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The dependence of recruitment on parent stock in different
groups of fishes

by

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Introduction

The variability of recruitment to a fish stock is very high and precludes the choice, from the data alone, of a curve describing the dependence of recruitment on parent stock. An attempt was made to extract the constants from the curves of Ricker (1954, 1958) and of Beverton and Holt (1957), for a number of fish stocks: tuna, cods, flatfish, salmon and herrings. It was hoped to generalize from a considerable body of data on disparate stocks. The attempt failed because the differences in constants within a group of fish were as great as those between groups. A method using a log log plot was tried.

Method

In Ricker (1958), variance was reduced by plotting recruitment in logarithms on stocks in logarithms. The simplest relationship of this form is

$$R = aS^b \quad (1)$$

where R is recruitment and S is stock in the same units, and where a and b are constants. The slope, b, is an index of the degree of density dependence, but it does not properly estimate the density-dependent mortality. The equation developed by Beverton and Holt (1957), but not used by them, is relevant:-

$$R = \alpha S e^{-\beta S} \quad (2)$$

where $\alpha = e^{-\mu_2 \cdot t_p}$ (μ_2 is the density-independent mortality, and t_p is the age of recruitment) and β is the density-dependent mortality for a specified time period. This equation gives a curvilinear relationship on a log log plot, and the slope, b in equation (1), estimates βS very roughly. However, it is probably good enough to establish differences between groups of fish. The only virtue of this method is that the variance about the slope is minimized by taking logarithms.

When $b = 1$, recruitment increases with stock, an unregulated state. When $b > 1$ recruitment, and as a consequence, stock, increases sharply during the period of observation. When $b < 1$, recruitment is dependent upon the density of the stock. A criterion of density dependence was that b should be significantly less than unity.

Results

About 24 stocks were analysed and classed in six groups: pink salmon, red salmon, Atlantic herring, Pacific herring, flatfish and cods. There are also data available from one stock of yellowfin tuna. Hence it was possible to average the constants from equation (1) for each group. The slopes are negative for tuna, cods and flatfish, and positive for the herrings and salmon. Figure 1 shows the stock-recruitment curves estimated in the same units, with the constants averaged from equation (1).

These curves should not be regarded as standard curves for any group, but only show the order of difference between groups. The Pacific salmon have virtually one age group and so the data group round the point of replacement. Herrings have more age groups, and cods and flatfish have many more age groups, and so the data tend to spread to the right. It will be seen that the dogma that recruitment is independent of stock size is most nearly true for flatfish. The control of Pacific halibut and of North Sea plaice was conceived and put into effect, taking the dogma as being axiomatic. But it does not apply to the other fish, particularly to cod.

In Table 1 are shown the sources of the data for the curves of Figure 1. Not all the observations survived the test that $b < 1$; Figure 2a is composed of all those surviving the test and Figure 2b comprises all the observations.

Figure 2 shows a relationship between the slope from equation (1) and an index of fecundity. Estimates of fecundity for such an array of stocks are not available. I have assumed that at W_{∞} the gonad weighs $0.16 W_{\infty}$ at spawning. Diameters of eggs are known and if eggs and fish are of about the same density, an index of fecundity is given by

$\frac{0.12 \cdot W_{\infty}}{\pi r^3}$; where r is the diameter of the egg in mm and W_{∞} is expressed

in mg. It is a fictitious estimate of fecundity, in that no individual or sample has so many eggs. Relative differences are based on differences in W_{∞} and in egg size; so it is assumed that the mean fecundity of a virgin stock would be given by a fixed fraction of this index.

The regression of the fecundity index on b is significantly different from zero. In Figure 2a are plotted only those data where $b < 1$, significantly; in Figure 2b are shown all the data, irrespective of this test. The figure shows all the slopes and one can see very clearly the positive slopes for the salmon and herring and the negative slopes for the demersal fish. It is worth recalling that the salmon, as large as cod, have large eggs and that their fecundity is very low.

The figure expresses the differences between stock and recruitment curves in another way. Where fecundity is high, density dependence is strong enough to generate a negative slope; typically the curves for demersal fish in Figure 1 are of this character. Where fecundity is low, density dependence is weak, as in salmon and herrings. The implication is that the true form of a stock/recruitment curve may be developed from an estimate of fecundity. If the relationship is as simple as it seems, another implication is that the density dependence is an effect of the density generated by a single parent. This would make sense if fish were a fixed distance apart, even in spawning shoals. A bigger stock spreads over a greater area of sea, and then differences in density dependence are generated by differences in fecundity only. A further consequence must be that the stock is virtually regulated on the larval drift between spawning ground and nursery ground, unless there is a mechanism for reinforcing densities, as, for example, sinking from a volume on to a surface.

Discussion

The negative slopes for tuna and demersal fish occur in five stocks of three groups. There is a trend of slope from positive to negative with increasing fecundity. Hence the stock/recruitment relations for cod, tuna and halibut are those to be expected. The important consequence is that a dome-shaped curve should be applied to the cod data. Figures 1 and 2 show how the curves for cods are one example of a family of curves, linked by differences in fecundity.

Of the two stock/recruitment curves in use for general purposes, that of Beverton and Holt (1957) (taking reciprocals of stock and recruitment and expressing the dependence of recruitment on parent stock, asymptotically in stock) appears to be misleading. Beverton (1962) showed that for plaice in the southern North Sea, recruitment was, in fact, independent of stock over the range of stock fished. Very nearly the same conclusion may be drawn from Fukuda's (1962) treatment of the Pacific halibut data. The same point is made in Figure 2, showing that the slopes for flatfish stocks (for North Sea plaice, two stocks of Pacific halibut, and the Petrale sole) are spread on either side of the zero line. So for flatfish, the dogma that recruitment is independent of parent stock was reasonable. For other stocks, cods, herring, tuna and salmon, the dogma misleads and the Beverton and Holt equation is not very useful. Because of the variability of slope within a group it is possible that dome-shaped curves should be used for some herring stocks and some salmon stocks.

The Ricker (1954, 1958) curve is dome-shaped, but the variation in recruitment remains intractable. As noted above, the variation in values of the constants did not permit any generalization. However, the intercepts could be ranked in the order shown in Figure 1. The

intercept in the Ricker curve is S_r/S_n , where S_r is the replacement value of stock and S_n is the value of stock at which maximum recruitment is found. The fact that this ranking coincides with that obtained by another method suggests that it is real. The differences in slope ($1/S_n$ which measures density dependence) were so high that all groups had very nearly the same ranking.

The curve used here suffers from a major disadvantage as compared with the two earlier curves, in that it is not deduced from first principles. Indeed it is only a piece of statistical brutality. As pointed out above it roughly resembles equation (2), but the latter is difficult to fit to the array of stocks used here. The only justification for using the present curve is to reach the generalizations given and to point the need for a new approach.

If the index of density dependence is related to fecundity, it implies that there is a fixed distance between spawning fish, because the density dependence is governed in a sense by the fecundity of one parent. Then if stocks vary in size, differences in abundance may well be reflected in differences in area of spawning ground, assuming that fish such as cod spawn in a layer. Presumably, in more fecund fishes, the period of density dependent mortality lasts for longer, declining with time until it becomes indistinguishable from the general level of natural mortality.

It should not be concluded from Figure 1 that the dogma of independent recruitment stands. The curves drawn are average curves on rather small scales to show the differences between groups. For herring and salmon there is a large proportion below the replacement point, and for any individual stock the effective curve may be near-linear. For cod a curve for an individual stock may be much more sharply dome-shaped than is suggested from the curve in Figure 1. Further it is possible that the curves for some herring stocks are dome-shaped.

A stock/recruitment curve expresses in summary form, for that stock, the fitness of the environment. It expresses the average recruitment under different conditions of stock. There is a sense in which a stock/recruitment curve only averages the changing environmental conditions, and because the environment changes any attempt at prediction is illusory. However, the stability of any fish stock should be contrasted with the very high fecundity; in other words, there is a finely adjusted control mechanism. An opposite sense is now put forward: there is a stock/recruitment curve which is a function of the stock's fecundity, an expression of the fine control mechanism. Then the variability of the recruitment expresses the fitness of the environment to the control mechanism in the fecundity. Hence a curve might be developed, from an understanding of fecundity, which is characteristic of a stock and is

not merely an expression of average conditions. Of course, it must express average conditions in an evolutionary sense, but it should be recalled that to master the environment, a biological mechanism must be independent of it to some degree.

If a stock/recruitment curve is characteristic of a species or group of species, it is likely that some of the forms of conservation in the North Atlantic will need modification. The shape of a yield curve changes with the shape of a stock/recruitment curve, and many detailed estimates might need alteration. The present state of conservation in the North Atlantic is that mesh regulation is now accepted and there is considerable determination to make it fully effective. However, it is admitted that there is a sense in which it is only the basic form of regulation and that it needs other measures, not in replacement, but in addition. A case in point is the Arcto-Norwegian stock of cod. It is now clear that the stock/recruitment curve suggested by Garrod (1966) is not a maverick, but one of the forms to be expected.

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TABLE 1 Sources of the data for the curves of Figure 1

Curve	Source of data
COD	
Stock: Arctic cod	Garrod (1966)
St. Lawrence cod	Paloheimo and Kohler (1967)
North Sea haddock	Beverton and Holt (1957)
FLATFISH	
Stock: North Sea plaice	Beverton (1962)
Petrale sole	Kotchen and Forrester (1966)
Pacific halibut (Areas 2 and 3, separately)	Fukuda (1962)
PACIFIC HERRING (<u>C. pallasii</u>)	
Stock: South-east Alaska	Hanamura (1961)
Kodiak Island	Hanamura (1961)
Sakhalin	Marty and Fedorov (1963)
British Columbia (North and Lower East)	Taylor and Wickett (1967)
ATLANTIC HERRING (<u>C. harengus</u>)	
Stock: Downs	Cushing and Bridger (1966)
Buchan	Burd (1966)
Dogger	Burd (1966)
Norwegian	Marty and Fedorov (1963)
SOCKEYE (RED) SALMON	
Stock: Bristol Bay	IIPFC (1962)
Columbia River	IIPFC (1962)
Karluk River	Rounsefell (1958)
Naknek-Kvichak	IIPFC (1962)
Egegik	IIPFC (1962)
Hushagak	IIPFC (1962)
Ugashik	IIPFC (1962)
Skeena River	Shephard and Withler (1958)
Fraser River	Killick and Clemens (1963)
PINK SALMON	
Stock: Alaska	IIPFC (1962)
Puget Sound	IIPFC (1962)
Kodiak	IIPFC (1962)
Karluk River	Ricker (1954)

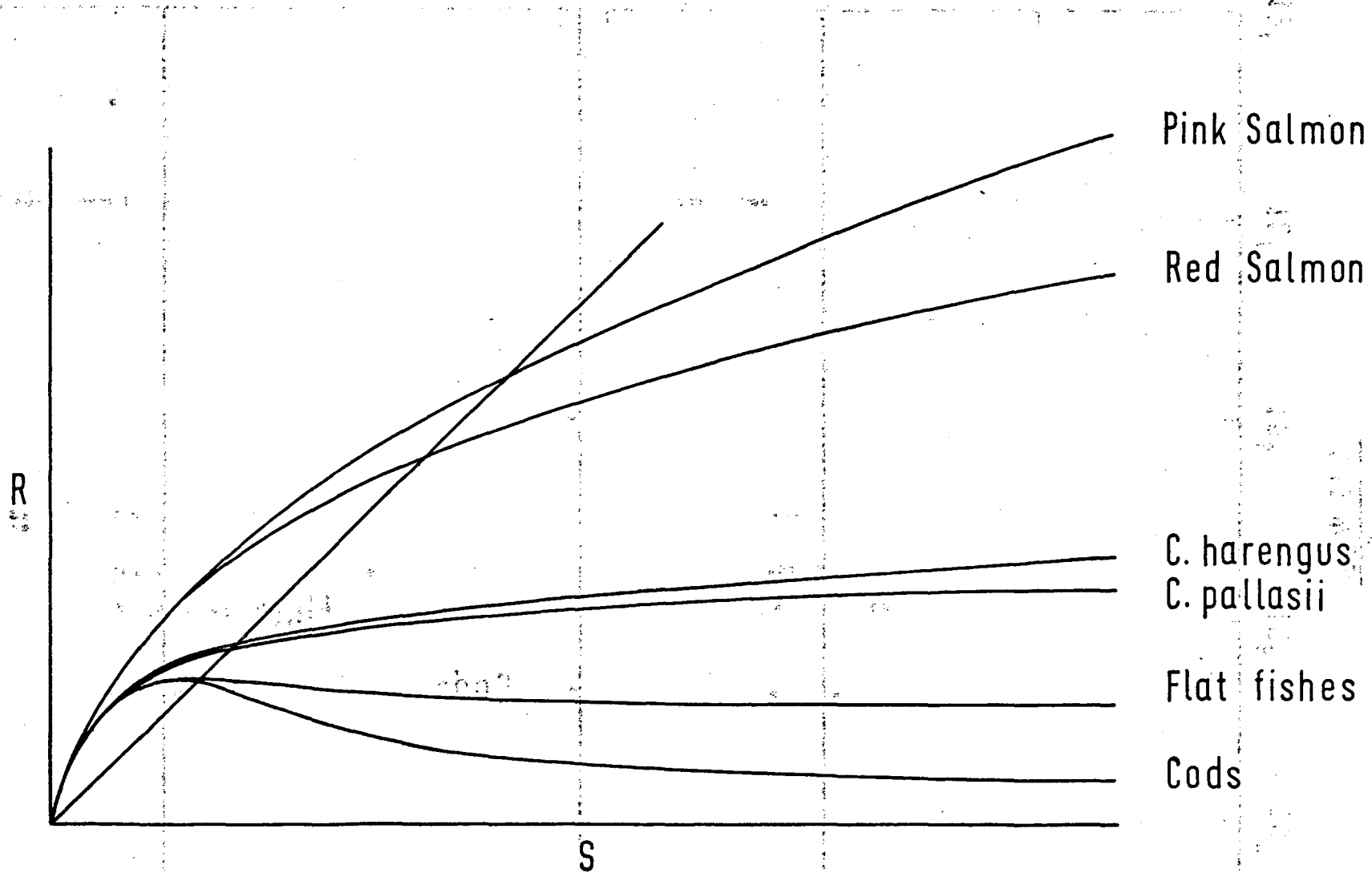


Figure 1 Stock and recruitment relations for six groups of stocks (45° line indicates replacement level).

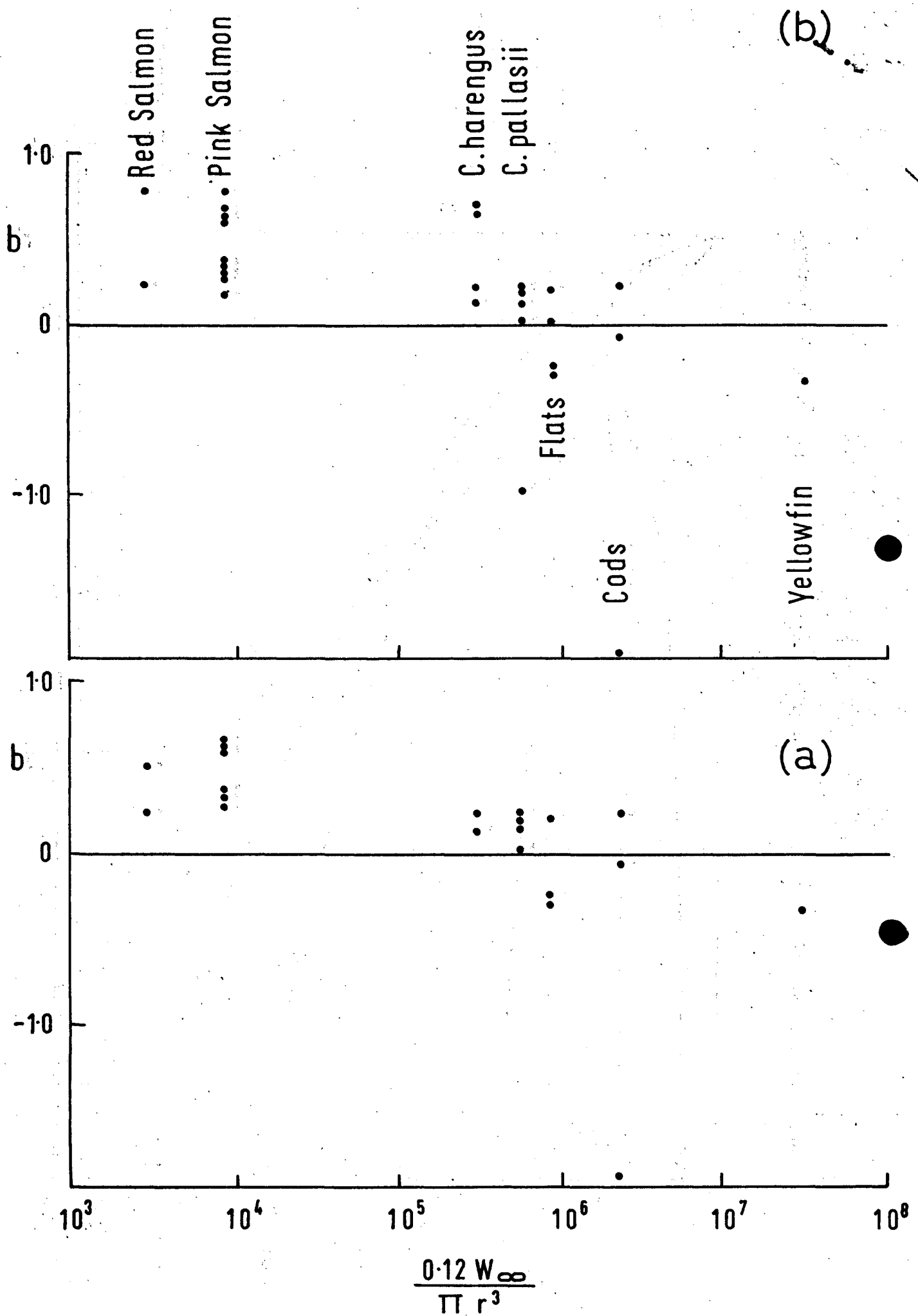


Figure 2 The relationship between the degree of density dependent mortality (as measured by the exponent b of equation 1) and an index of fecundity.

- (a) Stocks in which density dependent mortality is significant ($b < 1$).
- (b) All stocks.