Regulation in Fish Populations: Myth or Mirage? [and Discussion]

J. G. Shepherd, D. H. Cushing and R. J. H. Beverton

Phil. Trans. R. Soc. Lond. B 1990 **330**, 151-164
doi: 10.1098/rstb.1990.0189

Regulation in fish populations: myth or mirage?

J. G. SHEPHERD[1] AND D. H. CUSHING[2]

[1] *Ministry of Agriculture, Fisheries & Food, Directorate of Fisheries Research, Pakefield Road, Lowestoft, Suffolk, U.K.*
[2] *198 Yarmouth Road, Lowestoft, Suffolk, U.K.*

SUMMARY

There is abundant evidence of long-term changes in the abundance of fish populations, but the causes are not known. It is almost certain that climatic changes are responsible in part, but the role of population regulatory mechanisms is unclear. The evidence is conflicting. The ability of fish populations to sustain levels of fishing mortality several times the level of natural mortality suggests strong regulatory mechanisms. The persistence of stocks for centuries, with few extinctions or explosions, also implies some regulation, but not necessarily strong regulation. The high levels of fluctuation in recruitment suggest weak regulation except in the earliest stages of the life history. Under weak regulation the time taken for effective explosions or extinctions is long, maybe a century for 1000-fold changes in abundance. There are few historical records that imply greater stability (persistence) of stocks than this.

Analysis of stock-recruitment diagrams (the fisheries biologists' version of k-factor analysis) rarely yields clear evidence for or against regulation, because of high levels of fluctuation, which cannot therefore be because of single-species deterministic chaos (though multispecies chaos remains a possibility). Even the exceptions to this rule (North Sea herring, Georges Bank haddock) are not wholly convincing. Conversely, it is credible that these and other long-term declines of recruitment (Northeast Arctic cod, North Sea haddock) could be due to regulation, since stock sizes also fell. Regrettably we cannot distinguish the chicken and the egg.

It is indeed quite plausible that the only regulatory process operating for fish populations is a stochastic one: increased (and non-normal) variability at low stock sizes. This would give strong regulation in the mean, because of the increasing excess of the mean over the median at low stock sizes, but only because of increasingly large, but increasingly infrequent, outstanding year-classes. This sounds such an accurate description of heavily fished stocks that further exploration of this mechanism seems warranted.

1. INTRODUCTION

Recruitment to marine fish stocks often varies by one or two orders of magnitude, for reasons that are not well understood. This causes considerable difficulty when one attempts to study regulatory processes, since the variations obscure any relation that may be present. The variations seem to occur on a very wide range of timescales, with major fluctuations from year to year, and over decades and centuries.

The fishery biologist's standard approach to the study of regulation is the examination of stock-recruitment diagrams. For most fish species the breeding population consists of several age groups, and the most useful measure of stock is usually the spawning stock biomass. Total egg production is an even better measure, but the necessary data on fecundity are rarely available on a year-to-year basis. The major interest of fish populations when considering regulation is that many have been exploited very heavily. Total mortality rates exceeding five times the natural mortality rate are not uncommon, and may be sustained for decades. This led Shepherd & Cushing (1980) to believe that fish stocks must be strongly regulated. It also means that the populations have been 'exercised' over a wide range of spawning stock sizes, and the data for such stocks are potentially of great interest.

These aspects are discussed in more detail below, and a brief account is given of the results of attempts to find and quantify the regulatory process. This provides the motivation for the 'myth' in the title of this paper, since it is fair to say that most fish biologists believe in regulation even though they have been able to find remarkably little direct evidence for it. The latter part of the paper addresses the 'mirage' aspect, through a discussion of the possibility that deterministic density-dependent processes may be very weak, while stochastic processes may provide a rather effective mechanism for regulation of population size in practice. The mirage metaphor seems appropriate since the process becomes less clear as one tries to study it more closely. If this idea has any validity, it may resolve the classic conflict between the pro-regulation school of Nicholson (1933), and the anti-regulation school of Andrewartha & Birch (1954), since they would both be right if the variability is in fact an essential part of the regulatory mechanism.

Phil. Trans. R. Soc. Lond. B (1990), **330**, 151–164
Printed in Great Britain

2. THE EFFECT OF FISHING, AND EVIDENCE FOR DETERMINISTIC REGULATION

In the absence of regulatory processes, the expected relation between recruitment and parent stock size would be strict proportionality, a straight line through the origin on a stock-recruitment plot. This would be the result of constant fecundity and mortality rates, and this should in principle be the most appropriate null hypothesis, to be adopted in the absence of evidence to contradict it.

The consequence of such an assumption is, however, that the stock would tend exponentially to either zero or infinite size, with a characteristic timescale of a few years, depending on the level of total mortality on the stock (including fishing mortality), unless this happened to be just sufficient to keep the stock in a state of neutral equilibrium. Simple graphical simulations (see, for example, Beverton & Holt (1957) figure 6.1) can easily be used to show such behaviour, and the results are quite unlike anything normally observed in practice. It is for this reason that almost all fishery biologists believe that some sort of regulatory processes are at work, even though they cannot be described in any detail.

If the relation between recruitment and parent stock is nonlinear, then the possibility of regulation towards equilibrium states exists. These may, however, be either stable or unstable points, and are unlikely to be clearly observable in the presence of large variability. For single-cohort spawning stocks, these occur wherever the stock-recruit curve intersects a line of unit slope (through the origin) on a plot of recruits against numbers. The generalization of this to multiple-age spawning populations is straightforward, but seems not to be very well-known outside the world of fisheries. One simply calculates the steady-state level of spawning stock biomass per recruit for any desired regime of natural and fishing mortality, growth and maturity at age, and plots the line of the corresponding slope through the origin on the diagram of recruitment against spawning stock biomass. The intersections of these survival lines with the recruitment line again define potential equilibrium states. In fact the ratio of recruitment (R) to spawning stock biomass (SSB) must equal the reciprocal of the spawning biomass per recruit (BPR) so that:

$$\mathrm{R}/\mathrm{SSB} = 1/\mathrm{BPR}. \qquad (1)$$

Now, biomass-per-recruit is a measure of survival and decreases as total mortality increases because of fishing (see figure 1). Thus the slope of the survival lines increases (because we conventionally plot SSB on the x-axis) as fishing mortality (F) increases. The equilibrium stock size therefore decreases as F increases, as shown in figure 2. It is easy to see that the stock will collapse when fishing mortality is so high that 1/BPR exceeds the slope of the recruitment curve at the origin. This slope at the origin is therefore a quantity of great concern to fishery biologists. Regrettably it is not guaranteed to be positive definite. It could be zero, or effectively infinite, and techniques for determining this slope for real data sets are in their infancy.

In practice there is a tendency among fishery biologists to take constant recruitment as the null hypothesis. This is dangerous, because a stock capable of generating constant recruitment at any stock level cannot be collapsed, however great a fishing mortality is applied. It is also remarkable, because this assumption is often maintained with great tenacity, and without any appreciation that it corresponds to the

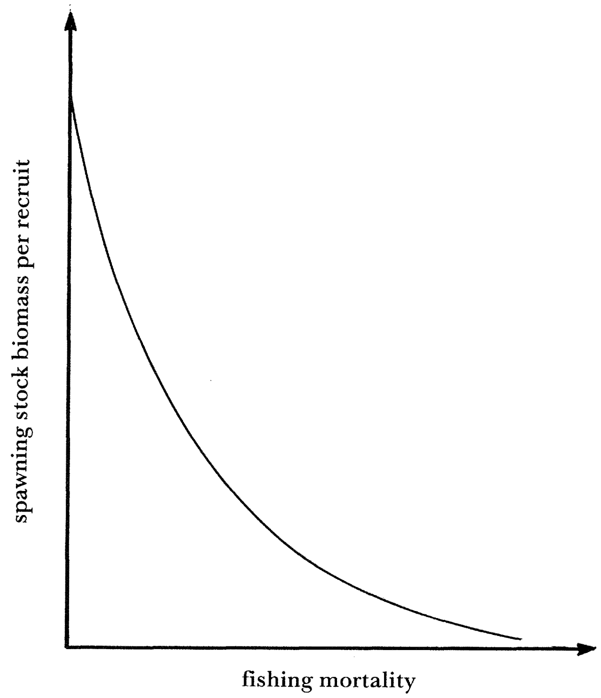


Figure 1. Survival in exploited stocks, as measured by spawning stock biomass per recruit.

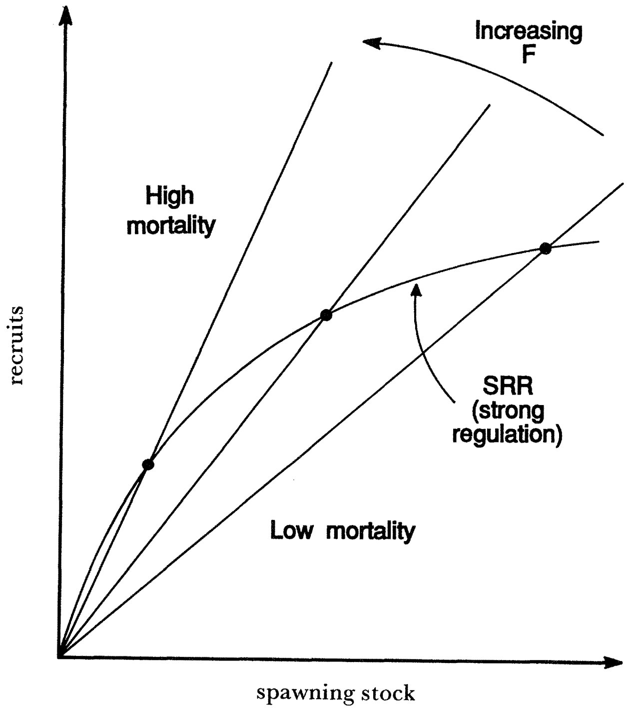


Figure 2. Stabilization of a regulated stock under various levels of exploitation.

operation of extremely strong regulatory processes. Such a powerful and persistent 'myth' is unlikely to have arisen by pure change, and it is presumably founded on the observation mentioned above, that fish populations do not in practice explode or collapse exponentially on decadal timescales, even where they have been subjected to large modulations of total mortality rates through fishing.

The evidence from detailed investigations of stock and recruitment data for marine fish is however distinctly equivocal. It is hard to distinguish on statistical grounds between constant recruitment (corresponding to strong regulation) and a constant R/SSB ratio (corresponding to no regulation). This is because of the high level of variability in the recruitment time series, and partly to the shortness of the time series available (rarely more than 30 years). Nevertheless, adding appropriate levels of noise to simple simulations of unregulated stocks, as described below, shows that simple variability does not alter the conclusion that an unregulated stock should collapse or explode in a quite characteristic manner, on a decadal timescale, and be very dependent on the level of fishing mortality applied.

Furthermore, it is clear that an unregulated stock must, to have survived, have evolved reproductive processes just capable of generating an R/SSB ratio which is sufficient to balance the effects of natural mortality. It is easily seen, by sketching or simulation, that such a stock would collapse rapidly under any significant fishing mortality (such as, for example, $F = M$, a very modest rate in the real world), as was pointed out many years ago by Beverton & Holt (1957).

It is therefore reasonable to conclude that there is some basis for the belief that fish populations are regulated in some way. In fact, the evidence is twofold: first, that they do not explode when subjected only to low (natural) levels of mortality: secondly, that they do not collapse at all quickly, when subjected to high levels of mortality. We regard these pieces of evidence as separate, as their implications are in fact rather different. It has been recognized for many years (see, for example, Reddingius (1971)) that only rather weak regulation is required to prevent a stock exploding at low mortality rates. This is easily verified, again, by a little sketching or simulation. In this context 'weak regulation' means a modest modulation of the R/SSB ratio. Such a weak regulation could be described for example by a Cushing-type non-asymptotic power-law relation with any power marginally less than one (Cushing 1973), or by any straight-line relation with a small positive intercept (though it should be remarked that both these relationships imply very strong regulation, large modulation of the R/SSB ratio, at low stock levels). There is no necessity to postulate a strongly regulatory process, such as a finite asymptotic value of recruitment at high stock level, to prevent unrealistic behaviour at low mortality. In passing, we note that there is *a fortiori* no need whatever to postulate an overcompensatory relation, where recruitment ultimately reduces as stock size increases, such as that inherent in the Ricker formulation (Ricker 1954). This is not to say that overcompensation may not occur, only that it is a much stronger assumption than is required, and should not be regarded as typical.

Conversely, at the low stock sizes that may be (and are) generated under heavy fishing, strong regulation is required. As a first approximation, spawning biomass per recruit (BPR) is approximately inversely proportional to total mortality (see figure 1). Fishing mortality rates up to and beyond five times the natural mortality rate are by no means uncommon for heavily fished stocks (e.g. for the North Sea gadoids in recent years). If a stock is to survive for more than a few years under such a mortality regime, the R/SSB ratio must be capable of increasing more than fivefold so as to compensate.

Thus the qualitative evidence is that some possibly rather weak regulatory process is required to prevent stocks increasing indefinitely when fishing mortality is small ($F < M$, say), but that very strong regulation is needed to prevent stocks collapsing rapidly under heavy fishing ($F > 2M$, say). There is no particular reason to suppose that the same biological mechanisms operate in both cases (though there is no reason why they should not either). It may be, for example, that processes such as density-dependent growth or fecundity, which can hardly be envisaged as capable of generating the high modulation of R/SSB required at low stock size, could be entirely adequate to provide the necessary modest modulation at high stock size. The strength of regulation is of course important, because it determines the maximum fishing mortality which a stock can sustain for very long, a crucial piece of information in developing rational stock management.

Table 1 summarizes the strength of regulation

Table 1. *Strength of regulation implied by various stock-recruitment relations at low and high stock size*

mortality... stock level...	high low	low high
constant R/SSB	none	none
constant R	very strong	strong
Cushing-type	very strong	moderate/weak
linear (positive intercept)	very strong	weak
Beverton–Holt	moderate[a]	strong
Shepherd	moderate[a]	variable
Ricker	moderate[a]	very strong

[a] Depends on parameter values, but R/SSB has a finite maximum at zero stock size.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

implied by various well-known stock-recruitment relations, at both low and high stock sizes, just to illuminate the situation. The qualitative evidence suggests that one needs strong regulation at low stock size, but only weak regulation at high stock size. Apart from the constant R/SSB (no regulation) case, which is clearly inadequate, it is evident that all of these provide more than enough regulation at both high and low stock size. Nothing quite so powerful is required to explain the observed behaviour of real fish stocks. There is no problem in postulating mechanisms capable of producing weak regulation at high stock size, i.e. capable of modulating R/SSB by a factor of, say, two either way around the value appropriate to the natural (unfished) population. The problem is rather to identify the processes capable of generating very high R/SSB levels at low stock sizes. This remains an unsolved problem for most stocks. The possibility that this is because there is no deterministic regulatory mechanism at low stock size, only a stochastic one, is discussed below.

At first sight there seems to be a paradox here: qualitative evidence suggesting strong regulation at low stock size, but great difficulty in detecting any relation from the detailed data. However, we observe that a powerful regulatory mechanism at low stock size (i.e. one capable of generating high R/SSB ratios) may look quite unremarkable on a stock-recruitment diagram, and could be extremely difficult to detect by statistical analysis. For example, a straight-line relation with any small positive intercept would suffice; this relation generates R/SSB ratios which tend to infinity as stock size reduces. The same is true of a Cushing-type power law relationship with a slope even fractionally less than one. Such relations would be adequate to explain the qualitative observations, but would be extremely difficult to distinguish from a straight line through the origin, either visually or statistically. This could perhaps explain why it has proven so difficult to determine stock-recruitment relations from real data. The paradox may therefore be more apparent than real. Nevertheless, one should beware of adopting such relations for practical use, because they imply infinitely strong regulation at zero stock size, and exclude the possibility of stock collapse even under massive fishing mortality. This is a much more extreme assumption than is warranted by the evidence, and it would be imprudent to make it.

3. THE DEPENDENCE OF RECRUITMENT ON PARENT STOCK

In the light of the above discussion, we now consider the data for a number of stocks for which long time series of data (more than 30 years) are available. In each case we first show the time series of recruitment, and then the plot of these data against spawning stock biomass. To these data we have simply fitted the functional form proposed by Shepherd (1982), that is,

$$R = aB/\{1+(B/K)^{\beta}\}, \qquad (2)$$

where R is recruitment in numbers; B is spawning stock biomass in tonnes; a, the slope at the origin, is maximal survival (recruits per unit biomass); K is the threshold biomass (at which recruitment is reduced to half aB), and above which density dependent effects predominate; β expresses the degree of compensation. These fitted lines are simply to guide the eye.

Five stocks were examined; North Sea sole, North Sea plaice, Iceland cod, Northeast Arctic cod and North Sea herring. They have been chosen because each is supported by about 30 or 40 years of observations; in all cases, recruitment and stock were estimated by virtual population analysis (VPA). The data have been taken from the reports of relevant International Council for the Exploration of the Sea (ICES) working groups, augmented by recent data provided by T. Jakobsen, J. Jakobsson, and staff at the Fisheries Laboratory, Lowestoft. The equation was fitted with the Marquardt algorithm by using a program called Fishparm (C. Walters, personal communication).

The five stocks are described in two figures for each: the time series of recruitment, with mean and standard deviation, both logarithmic, and the stock recruitment relation (see figures 3–7). In the North Sea sole there are three large year-classes, 1958, 1963 and 1987. There was a sharp decline in stock as the 1963 year-class was finished out. During a cold winter (as in 1963), with very cold easterly winds across the southern North sea, sole move into deeper water where the fishermen go to catch them, for example, in the Silver Pit (so named from the money made in a cold winter

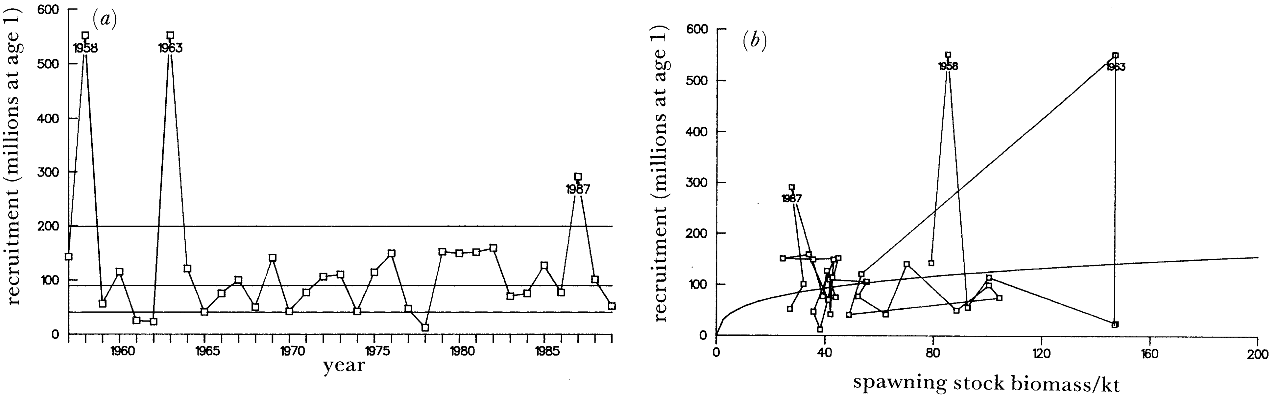


Figure 3. North Sea sole. (*a*) Time series of recruitment. (*b*) Stock-recruitment diagram.

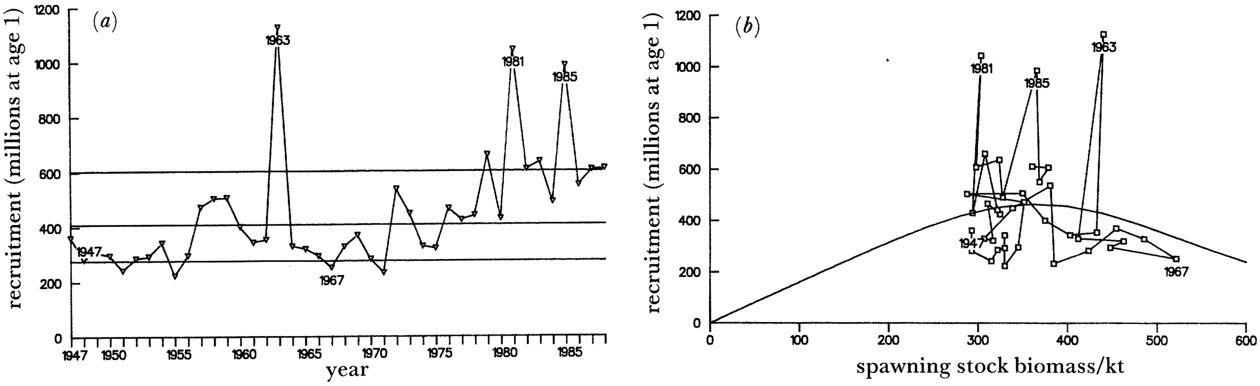


Figure 4. North Sea plaice. (*a*) Time series of recruitment. (*b*) Stock recruitment diagram.

in 1838). In contrast, after the 1958 year-class, stock built up steadily to 1962. The time series shows quite low variability except for the three high year-classes, but in 1979–1982 there were four quite good year-classes in succession.

In the plaice of the southern North Sea, the coefficient of compensation (β) appears to be high because of the low recruitment from 1964 to 1971 when stock size was quite high. There are three high year-classes, 1963, 1981 and 1985, the first and last of which were associated with cold winters. The cold winters are believed to have produced high recruitment because the shrimps (which generate density dependent mortality), move away into deeper water (van der Veer 1986), but there was no high recruitment from the cold winter of 1947. The time series of recruitment shows a slight decline to 1971 and a steady rise subsequently. The reason for this increase is unknown, but the increment is responsible for the anomalously high coefficient of compensation.

In the Iceland cod we see the quick exploitation of year-classes as they appear (1964, 1973 and 1983) because the fish are first caught at three years of age, and do not spawn until seven or eight, and so suffer a long period of exploitation as juveniles. The time series shows the high year-classes 1964, 1976 and 1986. During earlier years the spawning stock at Iceland received immigrant spawners from West Greenland. The West Greenland stock collapsed in the late sixties, and the last immigrations occurred in 1961 and 1963. An interesting point is that there was no reduction in recruitment during the passage of the Great Salinity Anomaly of the 1970s described by Dickson *et al.* (1988) through north Icelandic waters in 1965–71, presumably because the cod spawn off southern Iceland.

In the Northeast Arctic cod, there was an increase in recruitment, even though the stock declined after the second world war, culminating in a strong year-class in 1950. But there were also three strong year-classes at low stock in 1963, 1964 and 1970. There seems to be a fairly systematic seven-year quasi-periodicity in these data, but the very low year-classes of 1977–80 may also be associated with the passage of the Great Salinity Anomaly (Cushing 1988). It is worrying that the last peak in recruitment in 1983 was not very high, and the data are quite suggestive of a reduction of recruitment at low stock size, especially if the seven-year cycle is filtered out.

The North Sea herring shows a real collapse in the early 1970s but also strong year-classes in 1956, 1960 and 1985. The time series shows the collapse and recovery; catches were banned between 1977 and 1982 when the very poor year classes, 1974 to 1977, appeared. The ban on catches was very timely and assisted recovery. Here again the reduction of recruitment at low stock size looks quite convincing.

These data show the difficulty of determining the relation between recruitment and parent stock from historic data. They are atypical only in that they are some of the longest time series available and include two of the most convincing examples of possible reduction of recruitment at low stock (for the North Sea herring and the Northeast Arctic cod).

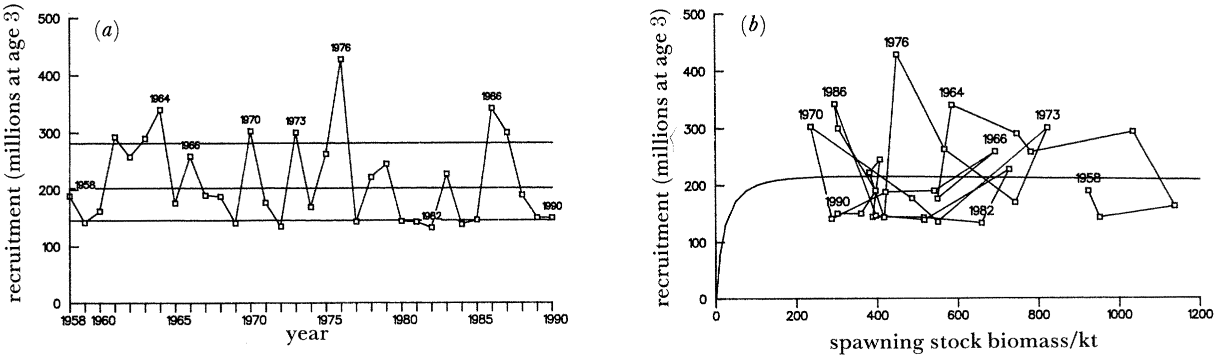


Figure 5. Iceland cod. (*a*) Time series of recruitment. (*b*) Stock recruitment diagram.

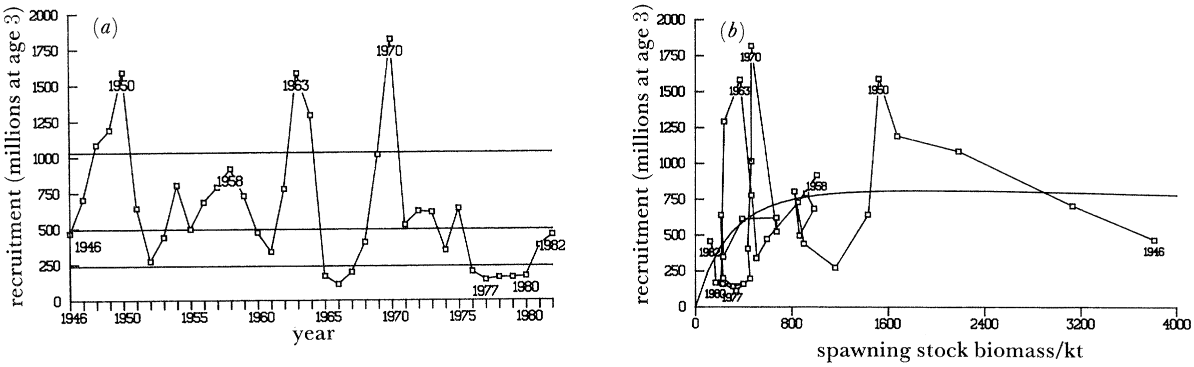


Figure 6. North east Arctic cod. (*a*) Time series of recruitment. (*b*) Stock recruitment diagram.

The relations we have fitted are only illustrative, and not to be taken seriously as attempts to determine the relation. We have ignored serious technical difficulties associated with autocorrelation in the recruitment time series (for which the reasons are incidentally far from clear), and the lagged cross-correlation due to the known causal relation between recruitment and the resultant stock size. It is still possible that purely empirical attempts to estimate such relations may yet be successful, if appropriate statistical techniques are used. It is more likely that it will be possible to obtain reasonable estimates of the slope at the origin by using suitable weighted averages that emphasize values obtained at low stock size (J. Pope, personal communication) and this may be sufficient for pragmatic fishery management. Nevertheless, attempts to analyse such data in similar ways have been conducted for several decades, without much success. The stock-recruitment relation remains elusive.

Is this because we are dealing with a chaotic system? On the face of it, this seems unlikely. First, to enter a chaotic regime, it is necessary that the recruitment curve should cut the survival line while descending rather steeply (Beverton & Holt 1957). This can only occur with a strongly domed over-compensatory relation, and there is no evidence that these are common. Secondly, and more conclusively, the stock-recruitment relation ought to be the underlying deterministic map for the system. If we were just dealing with deterministic chaos, the stock-recruitment plot would be clean, even though the time-series would be chaotic (Holden 1986). Clearly, this is not so. However, before dismissing chaotic dynamics entirely, we should recall that most fish stocks are components of multispecies systems, so that a single-species stock-recruitment diagram is just a projection of a more complicated system. For the moment the possibility of multispecies chaos must therefore be left open. However, attempts by the ICES Multispecies Working Group (Anon 1986) to clean up the stock-recruitment picture by allowing for predation by other species have not so far been successful, and most investigators remain convinced that much of the variation is due to environmental factors, or predation during the egg and larval stages.

4. MECHANISMS FOR DENSITY-DEPENDENT REGULATION

Despite the difficulty of showing density-dependence of recruitment in fish populations, there is no shortage of proposed mechanisms for generating the effect. One obvious possibility is the modulation of fecundity or maturation rates. The other main possibility is, of course, density-dependent juvenile mortality.

The processes concerned are presumably predation, starvation and cannibalism. The predator may be considered as an adventitious one, and so, as the larva or juvenile grows through fields of successively larger and less abundant predators, mortality tends to decrease with age. A predator could aggregate on its prey as Ricker (1957) suggested, but fish larvae tend to be rather thinly distributed (one per cubic metre or less). Starvation must increase mortality, but a more realistic thesis is that of Ricker & Foerster (1948), which combines the effects of predation and lack of food; if the specific growth rate is less than the maximum, so the animals are exposed longer to

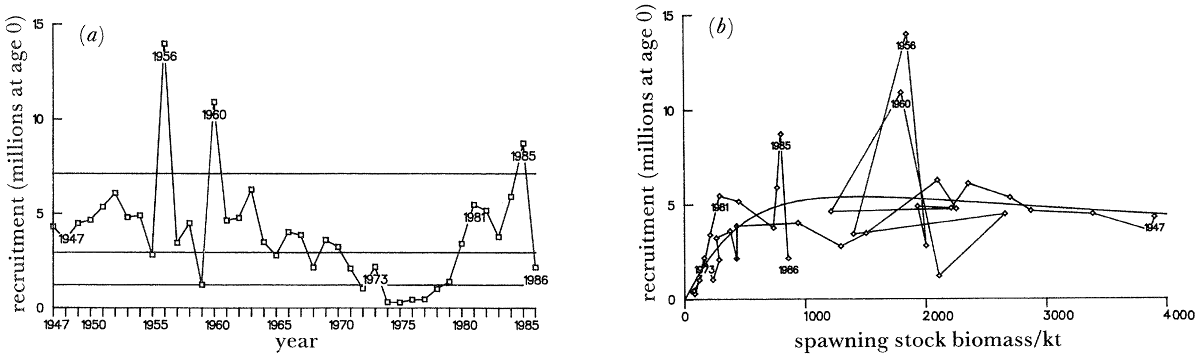


Figure 7. North Sea herring. (*a*) Time series of recruitment. (*b*) Stock recruitment diagram.

mortality generated by the adventitious predator. This idea was developed by Shepherd & Cushing (1980). Cannibalism is potentially a source of stock-dependent mortality, as big cod eat codling, but decisive evidence is lacking perhaps because the big cod could play the part of any adventitious predator. The only process that determines compensation so far discovered is the establishment of territories by the migratory trout in Black Brows Beck (Elliott 1990). In a small area of Black Brows Beck in Cumbria, Elliott (1984*a*) sampled eggs, alevins and parr of migratory trout for 22 years. Eggs were counted, and alevins were sampled by quadrat or cylinder sampling in February, and the parr were caught by repeated electrofishing in May–June and in August–September. The parr were thus sampled in the first and second year of their lives. The mortalities of eggs and alevins were very low, as were losses due to migration as shown by low surface net catches downstream.

Elliott (1984*b*, 1990) found that the number of parr surviving depends on the parent stock according to a Ricker curve, with remarkably little scatter of the data. This study is a very special one in that the population is very small, and the scale of observation is really that of the parr territories. The density-dependent mortality occurs during the earliest free feeding stage of the life history, and endures for about four or five weeks. The most remarkable point is the very low standard error about the Ricker curve, in sharp contrast to the observations on the larger stocks at sea. The conclusion is that the effect seems to be well-established, though it is still not clear how or why the mortality is proportional to initial cohort size, nor whether similar processes occur in marine populations.

In general, density-dependent growth is not very prominant, although it can be seen quite clearly in a large and long-lived fish like the Pacific halibut (Deriso 1985). After the predatory pike had been fished out in Windermere during the second world war, the stock of perch increased by a factor of 33, and then growth and fecundity were density-dependent (Le Cren 1958; le Cren *et al.* 1977). Horwood *et al.* (1986) found that the fecundity of plaice increased by 60% for a small increase in stock of 16%, which was not a compensatory change. Bailey & Almatar (1989) came to a similar conclusion for herring, but suggest that density-dependent fecundity might be more prominent in unexploited stocks.

Density-dependent mortality has been equally difficult to establish. Long ago, Hjort (1914) suggested that there might be a critical period of high mortality when the yolk had been exhausted, and the larvae started to feed. Sette (1935), Marr (1956) and May (1974) denied this thesis but in the past decade or so such an increment in mortality has been detected in single years (Lasker & Smith 1977; Kondo 1980). Daan (1981) and Ware & Lambert (1985) have found density-dependent mortality in the egg and larval stages; van der Veer (1986) established that the mortality of plaice at settlement was density-dependent due to predation by shrimp. Cook & Armstrong (1986) showed that the mortality of young haddock between the pelagic and demersal phases was density-dependent. The death rate of the Northeast Arctic cod between pelagic and demersal phases is also density-dependent (Sundby *et al.* 1989). Density-dependent mortality can occur at any early stage in the life history, but there is not yet enough information to relate it to the coefficient of density-dependence in the stock recruitment relation equation, or to establish that the mechanisms considered are in fact the right ones.

An interesting point is revealed by the observations on plaice eggs and larvae in the Southern Bight of the North Sea. Of eleven observations on eggs, and of four on larvae, there was no relation of either instantaneous or cumulative mortality upon initial numbers (Bannister *et al.* 1974). Estimates of the mortalities of eggs and larvae are available for four year-classes; at the larval stage the 1969 year-class was 100 times more abundant than the other three. It became an average year-class, the excess being presumably eaten by the shrimps at settlement. Yet, with another six year-classes, van der Veer (1986) found a link between the numbers of late larvae and an index of recruitment. The essential processes may occur between late larval stages and settlement.

Sinclair (1988), Sinclair & Iles (1989) have proposed the member-vagrant hypothesis: members of a population return to their native spawning grounds (as do the Pacific salmon) and vagrants do not. Then 'there is no necessary requirement for food availability or predators...losses due to spatial processes can be sufficient for the regulation of absolute abundance and temporal variability'. There must be some loss of animals on the migration circuit because the water movements are variable. The proportion of vagrants could be density-dependent, more leaving as stock increases, like the locusts, but the precise mechanism for this is not known. This would be best established by the appearance of tagged fish at a spawning ground distant from the native one. The stray of the Pacific salmon is very low indeed, and this is part of the evidence of return to the native stream. The west Greenland stock of cod was probably supported by emigration of eggs, larvae and juveniles from Iceland in the Irminger current across the Denmark Strait. For a period a proportion of mature fish returned from west Greenland to Iceland to spawn (see Cushing (1982), for an account of these migrations). These are, however, probably exceptional events, and such losses are in general unlikely to be density-dependent.

5. THE EFFECT OF ENVIRONMENTAL FACTORS

This paper is concerned with regulation in fish populations, and therefore deals primarily with endogenous (stock dependent) effects. However, exogenous effects such as weather and currents almost certainly play a large part in determining recruitment, and are believed to be the cause of the large variability characteristic of most marine fish stocks. We may use the term 'crucial period' to denote that stage in the life-history when density-dependent processes are largest, to avoid confusion with the 'critical period' of Hjort (1914) which has been re-interpreted in various ways, but is often taken to be the period when cumulative mortality is greatest, or when year-class strength is determined. Then exogenous variability occurring before the crucial period will be suppressed to some extent by the density-dependent processes, while that occurring during or after the crucial period is likely to be transmitted in full to the final year-class size. The consequences of this have been explored recently by an ICES Study Group on Models of Recruitment Processes (Anon 1990).

There is a large literature on the effects of the environment on recruitment to marine fish stocks (see, for example, Cushing (1982); Koslow *et al.* (1987); Shepherd *et al.* (1984); Garrod & Colebrook (1978)). There is once again no shortage of candidate mechanisms, but severe difficulty in separating correlations due to cause and effect from those due to a common cause (such as coincident trends). Given that controlled experiments are hardly possible for marine systems, this situation is likely to endure.

6. STOCHASTIC REGULATION

In view of the difficulties encountered in establishing the existence of density-dependent regulation, we now explore an intriguing possibility, that the deterministic regulatory processes may indeed be weak, weaker than anything envisaged within conventional stock-recruitment relations, and that regulation at low stock size may be due almost entirely to stochastic processes.

The genesis of this idea is quite simple. Stock-recruitment data invariably display high variability of recruitment. Being highly variable, but nevertheless non-negative, the probability distribution of recruitment is inevitably skewed, and better described by, for example, a log-normal distribution than by a symmetric (e.g. normal) distribution. It has also often been remarked that it seems that the variability of recruitment increases as stock size declines, although we are not aware of any very convincing demonstrations of this, nor is it probable that one could be prepared with less than 40 or 50 years of data. Garrod (1983) sought but failed to find the effect. Nevertheless, if it does occur, it could lead to a stochastic regulatory process, in the following way.

Assume that the variability of recruitment, expressed as the logarithmic standard deviation (σ) of a log-normal distribution, increases as stock size declines. It is well-known that the arithmetic mean of a log-normal distribution exceeds its geometric mean (or median) by an amount which is approximately $\exp(\sigma^2/2)$. This excess would therefore also increase as the stock size decreased. The stock size is of course some weighted arithmetic moving average of previous recruitment values. Dynamically, therefore, the stock size will depend on something like the recent arithmetic mean of recruitment. If, however, it is the median or geometric mean of the distribution of recruitment which is determined by a weakly regulatory (or even non-regulatory) deterministic process, the effect will be to generate larger arithmetic average R/SSB ratios at lower stock sizes.

The same mechanism would of course work equally well for any skewed distribution whose skewness increased as stock size declined: the assumption of log-normality is merely convenient. The essential ingredients are: (i) skewness of the distribution; (ii) increasing variability as stock size decreases; (iii) median recruitment controlled by deterministic process. Of these, (i) is inevitable, (ii) is plausible, and (iii) is perhaps more controversial. These aspects are discussed later. For the moment it is interesting to explore the consequences in more detail.

First, there need be little or no deterministic regulation in operation: this means that the ratio R/SSB may be distributed around some level which is effectively constant over the range of stock sizes observed. The points on a stock-recruitment diagram may be scattered widely around a straight line through the origin, with no apparent pattern which would correspond to a conventional stock-recruitment relation. A plot of ln(R/SSB) against SSB would in fact show more-or-less symmetrical scatter about a horizontal line, with (if it were detectable) a rather greater scatter at low stock sizes. Thus conventional methods for seeking stock-recruitment relations would almost certainly fail.

Secondly, the mechanism provides only regulation in the mean, and does so because of the increasing contribution made, as the stock declines, by increasingly rare, increasingly extreme recruitment events, as the distribution of year-class strengths becomes increasingly skewed. This sounds so much like a photofit description of recruitment to heavily fished stocks that we feel that this possibility warrants serious consideration.

7. SIMULATION STUDY

We have therefore carried out a simulation study of this process, to see whether it is indeed capable of maintaining non-zero stocks over a wide range of fishing mortality rates. We set up a standard age-disaggregated catch forecast model, in which the recruitment is controlled by a stock-recruitment relation with pseudo-random noise superimposed, and where the variance of the noise is (if required) determined by the stock size. The vital parameters were based on the North Sea plaice stock, for which the observed standard deviation of ln(R/SSB) is about 0.5, but the details are almost certainly of no consequence.

By using various stock-recruitment relations (i.e. none (constant R/SSB), constant recruitment, Beverton–Holt, and Cushing) we first verified that the system behaved as expected in the absence of recruitment variability. For these tests we simulated the effects of various fishing mortality rates in the range 0–1.0 per year. The stock recruitment relations were set up to pass through the observed mean recruitment and SSB values, any other parameters being chosen by intelligent guesswork. The behaviour, in terms of expansion, collapse and stabilization was qualitatively as expected from the simple graphical approach to the problem.

Next, we verified that adding a constant level of variability (as a normally distributed perturbation of log recruitment) did not alter the results in any essential respect. In fact, multiplying by a log-normal perturbation in this way increases the average level of recruitment by the constant factor $\exp(\sigma^2/2)$ mentioned above, and this effect is visible in the simulation results, as will be seen. It does not, however, alter the expansion/decline/stabilization behaviour in any significant way, as expected.

Finally, we implemented the variable variance stochastic mechanism discussed above, as an embellishment of several of the stock-recruitment models. In principle, and indeed in practice to some extent, the mechanism can be superimposed on a purely unregulated deterministic relationship (constant R/SSB). However, such a system is very sensitive to the parameters selected, the population has a tendency to grow very large at low mortality levels, and it is difficult to control the simulations so as to produce plottable results. Wishing to introduce a little regulation, we superimposed the mechanism on both the Beverton–Holt and Cushing (power law) relations. This achieved rather more than the desired result, however, because (as shown in table 1) the Beverton–Holt relation provides strong regulation at high stock levels, and the Cushing relation at low levels.

To achieve the desired minimal effect, we therefore again used instead the functional form of Shepherd (1982), given in equation (2). Selecting $a = 2R_0/B_0$, $K = B_0$ and $\beta = 0.5$, (where R_0 and B_0 are the mean observed recruitment and SSB) this interpolates between a Cushing curve (with a power of 0.5) at high stock levels, and an unregulated relation at low stock levels. The maximal deterministic value of R/B at zero stock size is in fact only double that at the reference level K (taken to be the average stock size).

The variability was applied as a normally distributed perturbation $N(0, \sigma^2)$ with:

$$\sigma^2/\sigma_d^2 = 21.2\,B_0/(21.2\,B+B_0), \tag{3}$$

where σ_d^2 is the observed variance of $\ln(\text{R/SSB})$, equal to 0.24 for the North Sea plaice stock. This strange expression effectively makes the variance inversely proportional to biomass, which is just a plausible way of making it increase as biomass decreases, chosen by analogy with the variance of a mean (which is inversely proportional to the size of the sample). The extra terms involving 21.2 and B_0 are just to limit the ratio σ/σ_d to 4.6 when the stock gets very small. Without this modification, one can get computer overflow when the occasional large random number occurs, which can crash the calculation. This effectively limits the arithmetic mean slope at the origin of the effective stock-recruitment curve, where otherwise it would be infinite.

The arithmetic mean recruitment is obtained by multiplying the deterministic (median) value given by equation (2) by the inflation factor $\exp(\sigma^2/2)$. Both the median and the arithmetic mean values are plotted in figure 8. The weakness of the regulation in the deterministic relationship, and the effectiveness of the stochastic mechanism in increasing R/SSB at low stock size, are both clearly apparent.

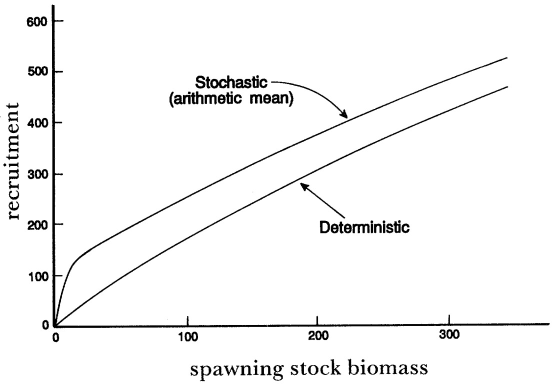


Figure 8. Deterministic and stochastic stock-recruitment relations used for simulation.

We first carried out a series of 100 year simulations by using these relations, starting from their recent average levels of recruitment (488 million) and SSB (372 kt). The results, for a range of fishing mortalities from zero to 0.8 are summarized in figures 9–12. These show the evolution of recruitment for three cases: (i) deterministic; (ii) with constant noise level; (iii) with stock-dependent noise. When there is no fishing (figure 9) recruitment rises to about 2000 million in the deterministic case. With constant noise, the average level is (of course) a little higher, and the variability is very apparent. With the stock-dependent stochastic relationship, the variability is reduced at the high stock levels, and the result is almost indistinguishable from the deterministic case.

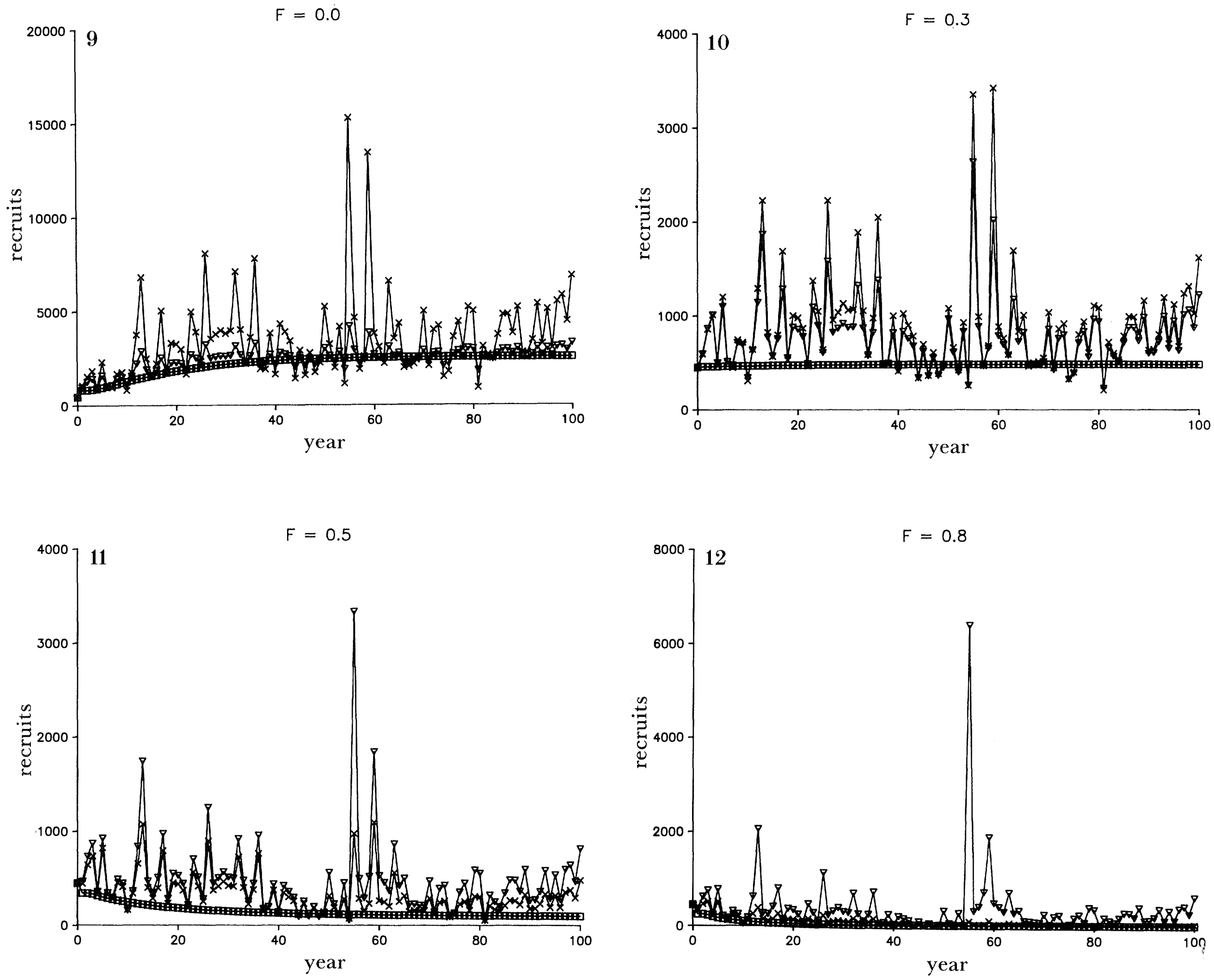
At a fishing mortality of 0.30 (figure 10) deterministic recruitment stays more or less constant at about 500 million, and there is little difference between the constant and variable noise cases (the variance for the latter is now only a little reduced).

At a fishing mortality of 0.5 (figure 11), recruitment declines to about 100 million in the deterministic case. The recruitment for the variable variance case now exceeds that for the others by a substantial margin, and recruitment appears to have stabilised at around 500 million after 100 years.

At a fishing mortality of 0.8 (figure 12) the stock collapses to zero for both the deterministic and the constant variance cases, but with variable variance it persists, with recruitment still fluctuating in the low hundreds after 100 years, following a massive year-class around year 58.

All of this is pretty much as expected. It merely shows that the mechanism postulated does in fact work as predicted. However, when we attempted to find the level of F at which the stock would collapse, even with the variable variance mechanism, we got a surprise. This is shown in figure 13, for a fishing mortality of 2.0, now with a 1000-year time horizon.

The stock survives its first 100 years, probably because of the massive year-class in year 58, now even more pronounced. Thereafter it ‘collapses’ to a very low level, and remains there for 150 years. At around year 250, another extreme year-class occurs, leading to a century or so of modest but variable recruitment. The stock then disappears for almost 200 years, before reappearing for three centuries or so. After year 850 it



Figures 9–12. Simulated recruitment time series for various levels of fishing mortality. Figure 9, $F = 0$; figure 10, $F = 0.3$; figure 11, $F = 0.5$; figure 12, $F = 0.8$. (□, deterministic (no variability); ×, constant variability; △, stock-dependent variability.)

collapses again, but we clearly cannot rule out the possibility of further recoveries; indeed, they seem to be rather probable.

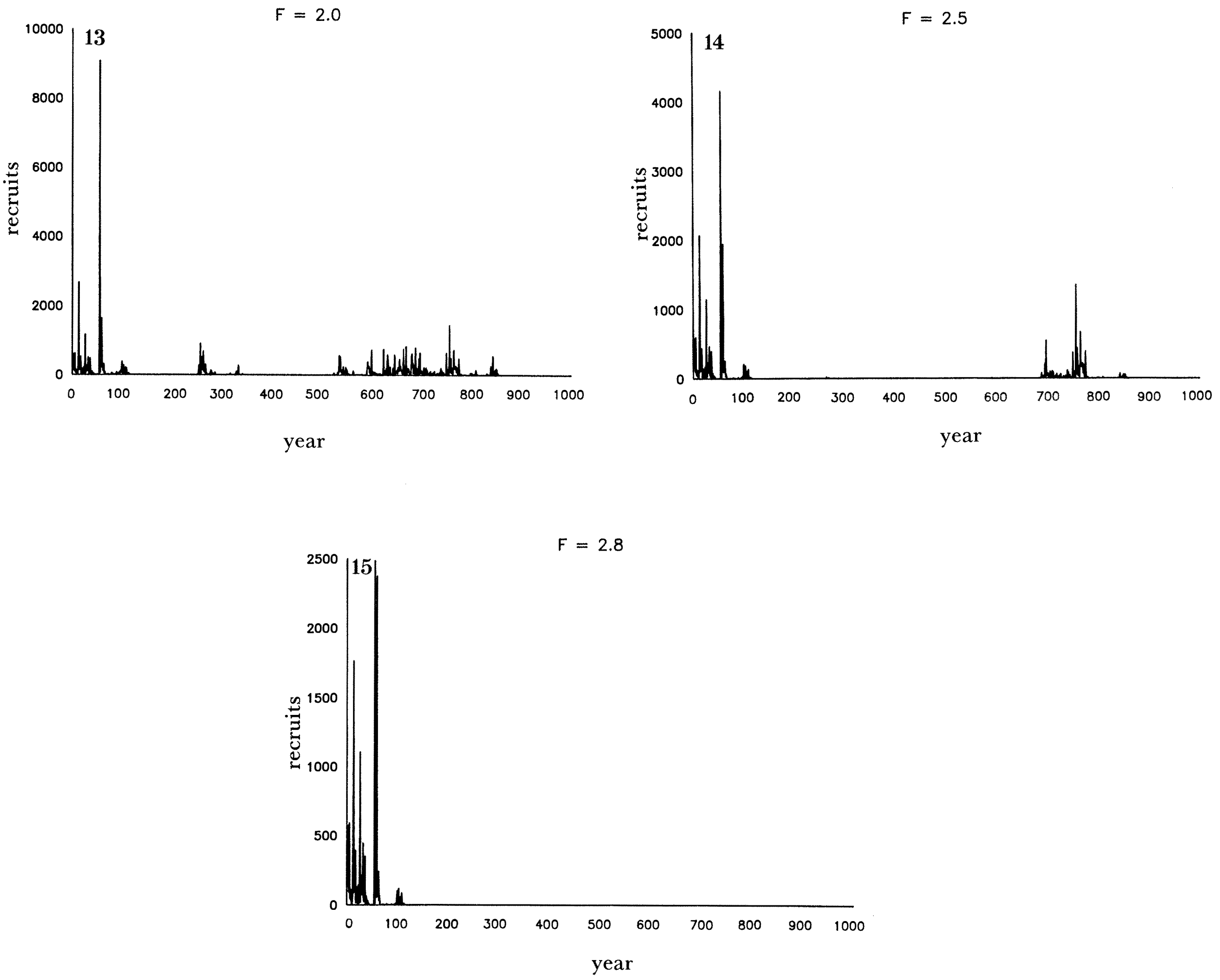
At a fishing mortality of 2.5 (figure 14) the last episode of good recruitment is restricted to only about one century starting at year 700. Only with $F = 2.8$ (figure 15) does the stock collapse, and stay extinct for the remaining 900 years of the simulation.

This behaviour is of course explicable with hindsight, but was not expected by us. It should be stressed that this episodic behaviour on a timescale of centuries is obtained without any time-variation of the parameters of the model. There is no climatic variation, no change of fishing mortality, predator abundance or anything. It is entirely self-generated: the stock bootstraps itself back up from near-extinction every now and then, purely by chance events.

We have in fact, without deliberately setting out to do so, created a highly non-stationary stochastic process. Neither the mean nor the variance of this process is constant, but each depends on the other, and they fluctuate together over time, without any systematic external control at all. Results generated by such a process violate the assumptions of stationarity implicit in conventional methods of time series analysis. They will defy understanding using these tools. If such a mechanism operates, it is perhaps not surprising that attempts to analyse such data have met with little success.

The ability of the stock to bounce back after six centuries in the wilderness (figure 14) even when held down by a level of fishing mortality which is extremely high even by North Sea standards, is a little uncanny. It is, nevertheless, distinctly reminiscent of the long-term behaviour of quite a few real stocks (as described earlier in this paper). These long-term changes are usually attributed to climatic changes, or interaction between stocks (for example, the Californian sardine–anchovy switching). Our simulations now suggest an alternative hypothesis: that they are due to pure chance. There may, in fact, be no deterministic regulatory mechanism to be found, beyond that which would lead to increasing variability at low stock size. So far as we are aware, this is a new and rather exciting result. It removes the apparent conflict between the ideas of regulation and variation of recruitment as dominant mechanisms. Here they are inextricably linked aspects of the same stochastic process.

For completeness, we plot the 'observed' stock-recruitment plot from the simulations (figure 16): this is a composite diagram built up from the results for fishing mortalities of 0.3, 0.5 and 0.8. Whether or not



Figures 13–15. 1000-year time series of recruitment from stochastic simulation with stock-dependent variability. Figure 13, $F = 2.0$; figure 14, $F = 2.5$; figure 15, $F = 2.8$.

it resembles the real data sets is perhaps a matter of opinion! Finally, figure 17 shows the time series of ln(R/SSB), the crucial parameter describing reproductive success, for $F = 0.8$. This shows no systematic trend, as expected, and the changing variability is not immediately apparent, and would be difficult to detect statistically.

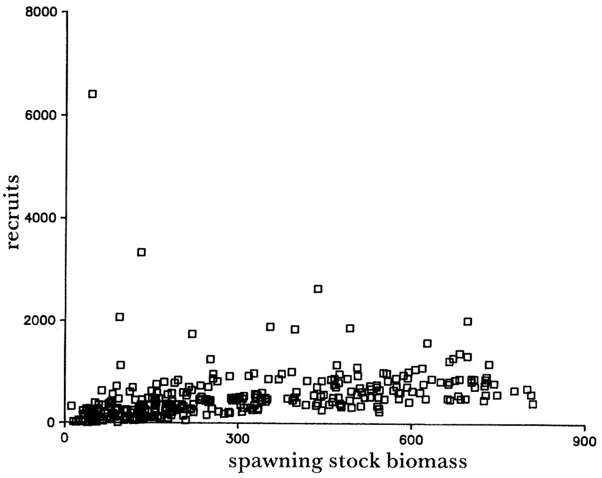


Figure 16. Simulated stock-recruitment scatter plot (composite diagram for $F = 0.3$, 0.5 and 0.8).

8. MECHANISMS FOR STOCHASTIC REGULATION

These results are rather suggestive, and would have considerable implications for stock-recruitment research; these are discussed later. First, it is necessary to ask whether the mechanism proposed bears any relation to reality, or whether it is just a figment of our

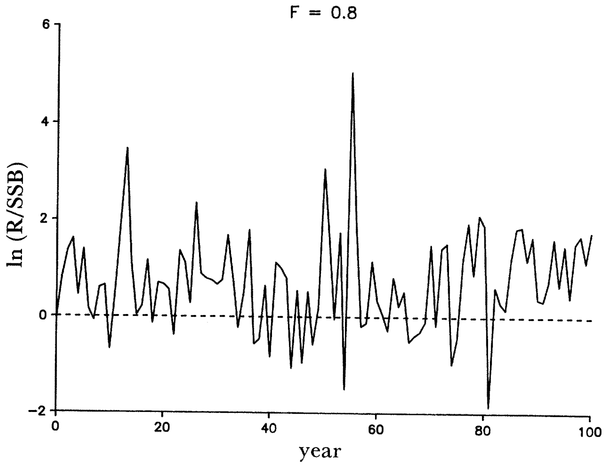


Figure 17. Simulated time series of ln(R/SSB) for $F = 0.8$.

imagination. The three essential ingredients are skewness, increasing variability as the stock size decreases, and control of the median (rather than the arithmetic mean) by whatever deterministic processes operate. The first of these is almost inevitable for a highly variable non-negative quantity, is confirmed by observation, and need not detain us.

The second is plausible. There are doubtless various mechanisms that could lead to such behaviour. The most obvious is patchiness, in either space or time. There is considerable literature on this subject (see Steele (1976) for an account in relation to marine systems), and there is no doubt that it occurs, probably for most populations and certainly for marine fish. The recruitment to the stock (a rather large unit) is the result of a summation over space and time of all the components of the stock. We know that there is extreme variability of abundance in the plankton at small space and timescales, and almost certainly of mortality too. By the central limit theorem, we should expect the variability (expressed by the coefficient of variation, perhaps) of the resultant total to be less than that of any of the component parts. Just how much less depends on the relative space and timescales, and the distribution of variability itself. However, will modulation of the size of the stock lead to any variation of the total variability? Clearly, if the effect is simply to reduce the abundance everywhere by the same factor, the answer would be no. If, on the other hand, the reduction were expressed as a reduction in the range, in space or time, of the population, the answer is most likely yes, because there would be fewer components contributing to the total. Beyond that, if as the stock declines the areas of high abundance are affected more than those of low abundance (or vice versa), then greater or lesser modulation of variability could be expected. Observations on fish stocks suggest that such effects do in fact occur (Myers & Stokes 1989).

Effects of this sort would of course also be generated by density-dependent processes acting locally, at high abundance the variability would be reduced by regulation. It is, however, an intriguing possibility that the effect could be generated just by chance. The coefficient of variation of a compound probability distribution describing the patchy spatial distribution of animals (e.g. a negative binomial distribution) seems quite likely to behave as hypothesized, for example. The answer to this question must therefore be: ‘quite possibly’. It is a concrete question which can be studied by field observations: the hypothesis is testable. The strength of the effect will depend on the spectrum of space and timescales concerned. To understand the process one would need to study the structure of the patchiness, and such work is closely related to modern ecological studies carried out purely for their intrinsic interest. Here perhaps, is yet another example of a practical question (of considerable economic importance) suddenly focussing attention on the results obtained from decades of basic research driven only by curiosity.

The third question is quite tricky. The answer depends on how the variability arises, on what is determined by what, and how the perturbations enter the process. The arithmetic mean is the classic measure of location of a statistical distribution, and statisticians even use the term ‘expectation’ for it, which lends it an air of universality it does not deserve. The key question is, as the variability reduces, onto which measure of location does the distribution collapse? A simple real example suffices to show that this may be the geometric mean or median rather than the arithmetic mean, in at least one relevant case. Consider, in fact, the abundance of fish eggs just before hatching. Suppose that they have been subjected to mortality by predators since they were laid, and that the abundance of the predators varies according to a normal distribution. Then, if the mortality rate is proportional to the predator abundance, the number of eggs which survive will be log-normally distributed. If the variation of the predator abundance is suppressed, so that it stabilizes at its arithmetic mean, then the egg abundance will stabilise at its previous geometric mean (the same as the median in fact). If the variation of predator abundance is not normally distributed, something more complicated will happen, but it seems plausible that, for perturbation processes of this sort, one should think of things being distributed about their medians, rather than their arithmetic means. This is not true for pure sampling (counting) variability but we have not so far thought of any other counter-examples. These are, however, deep probabilistic waters, and for the present purpose it suffices that deterministic control of medians rather than arithmetic means seems to be entirely plausible. Laurec *et al.* (1980) considered a somewhat similar model where the arithmetic mean rather than the median was controlled, and found that this increased the frequency of stock collapse. This is to be expected, because in this case the variability acts to produce depensatory rather than compensatory density-dependence.

9. DISCUSSION

We conclude that the stochastic mechanism proposed is plausible, and perhaps even likely to occur in practice. Whether it is indeed powerful enough to produce effects of the magnitude we have simulated is another question, that can only be answered by analysis of real data sets. However, our results do provide a new perspective for stock-recruitment studies, and suggest that we could be missing the point in seeking processes that would deterministically regulate total recruitment. We should instead perhaps study the causes of the variability itself, since that might be an equally or even more important part of the problem of regulation. The role of density-dependent processes may be primarily local, and they may act mainly to modulate variability, and therefore only indirectly affect total recruitment to the stock.

Studies of variability in space and time of abundance, at as wide a range of scales as possible, for a wide range of stock sizes, are clearly indicated. We may need not patch studies, but patchiness studies. These will be expensive. Before committing a lot of resources to such work, it would be wise to seek, in the few long-term series available, for any evidence of variation of variability as a function of stock sizes. This will be difficult to detect (Garrod 1983); it takes 10 years of data to determine one variance with a precision of 30% and several estimates of variance for each stock will be required to establish any changes. Nevertheless, something may show up, and the search should be made as soon as possible. Meanwhile, those responsible for operational stock assessments should bear in mind that not only is the casual assumption of constant recruitment dubious and dangerous, but also that the ability of fish stocks to withstand heavy exploitation may have been bought at the price of extreme variability at low stock sizes.

The simulation calculations for the evaluation of the stochastic mechanism were carried out by Dr M. Sun.

REFERENCES

Andrewartha, H. G. & Birch, L. C. 1954 *The distribution and abundance of animals*. (781 pages.) Chicago University Press.

Anon 1986 *Report of the ICES ad hoc Multispecies Assessment Working Group 1985*. ICES CM 1986/Assess: 9.

Anon 1990 *Report of the ICES-IOC Study Group meeting on Models for Recruitment Processes, Paris, May 1990*. ICES CM 1990/A: 5.

Bailey, R. S. & Almatar, S. 1989 Variations in fecundity and egg weight of herring (*Clupea harengus* L) Part II. Implications for hypotheses on the stability of marine fish populations. *J. Cons. perm. int. Explor. Mer.* **45**, 125–130.

Bannister, R. C. A., Harding, D. & Lockwood, S. J. 1974 Larval mortality and subsequent yearclass strength in plaice (*Pleuronectes platessa* L). In *Early life history of fish* (ed. J. H. S. Blaxter). Berlin: Springer.

Beverton, R. J. H. & Holt, S. J. 1957 On the dynamics of exploited fish populations. *Fishery Invest. Ser.* **2**, no. 19.

Cook, R. M. & Armstrong, D. W. 1986 Stock-related effects in the recruitment of North Sea haddock and whiting. *J. Cons. perm. int. Explor. Mer.* **42**, 272–280.

Cushing, D. H. 1973 The dependence of recruitment on parent stock. *J. Fish Res. Bd Canada* **30**, part 2, 1965–1976.

Cushing, D. H. 1982 *Climate and fisheries*. (373 pages.) London: Academic Press.

Cushing, D. H. 1988 The northerly wind. In *Toward a theory on biological–physical interactions in the World Ocean* (ed. B. J. Rothschild), pp. 235–244. Kluwer.

Daan, N. 1981 Comparison of estimates of egg production from the Southern Bight cod stock from plankton surveys and from market statistics. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.* **178**, 242–243.

Deriso, R. B. 1985 Stock assessment and new evidence of density dependence. In *Fisheries dynamics; harvest management and sampling* (ed. P. Mundy, T. S. Quinn & R. B. Deriso), pp. 49–60. Univ. Washington, Seattle.

Dickson, R. R., Meincke, J., Malmberg, S.-A. & Lee, A. J. 1988 The great salinity anomaly in the northern North Atlantic, 1968–1982. *Prog. Oceanogr.* **20**, 103–151.

Elliott, J. M. 1984*a* Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *J. Anim. Ecol.* **53**, 327–350.

Elliott, J. M. 1984*b* Growth size, biomass and production of young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *J. Anim. Ecol.* **53**, 979–994.

Elliott, J. M. 1990 Mechanisms responsible for population regulations in young migratory trout, *Salmo trutta* III the role of territorial behaviour. *J. Anim. Ecol* (In the press.)

Garrod, D. J. 1983 On the variability of yearclass strength. *J. Cons Perm. int. Explor. Mer.* **41**, 63–66.

Garrod, D. J. & Colebrook, J. M. 1978 Biological effects of variability in the North Atlantic Ocean. *Rapp. P.-v. Cons. int. Explor. Mer.* **173**, 128–144.

Hjort, J. 1914 Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.* **20**, 1–228.

Holden, A. V. (ed.) 1986 *Chaos*. (324 pages) Manchester University Press.

Horwood, J. W., Bannister, R. C. A. & Howlett, G. J. 1986 Comparative fecundity of North Sea plaice (*Pleuronectes platessa* L). *Proc. R. Soc. Lond.* B **228**, 401–431.

Kondo, K. 1980 The recovery of the Japanese sardine – the biological basis of stock fluctuations. *R. P.-v. Réun. Cons. perm. int. Explor. Mer.* **177**, 322–354.

Koslow, J. A., Thompson, K. R. & Silvert W. 1987 Recruitment to north west Atlantic cod (*Gadus morhua* L) and haddock (*Melanogrammus aeglefinus* L) stocks: influence of stock size and climate. *Can. J. Fish Aquat. Sci.* **44**, 26–39.

Lasker, R. & Smith, P. E. 1977 Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. *Calcofi Rep.* **19**, 128–137.

Laurec, A., Fonteneau, A. & Champagnat, C. 1980 A study of the stability of some stocks described by self-regenerating stochastic models. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.* **177**, 423–438.

Le Cren, E. D. 1958 Observations on the growth of perch (*Perca fluviatilis* L) over twenty-two years with special reference to the effects of temperature and changes in population density. *J. Anim. Ecol.* **27**, 287–334.

Le Cren, E. D., Kipling, C. & McCormack, J. 1977 A study of the numbers, biomass and yearclass strengths of perch (*Perca fluviatilis* L) in Windermere from 1941 to 1966. *J. Anim. Ecol.* **46**, 281–307.

Marr, J. C. 1956 The 'critical period' in the early life history of marine fishes. *J. Cons. perm. int. Explor. Mer.* **21**, 160–170.

May, R. C. 1974 Larval mortality in marine fishes. In *The early life history of fish* (ed. J. H. S. Blaxter), pp. 3–20. Heidelberg: Springer.

Myers, R. A. & Stokes, T. K. 1989 Density-dependent habitat utilisation of groundfish and the improvement of research surveys *ICES CM 1989/D: 15*.

Nicholson, A. J. 1933 The balance of animal populations. *J. Anim. Ecol.* **2**, 132–178.

Reddingius, J. 1971 Gambling for existence. *Acta Biotheor.* **20** (Suppl. 1), 1–208.

Ricker, W. E. & Foerster, R. E. 1948 Computation of fish production. In *A symposium on fish populations* (*Bull. Bingh. Oceanogr. Collection* **11**), pp. 173–211.

Ricker, W. E. 1954 Stock and recruitment. *J. Fish Res. Bd. Canada* **11**, 559–623.

Ricker, W. E. 1958 Handbook of computations for biological statistics of fish populations. *Bull. Fish Res. Bd. Canada* **119**, 1–300.

Sette, O. F. 1935 Biology of the Atlantic mackerel (*Scomber scombrus*) of North America: its early life history including the growth, drift and mortality of egg and larval populations. *Fish Bull. U.S. Fish Wildlife Serv.* **50**, 149–234.

Shepherd, J. G. 1982 A versatile new stock-recruitment relationship for fisheries and the construction of sustainable yield curves. *J. Cons. perm. int. Explor. Mer* **40**, 67–75.

Shepherd, J. G., Pope, J. G. & Cousins, R. D. 1984 Variations in fish stocks and hypotheses concerning their links with climate. *Rapp. P.-v. Réun. Cons. perm. int. Explor Mer.* **185**, 255–267.

Shepherd, J. G. & Cushing, D. H. 1980 A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons. perm. int. Explor. Mer.* **39**, 160–167.

Sinclair, M. J. 1988 *Marine populations: an essay on population regulation and speciation.* (252 pages), Seattle and London: University of Washington Press.

Sinclair, M. J. & Iles, T. D. 1989 Population richness of marine fish species. *Aquat. Living Res.* **1**; 71–83.

Steele, J. H. 1976 Patchiness. In *The ecology of the seas* (ed. D. H. Cushing & J. J. Walsh), pp. 98–115. Philadelphia & Toronto: W. B. Saunders.

Sundby, S., Bjorke, H. Soldal, A. V. & Olsen, S. 1989 Mortality rates during the early life stages and yearclass strength of north east Arctic cod (*Gadus morhua* L). *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.* **191**, 351–358.

van der Veer, H. W. 1986 Immigration, settlement and density dependent mortality of a larval and post-larval O group plaice (*Pleuronectes platessa* L) population in the western Wadden See. *Mar. Ecol. Progr. Ser.* **29**, 223–236.

Ware, D. M. & Lambert, T. C. 1985 Early life history of Atlantic mackerel (*Scomber scombrus* L) in the southern Gulf of St Lawrence. *Can. J. Fish Aquat. Sci.* **42**, 577–592.

Discussion

R. J. H. Beverton (*Montana, Old Roman Road, Langstone, Gwent, U.K.*). Dr Shepherd has shown a most intriguing way in which extreme episodic fluctuations, apparently density-independent, can nevertheless have a regulating influence on the long-term dynamics of the population. I would like to make two comments.

One is that I believe that a further search for evidence of higher variability of recruitment at low population sizes may prove rewarding, perhaps by using the statistics of extreme events as well as the conventional measures of variance.

The other is that an exceptionally large recruitment may set in train events other than the purely structural changes in the size and age composition of the adult population when the yearclass becomes mature.

The North Sea haddock is a good example. The three largest yearclasses ever recorded, those of 1962, 1967 and 1974, were each followed by year-classes significantly smaller than average; indeed, the inhibiting effect of the very large year-class was detectable, though muted, in two or even three of the year-classes that immediately followed it. Whatever the mechanism (not intra-specific predation in the case of haddock, which is primarily a benthic feeder), the result is that the haddock system evidently does not permit an extremely large year-class more often than once every five years or so (at best), however favourable the other circumstances may be. This puts a form of density-dependent 'capping' on the upper end of the range of populations size, but at the cost of higher short-term variability. Perhaps these dynamics would be worth investigating as a follow-up of Dr Shepherds paper.

J. G. Shepherd. I agree with Professor Beverton that we need to look harder at levels of variability at various stock sizes, and that we may need to use non-standard statistical tools to do so. His point about the apparent effect of large year-classes is also interesting. Armstrong & Cook (loc cit) have carried out an investigation for the North Sea haddock, but in general serial autocorrelation, including the negative correlation he mentions, appears to be quite common. I am sure that this aspect also warrants further investigation. For example, is there a similar effect after small year-classes?