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The South African pilchard and anchovy stock complex - an example of the effects of biological interactions between species on management strategy[2]

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1. THE DEVELOPMENT OF AN INTERACTIVE MODEL OF THE SOUTH AFRICAN PILCHARD AND ANCHOVY FISHERY

Stander and Le Roux (1968) suggest that the South African pilchard and anchovy have a common ecological niche and state that "As the two species compete among others, for a common food supply there is presumably an equilibrium between the respective populations, which is liable to be disturbed by external factors such as the continued high rate of exploitation and reduction in numbers of one of them". It is interesting to try to express this statement in mathematical terms in order to understand its implication more fully.

Following Walter (1975) Schaefers model of a fishery can be written as

$$\frac{1}{p}\frac{dp}{dt} = b - ap - qf$$

where p is the stock biomass and f is the fishing mortality and q the catchability. Thus this could be rewritten as

$$\frac{1}{p}\frac{dp}{dt} = b - ap - F$$

where F is the fishing mortality, that is, the proportion of the stock removed by fishing. If P is the biomass of pilchard and A is the biomass of anchovy and F(P) and F(A) are the respective fishing mortalities, then a simple way to describe the the interaction of the two species is by the following two equations

$$\frac{1}{P}\frac{dP}{dt} = b - aP - cA - F(P) \quad 1$$

and

$$\frac{1}{A}\frac{dA}{dt} = b - aA - cP - F(A) \quad 2$$

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[1] This number was originally assigned to a paper by S.J. Crabtree who subsequently withdrew it from this series. For administrative purposes, it is necessary to re-use this number for the present paper.

[2] This paper was originally presented to the Seventh Special Commission Meeting, Montreal, Canada, September 1975 as ICNAF Working Paper 75/IX/1.

These incidentally correspond to the simple competition model, see for example Bartlett 1960. In order to fit the various constants to the model it is necessary to have values of A, P and the fishing mortalities for a series of years. Fortunately catch at age data has been collected for the pilchard since 1950 and for the anchovy since 1964 (the anchovy fishery started in 1963). Therefore it is possible to perform virtual population analysis on these two stocks and to estimate the numbers of fish at each age in the stock and to then estimate the biomass for each year using the weight at age data. The fishing mortality for each year was estimated as the proportion the catch formed of the annual biomass. Estimates of biomass and fishing mortality for the pilchard were thus available from 1950 to 1972 and for the anchovy from 1964 to 1972. Results for 1973 and 1974 were also available but were rejected as being liable to error from the estimates of fishing mortality assumed for 1974 in the Virtual Population Analysis; see Pope (1972).

In order to fit the various constants of equations 1 and 2 an extension of the method proposed by Walter (1975) was used. This consisted of regressing the population in year i + 1 against the appropriate fishing mortality for year i and the biomass of the other species for year i.

Thus a multiple regression was made of P_{i+1} against $F(P)_i$ and A_i and a second regression was made of A_{i+1} against $F(A)_i$ and P_i. This procedure was extremely successful for the anchovy yielding an equation

$$A_{(i+1)} = 1100 - .5P_i - 1000\ F(A)_i \qquad 3$$

implying

$$\frac{1}{A}\frac{dA}{dt} = 1.1 - 0.001A - 0.0005P - F(A) \qquad 4$$

The regression coefficients were both significant and the regression explained 97% of the variance. It should however be noted that the two independent variables used in fitting this equation were highly correlated (r = 0.79, N = 9) and thus rather different constants could have been found with no great loss of fit.

The pilchard regression was less successful yielding only a significant coefficient for the A_i term and finding no significant effect for the F(P) term. This was due in part to the intercorrelation of the two estimates $F(P)_i$ and A_i for the 8 years for which A_i was available (r = .61) and in part to the fact that during this period F(P) was at a high level and did not exhibit sufficient contrast to provide a good regression. An alternative method was therefore used based on the following relations. A simple regression of

$P_{(i+1)}$ on A_i yields

$$P_{(i+1)} = -1.1474A_i + 948 \qquad 5$$

which is a significant correlation, r = 0.81 N = 8

A simple regression of $P_{(i+1)}$ on $F_{(i)}$ for the 17 years from 1956 to 1972 yields

$$P_{(i+1)} = -7190F\ (P)_{(i)} + 2660 \qquad 6$$

The 1950-1955 data was eliminated from this analysis due to possible interactions with a third species the Maas-banker.

The correlation was significant r = .86 N = 17 and it was considered best to make a combined equation of the two regressions giving with some simplifications

$$P_{(i+1)} = 3000 - A_{(i)} - 7000F\ (P)_{(i)} \qquad 7$$

$$\frac{1}{P}\frac{dP}{dt} = .43 - 0.000143\ P - 0.000143A - F(P) \qquad 8$$

Thus Equations 4 and 8 are the best available estimates of the effect of fishing mortality and of the biomass of the competitive stock on each of the stock biomasses. They imply what steady state conditions will exist for the two stocks when

$.43 - 0.000143P - 0.000143A - F(P) = 0$

and

$1.10 - 0.001A - 0.0005P - F(A) = 0$

The rather unsatisfactory method of fitting used for equation 7 should be kept in mind during the interpretation of the results in the next section.

2. AN INTERPRETATION OF THE STEADY STATE EQUATIONS

The two equations

$$.43 - 0.000143P - 0.000143A - F(P) = 0 \quad 1$$

and

$$1.10 - 0.0001A - 0.0005P - F(A) = 0 \quad 2$$

represent an attempt to explain the conditions for equilibrium states for the Pilchard and Anchovy system.

Equations 1 and 2 have quite complicated consequences. The two stock model breaks down when P = 0 or A = 0. Negative biomasses are not possible! Therefore there must be constraints on the two stock interaction model such that

$$.43 - 000143A - F(P) \geqslant 0 \quad 3$$

$$1.10 - .0005P - F(A) \geqslant 0 \quad 4$$

From equations 1 and 2, P and A can be expressed in terms of F(P) and F(A) as follows

$$P = 3814 - 13986F(P) + 2000 F(A) \quad 5$$

$$A = -807 + 6993 F(P) - 2000 F(A) \quad 6$$

Hence 3 and 4 may be rewritten as in terms of F (P), F (A) as follows

$$3814 - 13986 F(P) + 2000 F(A) \geqslant 0 \quad 7$$

$$-807 + 6993 F(P) - 2000 F(A) \geqslant 0 \quad 8$$

If the constraint (7) is violated the Pilchard biomass becomes zero and the yield of Anchovy Y (A) becomes the total yield. This is given by

$$Y(A) = 1.10A - .001A^2 \quad 9$$

or substituting A = 1100 - 1000 F (A)

$$Y(A) = 1100 F(A) - 1000 F(A)^2 \quad 10$$

This has a maximum yield of 302500 metric tons when F (A) = .55.

Similarly if constraint 8 is violated the anchovy biomass becomes zero and the yield of Pilchard (Y (P)) becomes the total yield. This is given by

$$Y(P) = .4300 P - 0.000143 P^2 \quad 11$$

or substituting P = 3007 - 6993 F (P)

$$Y(P) = 3007 F(P) - 6993 F(P)^2 \quad 12$$

This has a maximum yield of 323,254 metric tons when F (P) = 0.215. Thus outside of the constraints 7 and 8 the two stock model breaks down and the yield is given by a Schaefer type parabolic yield curve. In the region between the two constraints the total yield (Y) is the sum of Y (P) and Y (A). These are derived as follows

$$Y(P) = .43P - .000143 P^2 - .000143 PA \quad 13$$

$$Y(A) = 1.10A - .001 A^2 - .0005 PA \quad 14$$

Thus total yield is given by

$$Y = .43 P + 1.10 A - .000643 PA - .000143 P^2 - .001A^2 \quad 15$$

and the contours of equal yield are ellipses when drawn against the population biomasses of the two stocks. Alternatively the total yield can be given in terms of

F (P) and F (A) as follows (by multiplying equations 5 and 6 by the appropriate fishing mortality).

$$Y = 3814\, F(P) - 807\, F(A) + 8993\, F(P) * F(A) - 13986\, F(P)^2 - 2000\, F(A)^2 \qquad 16$$

Thus the contours of equal yield are also ellipses when plotted out against the fishing mortalities of both stocks. Simple algebric manipulations indicate that the maximum yield of the two stock system is 339270 metric tons and this occurs at F (P) = 0.2579, F (A) = 0.3781. Furthermore the major and minor axes of the ellipses described by equation 16 are inclined at an angle of -18.44° to the F (P), F (A) axes and the semi-major axis is of length $\sqrt{\frac{339 - Y}{501}}$ in mortality units and the semi-minor axis is of length $\sqrt{\frac{339 - Y}{15485}}$ in mortality units. The ratio of the major axis to the minor axis is therefore approximately 1 to 5.6 in all cases making the ellipses rather long and thin.

Figure 1 shows the contours of equal yield for the 3 regions thus described. Region A is the area of values of F (P), F (A) where the constant 8 is violated and thus the anchovy biomass and yield becomes zero. Therefore lines of equal yield are parallel to the F (A) axis in this region because no anchovy exist and any level of fishing for it cannot alter the yield. A similar situation exists for pilchard in region C with the yield is composed entirely of anchovy. Region B is the area of mixed fishery where the yield is composed of both anchovy and pilchard in varying proportions. It can be seen that the system has a maximum yield of approximately 340,000 metric tons but,while this is attained in a mixed fishery,the maximum is only slightly larger than the maximum yield of pilchard alone which is 320,000 and not greatly larger than the maximum yield of anchovy alone which is 302,000. This it would seem that in a highly interactive fishery, as this appears to be, that the total yield the system can deliver is fairly constant despite changes in species composition. Another effect would seem to be that the region of the F (P), F (A) plane that gives a mixed fishery is comparatively small. Therefore holding the fishery in this region would probably be a difficult operation akin to standing a pencil on end,and it is likely the fishery would fall out of region B into either region A or region C. It might be considered superficially unlikely that the fishery would remain in region C since this implies a continuing fishing effort on pilchard when the pilchard have ceased to exist. However this could be caused by a by-catch of pilchard in the anchovy fishery: this is entirely possible since young pilchard shoal with the anchovy. A catch rate of pilchard with anchovy of about 0.66 would be sufficient to hold the fishery in region C.

The consequences described above,of course all follow from the choice of the constants in equations 1 and 2. The results of the analysis would be critically effected by the values of these parameters; therefore it is not suggested that the precise estimates of MSY and of the value of F (A) and F (P) that attain it should be taken at their face value for managing this stock. Indeed the consequences of Figure 1 would suggest that the approach used by the South African government of imposing an overall catch quota for all pelagic fish is a good one since whatever the species the yield of the fishery is substantially the same. A TOTAL EFFORT QUOTA WOULD PROBABLY BE UNSUCCESSFUL BECAUSE THE APPROPRIATE LEVEL OF EFFORT FOR MSY WOULD DEPEND ON THE PROPORTION OF THE EFFORT WHICH WAS DIRECTED AT THE TWO SPECIES. Figure 2 shows plots of total yield against total effort based on different proportionate fishing mortalities on the two species. So while the maximum yield attainable for the different proportions is fairly constant the level of joint fishing mortality at which it is attained varies considerably.

Apart from the implications of Figure 1 to the management of a mixed fishery where the species interact biologically, it has some interesting biological aspects and, coupled with a knowledge of the development of fishing on this stock provides considerable insight into how the stock complex may have been influenced by fishing.

It is particularly interesting that region A includes the unfished state F (P) = 0, F (A) = 0 since this implies that in the natural state the pilchard would be the more successful stock and dominate anchovy. The implication that the anchovy biomass is zero at this point is of course not strictly correct since there must have been some to provide the subsequent development of anchovy biomass. If however we assume that zero biomass simply means very small and that the relationship of anchovy biomass to pilchard biomass becomes asymptotic to zero at low values, the interpretation previously made is not seriously changed. Figure 3 shows the regions shown in Figure 1 with the development trajectory of fishing mortality on the two stocks.

The contour levels shown in Figure 1 have been omitted for the sake of clarity.

The fishery development trajectory shows a pure fishery on pilchard up until 1962 when a small mesh fishery for anchovy was developed. The level of pilchard fishing mortality was apparently sufficiently low to remain in region A until 1960 at which time the pilchard fishing mortality moved into region B thus allowing the anchovy to develop. While it would be unrealistic to suppose that the situation would be as cleancut as this, it is interesting to compare the implications of the diagram (Figure 3) with Table VIII of Stander and le Roux (1968). This shows that the ratio of larval anchovy to larval pilchard in South African blanket net samples changed from 1:15 in favour of pilchard in 1955/56 to 19:1 in favour of anchovies in 1963/64. The fishing mortality subsequent in 1962 shows an explosive development of fishing on anchovy and further increases in the fishing on pilchard in some years. The fishing fluctuates between all 3 regions indicating the likely problems of keeping such a fishery in the most productive configuration, but the tendency has been towards a shift into region C, the region of no pilchard. This would seem consistent with the change in calculated biomass from pilchard from a high of 2,490,000 metric tons in 1959 to a low of 138,000 in 1972, an 18 fold reduction.

Thus while it is not claimed that this model is a precise description of this stock complex, it would appear to explain most of the important biological changes in these two species.

DISCUSSION

The model developed in this paper to explain the effect of inter-specific competition between South African pilchard and anchovy on the combined yield of the two species is, in effect, an extension of Pope's 1975 paper on mixed fisheries to include species interaction terms. While the inevitable problems of fitting this model to the short-term series available for the anchovy must leave considerable doubts as to the precise shape and magnitude of the total yield function, it is nevertheless true that the model developed does explain most of the significant developments in this stock complex since 1956 in an intuitively attractive fashion. Perhaps, more importantly, the shape of the total yield function for this highly interactive stock complex suggests that overall catch quotas are more likely to prove successful than overall effort quotas. This has considerable implications for stocks where similar interactions between species are inferred. Moreover the high level of correlation of the interaction terms suggest that where they exist they are fairly obvious.

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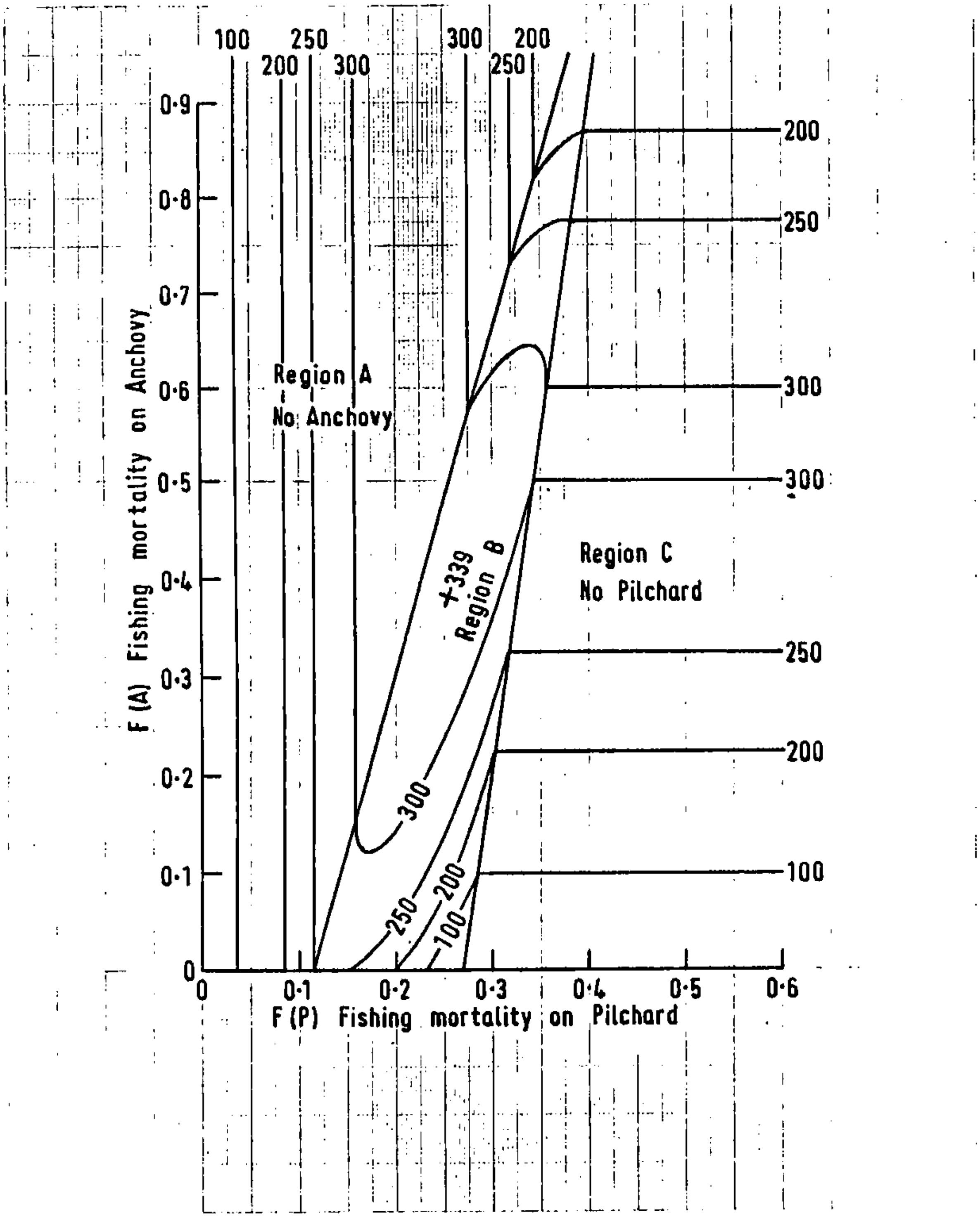

FIGURE 1 Total yield contours drawn against the fishing mortality of South African anchovy and pilchard and the region of mixed fishery (region B) and of pure fisheries for the two stocks (regions A and C).

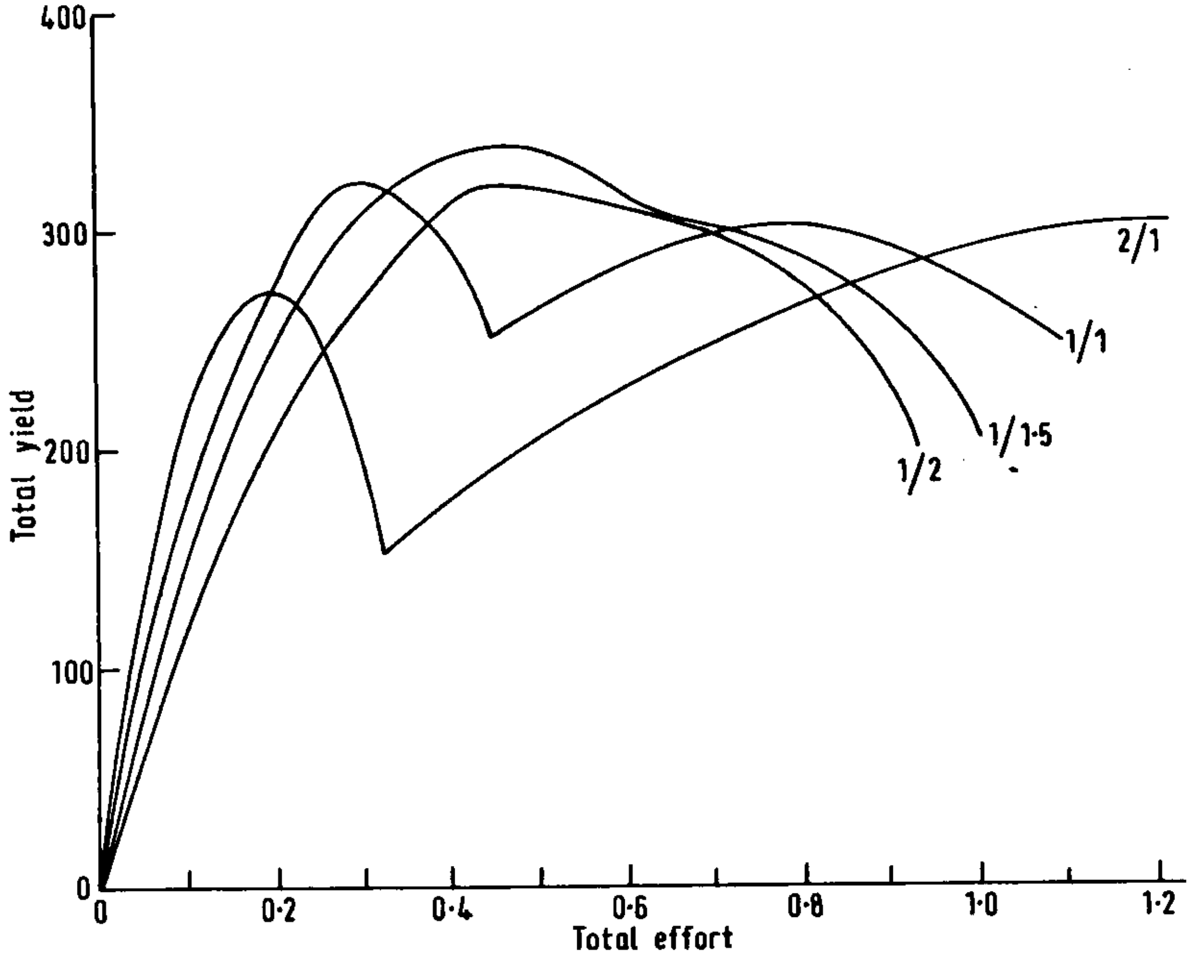

FIGURE 2 The shape of yield curves produced when fishing effort develops on both stocks in various constant proportions. (The figures at the ends of the yield curves are the ratio of pilchard effort to anchovy effort.)

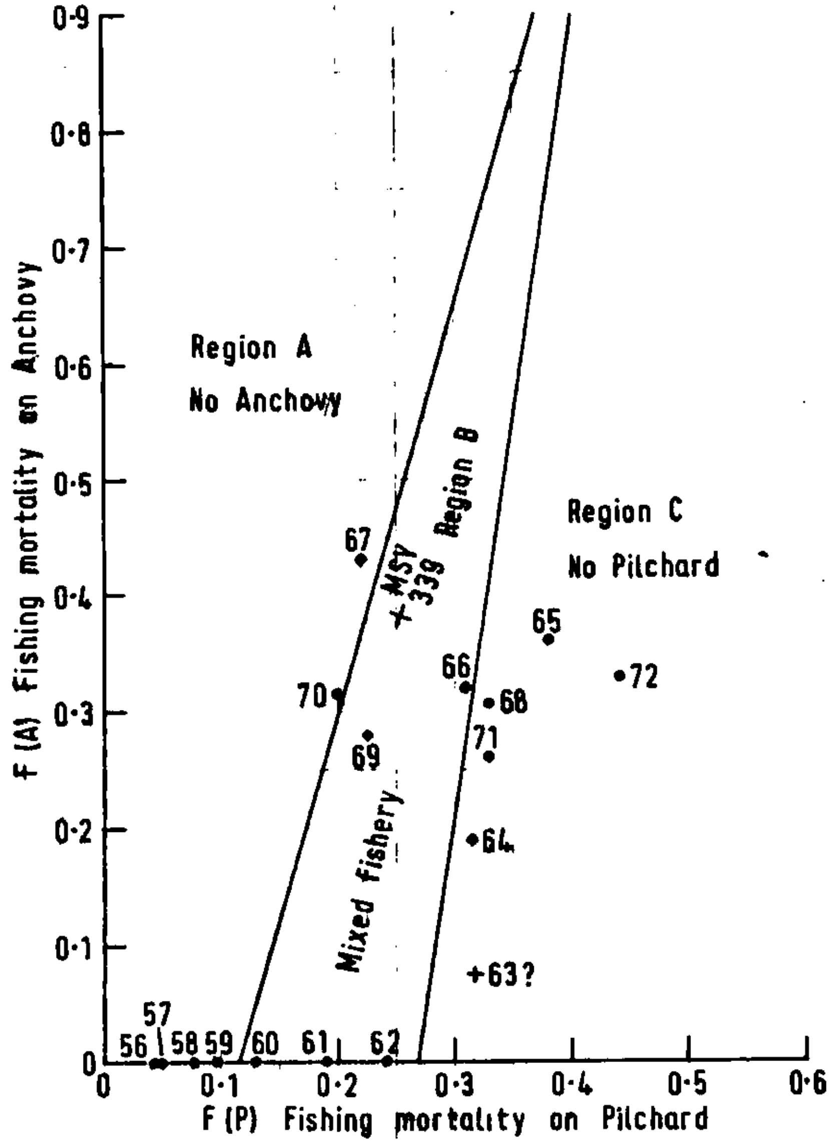

FIGURE 3 The fishing mortality on each stock each year (the development trajectory) plotted over the region of mixed fishery (region B) and the regions of pure fisheries for the two stocks (regions A and C).