

THE FLUCTUATION OF YEAR-CLASSES AND THE REGULATION OF FISHERIES

By

DAVID H. CUSHING

Fisheries Laboratory, Lowestoft

INTRODUCTION

Fishermen contrast the considerable regularity in the positions of capture of fish with the variation in quantities caught at those positions from year to year. The regularity is that of the migratory circuit from spawning ground to feeding ground and back again (HARDEN JONES 1968); for example, spawning cod have been caught in the Vestfjord for centuries (ROLLEFSEN 1956) and, since the thirties, fish of the same stock have been caught on the Svalbard Shelf west of Bear Island in early June. Similarly, the East Anglian herring have been caught in October and November off Lowestoft and Yarmouth for centuries as they migrated southward to spawn. But both stocks, cod and herring, vary from year to year due to differences in the recruiting year-classes. These differences can be grouped in three categories:

1. Annual changes due to density independent effects.
2. Density dependent changes following changes in stock.
3. Long term changes associated with changes in climate.

THE THREE CATEGORIES OF VARIANCE IN RECRUITMENT

Fig. 1 shows how the three categories of variation may be represented on a stock and recruitment curve. The curve of recruitment cuts the bisector at the point at which stock replaces itself in recruitment; in effect, it is the level of stock about which it stabilizes itself under natural conditions without fishing. Variance in recruitment about the stock and recruitment curve is represented on the ordinate (a) below the replace-

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

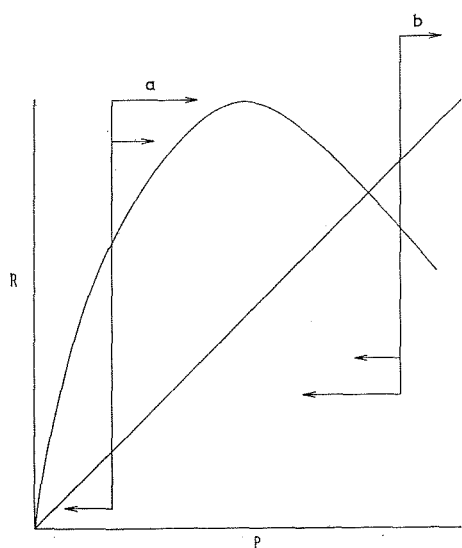


Fig. 1. The three sources of variance in recruitment shown on a stock and recruitment curve; see text for discussion.

ment point in stock and on the ordinate (b) above it in stock. Both represent the first category of fluctuation, variance in recruitment from year to year due to density independent causes. The second category is represented by the stock and recruitment curve itself; as stock increases, the recruitment per unit stock decreases and this is the effect of density dependence. The third category of variation occurs if recruitment falls below stock when stock is very low and then downward instability in stock is generated, which is represented in Fig. 1 by the variance of recruitment on the ordinate (a) falling below the bisector; an upward instability—at high stock—can be generated in an analogous way by the variance of recruitment on the ordinate (b) appearing above the bisector. If such instabilities occur randomly, subsequent recruitments must return the stock in the direction of stability. If, however, they occur in sequence, the stock collapses or expands, which are the conditions under which climatic change can affect the fluctuations.

PROCESSES DURING THE PERIOD OF LARVAL DRIFT

To survive, the larvae need food, not only when the yolk-sac is exhausted, but all through their lives during the period of larval drift. Although algae are often found in the guts of larvae at the first stages of active feeding, the baby fish subsist in the main on copepod nauplii (LEBOUR 1918a, b and 1919) and their analogues. In temperate seas, the production of nauplii is linked to the feeding of adult copepods in the early stages of the production cycle (MARSHALL and ORR 1952). So food

is available to fish larvae at a fairly early stage in the cycle and this accounts for the link shown below between the herring populations and the form of production cycle.

However, the production cycle is variable in timing, in amplitude and in spread (COLEBROOK 1965) and if fish in temperate seas spawn at relatively fixed seasons (CUSHING 1969a) then the food available to the larvae must vary as the cycle varies. The variability of the production cycle tends to increase with depth of water as it depends much upon the vagaries of the depth of mixing, largely governed by wind strength and direction. This accounts for the greater variability in recruitment observed in stocks living over deep water in temperate seas. In the relation of spawning and the production cycle, time is critical to the survival of the larval fish, and the observed variance implies that the major processes determining recruitment may lie between spawning and nursery ground.

The separation of the three categories of variance in recruitment is perhaps a little artificial as all three may be but facets of a single set of processes. In temperate seas, the variance of recruitment to herring stocks tends to increase with depth (CUSHING 1967) and it has been shown that the three groups of autumn-, winter- and spring spawning herring stocks are associated with three forms of production cycle in the north-east Atlantic (CUSHING 1967). The increased variance in recruitment with depth can be associated with increased instability in the timing of the production cycle providing food for the larval fish. The two results lead to the conclusion that the processes determining the major proportion of larval mortality must lie between spawning ground and nursery ground because the production cycles on the nursery ground must differ from those in the open sea, if only because of differences in depth. The argument depends on the biology of the herring; it can be extended to other species when it is recalled that fish of many species spawn at about the same time. For example, in the Southern Bight of the North Sea, when herring spawn there so do cod, whiting, dabs, sandeels and plaice.

Of the three sources of loss to which the larvae are subject, predation, diffusion and advection, it is likely that predation is by far the most important. The loss rate of plaice larvae in the Southern Bight of the North Sea is 80 per cent per month as an apparent mortality (HARDING, in preparation), which is considerably more than might be expected from the physical causes. It is assumed that a larva, which has moved out of the larval drift and fails to reach the usual nursery ground, is lost to the stock, i.e. it fails to return to the native spawning ground as an adult. The real question is how can predation in the larval drift effect the three categories of fluctuations which are illustrated in Fig. 1.

The fish larvae feed and as they feed they grow. As they grow they

swim more quickly and reduce the chance of predation. If they fail to feed adequately they swim more slowly and the chance of predation is increased. So with constant predation, variations in mortality rate can be generated merely by differences in the availability of food. Then, variations in stock change the food availability and so the mortality rate generated by the predators is also density dependent. The assumption of constant predation may appear to be unreal, especially if a particular predator is in view. The fish moves through three trophic levels as it grows and within any one level it is likely to be subject to a succession of predators, each larger than the last, but each less numerous. The differences between densities of each predator may tend to average out and then the low variability of recruitment as proportion of total mortality between egg and adult is not surprising. It is possible, in an evolutionary sense, that the fecundity of a fish stock is a function of the mortality generated by the network of predators along the larval drift and on the nursery ground.

VARIANCE OF RECRUITMENT ABOUT THE STOCK AND RECRUITMENT CURVE

Although it is unlikely that year-classes are completely determined during the period of larval drift, because by then only a small fraction of life to recruitment has elapsed, much of the variance of recruitment might be attributed to variance in food availability, itself due to variation in the timing of the production cycle. Many attempts have been made to correlate recruitment with environmental factors, but usually they have failed. An important exception is the correlation of catches of cod at Lofoten with the number of rings on pine trees in northern Norway for a long time period (ORTTESTAD 1942). The reason for success is that a well-known result of climatic change was correlated with the catches. A particular cause was not specified, like the strength of a wind from a given direction over a very broad area, but a general result was indicated. The variation in the production cycle is governed by the rate of change of the algal reproductive rate, which in its turn is controlled by the rate of change of the ratio D_c/D_m , where D_c is the compensation depth and D_m is the depth of mixing (CUSHING 1962). Very roughly, this ratio is affected by changes in sunlight and by changes in wind strength and direction. It follows that these climatic parameters need be sampled only on the track of the larval drift from spawning ground to nursery ground.

Correlations between recruitment and winds were often successful for a period of years, after which they failed catastrophically. Any examination of trends in wind strength and direction, at one position at the same

season for a long time period, shows that there are shifts in strength and direction of wind all the time (DIETRICH 1954). Hence to take wind strength variations from a single direction is to ignore perhaps the most important source of variation. In temperate seas, the track of larval drift is usually not far from a coastline, where a small shift in direction can have considerable effects.

A considerable source of variation can lie in the stock and recruitment curve itself. That for the Arctic cod is dome-shaped as has been shown by GARROD (1966). At middle levels of stock, average recruitment is considerably higher than at low levels and at high levels. In contrast, the curve for the East Anglian herring is not far from a linear one, with only a slight dome before it passes through the replacement point. Differences in recruitment at different levels of stock are considerable. So if we need to know the true relationship between recruitment and environmental factors, recruitment should be measured as deviation from the stock and recruitment curve. If it is believed that such a curve should be fitted from the data on recruitment and data on stock only, then the argument is circular. The circle can be broken if it is assumed that there is a curve characteristic of any fish species and that differences, for example between that for the Arctic cod and that for the East Anglian herring, are real and not merely statistical fantasies.

AN INDEX OF DENSITY DEPENDENCE AND ITS CONSEQUENCES

CUSHING (1969b) has examined the possible stock and recruitment curves for thirty-one stocks. No differences between constants were found using the RICKER equation (1954, 1958) or the BEVERTON and HOLT (1957) equation. An index of density dependence, b , was calculated from the equation $R = KP^b$ (where R is recruitment, P is stock, and K is a constant), used at mid to high stock levels. It was found that $b = a \bar{f}^{1/3}$, where \bar{f} is the average fecundity of the stock, over a range in b from $b = 0.8$ to $b = -1.95$. In effect, this means that there is a series of curves ranging from the near linear curve of the East Anglian herring to the pronounced dome of the Arctic cod, each of which is specified by the fecundity of the fish. Fecundity is a function of weight, and density dependent growth decreases with size in fish (RAITT 1939, ILES 1967, SOUTHWARD 1967) and so it is effectively independent of the index, i.e. density dependence must be achieved in density dependent mortality. Thus, we return to the point that in an evolutionary sense, fecundity is a function of the network of predators along the track of the larval drift. Because there is a fixed

quantity of eggs available, fecundity may be regarded as a homeostatic mechanism which creates stability in a variable environment.

Larval density is a function of the density of spawning females and of fecundity. With fish like the herring which do not grow much during their mature lives, fecundity must play less part in determining larval density than the density of spawning females. With fish like the cod which grow a great deal as mature animals, fecundity may not stabilize the population: a stock at the replacement point which suffers a recruitment failure must suffer an increase in average weight and fecundity, which by itself must generate instability. At the same time, after a recruitment failure, the density of spawning females must decline which will generate greater recruitment per unit stock which is a stabilizing change. So it is likely that stock differences affect larval density merely through differences in the densities of spawning females. Then fecundity controls differences in the degree of density dependence between stocks as might be expected from its supposed homeostatic character of evolutionary origin.

A DIFFERENCE BETWEEN HERRING-LIKE FISHES AND COD-LIKE FISHES

On Fig. 1 variance in recruitment due to differences in stock density is expressed in the stock and recruitment curve itself. In larval density, differences in stock affect the availability of food, more being available to the larvae at low stock and less at high; and from the preceding argument such differences within a stock are generated by differences in the densities of the spawning females rather than fecundity. The question of how much of the variance of recruitment is due to density dependent causes and how much to density independent causes cannot readily be answered in general terms. However, D. J. GARROD has analysed the variances in the recruitment of spawners to the Arctic cod stock and has separated those due to environmental changes and those due to stock changes. Because the stock and recruitment curve for the Arctic cod is markedly dome-shaped, it is likely that for other fish stocks the ratio of density independent variance to density dependent variance may be greater. Indeed, it is possible that the ratio is correlated with the index of density dependence, or with fecundity. As further consequence, it might be concluded that the herring-like and salmon-like fishes were more vulnerable to environmental change than the cod-like fishes. Another way of saying the same thing is that the cod-like fishes have a greater capacity for stabilizing their populations than have the herring-like fishes. The stock of the Arctic cod has varied in quantity to some extent during the long centuries of its recorded existence (ROLLEFSEN 1956). In contrast, the Norwegian herring

fishery, which is worked in a somewhat less adverse environment than the Arctic cod, has suffered a series of temporary extinctions over about the same historical period (DEVOLD 1963).

The dramatic changes in pelagic fish stocks are exemplified well by the Norwegian herring periods which have been correlated with ice cover periods north of Iceland by BEVERTON and LEE (1965). There are periods in climatic change lasting about fifty to a hundred years of somewhat irregular occurrence. A recent change in climate has been expressed as a warming of the north-east Atlantic since the late twenties which may have ended in the early sixties of the present century (BJERKNES 1964). A decline in the average strength of the westerlies in the North Atlantic left more residual heat in the water. Towards the European coasts the decline of the westerlies allowed southerly winds to predominate (DICKSON, in preparation). Over a long time period the wind direction slowly shifts and the long-term consequence may be that the production cycle shifts away in season from the time of spawning of a fish stock. Equally, a production cycle may shift towards the time of spawning of a fish stock. Fig. 1 shows how a marginal instability in sequence (shown where the variance of recruitment falls below stock at low stock and where it rises above stock at high stock) can lead to the marked reduction or the full expansion of a stock. Such a capacity to respond to environmental change by changes in numbers is the means by which the herring-like fishes survive under adverse conditions. The lack of homeostasis is a primitive character and perhaps the evolutionary step from the primitive herring to the developed cod was the use of growth and hence fecundity to achieve a more powerful mechanism by which the population could be stabilized.

In Fig. 1 are shown the three sources of variation which might affect recruitment, the year to year environmental changes, the larger scale climatic changes and the differences due to stock density. It is possible that all three are mediated by the same processes in food availability during the period of larval drift. A perennial problem facing fisheries biologists is how to distinguish the effects of environmental change on recruitment from those induced by the fishery. The first distinction to be made is between the year to year density independent effects and those associated with large-scale climatic change. The year to year effects, although contributing perhaps a high variance, are considered to be randomly distributed about the stock and recruitment curve and therefore are of no further interest. If the stock and recruitment curve for a given fish species is established independently of the values of recruitment and parent stock then we may consider the curve as given and recruitment as distributed about that curve.

An assumption here is that within an environmental period, recruitment fluctuates randomly and that when the environment changes, recruitment changes markedly and sharply. This concept follows from the supposed homeostatic nature of fecundity, i.e. that the fixed fecundity insulates the stock from minor environmental changes, but allows it to adapt in a favourable or unfavourable manner to major changes.

CONSEQUENCES IN THE REGULATION OF FISHERIES

The more important problem is whether a large scale climatic change has effects on recruitment which can be distinguished from those following a reduction of stock due to fishing. Consider a virgin stock oscillating in time about its replacement point. A failure of recruitment, complete as that in the Plymouth herring (CUSHING 1961), would yield a series of points along the abscissa, decreasing in stock as stock fell in consequence. In general, the recruitment/unit stock should decline more quickly with stock than that expected from the stock and recruitment curve. In a stock with a dome-shaped stock and recruitment curve the distinction could perhaps still be made as long as the stock were not too heavily exploited. For herring-like fishes, in which the curve of stock and recruitment is only lightly convex, there would be a real problem of distinction. One would depend upon the difference between the average falling recruitment and that expected about the stock and recruitment curve. If it becomes possible to specify the variance to a stock and recruitment curve, a failing recruitment due to abnormal environmental causes might be distinguishable by ordinary statistical procedures. There is, however, a strong possibility that failure would take place quickly and so there would not be enough information on which to base a judgement. There is, however, a more practical way of achieving the same end. On any stock and recruitment curve there is a point in stock at which recruitment is maximal—RICKER's (1958) point of maximum surplus reproduction at stock P_s with a corresponding exploitation rate E_s . At stock levels below this point, if fishing effort is constant, yield will be reduced and if fishing effort increases at such levels, there is considerable danger that the fishery will be extinguished, if not the stock. There is a limiting exploitation rate, E_1 ($= 1 - e^{-a}$ where $a = P_r/P_m$, P_r is the replacement level of stock and P_m is the level of stock at which maximum recruitment occurs) beyond which the stock is extinguished. If the stock in numbers collapses when the exploitation rate is set at E_s , it must do so through a failure of recruitment due to environmental change. So any stock can be exploited down to the stock level, P_s , at which maximum recruitment is obtainable. Then,

if environmental collapse occurs, the maximum yield has been obtained until the point of collapse.

From a regulatory point of view this means that environmental changes in recruitment can be to some extent ignored. The value P_s can be established from the character of the stock and recruitment curve, i.e. to some extent from the fecundity of the fish. The effect of growth can be taken up in a self-regulatory yield curve of the form proposed but not fully developed by BEVERTON and HOLT (1957). The maximum of such yield curves may tend to lie at stock levels of $P < P_s$, because the exploitation rate E_s may tend to be too high to exploit the benefits of growth to the full. The effect of variance in recruitment about the curve is an important one. In the extreme case of a one-year-class stock under heavy fishing pressure, the variance of stock is essentially the variance of recruitment and so collapse of the fishery could occur near the level of P_s ; obviously the variance of the stock is that of the recruitment divided by the number of year-classes.

It might be suggested that if the stock were fished to the maximum sustainable yield on a yield-per-recruit basis, the stock is not vulnerable to recruitment failure through heavy fishing. Fig. 2 (after GULLAND 1967) shows a yield per recruit curve and a yield curve calculated in terms of a stock and recruitment curve. The obvious point is made that the new maximum is at a lower level of stock than that on the yield per recruit curve. But, where yield decreases from the maximum at increasing levels of fishing mortality, and $P < P_s$, the variance of recruitment might generate sufficient variability in stock to endanger it. The danger is greater for the herring-like fishes with a slightly convex stock and recruitment curve than for the cod-like fishes with a curve which is markedly dome-shaped. Indeed the limiting rate of exploitation for herring may

occur at levels of fishing mortality hitherto considered as comparatively low.

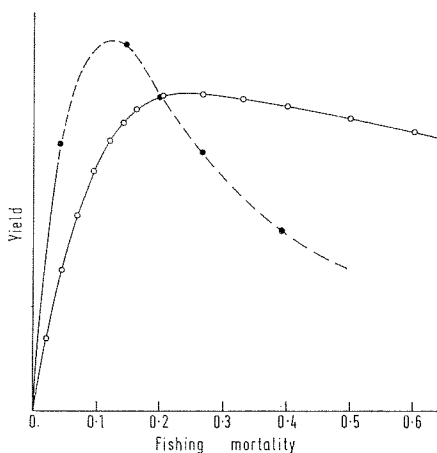


Fig. 2. A yield-per-recruit curve for plaice (full line) and with a stock and recruitment curve (broken line) incorporated (After GULLAND 1967).

The failure of the East Anglian herring stock was one in which $E < E_s$ for a long period during the fifties (CUSHING and BRIDGER 1966) and so the ascription of failure is to fishing. An interesting point is that the fishery took a long time, about a decade, to finally vanish. This was because the variance in recruitment (and hence stock, because during its last decade, it was a one-year-class fishery) was rather low, and because the stock and recruitment curve is only slightly convex. The Arctic cod stock is in danger at the present time, because recruitment has been reduced under pressure of fishing. If we were given the chance to solve the problems of these ancient fisheries again, we should recommend that the stocks be exploited at the best rate of exploitation for the recruitment (either at E_s in numbers, or at the maximum of a self-regulatory yield curve). Then if collapse occurred subsequently through an environmental effect on recruitment, the best yield to that point had been taken. Thus, from the point of view of regulation the environmental factors need not concern us unduly, which is not to say that they should not be predicted.

SUMMARY

There are three sources of variation of recruitment; first that due to random fluctuations alone, secondly that, due to variations in stock and thirdly variations which are extreme at low and high levels of stock and if these occur sequentially can cause catastrophic declines or sharp increases in stock density. From a study of stock/recruitment curves of a number of fish species, it appears that the curve for herring-like fishes differs markedly from those, for example, of cod-like fishes or in more general terms that the shape of the stock/recruitment curve is really a function of its fecundity. That for the herring-like fishes is a near linear curve whereas that for the cod-like fishes is markedly dome-shaped. It follows that the herring-like fishes are very vulnerable to long-term climatic changes and that the cod-like fishes are able to stabilize their populations through long-term climatic changes merely because the increased recruitment when stock is slightly reduced is very much greater than that for the herring-like fishes. If stocks of fish are to be managed then the stock/recruitment relationship has to be taken into account; a form of self regenerating yield curve combining stock/recruitment and yield-per-recruit was in fact put forward by BEVERTON and HOLT. A development of such a curve is needed and one of the uses of such a curve would be that management need not take too much notice of environmental change, because if it occurred the stock would have been exploited at its best rate before any environmental collapse took place.

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