THE DEPENDENCE OF RECRUITMENT ON PARENT STOCK IN DIFFERENT GROUPS OF FISHES

by

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An attempt was made to establish differences between groups of fishes in the nature of their stock and recruitment curves. Recruitment in logarithms was plotted on stock in logarithms and the slope was used as an index of density dependence. A number of stocks of Pacific salmon, Atlantic herring, Pacific herring, flatfish and gadoids were examined. It was found that the index of density dependence was inversely correlated with the cube root of the fecundity, which implies that for stocks of the same size, the distance apart of the larvae plays an important part in the determination of density dependence.

Four pelagic stocks, Hokkaido herring, Norwegian herring, Japanese sardine and Californian sardine, were examined. The stocks collapsed when fishing effort was high, and it was suggested that in two cases RICKER's limiting value of the exploitation rate might have been reached.

INTRODUCTION

The variability of recruitment to a fish stock is very high and allows a wide 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 some of the fish stocks for which the relevant data are published: tuna, cod, flatfish, salmon and herring. It was hoped to generalize from a considerable body of data on disparate stocks. This attempt failed because the differences in constants within a group of fish were as great as those between groups; this does not mean that either curve fails to fit the data, but the differences between the relevant constants were great. The data were used to estimate an index of density dependence by plotting recruitment in logarithms on stock in logarithms.

METHODS

THE INDEX OF DENSITY DEPENDENCE

To determine an index of density dependence in different species the simplest relationship of this form is:

$$R = kP^b, \tag{1}$$

where R is recruitment and P is stock in the same units, and where k and b are constants. The slope, b, is an index of density dependence, but it does not

estimate density dependent mortality. This equation has been used by MORRIS (1963) in his analysis of the "key factors" determining recruitment in insect populations.

A form of RICKER's curve, also developed by BEVERTON and HOLT (1957) is:

$$R = \alpha P e^{-\beta P}, \tag{2}$$

where α expresses the density independent mortality and β is the density dependent mortality. RICKER's curve, fully developed, is:

$$R = P e^{P_r/P_m(1-P/P_r)},$$

where P_r is the stock level at which recruitment replaces stock; P_m is the stock level at which maximum recruitment occurs.
Then, if $a = P_r/P_m$,

$$R = P e^{a(1-P/P_r)}. \tag{3}$$

This curve describes the stability of the population about P_r; it is illustrated in Figure 3. The rest of this paragraph summarizes RICKER's development (1958). When stock is less than the replacement stock $(P < P_r)$, recruitment is greater than stock $(R > P)$; when stock is greater than replacement stock $(P > P_r)$, recruitment is less than stock $(R < P)$. As recruitment is added to the stock, these processes tend to bring the stock to P_r. Between P_0, zero stock, and P_r there is P_s, the stock at which maximum surplus recruitment occurs, i.e. at which the greatest equilibrium catch in numbers can be taken. There is a rate of exploitation, E_s, at which P_s can be sustained under equilibrium conditions. Fishing can be sustained at lower stock levels, but below
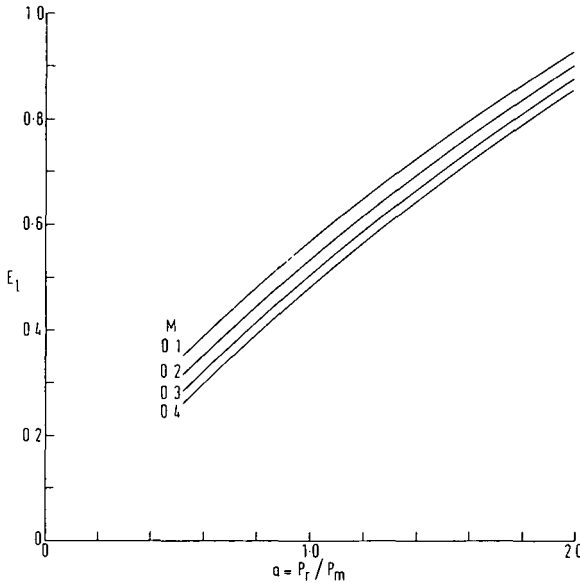

Figure 1. The relation between the limiting exploitation rate, E_l, and a, for four values of M. The values of E_l are corrected by the ratio (F/Z).
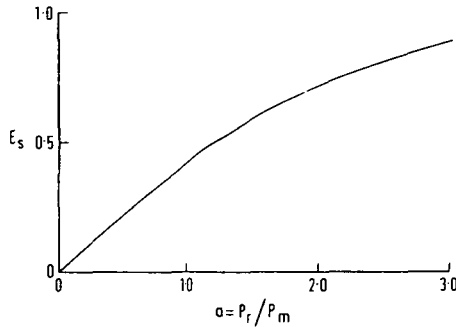
Figure 2. The relation between E_s, the exploitation rate needed to maintain maximum catch in numbers, and a, the constant which describes the stock and recruitment curve.

P_s an *increase* in fishing can reduce stock to P_0. If all values are in equilibrium, the exploitation rate

$$E = (R - P)/R = (Pe^{a(1 - P/P_r)} - P)/(Pe^{a(1 - P/P_r)}) = 1 - e^{-a(1 - P/P_r)} \quad (4)$$

In the limit, as $P \to 0$ the value of exploitation, $E_l = 1 - e^{-a}$ (Ricker 1958). Widrig (1954b) has defined the exploitation rate in a fishery in which F and M operate concurrently as:

$$E = (F/Z) (1 - e^{-Z}).$$

Dr Ricker has pointed out to me that the exploitation rates in expression (4) carry the implication that fishing operates before natural mortality in any biological year. Then $E = 1 - e^{-F}$ and is independent of M. If F and M were operating concurrently, then $(R - P)/R$ represents the loss by both forms of death and any exploitation rate should be reduced by F/Z, i.e. $E_l = (F/Z)$ $(1 - e^{-a})$. Figure 1 shows the relation between E_l and a for different levels of natural mortality. P_s/P_r may be determined from $(1 - aP_s/P_r)e^{a(1-P_s/P_r)} = 1$; then $E_s = 1 - e^{-a(1 - P_s/P_r)}$. Figure 2 shows the relation between E_s, the rate of exploitation needed to take the maximum catch in numbers, and a; E_s is derived on the basis of expression (4) above and must be reduced by the ratio (F/Z) in a given situation.

Data on stock and recruitment have been published for a number of stocks of different groups of fishes. In fitting the Ricker curve, no differences in the constants between groups were detected, implying that there was no curve characteristic of a given group of fish. Figure 3 shows a number of Ricker curves, the dome of which becomes more pronounced as the constant a increases. Equation (1) cannot strictly be used to fit a fully dome-shaped curve at all, but could well be used to fit a left-hand limb or a right-hand limb. A lightly convex curve (curves (a) or (b) in Fig. 3) would be reasonably fitted by equation (1) and then the index of density dependence, b, would be positive and less than unity. If the index is zero, a flattish dome is indicated, as in curve (c) in Figure 3, or there are points distributed about both left and right-hand limbs of a more sharply dome-shaped curve. If the index is negative, then the right-hand limb of the dome is indicated, but it is perhaps under-estimated.
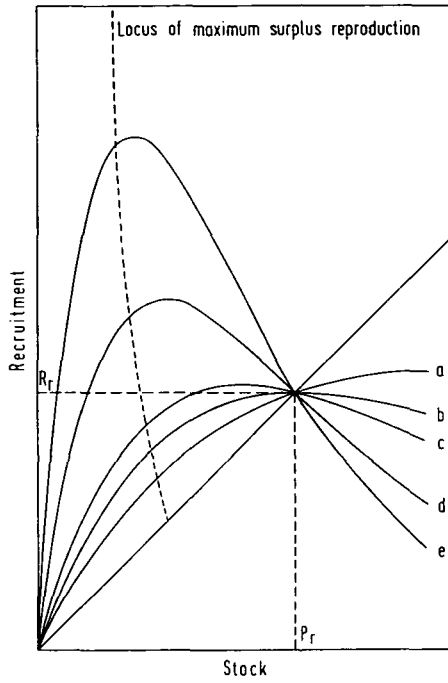
Figure 3. A family of stock (P) and recruitment (R) curves as formulated by RICKER (1958):
$R_r = P_r$ at the replacement level of stock, P_r.

Stock (P) and recruitment (R) curves

When stocks are heavily fished, like the Arctic cod (GARROD, 1966) or Georges Bank haddock (HERRINGTON, 1948), the points of recruitment are obviously distributed on both sides of a dome-shaped curve (*i.e.* of the type of (d) or (e) in Figure 3). But a less heavily exploited stock like the St. Lawrence cod exhibits only the right-hand limb of the dome. Thus, for lightly exploited stocks, in which the points of recruitment were distributed from P_r to P_s, the shape of dome is fairly well estimated by the index of density dependence, *b*. For more heavily exploited stocks the shape of dome expressed by the constant *a* in the RICKER equation is underestimated by the index of density dependence, *b*.

NUMERICAL DATA

A number of stocks were analysed and classed in six groups: pink salmon, red salmon, Atlantic herring, Pacific herring, flatfish and gadoids. There are also a few data available from one stock of yellowfin tuna. The sources of the data are shown in Table 1.

Fecundity

Because the fish stocks examined are all exploited an attempt has been made to obtain estimates of mean fecundity from each. Inevitably the quality of

Table 1. Sources of the stock and recruitment data plotted in Figures 4–10.

Group	Source of data
Pink salmon	
Alaska	Anon. (1962)
Puget Sound	Anon. (1962)
Kodiak	Anon. (1962)
Karluk River	Ricker (1954)
Chum salmon	
Tillamook Bay	Henry (1953, 1954)
Sockeye (red) salmon	
Columbia River	Anon. (1962)
Karluk River	Rounsefell (1958)
Naknek-Kvichak	Anon. (1962)
Egegik	Anon. (1962)
Nushagak	Anon. (1962)
Ugashik	Anon. (1962)
Skeena River	Shepard and Withler (1958)
Fraser River	Killick and Clemens (1963)
Atlantic herring (C. harengus)	
Downs	Cushing and Bridger (1966)
Buchan	Burd (1966)
Dogger	Burd (1966)
Norwegian	Marty and Fedorov (1963)
Sardine (Sardinops caerulea)	Clark and Marr (1955)
Pacific herring (C. pallasii)	
South-east Alaska	Hanamura (1961)
Sakhalin	Marty and Fedorov (1963)
British Columbia	Taylor and Wickett (1967)
(north and lower east)	
Flatfish	
North Sea plaice	Beverton (1962)
Petrale sole	Ketchen and Forrester (1966)
Pacific halibut	Fukuda (1962)
(Areas 2 and 3, separately)	
Tuna	
Yellowfin	Anon. (1966b)
Gadoids	
Arctic cod	Garrod (1966)
St. Lawrence cod	Paloheimo and Kohler (1967)
North Sea haddock	Beverton and Holt (1957)
Georges Bank haddock	Herrington (1948)

such estimates is variable. For example, for all four pink salmon stocks, a relationship between length and fecundity has been used from Hunter (1959). For the red salmon, estimates of fecundity were taken from Rounsefell (1957) and Mathisen (1962); mean lengths of spawning fish were taken from Penn-oyer and Seibel (1964) for the Bristol Bay group. For the Skeena stock, the Babine Lake fecundities were used because the greater part of the stock spawns in that lake (Larkin and McDonald 1968); for the Columbia River, mean lengths were taken from Rich (1942) and Burner (1951). Data for the chum salmon were taken from Henry (1953, 1954).

The herring material on fecundity is summarized for the Atlantic herring in Cushing (1966); for the Pacific herring I have used data in Nagasaki (1958) for the British Columbia stocks, in Rounsefell (1929) for the south-east Alaska stock, and in Motoda and Hirano (1963) for the Hokkaido-Sakhalin stock. Simpson (1951) gives fecundity estimates for North Sea plaice, as does

RAITT (1933) for North Sea haddock. The estimate for Pacific halibut was taken from NIKOLSKI (1961) and that for the Arctic cod was from GARROD (personal communication). No estimates were available for the Petrale sole or for the St. Lawrence cod, and the same figures were used as for plaice and Arctic cod. For the yellowfin tuna the figures given by JOSEPH (1963) were used. The estimates of fecundity are in general of slight value statistically; the sampling is made casually and with no attempt to impose the discipline of a market system of sampling.

<div align="center">STATISTICAL TREATMENT</div>

The basic method was to plot recruitment in logarithms on stock in logarithms. There are positive, zero and negative values of b as the data approximate to different parts of the stock and recruitment curves shown in Figure 3.

If the index of density dependence, b, estimates the stock and recruitment curve then a negative value must indicate a marked dome in the curve and data grouped on the right-hand limb. As exploitation increases, so the dome, if it exists, becomes more pronounced in the display of the data. If there is no dome, then the estimate of the index may not change much under exploitation. Hence the index is underestimated when the stock and recruitment curve is dome-shaped and the population is well exploited. Although the degree of exploitation is known well for many of the stocks it is not known for all of them and so the effect of exploitation upon the estimation of the index of
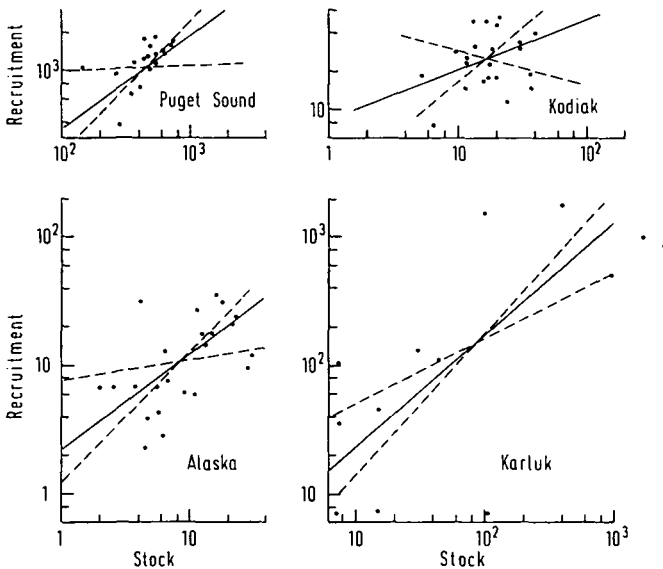

Figure 4. The relationship between stock and recruitment (in logs) for pink salmon. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, b. Broken lines are the 95% confidence limits.

density dependence cannot be measured. The following method was devised to mitigate this difficulty to some degree.

An attempt was made to improve the estimate of the index of density dependence by recalculating the slope for all observations in stock greater than the mean; the exercise was restricted to those stocks for which more than twenty observations were available. The data for twenty stocks could be used in this way. For six, no change in the coefficient was found, *i.e.* less than the standard error in the original analysis. In twelve stocks, differences greater than the standard error of the original analysis were found, but they were less than that of the second treatment, which, of course, included fewer observations. Only in two stocks (Skeena sockeye and Arctic cod) was a difference found which was greater than the standard error of the slope in the second treatment. For the Skeena sockeye, the slope was reduced from 0·679 to 0·315 (s.e. 0·343), a difference which, however, is not significant. For the Arctic cod, *b* was increased from −0·067 to −1·989 (s.e. 0·449) a difference which is significant. It is interesting to notice that the slope for the St. Lawrence cod, a stock probably less well exploited than the Arctic stock, is −1·953 (s.e. 0·479). This estimate is considered to be a better estimate of density dependence than that from all the data for the Arctic cod and is used in the subsequent treatment.

There is another conclusion to be drawn from the study of those observations greater than the mean. It is that the original values of the index of density dependence are estimated as well as can be expected, given the high variance of recruitment, despite the convex nature of the curve to which the index is fitted.

RESULTS

THE RELATIONSHIP BETWEEN THE INDEX OF DENSITY DEPENDENCE AND AN INDEX OF FECUNDITY

The data with slopes fitted through the logarithmic means are shown in Figures 4–10 grouped as sockeye (red) salmon, pink salmon, chum salmon, Atlantic herring, Pacific herring, sardine, flatfish, tuna and gadoids; also given are slopes at the 95 per cent confidence limits, based on the standard errors of the slope. It will be seen by inspection that there are real differences between slopes, but that there is considerable variability.

Figure 11 shows the mean values of *b* (±2 standard errors about the slope) for all the stocks examined. The slope for the St. Lawrence and Arctic cods are significantly different from the slopes of all other stocks. In general there is a trend in mean value from the bottom left-hand corner to the upper right-hand corner. The indices for Egegik Red, Skeena Red and Puget Sound Pink differ from those of St. Lawrence cod and Georges Bank haddock. Further, the indices for plaice and halibut differ from some of the salmon stocks and the Atlantic herring. In other words, the grouping of indices of density dependence corresponds to groups of fish species. On the other hand estimates of the index for Karluk pink salmon, North Sea haddock, south-east Alaska and Sakhalin herring are poor ones in that they differ only from that of the St. Lawrence cod.

Table 2 gives the indices of density dependence, *b*, by groups of fish, with their standard errors and their average fecundities, $\bar{f}$; the average fecundity

TABLE 2. Data on the index of density dependence, *b*, and mean fecundity
(in thousands of eggs) for different stocks

Stock	Index of density dependence, *b*	Standard error S.E.	DF	Mean fecundity $\bar{f}$
Pink salmon				
Alaska	5·581	0·202	21	1 754
Kodiak	0·245	0·206	20	1 754
Karluk	0·788	0·199	12	1 754
Puget Sound	0·538	0·215	16	1 754
Chum salmon				
Tillamook Bay	0·231	0·219	18	2 890
Red salmon				
Columbia	0·386	0·134	17	about 4 000
Fraser	0·614	0·119	40	4 074
Skeena	0·679	0·128	43	3 273
Karluk	0·292	0·151	60	3 199
Egegik	0·798	0·189	30	4 011
Naknek	0·622	0·157	30	4 011
Ugashik	0·175	0·217	30	4 011
Nushagak	0·348	0·151	30	4 011
Atlantic herring				
Norwegian	0·668	0·206	45	51 000
Downs	0·706	0·209	25	38 000
Dogger	0·152	0·404	22	70 000
Buchan	0·231	0·277	28	80 000
Californian sardine				
Sardine	0·448	0·148	20	33 000
Pacific herring				
British Columbia, (lower east)	0·245	0·161	24	16 000
Sakhalin	0·205	0·107	44	45 000
South-east Alaska	0·168	0·293	16	20 000
British Columbia, (north)	0·031	0·266	22	20 000
Flatfish				
Halibut 2	−0·263	0·340	28	210 000
Halibut 3	−0·281	0·269	33	210 000
Plaice	0·001	0·128	23	140 000
Petrale sole	0·217	0·209	18	(100 000)
Tuna				
Yellowfin	−0·339	0·643	7	3 000 000
Gadoids				
Arctic cod	−0·067[1]	0·162	22	1 500 000
St Lawrence cod	−1·953	0·479	9	(1 100 000)
North Sea haddock	0·230	0·133	14	250 000
Georges Bank haddock	−0·957	0·474	29	(250 000)

[1] Revised to −1·989 (see text).

is that at the mean weight of the stock under exploitation. The slopes are
negative for tuna and cod, and positive for the herring and salmon. The
average index of density dependence for flatfish was about zero. In general,
fecundity is poorly sampled and we cannot be certain that the values quoted
are always properly taken at the mean weight. The average indices (number of
observations contributing to the average in parentheses) for each group
are given in Table 3, with average fecundities. Thus there is a distinct trend
in the index of density dependence from top to bottom of the table and this
order in fish groups is an order in fecundity, the least fecund at the top and
the most fecund at the bottom.

It would not be surprising if there were differences in the index of density
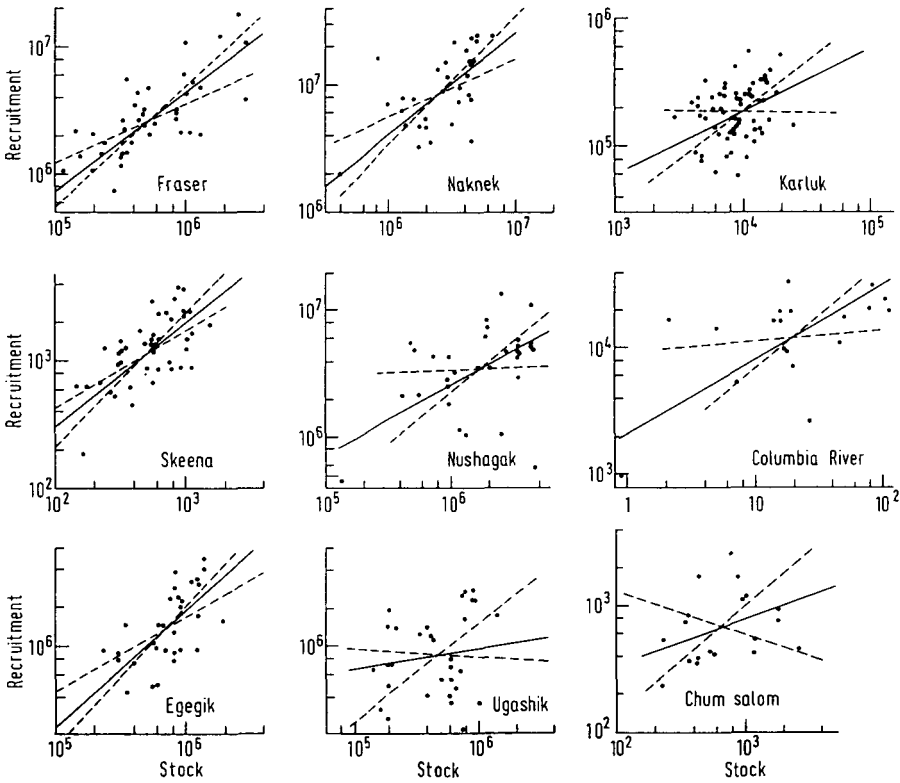
Figure 5. The relationship between stock and recruitment (in logs) for sockeye and chum salmon (bottom right). Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, b. Broken lines are the 95 % confidence limits.

TABLE 3. Average indices of density dependence (b) and average fecundity ($\bar{f}$) for the main groups of fish in Table 2

Group	Mean index of density dependence ($\bar{b}$)	Mean fecundity in thousands of eggs ($\bar{f}$)
Pink salmon	0·524 (4)[1]	1·75
Red salmon	0·468 (8)	3·2–4·1
Chum salmon	0·231 (1)	2·9
Atlantic herring	0·441 (4)	33–80
Sardine.......................	0·448 (1)	33
Pacific herring.................	0·162 (4)	16–45
Flatfish.......................	−0·081 (4)	100
Gadoids.......................	−1·168 (4)	500
Yellowfin tuna	−0·339 (1)	3 000

[1] Numbers of stocks contributing to the mean indicated in parentheses

dependence within the groups shown above. In general the indices for pink salmon are high (the highest average slope and the lowest fecundity), despite their geographical range in the group from Puget Sound to Alaska and the
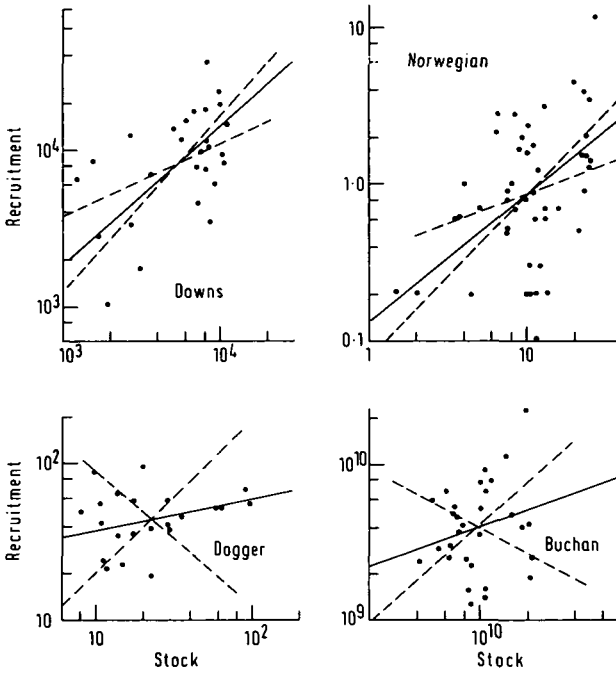
Figure 6. The relationship between stock and recruitment (in logs) for Atlantic herring. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, *b*. Broken lines are the 95% confidence limits.
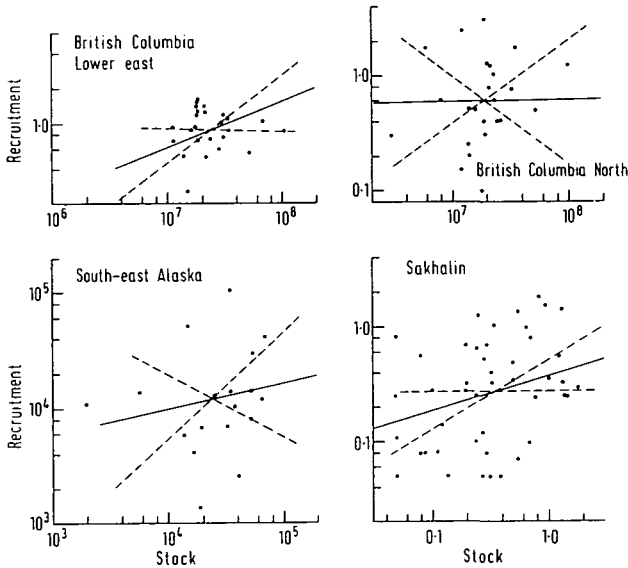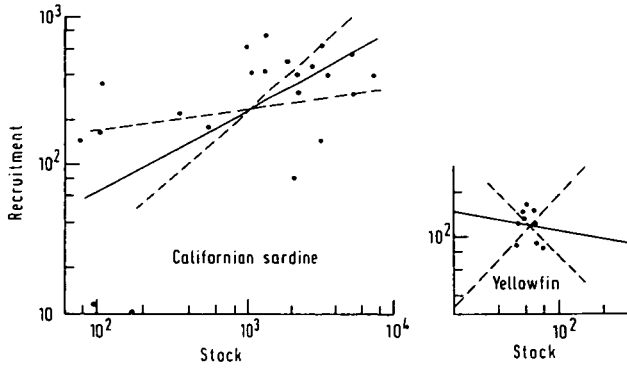

Figure 7. The relationship between stock and recruitment (in logs) for Pacific herring. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, *b*. Broken lines are the 95% confidence limits.

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Figure 8. The relationship between stock and recruitment (in logs) for California sardine and yellowfin tuna. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, b. Broken lines are the 95% confidence limits.
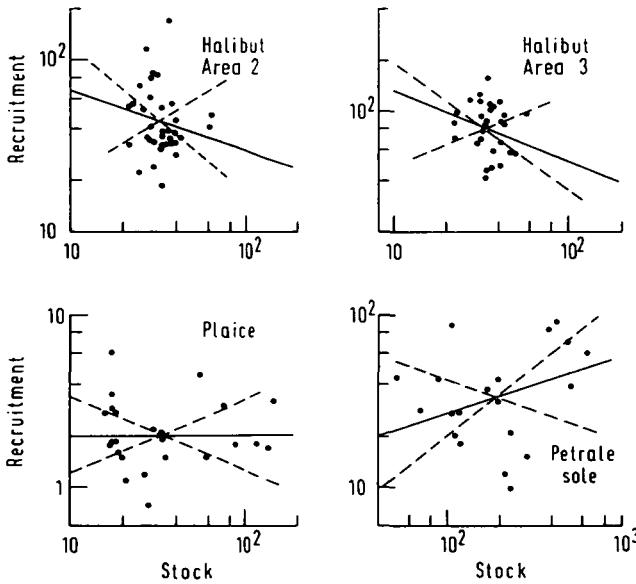

Figure 9. The relationship between stock and recruitment (in logs) for halibut, plaice, and Petrale sole. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, b. Broken lines are the 95% confidence limits.

uncertainties of stock identity. Within the red salmon or sockeye group there are two groups: (a) Columbia River, Fraser River and Skeena River in Washington State and British Columbia, (b) Egegik, Naknek, Ugashik and Nushagak, the Bristol Bay group – with the Karluk River stock perhaps between the two. There is a real difference between the two in that the first southern group is larger at spawning and spawns in one or two age-groups (4_2 and 5_2;
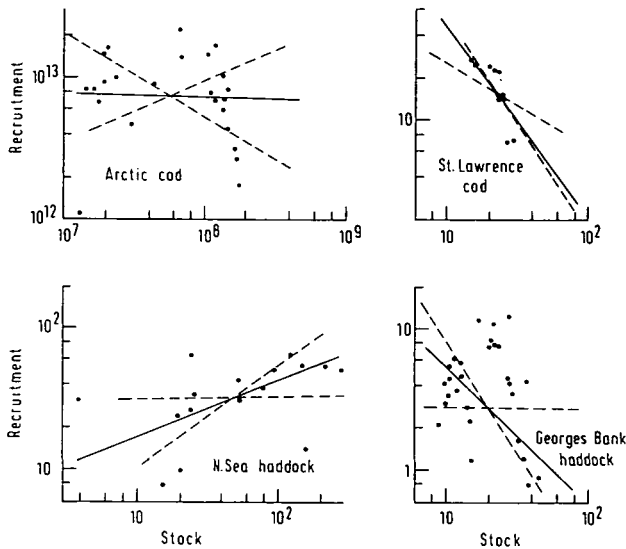
Figure 10. The relationship between stock and recruitment (in logs) for cod and haddock. Sources of data as shown in Table 1. The full line represents the slope of the regression of recruitment on stock which is the index of density dependence, b. Broken lines are the 95 % confidence limits.

the subscript indicates the number of years spent in fresh water), whereas the smaller Bristol Bay red salmon spawns in perhaps three age-groups (4_2, 5_2, 5_3, 6_3, 6_4). There is a slight difference in index between the two groups (a) southern, 0·559 (b) northern, 0·485, of no significance statistically. There are cycles in the Pacific salmon, a 4-year one in the sockeye and a 2-year one in the pink. It was considered that the advantage of a greater number of observations outweighed differences due to cycles.

Within the group of Atlantic herring, there is a distinct difference between the winter and spring spawners, Downs and Norwegian, and the autumn spawners, Dogger and Buchan. The average fecundity of the winter-spring group is 45 000, with an average index of density dependence of 0·687. The average fecundity of the autumn spawners is 75 000, with an average index of 0·191. So the difference in fecundity is associated with difference in the index of density dependence within this group. No such differences can be detected within the Pacific herring group, but the average index, 0·162, is much lower, with an average fecundity of about 25 000.

Within the flatfish group the index of density dependence is greater for the halibut than for the plaice or Petrale sole, which probably have lower fecundities. The same trend can be detected within the gadoid group: the cod, with greater fecundity, have higher indices than the haddock.

Figure 12 shows the relationship between b, the index of density dependence, and the average fecundity. An average curve has been fitted by eye to the data excluding the single observations on chum salmon, Californian sardine, and yellowfin tuna. Very roughly it appears that the index of density
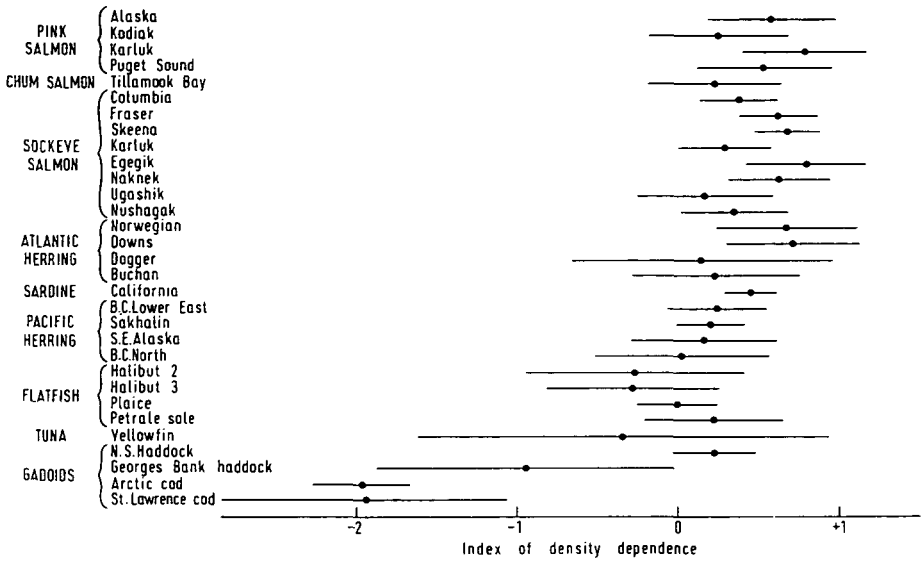
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Figure 11. The indices of density dependence, b, for thirty-one stocks ($\pm$ twice the standard error).

dependence is related to the cube root of the fecundity. Figure 13 gives the dependence of b on $\sqrt[3]{f}$. Given the variability of the data, it will be seen that the fit is reasonable. Eggs are released into the water and the spawning potential of a female fish could be expressed in numbers of eggs/m^3. If density dependence is related to $\sqrt[3]{f}$ then it is related to the distance apart of the larvae. The consequences of this argument are discussed in the next section. The main conclusion from this section is that there are differences between
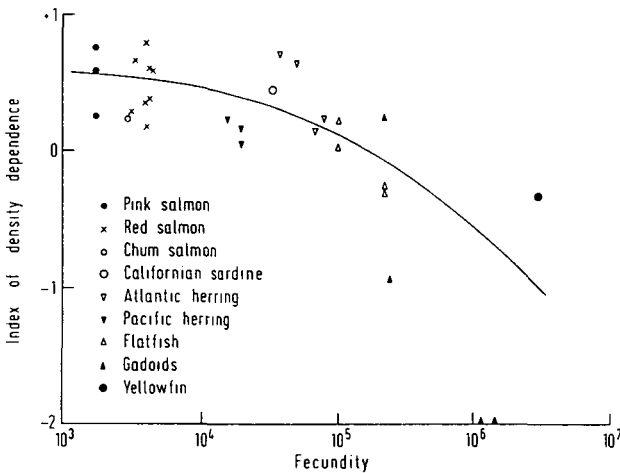

Figure 12. The relationship between the index of density dependence, b, and the average fecundity, $\bar{f}$, for a number of fish stocks.
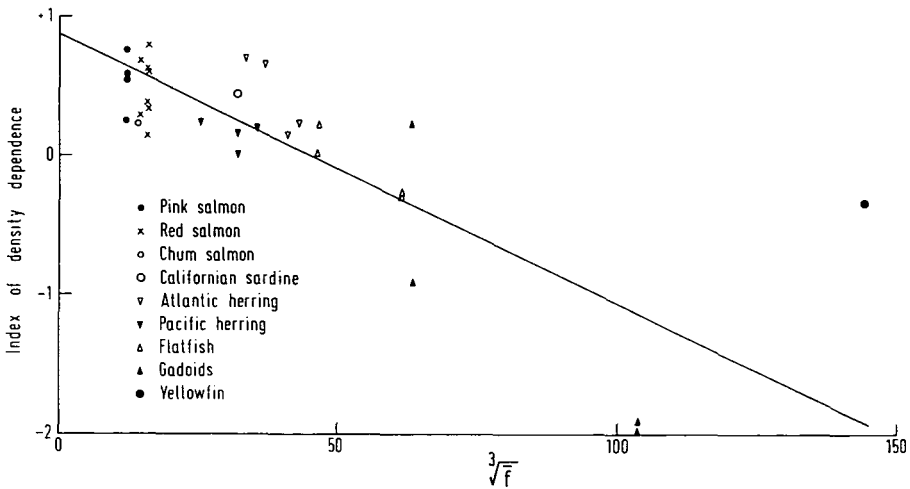
Figure 13. The relationship between the index of density dependence, b, and $\sqrt[3]{\bar{f}}$.

groups of fish species in density dependence – and hence, stock and recruitment curves – and that these differences are related to differences in fecundity[1].

THE ROLE OF FECUNDITY IN A STOCK AND RECRUITMENT RELATIONSHIP

Fecundity is a function of weight in an individual and of biomass in a stock; there is a mean fecundity, $\bar{f}$, at a mean weight, $\bar{w}$, in the stock. All the stocks under investigation are exploited and so the data will tend to be distributed in $P < P_r$ and so b is properly correlated with $\bar{f}$.

Let r ♀/m³ lay $f.r.$ eggs/m³ and that at a given time after hatching this quantity will be reduced by a loss rate. Pacific salmon may spawn in succession on the same redd and it has been suggested that density dependence in this species is effected by differences in r/m². Within a stock, density dependent effects could be achieved by differences in r or in $\bar{f}$, or both. An increase in mortality would decrease the mean weight of the stock and hence $\bar{f}$, and r, and so larval density would be reduced. But if recruitment to an unfished multi-age stock were reduced (by a random fluctuation), $\bar{w}$ and hence $\bar{f}$ must *increase*. Under such conditions of recruitment failure, numbers are reduced and so r, the density of spawning females, is reduced. So it is possible that the density dependent control in a given stock is exerted in the density in numbers of spawning females rather than in the fecundity of the stock. When stocks decline, the spawning grounds decrease in area (AHLSTROM 1966; Cali-

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[1] GULLAND (personal communication) has clarified the nature of the index of density dependence in the following way. Let survival be R/P, then $R/P = KP^{(b-1)}$; therefore log $R/P = \log K + (b-1) \log P$. Thus $(b-1)$ is the decrease in survival caused by a proportional increase in stock. So it is an index of density dependence, and as the stock and recruitment curves become more dome-shaped, so the density dependence becomes more intense.
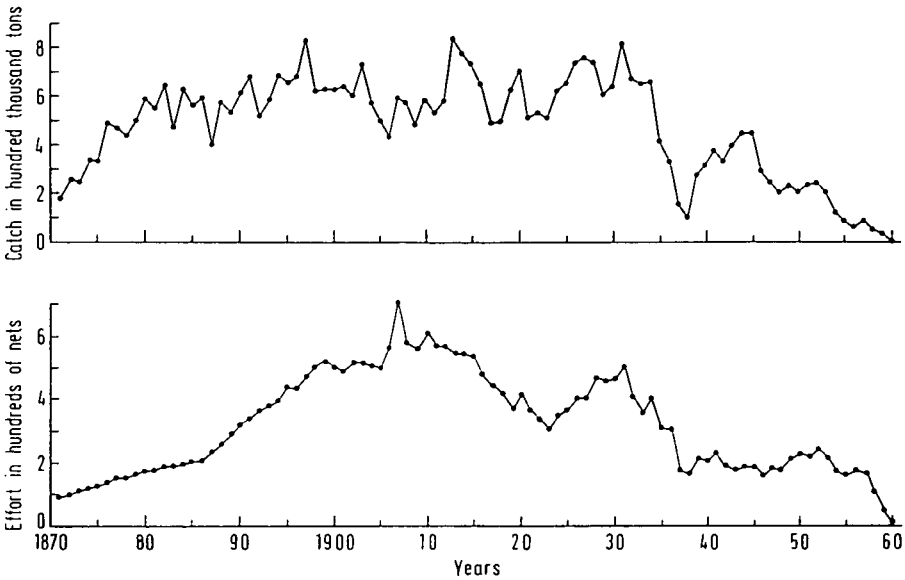
Figure 14. Catches and effort of the Hokkaido-Sakhalin herring, from MOTODA and HI-
RANO (1963) and AYUSHIN (1963).

fornian sardine), and when they increase, the spawning grounds increase in
area (AHLSTROM 1966; Californian anchovy). Such changes are accompanied
by considerable changes in density of larvae, much greater than can be ac-
counted for in terms of fecundity within the mature stock – because neither
sardine nor anchovy grows very much during adult life.

Demersal fish have long life-spans, grow much and increase greatly in
fecundity during their life-span. Any single recruit year-class supplies a num-
ber of age-groups of stock with eggs, thus damping variability as noted by
MURPHY (1967). When $P < P_r$, due to the damped failure of a year-class,
numbers are reduced but fecundity is relatively increased; consequently, in
terms of stock in eggs the effect of fecundity tends to return P to P_r, which
is a stabilizing tendency. The argument can be conducted in an opposed way
when $P > P_r$. Thus differences in fecundity tend to help stabilize the stock
about its replacement point P_r. The conclusion to this argument is that, within
a stock, density dependence may be mediated by differences in densities of
spawning females, r, but that between stocks, as shown in Figure 13, diffe-
rences are effected by differences in fecundity.

THE FATE OF FOUR PELAGIC STOCKS

There are four large stocks of herring-like fishes, each of which has suffered
a dramatic decline during periods when fishing effort was high. They are the
Hokkaido-Sakhalin herring, the Norwegian herring, the Japanese sardine and
the Californian sardine. In each case the effect of fishing, as cause of decline,
has been doubted as a sole cause, although YAMANAKA (1960) suggested that

fishing might have played a significant part in the decline of the Japanese sardine and MURPHY (1966) produced evidence that fishing on the Californian sardine reduced the spawning potential of that stock considerably. Environmental causes of a rather generalized nature have been associated with the four declines, but little of the evidence adduced is convincing.

From Figure 13 the index of density dependence for sardines and for the Atlantic herring should be about 0·40 and that for the Pacific herring should be about 0·20. These figures correspond to values of $a = 0·50$ and $a = 0·75$ respectively. The limiting exploitation rates E_l for sardines and Atlantic herring should then be about 0·27–0·35 and for Pacific herring about 0·39–0·48. At a steady and moderately high rate of exploitation, $E; E_l > E > E_s$, provided that the variance of recruitment is relatively low, a stock can continue to yield catches in numbers at a less rate than the maximum. But if exploitation were increasing to E_l, or if the variance of recruitment were high, there is danger of recruitment failure, a collapse of stock and total loss of catches.

Catches of the Hokkaido herring increased during the last century to a peak at the end of the century (1897), oscillated until 1931, after which they declined. Effort increased to a maximum in 1907, declined till 1922, increased to 1931 and subsequently fell. Catches in hundred thousand tons and effort in hundreds of nets are shown in Figure 14 from MOTODA and HIRANO (1963) and AYUSHIN (1963) for the Hokkaido and Sakhalin herring; the catches from the Sakhalin area in AYUSHIN were added to those off Hokkaido in MOTODA and HIRANO. From a relationship established from the catch and effort data in Figure 2 of MOTODA and HIRANO, the Sakhalin catch was roughly converted to effort and Figure 7 also shows an index of total effort exerted in the fishery. The survival rates of herring of fully recruited fish of five years of age ranged from 0·46–0·53 for the whole period 1910–1950; in 1910–1916 it was 0·36–0·43 and in 1944–1948 it was 0·79 (ISHIDA 1952). If the natural mortality is well estimated in the latter survival rate, then the exploitation rate in the earlier period must have been fairly high. It is possible that the catches declined after 1931 merely because $E > E_s$. The only point of evidence needed here is that catch declined under high effort, when the exploitation rate was probably high, and it is suggested that the decline in catch was due to a moderate failure in recruitment.

Catches of the Norwegian herring increased steadily during the early part of the present century. Since 1946 catches of all countries (ANON. 1966a) increased to a peak in 1956 after which catches fell by a factor of nearly three. A minimal index of effort is given by the number of purse seiners (ØSTVEDT 1963); to this has been added the number of drifters, assuming that 1 purse seiner is equivalent to 8 drifters (see Figures 2 and 3 in ØSTVEDT 1963). For the period 1947–1958, in each year 500 purse seiners caught about $2·10^9$ herring and in the same period 2000 drifters caught $1·10^9$ herring in each year. The total Norwegian effort obtained in this way was raised by the ratio of total international catch to Norwegian catch. The trends of international catch in thousands of tons and effort derived in this way are shown in Figure 15. DRAGESUND and JACOBSSON (1963) have analysed tagging results for the Atlanto-Scandian stock in the Iceland fishery in summer for the period 1952–1959; their maximum estimate of M was 0·23. Because this estimate includes tagging mortality, the true value of M would have been less. Estimates of exploitation rates are given in the inset figure above Figure 15. (DRAGESUND
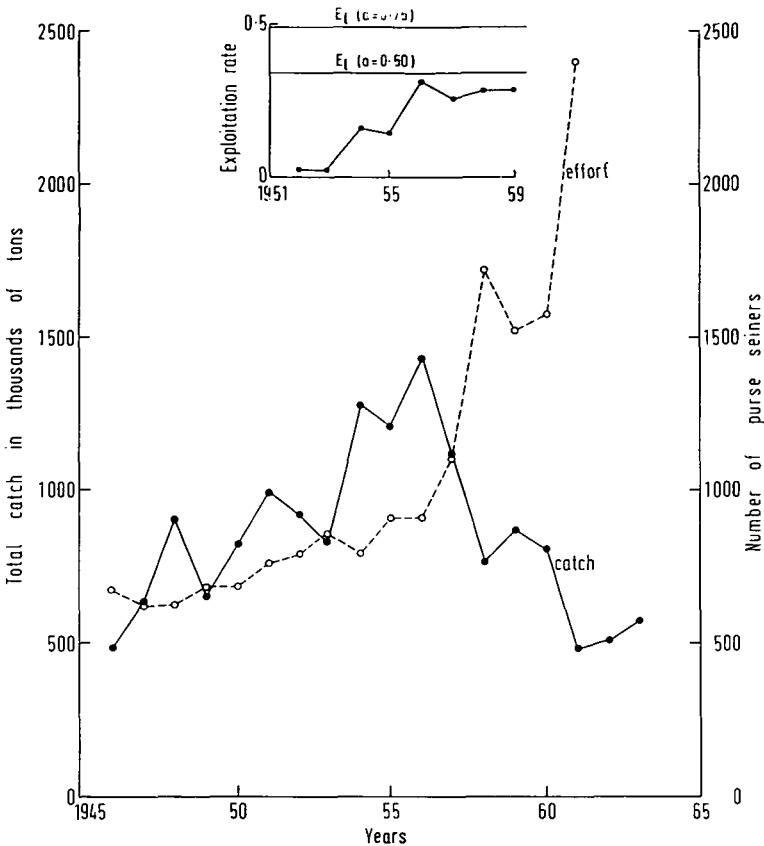
Figure 15. International catches and effort for the Atlanto-Scandian stock of herring (Anon. 1966, Østvedt 1963), together with the exploitation rate during the period (Dragesund and Jakobsson 1963).

and Jacobsson 1963). The inset figure shows the estimated value of E, $i.e.$ $(F/Z)(1 - e^{-Z})$, together with values of E_l, for $a = 0.50$ and for $a = 0.75$. It will be seen that in 1956 E rose high and if the exploitation rate is under-estimated, it may have exceeded E_s, which would be low if $a < 1.0$ (see Figure 2). In the years 1958–1961, effort increased further but no increase in exploitation rate was observed in 1958–1959. The point of evidence from the Atlanto-Scandian herring stock is that the collapse of catches came at a time when perhaps $E < E_s$. The life-span of this stock of herring is long and the good year-classes occur only sporadically. During the fifties the stock was dependent upon one year-class, that of 1950, which in effect was not replaced. John Gulland has pointed out to me that the extreme fluctuation of year-classes in the Norwegian herring stock complicates the question. Perhaps the probability of good year-classes is high only at moderate ranges of stock size; then, if the exploitation rate is high, the stock from a good year-class lasts in the moderate range for a short time. It remains true that recruitment has
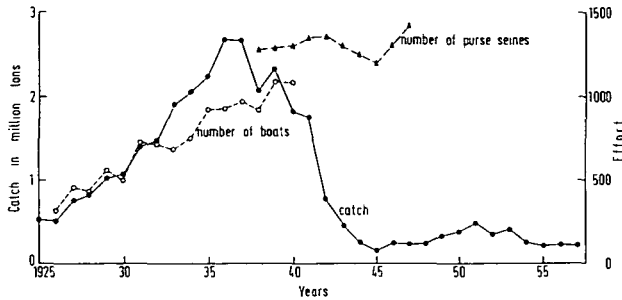
Figure 16. Catches of the Japanese sardine (NAKAI 1960) and effort as purse seiners and as purse seines (KURITA 1960).

reduced in the stock since the 1950 year-class reached its peak during a period of high effort.

Catches of the Japanese sardine in tons increased to a peak in 1936 and 1937, after which they declined to very low values within ten years (NAKAI 1960). Effort is given as the number of purse seiners registered or as the number of seines worked (KURITA 1960); the two indices overlap for only two years, but KURITA says that the effort was steady from 1935 to 1947 (Figure 16). YAMANAKA (1960) suggested that $M = 0.37$, before and after the decline. He estimated that $F = 0.50$–0.70 after the decline and as effort was said to be constant for twelve years, a reasonable value of the exploitation rate would be $E = 0.38$ (then $E < E_s$ if $a < 1.0$; see Figure 2). It is even possible that the exploitation rate approached the limiting rate, E_l (= 0.40–0.53). These are the conditions under which recruitment is reduced and perhaps catastrophically so.

Catches of the Californian sardine reached a peak in 1936 and subsequently declined; effort as boat-months remained high until 1950 (CLARK and MARR 1955); I have used catch and effort for the State of California (Figure 17). From tagging experiments, CLARK and MARR give values of M of 33 per cent to 39 per cent. The top inset shows the trend in exploitation rate estimated from mortality rates. There are two forms of estimate, that for the available population and that for the whole population. The values for the available populations are calculated for the two estimates of natural mortality ($M = 0.40$, 0.50) derived from tagging experiments; MURPHY (1966) suggests that these values are a little too high for the period 1937–1945. The difference between the values for the available population and those for the total population is that discussed by WIDRIG (1954a). The lower inset shows the trend in exploitation rate calculated from the ratio of catch to stock.

The collapse of the fishery took place in three stages, after 1936, after 1944 and after 1950. The rate of exploitation reached high levels in 1936, by all three methods of estimation; indeed in 1936 itself, E approached E_l in all methods, so the year-class of 1936 must have been vulnerable, although it was not in fact reduced. During the years 1943–1945, the exploitation rate approached E_l in all three methods and so the year-classes 1943, 1944 and 1945 were low in consequence. Relatively, the year-classes 1947 and 1948 recovered somewhat, but the year-classes 1949 and 1950 collapsed completely. In the
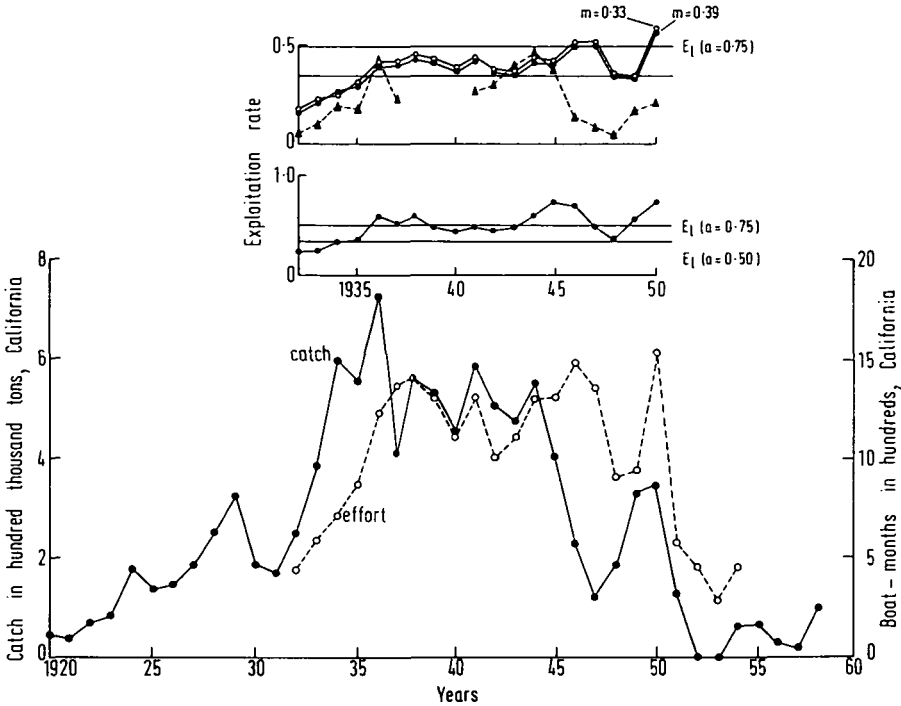
Figure 17. Catches and effort of the Californian sardine (CLARK and MARR 1955). Exploitation rates from data in CLARK and MARR.

two latter years the exploitation rate may well have exceeded the limiting rate; in 1950, two estimates out of three did actually exceed it, whereas that based on WIDRIG's method did not. Now, WIDRIG's method requires constant recruitment. It is interesting that the estimated E using WIDRIG's method falls away when the three failing year-classes 1943, 1944 and 1945 enter the fishery. Hence we may conclude that the fishery collapsed because $E > E_s$ and that E might have been greater than E_l for the three crucial year-classes. The preceding discussion is based on data on vital rates and year-classes given in CLARK and MARR (1955). More recently MURPHY (1966) has distinguished two forms of stock-and-recruitment curve in the Californian sardine. From the same spawning biomass, the potential biomass in recruitment (with the year-class reduced by natural mortality) and the actual biomass (with the year-class reduced by total mortality) were estimated. In the latter there were more negative deviations from the bisector, showing that the decline in recruitment was probably due to fishing.

It is suggested that the four great pelagic stocks have suffered recruitment failure because the rate of exploitation was too high. It is likely that the best rate of exploitation was exceeded and that recruitment was reduced to a lower level as a consequence. It is possible that the limiting rate of exploitation

was reached in the Norwegian herring stock and probable that it was reached in the Californian sardine stock.

For each fishery the collapse has been attributed to environmental causes and in the Norwegian herring stock and the two sardine stocks the proximate cause of collapse was recruitment failure. In no case has the environmental mechanism been described properly and the postulated causes in the four cases are disparate. The simplest explanation is that collapse was due to heavy fishing which reduced recruitment. The purpose of grouping the four fisheries in this way was to provide independent evidence that the stock and recruitment curve for the herring-like fishes was of the form suggested, *i.e.* that $b = 0.2$–0.4 or that a (in RICKER's curve) $= 0.50$–0.75. To extend the argument, for salmon $E_l < 0.53$ and for flatfish and cod $E_l > 0.53$.

DISCUSSION

Figure 13 shows a relationship between the index of density dependence and $\sqrt[3]{f}$. Where fecundity is high, the dome-shaped curve characteristic of cod, haddock, some flatfish and perhaps tuna is to be expected. This dome shape has been attributed to cannibalism (BEVERTON and HOLT 1957) and so has been considered a special form of density dependence. The evidence presented here does not deny this argument but suggests that density dependence is a function of fecundity and that therefore the gadoid dome is not necessarily a special case.

Of the two stock and recruitment curves in use for general purposes, that of BEVERTON and HOLT (1957), which expresses the dependence of recruitment on parent stock asymptotically in stock, does not describe a dome. 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 the treatment of the Pacific halibut data by FUKUDA (1962) and SOUTHWARD (1968). The same point is made in Figure 4, showing that the slopes for flatfish stocks (for North Sea plaice, two stocks of Pacific halibut, and the Petrale sole) are averaged at $b = 0$. So for flatfish, the idea that recruitment was independent of parent stock was reasonable over the range of fishable stock. It is an unfortunate accident that the two authors (THOMPSON and BELL 1934; GRAHAM 1935) who enunciated the dogma of recruitment independent of parent stock should have been working on flatfishes. However, in other stocks – cod, herring, tuna and salmon – recruitment depends markedly upon parent stock.

From the indices of density dependence, it was suggested that the stock and recruitment curves for salmon- and herring-like fishes were only lightly convex, that those for flatfish resembled asymptotic curves and that those for gadoids and tuna were rather marked domes. To test this hypothesis, the fate of two stocks of herring and two stocks of sardines were examined to see if the decline in catches could be accounted for by reduced recruitment under the pressure of high effort. It is possible that the decline in each could be accounted for in this way; in particular the collapse of the Californian sardine stock is described in some detail. The evidence is strong enough to throw considerable doubt on the disparate environmental hypotheses put forward to account for the four collapses. The point of evidence is that considerable

support is given for the hypothesis that the stock and recruitment curve of the herring-like fishes is near linear, being only slightly convex, as indeed is suggested by CUSHING (1968) for the Downs herring.

Perhaps the difference between herring-like and cod-like species is clarified to some extent. The herring-like fish are subject to violent fluctuations, not only due to high fishing effort, but also due to environmental effects. The cod-like fishes until recently did not appear to be so vulnerable to fishery or environmental changes. The reason for this may be that the index of density dependence of herring-like fish is low and that that for the cod-like fish is high.

Another way of putting it is that the more highly developed gadoids have greater capacity for stabilizing their populations than have the clupeids. It follows that the clupeid populations can suffer greater damage from un-regulated fishing than the gadoid ones.

Historically, the demersal fish species have been protected first, partly because they are more valuable, and so the fishing mortality was higher, and partly because the catches were less variable. This suggested that recruitment was independent of parent stock, but the real reason for the steady catches was the stabilizing tendency of recruitment with respect to parent stock. The greater the density dependence, the greater the stability.

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