1976, 1977b) and Perrin and Henderson (1979). The parameter values used are given in Table 2.

Two criteria were used to judge whether the estimated survival rates were consistent with the data and biological realism. The first criterion is the obvious constraint that survival rates can be no greater than 1.0. The second criterion is that juvenile survival rates must be less than or equal to adult survival rates. This is usually considered a characteristic of the survival curve for long-lived organisms (e.g. Caughley, 1966).

In addition to generating survival estimates for these three dolphin stocks, general solutions for S_j and S_A are computed for versions I and II of the matrix M_2 when the dominant eigenvalue is constrained to 1.0. This is equivalent to solving the following expression.

$$\{ S_j, S_A | F_A, G, M, N \} \text{ such that } \begin{array}{l} \lambda = 1 \\ \text{and} \\ u = \hat{u} \end{array}$$

Solutions have been calculated for a range of values of F_A , \hat{u} and M . These general solutions provide estimates of S_j and S_A under a stationary age distribution for a large combination of possible values of the input parameters, and are useful in evaluating the sensitivity of the results for the three dolphin stocks to the values of the input parameters.

RESULTS

Northern Offshore Spotted Dolphin

The results of the analysis for the northern offshore spotted dolphin are presented in Table 3. For any adult survival rate value, version I requires the highest juvenile survival rate to balance the matrix while version II requires the least. Also for any fixed value of adult survival, version II yields the highest eigenvalue while version III yields the lowest. For any fixed adult survival rate, a lower fecundity rate requires a higher juvenile survival rate to balance the matrix, and produces a correspondingly higher eigenvalue, as is illustrated by the results for method I and method II pregnancies.

For the northern offshore spotted population, a wide range of adult and juvenile survival rates are consistent with the data using the two criteria listed above. Only a very narrow range of these survival estimates, however, yield a non-negative growth rate (i.e. have eigenvalues > 1). Positive growth only occurs when adult survival rates are very high. Only with version II is the eigenvalue of the matrix greater than 1 for adult survival rates less than 0.95, and even for this version adult survival rates below 0.92 result in a negative growth rate for the population.

Eastern Spinner Dolphin

For the eastern spinner dolphin population, only a very small range of adult and juvenile survival rates are consistent with the data even if only the first criterion that survival rates be less than or equal to one is applied (Table 4). For juvenile survival rates to be less than 1.0, adult survival rates must be less than 0.65. None of the combinations of adult and juvenile survival rates which balance the matrix with survival rates less than 1.0 yield an eigenvalue for the matrix approaching 1.0. In short, it appears unlikely that a viable population with a stable age distribution can exist given the observed values of the input parameters. In order to obtain estimates corresponding to a viable population, one or more of the input parameters must be assumed to have been underestimated (see below for further discussion of this point).

Northern Whitebelly Spinner Dolphin

The results for the northern whitebelly spinner dolphin (Table 5) are similar to those for the eastern spinner dolphin, but the range of biologically possible survival rate combinations is somewhat larger. No combinations of adult and juvenile survival rates which meet both criteria and balance the matrix result in a matrix for a viable population.

If juvenile survival rates are allowed to exceed adult rates and approach 1.0, there are some survival rate combinations with which versions I, III and IV yield positive growth rates. With version II, as the juvenile survival rate approaches 1.0, the eigenvalue also approaches 1.0, but does not reach it.

General Solutions

Since for all three stocks it is difficult to find combinations of adult and juvenile survival rates which yield viable matrices given the estimated values for the input parameters, I solved for the combination of input values which balance the matrix with an eigenvalue of one. Calculations are presented only for versions I and II of the projection matrix, since the inclusion of senescence (versions III and IV) severely increases the difficulty of balancing the matrix. The results of these calculations for version I are plotted in Figures 1-4. In these figures, the proportion mature has been plotted as a function of adult survival rates for a range of fecundity rates and ages of maturity. The point on each curve where $S_j = 1$, and the point on each curve where $S_j = S_A$ are indicated. All values on each curve to the right of those points meet the corresponding criterion for consistency.

For version II, when the eigenvalue of the matrix is constrained to 1.0, the relationship between the proportion mature and the adult survival rate is very insensitive to changes in the fecundity rate, but the corresponding relationship between the proportion mature and the juvenile survival rate

tends to be highly sensitive to changes in the fecundity. Therefore, the proportion mature has been plotted as a function of the adult survival rate for a range of ages of maturity and with a fixed fecundity rate of 0.25 in Figure 5. For fecundity rates between 0.10 and 0.25, the curves would be basically the same as Figure 5 but would be shifted by most by 0.02 along the axis of adult survival rates. Figures 6-9 show the relationship between the proportion mature and the juvenile survival rate for version II for a range of pregnancy rates. The point on each curve in Figures 6-9 where $S_j = S_A$ is denoted. All values to the left of this point meet the second criterion for consistency.

These nine figures can be used to judge how large a difference in the observed value of the input parameters for each stock is needed to yield viable matrices for both versions I and II of the matrix. For example, in Figure 2 it can be seen that, for the observed age of maturity of 6 and the observed proportion mature of 52% for the northern whitebelly spinner stock, the fecundity rate must be at least 0.20 in order to yield a version I matrix with an eigenvalue of 1 that satisfies both criteria for consistency. Similarly, Figure 7 suggests that a fecundity rate just slightly less than 0.20 would satisfy both criteria for version II.

These figures also illustrate the constraints created by the data when trying to balance the matrices with eigenvalues greater than or equal to one. They show that the more the proportion mature is underestimated, the more likely a viable matrix can be achieved, but only with increasingly high (unrealistic) adult survival rates. If senescence is considered (i.e. versions III and IV) with increases in the proportion mature, the biological constraint $S_A < 1$ is reached. Similar relationships are apparent with underestimates of pregnancy rates or age of maturity, although for version II, underestimates of pregnancy rates have little effect on adult survival rates. In contrast, to the extent that any parameter is overestimated, a viable matrix can be achieved with proportionately lower adult survival rates, but the constraints on juvenile survival (i.e. $S_j < 1$ and $S_j < S_A$) are then reached. It is worth noting that these opposing constraints can result in nonintuitive effects. Thus, in a situation where the constraints on adult survival are approached, a lowering in the estimated fecundity rate can lead to an increase in the estimated possible rate of increase. Similarly, when the constraints on juvenile survival are reached, an increase in the age of maturity results in an increase in the estimated possible rate of increase. When these relationships are considered along with the general range of values observed in porpoise stocks, they suggest, as illustrated in Figures 1-9, that the combination of values for the percent mature, age of maturity and fecundity rate which yields viable matrices is limited.

DISCUSSION

The results of the preceding analysis are rather disturbing, as they suggest that for the two spinner populations, the observed combinations of pregnancy rates, proportions of mature female and ages of maturity would likely only be found in declining populations. Even the results for the northern offshore spotted population are not encouraging, as they suggest that

the observed combination of input parameters could only be found in a viable population if adult survival rates are extremely high and juvenile and adult survival rates differ mostly at very young ages. Even then, the results suggest that the maximum current rate of increase consistent with the three input parameters is $\sim 2\%$, despite the fact that the abundance of this population has been greatly reduced as the result of purse seine fishery (Smith, 1979³). It should be noted that the difficulties in balancing these matrices are not the same for all three stocks. The eastern spinner and northern whitebelly stocks are constrained in their estimated rates of growth by biological limits on juvenile survival rates, suggesting that one or more of the input parameters may be underestimated. In contrast, the northern offshore spotted stocks are constrained by limits on adult survival rates, suggesting a possible overestimation of one or more parameters. These conclusions suggest that the robustness of the results to sampling error, bias in the input parameter estimates, and the assumptions of the method need to be examined.

These conclusions are not easily explained as the result of sampling error, especially for the eastern spinner stock. The proportion mature and the method I pregnancy rates can be considered as binomial proportions. Given the sample sizes on which these estimates are based, their 95% confidence intervals are about $\pm 3\%$ for the proportion mature and $\pm 5\%$ for the pregnancy rate (i.e. 2.5% for the fecundity rate). Considering the extremes for both of these intervals would not change significantly the results for the eastern spinner population. For the northern whitebelly spinner, the upper ranges of their confidence interval would yield viable matrices for both versions I and II (Figures 2 and 7) which satisfy both criteria for consistency. Similarly, within the lower range of the estimates for the northern offshore spotted stock, the range of viable matrices would increase with corresponding increases in the maximum eigenvalue to about 1.04. The age of maturity is a more uncertain quantity and assessing the likely sampling error of this parameter is not possible. The conclusions for eastern spinner are robust over a wide range for the age of maturity. If the age of maturity for the northern whitebelly is as high as eight, the conclusions for this stock would be similar to those for the northern offshore stock (i.e., with very high adult survival rates, the matrix would balance with a eigenvalue of one). The estimate of eight years of age for the northern offshore spotted appears most favorable for achieving a viable matrix given the other two parameters. A lower age of maturity tends to require unreasonably high estimates of juvenile survival to balance the matrix while older ages of maturity require adult survival rates even closer to 1.0 to achieve a viable matrix (Figures 1-9).

The conclusions about the current rate of increase appear to be fairly robust to all of the major assumptions of the method except that of a stable age distribution. Thus, the effect of the assumption of constant adult and juvenile survival rates are bracketed by versions II, III and IV. Although

³Smith, T. (ed.) 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Southwest Fisheries Center, Admin. Rep. No. LJ-79-41.

the effect of the assumption of a constant fecundity with age has not been considered, the fact that fecundity rates tend to decline with age in large mammals suggests that the consideration of age specific fecundity rates may not greatly change the results, at least for the spinner populations.

The effect of a nonstable age distribution is harder to assess. The method used in this paper should be less sensitive to random fluctuations around a stable age distribution than most methods of estimating survival rates based on the age structure of a population, since it is only the observed proportion which requires the assumption of a stable age distribution. This observed proportion is obtained by averaging across a number of age classes. Systematic deviations from a stable age distribution could result in estimates of the proportion mature which would yield inappropriate survival estimates. However, for the spinner stocks, the age structure would have to be skewed towards immature animals in relationship to the stable age distribution in order for the present reproductive estimates to yield viable projection matrices. The fact that the observed proportion mature for these three stocks for the five years that data exist has remained relatively constant with a possible slight downward trend (Henderson, et al., 1979²) would argue against the current age structure being highly skewed towards immature animals. While the effects of the purse seine fishery on the stable age distributions can only be speculated about, the fact that juveniles appear to be more vulnerable (at least for *S. attenuata*, see Powers and Barlow, 1979⁴) should have resulted in the age distribution being distorted in the opposite direction.

However, this potential increased vulnerability of juveniles raises the question of the representativeness of the samples used for estimating the input parameters. Clearly, a bias in the samples towards immature animals could alter the conclusions about the current rate of increase, since the major difficulty in obtaining viable matrices with parameters estimate from the observed data is that too few mature animals are sampled. However, the magnitude of the bias would have to be large, especially for the eastern spinner population. Thus, for the observed proportion mature of .438 for eastern spinner to come from a population in which the actual proportion mature was .50, juveniles would have to be over-represented in the samples by a factor of 1.3 (Polacheck, in press⁵). It should be noted that an attempt to correct for this potential bias has been incorporated in the estimates for *S. attenuata* by only using data from sets in which more than 40 animals were killed (Henderson, et al., 1979²) since Powers and Barlow (1979⁴) found that sets with small kills had a larger proportion of immature dolphins. No significant differences in the proportion of immatures was found for either of

⁴Powers, J. E. and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. NMFS-SWFC. SOPS/79/31.

⁵Polacheck, T. In press. A sensitivity analysis on the effects of biases in the kill on variances reproductive estimates for porpoise stocks in the eastern tropical Pacific. Southwest Fisheries Center, Administrative Report.

the spinner stocks.

The results of this study suggest that the observed reproductive estimates for the two spinner populations (especially the eastern spinner) would only be found in a declining population. While these conclusions warrant caution with respect to any evaluation on the status of these stocks, I would also urge caution in the use of these conclusions without further information and analysis on the representativeness of the kill. While the only analysis of potential bias suggests that no bias of sufficient magnitude exists to alter the conclusions, the fact that no samples are available which are independent of the purse seining operations and that numerous potential sources of bias could exist in these operations (e.g. see Stuntz, 1980⁶) clearly warrants caution. The biologically possible survival estimates and population growth rates derived from the method used in this paper seem unreasonably low for marine mammals, at least for the eastern spinner stock, which suggests that serious sampling problems may exist.

As this paper is being completed, initial examination of the age distribution of the samples of dolphins used here, based on preliminary age determinations, have revealed proportionately fewer young dolphins than would be expected in a random sample from an increasing population. It is not yet possible to determine if this is due to sampling biases with age, or if this reflects declining populations.

⁶Stuntz, W. E. 1980. Variation in age structure of the incidental kill of spotted dolphins, *Stenella attenuata* in the U. S. tropical purse-seine fishery. Southwest Fisheries Center, Admin. Rep. No. LJ-80-06.

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Table 1. Summary of the parameterization of the four versions of the matrix \tilde{M}_2 .

Version	Parameter		
	α	G	N
I	M	S_A	M+1
II	1	S_A	M+1
III	M	0	30
IV	M	0	50

Table 2. Parameter values used for estimating survival rates for the three dolphin stocks:

	Northern offshore spotted	Eastern spinner	Northern whitebelly spinner
Age of maturity	8 ¹	5 ²	6 ²
Proportion mature ³	.561	.432	.522
Pregnancy rate ³			
Method I	.376	.339	.356
Method II	.323	.446	.332

¹Rounded to the nearest year from the estimate in Perrin, et al., 1976.

²Rounded to the nearest year from the estimate in Perrin and Henderson, 1979.

³From Henderson, et al., 1979.

Table 3. Estimates of juvenile survival rate (S_j) and the current rate of increase (λ) as a function of adult survival rate for the northern offshore spotted dolphin (Stenella attenuata) based on the parameter values in Table 1.

S_A	Version I		Version II		Version III		Version IV	
	S_j	λ	S_j	λ	S_j	λ	S_j	λ
.6	.368	.603	.176	.635	*	*	*	*
.7	.478	.708	.265	.744	*	*	*	*
.8	.594	.815	.373	.853	*	*	.563	.786
.9	.715	.924	.500	.961	.621	.840	.689	.901
.95	.777	.980	.567	1.016	.687	.900	.753	.958
.6	.409	.607	.227	.637	*	*	*	*
.7	.525	.714	.335	.746	*	*	*	*
.8	.647	.823	.467	.851	*	*	.626	.805
.9	.775	.936	.615	.964	.704	.874	.758	.921
.95	.841	.993	.698	1.018	.774	.935	.827	.908

*Biologically unreasonable solutions which did not converge readily were not solved for

Table 4. Estimates of the juvenile survival rate (S_j) and the current rate of increase (λ) as a function of adult survival rate for the eastern spinner dolphin (Stenella longirostris) based on the parameter values in Table 1.

S_A	Version I		Version II		Version III		Version IV	
	S_j	λ	S_j	λ	S_j	λ	S_j	λ
.40	.399	.473	.399	.473	.396	.470	.399	.473
.50	.771	.727	.693	.597	.771	.727	.771	.727
.60	+	+	1.065	.720	+	+	+	+
.70	+	+	1.516	.844	+	+	+	+
.80	+	+	2.045	.967	+	+	+	+
.90	+	+	2.655	1.091	+	+	+	+
.95	+	+	2.989	1.153	+	+	+	+
.4	.274	.425	.251	.466	.256	.409	.271	.422
.5	.463	.575	.460	.590	.457	.571	.462	.575
.6	.748	.780	.730	.714	.747	.779	.748	.780
.7	1.375	1.180	1.057	.837	1.377	1.181	1.376	1.180
.8	+	+	1.45	.961	+	+	+	+
.9	+	+	+	+	+	+	+	+
.95	+	+	+	+	+	+	+	+

⁺No solution for the juvenile survival rate exists that will balance this version of the matrix for the combination of values for adult survival rates, fecundity rate, and age of maturity.

Table 5. Estimates of juvenile survival rate (S_j) and the current rate of increase (λ) as a function of adult survival rate for the northern whitebelly spinner dolphin (Stenella longirostris) based on the parameter values in Table 1.

S_A	Version I		Version II		Version III		Version IV	
	S_j	λ	S_j	λ	S_j	λ	S_j	λ
.6	.469	.630	.386	.663	*	*	*	*
.7	.620	.755	.568	.777	.595	.734	.612	.752
.8	.790	.888	.784	.891	.773	.875	.787	.887
.9	.980	1.031	1.0337	1.005	.968	1.022	.980	1.038
.95	1.083	1.107	1.171	1.062	1.074	1.100	1.083	1.106
.6	.496	.637	.430	.664	.468	.617	.491	.633
.7	.656	.766	.628	.779	.637	.750	.654	.764
.8	.837	.904	.862	.892	.824	.894	.836	.904
.9	1.040	1.054	1.133	1.007	1.032	1.048	1.040	1.053
.95	1.151	1.133	1.282	1.069	+	+	+	+

+ See footnote for Table 3.

* See footnote for Table 2.

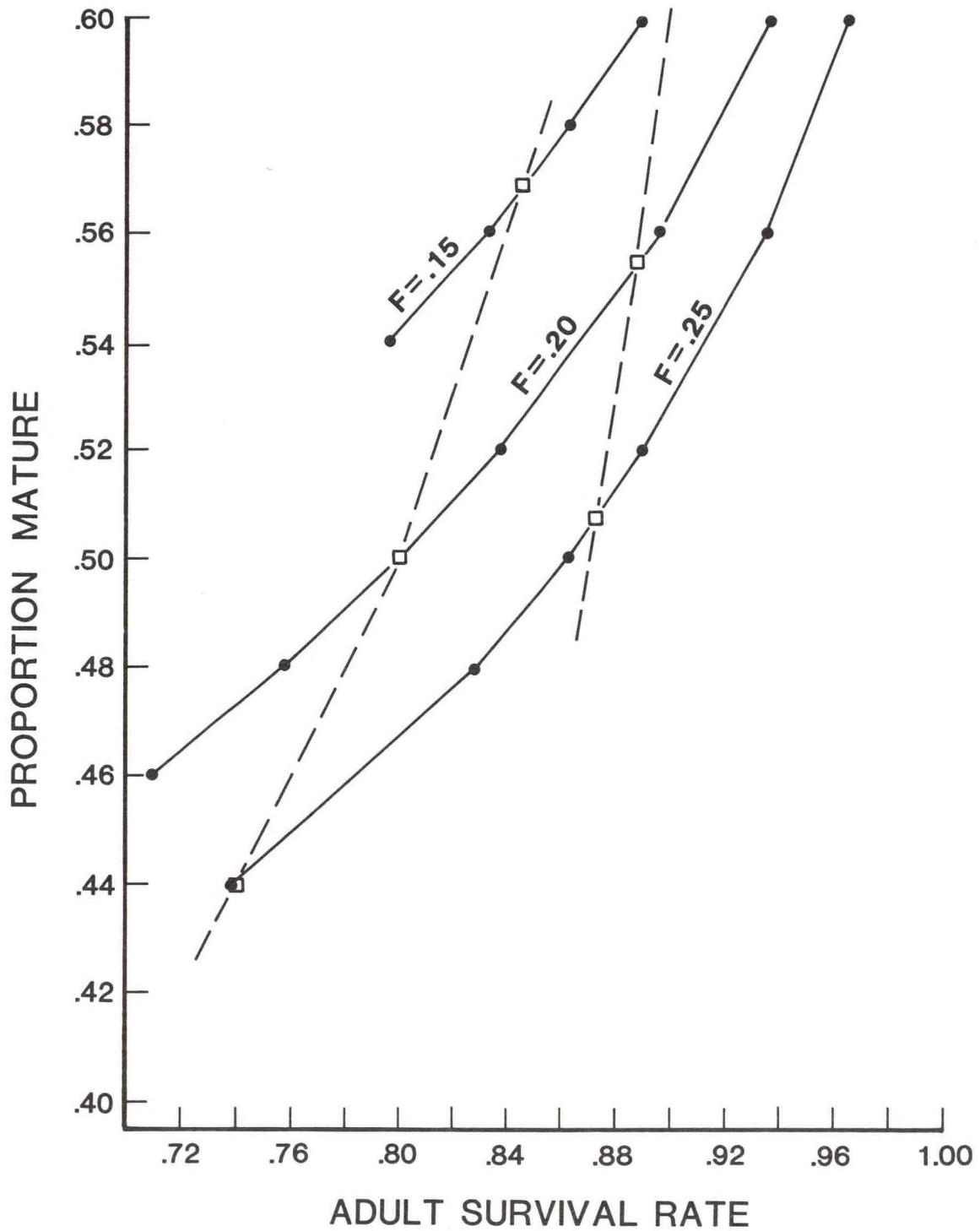


Figure 1. The proportion of mature females when the age of maturity is 5 plotted as a function of adult survival for a range of fecundities for Version I of the projection matrix when the eigenvalue is constrained to equal one. The leftmost dashed line indicates the points where $S_j = 1$ and the rightmost dashed line indicates the points where $S_j = S_A$.

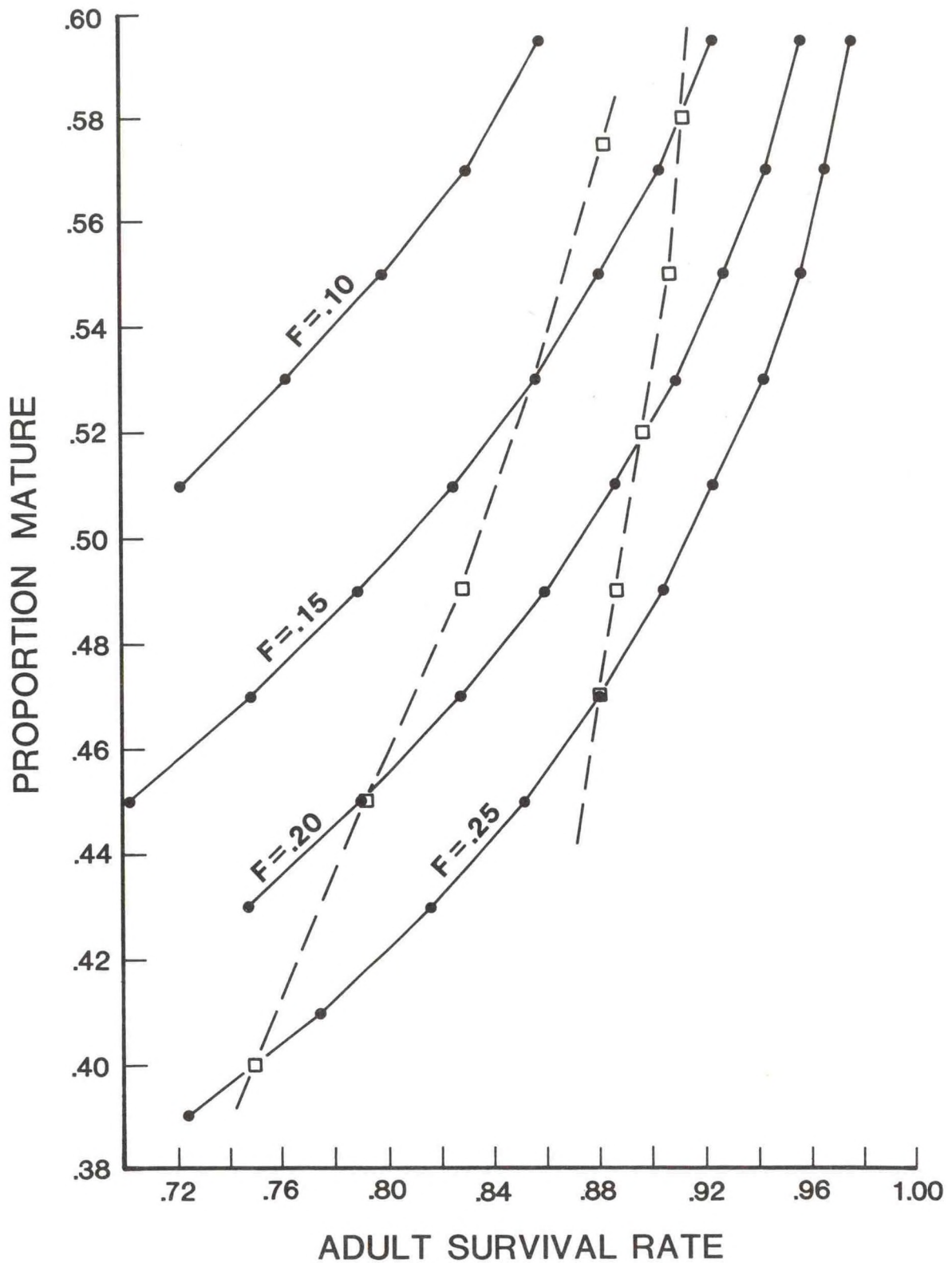


Figure 2. The proportion of mature females when the age of maturity is 6 plotted as a function of adult survival for a range of fecundities for Version I of the projection matrix when the eigenvalue is constrained to equal one. The dashed lines are as in Figure 1.

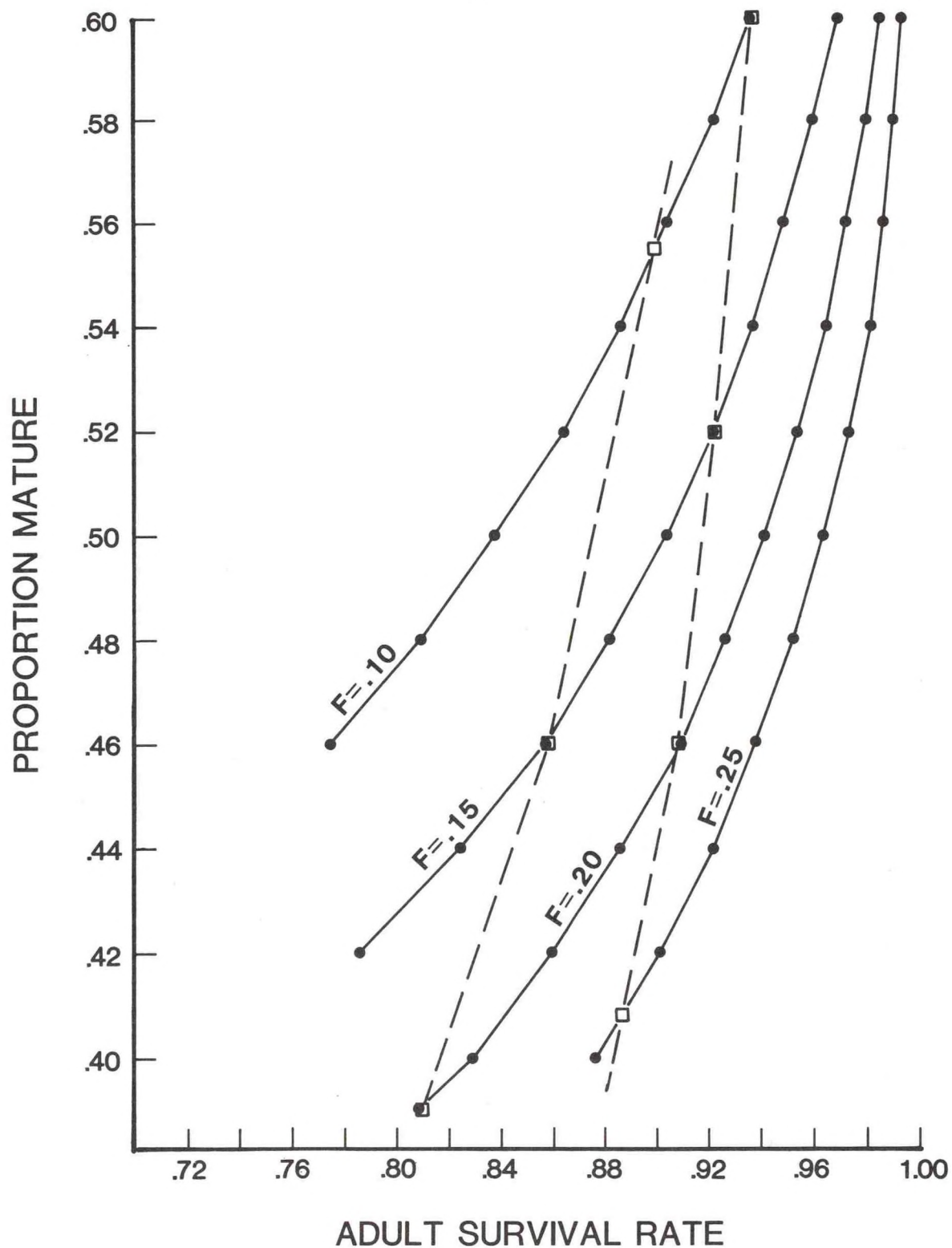


Figure 3. The proportion of mature females when the age of maturity is 8 plotted as a function of adult survival for a range of fecundities for Version I of the projection matrix when the eigenvalue is constrained to equal one. The dashed lines are as in Figure 1.

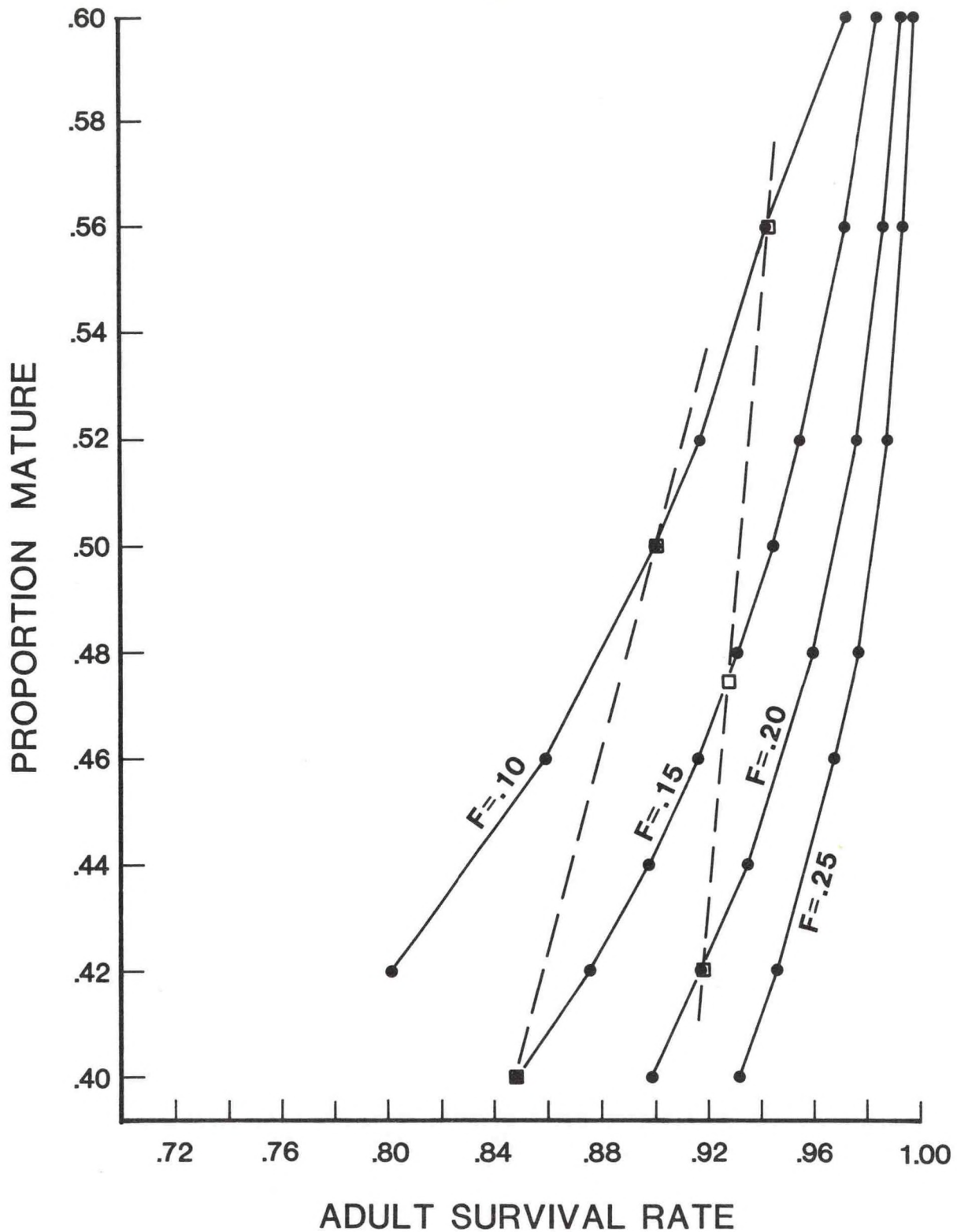


Figure 4. The proportion of mature females when the age of maturity equals 10 plotted as a function of adult survival for a range of fecundities for Version I of the projection matrix when the eigenvalue is constrained to equal one. The dashed lines are as in Figure 1.

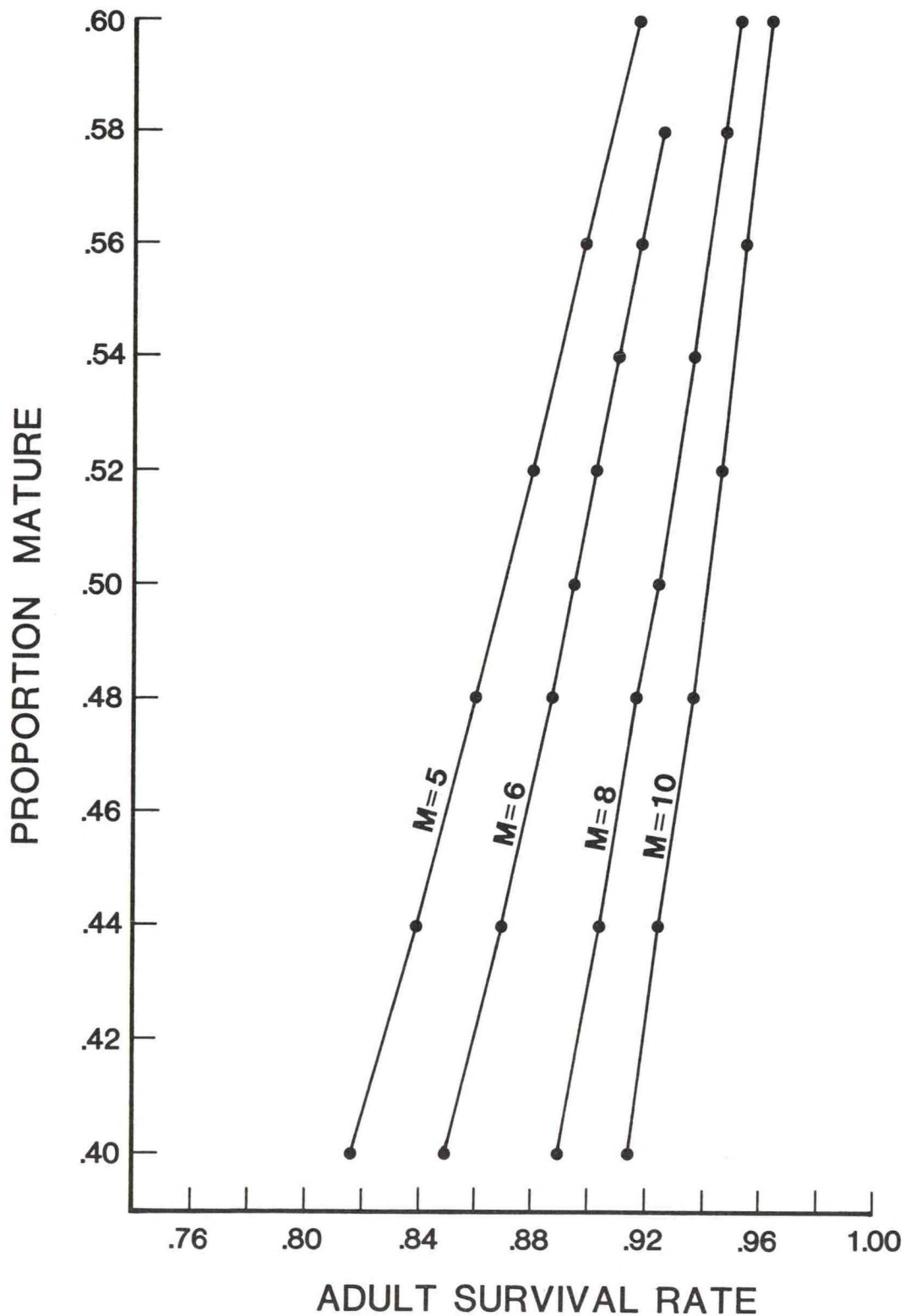


Figure 5. The proportion mature as a function of adult survival rates for Version II of the matrix when the eigenvalue of the matrix is constrained to equal one calculate for a range of ages of maturity. The fecundity rate is .25.

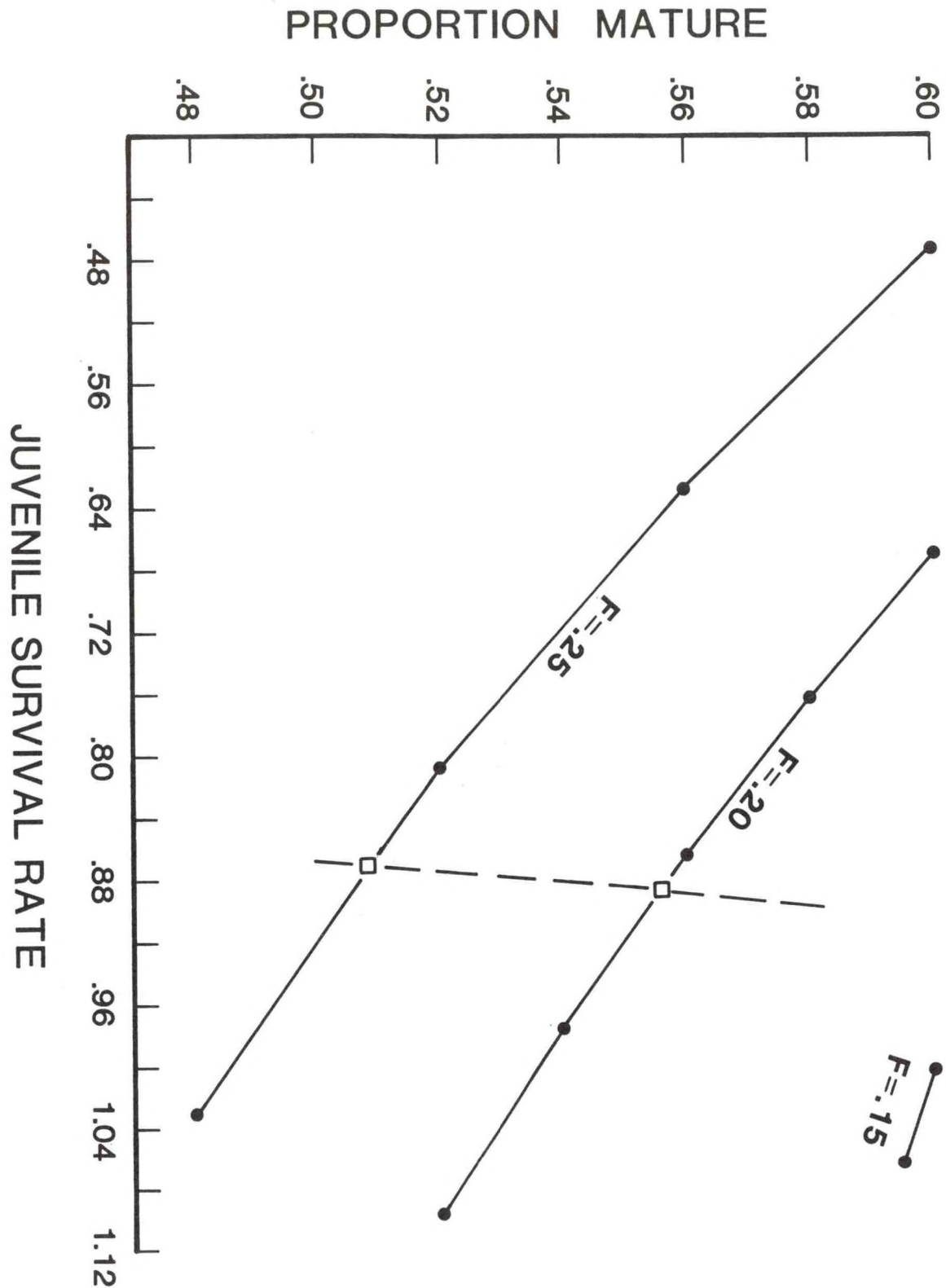


Figure 6. The proportion mature when the age of maturity equals 5 plotted as a function of juvenile survival for a range of fecundities for Version II of the projection matrix when the eigenvalue is constrained to equal one. The dashed line indicates the points where $S_j = S_A$.

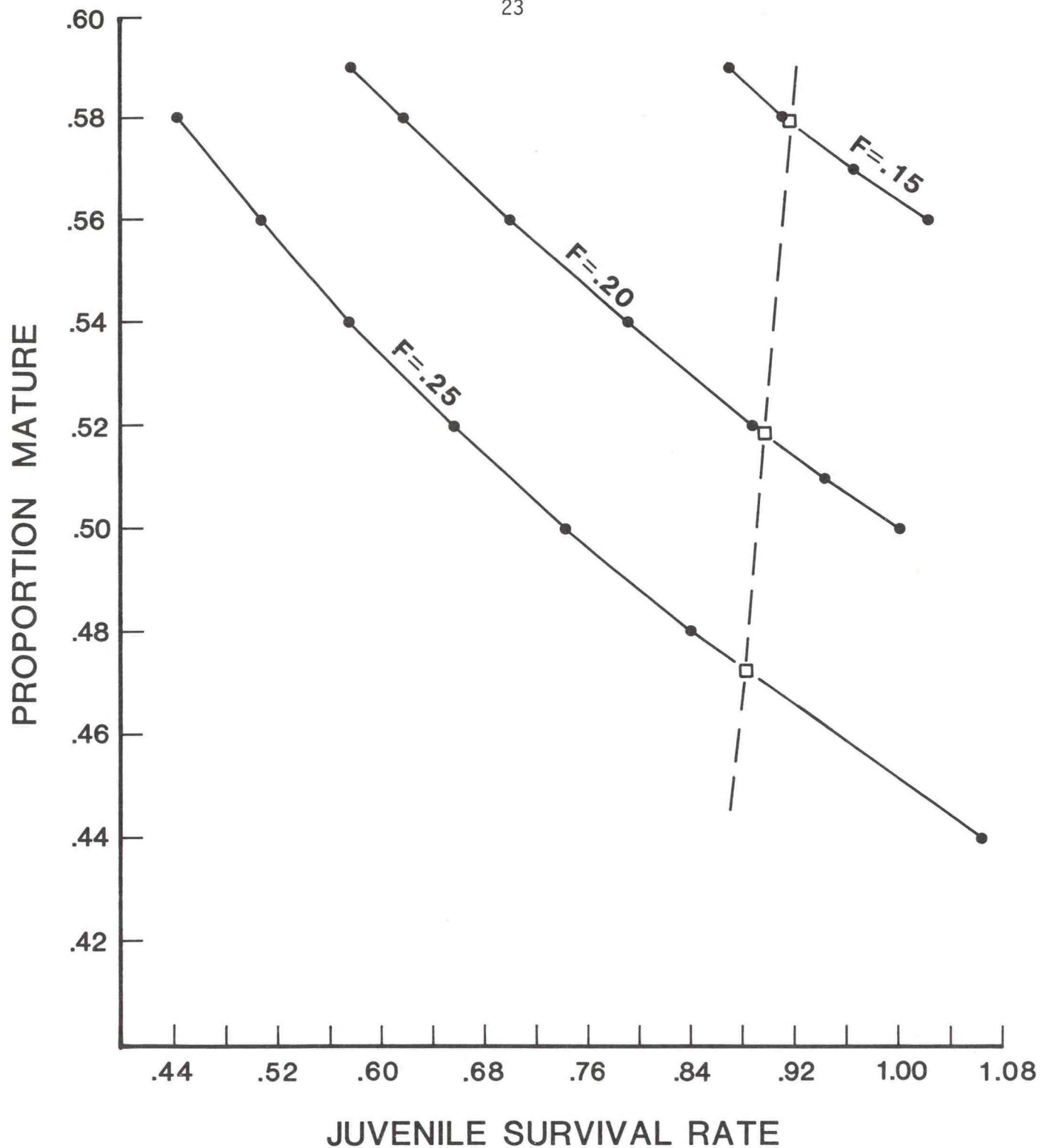


Figure 7. The proportion mature when the age of maturity equals 6 plotted as a function of juvenile survival for a range of fecundities for Version II of the projection matrix when the eigenvalue is constrained to equal one. The dashed line indicates the points where $S_j = S_A$.

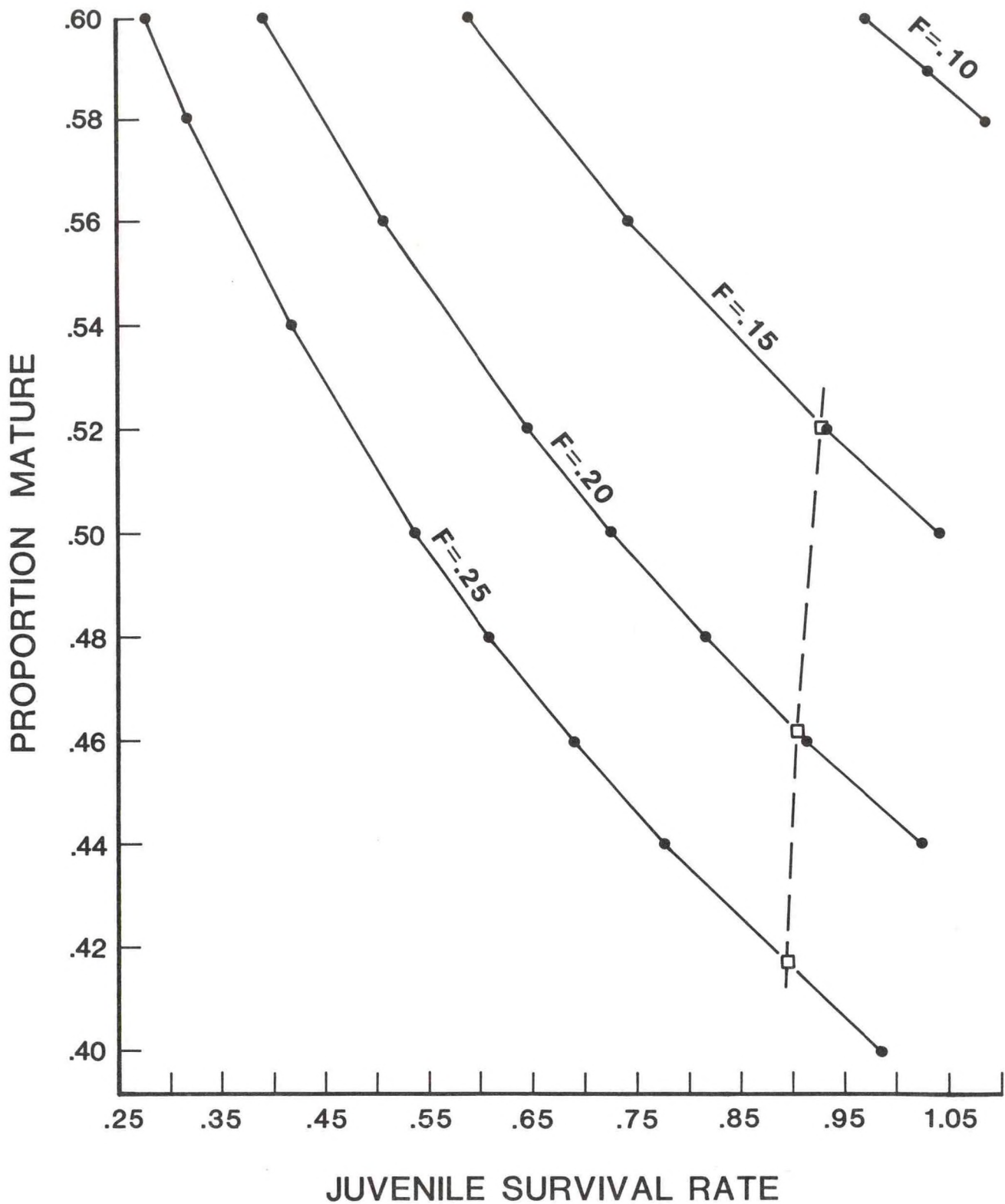


Figure 8. The proportion mature when the age of maturity equals 8 plotted as a function of juvenile survival for a range of fecundities for Version II of the projection matrix when the eigenvalue is constrained to equal one. The dashed line indicates the points where $S_j = S_A$.

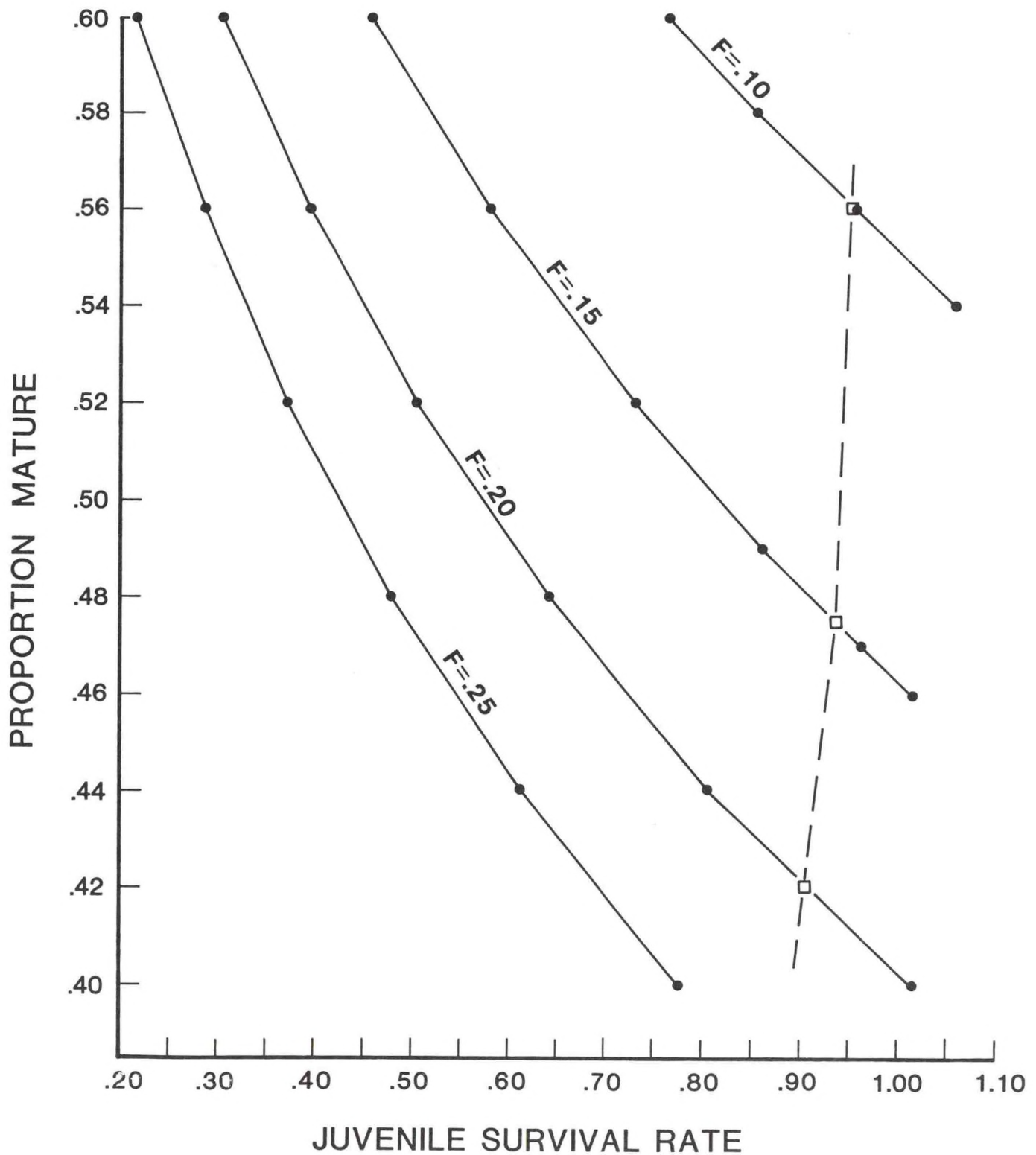


Figure 9. The proportion mature when the age of maturity equals 10 plotted as a function of juvenile survival for a range of fecundities for Version II of the projection matrix when the eigenvalue is constrained to equal one. The dashed line indicates the points where $S_j = S_A$.