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Plankton-generated chaos in the modelled dynamics of haddock

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SUMMARY

This study illustrates the feasibility of regimes of chaotic dynamics in gadoid populations. A previously developed plankton model related fish larval survival to larval density and their copepod food supply. This model is extended to a full-population model, incorporating age structure, fishing and a stock-recruitment relation implicit in the plankton model. Parameterization is based upon the Georges' Bank haddock. It is shown that regions of stability, aperiodic and chaotic-like dynamics exist as both the copepod food-supply and fishing rates are varied. The deterministic aperiodic dynamics are significantly complicated by additional stochastic elements. The implications are that chaotic dynamics are plausible and that analyses of output data on stock and recruitment can reveal relatively little; field and laboratory studies are needed to elucidate the underlying mechanisms. Traditional fitting of stock and recruitment relations may give an overly optimistic interpretation for fisheries managers.

1. INTRODUCTION

The problems of 'stock and recruitment' are the most difficult, important and pressing in fisheries science and management. They are difficult to address because the knowledge needed embraces the totality of marine ecology, and adequate synoptic sampling at sea is expensive. They are important because they attempt to explain and predict the short- and long-term dynamics of fish populations, or stocks, and the maximum rates of exploitation that the populations can sustain. They are pressing because most of our major temperate-water stocks are at historically low levels. The mature biomass of many populations is less than 10% of unexploited levels. Warnings have been given, and major fisheries closed, because it is feared that populations might be reduced to unsustainable levels (Anon. 1994*a*,*b*).

The problems of 'stock and recruitment' fall into two related categories. The first seeks to explain the variations in the numbers of juvenile fish that enter the fisheries, termed the 'recruitment'. This variation is one of the main features of marine fisheries (Cushing 1975), with the variance of logged-recruitments in the range 0.4–1.0 (Garrod 1983). For example, the North Sea haddock has displayed a 100-fold difference between recruitments in consecutive years (Anon. 1993*a*).

The second problem is to describe and explain the functional relation between the parent stock size and the recruitment spawned by those parents (Cushing 1975; Rothschild 1986). Over a large range of stock size the production of recruits is on average constant, but very variable as described above. This implies an approximate density dependence of the form $1/n$ over the range of stock size. But this cannot be sustained as the stock size n becomes very small, and, if there are no parents there will be no young: a line through the origin is implied. This has lead to the construction of largely empirically based functions to describe the stock and recruit relation (e.g. Ricker 1954; Beverton & Holt 1957; Cushing 1971; Shepherd 1982). It is an injustice to assert that they are all only empirical, but they are influenced by the need to have few parameters to express the density dependence, given the paucity of understanding of the mechanisms and the few and very noisy data.

The stock and recruit relation is by far the most important source of density dependence in the populations. The shape of the relation, specifically the slope of the function at the origin, determines the maximum rate of fishing that the population can sustain. All the above functions provide visually adequate fits to most data, and are statistically indistinguishable. To provide better resolution, data from many stocks have been considered together (Anon. 1993*b*; Myers *et al.* 1994, 1995). These studies have indicated a reduced recruitment at low stock sizes, but have had limited success in elucidating the underlying structures. However, the functions are not guaranteed to give useful information on the maximum rates of exploitation. The Cushing power-curve, for example, has an infinite slope at the origin. It can be appreciated that the family of curves gives little insight into the behaviour of the populations at low numbers, and that they cannot readily be used for management. The position would be different if stocks were allowed to collapse, and the character of the stock-recruitment relation observed:

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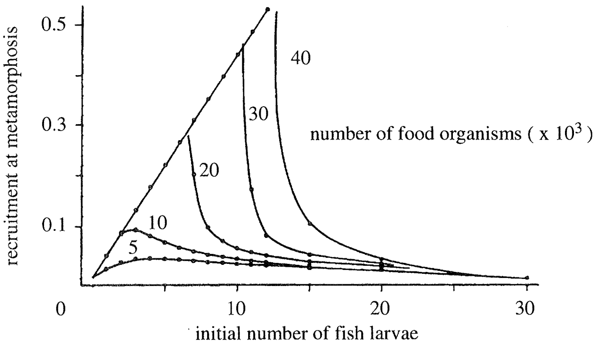

Figure 1. The relation between haddock larvae at first feeding (*lo*) and at metamorphosis (*lm*), m^{-3}, for initial copepod densities of 5, 10, 20, 30 and 40 10^3 m^{-3}. (Redrawn from Cushing & Horwood 1994.)

as for in North Sea herring (Horwood 1982; Myers *et al.* 1995). This is clearly not prudent, although current management practice is giving us an opportunity to observe too many stocks at low levels.

A different approach was adopted by Cushing & Horwood (1994). They modelled the growth and death of Georges' Bank haddock (*Melanogrammus aeglefinus* L.) based upon laboratory and field observations of the larvae. The model assumed that the larvae grow with their cohort of copepod food. The mortality rate is independent of density, but the duration over which the pre-metamorphosis mortality operates varies with the growth of the larvae, in a similar manner to that modelled by Shepherd & Cushing (1980,1990). In this model, the growth is dependent upon the density of the copepods, which itself is determined by the abundance of fish larvae. Two features of the model are notable. First, with adequate food levels, the survival rate of larvae is constant giving a constant slope at the origin. Second, some food levels allow the larval cohort to develop rapidly, but can then be inadequate to sustain the increasing larval biomass, resulting in a collapse. This is similar to the 'scramble' competition familiar in entomology (Nicholson 1959; Varley *et al.* 1973). Both features have significant implications for the dynamics of the population.

This study extends the Cushing & Horwood model, of early larval growth, to a full population model of the 'Georges' Bank' haddock. It is a caricature, based on the population biology of the larvae and adult haddock of Georges' Bank, and is intended to illustrate the spectrum of possible dynamic behaviour rather than assert that this is the most appropriate model. The dynamics are explored, and the limit cycle, aperiodic and chaotic-like behaviours are illustrated.

2. MODEL DEVELOPMENT

The model developed by Cushing & Horwood (1994) related the numbers of first-feeding larvae, of Georges' Bank haddock, to the numbers at metamorphosis, one to three months later, at different densities of copepod nauplii. The resulting functional forms are illustrated in figure 1, for initial densities of fish larvae of 0–30 m^{-3} and initial densities of copepods of 5000–40000 m^{-3}. It is necessary to translate the numbers of larvae from m^{-3} to numbers in the population, and to translate the axes to numbers of recruits to the fishery and to the biomass of the mature population. Later the model is 'scaled' to an appropriate unexploited population size at an initial copepod density of 15000 m^{-3}. This is higher than the average copepod densities of 5–10000 m^{-3} but the larvae tend to concentrate, in the water column, at the highest prey densities (Lough & Potter 1993). Table 1 gives the parameters used in the model.

The mature female biomass is assumed to spawn a fixed number of eggs g^{-1}, (f). The eggs and pre-feeding larvae are subject to a planktonic mortality rate (M_e) to give the numbers of first feeding larvae (lo) in the population. This number is divided by the appropriate water volume (V) of Georges' Bank to give lo m^{-3}. The original model then returns the numbers of metamorphosing larvae (lm), which can be multiplied by the same volume to give the numbers in the population. A mortality from metamorphosis to age 1 is then applied (M_j). Let the functional relation be defined by $lm = h(lo\,|\,n)$, where n is density of the copepods.

The post-larval model has 14 age classes with a 15th 'plus-group'. The proportion mature (pm_i), mass (w_i) in kg, and selectivity to fishing (s_i), at age i, are age dependent, but otherwise constant. A constant instantaneous natural mortality, M is assumed, and F is the instantaneous rate of fishing mortality, which is usually constant over time. The total instantaneous mortality rate, Z_i, is given by $M+s_i.F$, and the annual survival rate, S_i, by exp(-Z_i). The fish spawn in March and 20% of the natural and fishing mortality occurs before spawning (Gabriel *et al.* 1989). The mass of fish is that at spawning.

Define $X_{i,t}$ as the number of haddock, in millions, of age i, at the beginning of year t, and $g(SSB_t)$ as the recruits of age 1, in millions, as a function of the spawning stock biomass (males plus females), in thousands of tonnes. The model can be expressed as:

$$X_{1,t+1} = g(SSB_t)$$

$$X_{i+1,t+1} = X_{i,t}.S_i \qquad i \in (1,13)$$

$$X_{15,t+1} = X_{14,t}.S_{14} + X_{15,t}.S_{15},$$

$$SSB_t = \Sigma_i\, X_{i,t}.pm_i.w_i.\exp\,(-0.2Z_i).$$

We need to develop $g(SSB)$ in terms of lo and lm. The density dependence will appear in the survival rate of larvae. The result is to modify fish fecundity to an effective fecundity, and then the model can be recognized as relatively standard.

The number of eggs produced by the mature female biomass in year t is, $1/2.SSB_t.f.10^9$. The eggs are subject to a planktonic mortality (Me) during the period of incubation (ti) and between hatching and first feeding (tf); the survival rate over the period, Se, is exp(-($ti+tf$).Me). Thus

$$lo_t = 1/2.SSB_t.f.10^9.Se/V, \text{ and } lm_t = h(lo_t).$$

The metamorphosis of the gadoids is protracted. Following Lawrence (1982), the Cushing & Horwood model considered 'metamorphosis' at about 12 mm. They are still in the plankton at 45–50 mm (Schmidt 1905; Russell 1976) before they take up a more demersal phase in the later months of the year, as

Table 1. *Parameters used in the model and their dimensions if not dimensionless*

F	instantaneous rate of fishing mortality mortality at full selectivity (per year)
f	number of eggs produced per gramme of female
$g(SSB)$	the adult stock-recruitment relation (millions)
$(lo\,\vert\,n)$	the larval stock-recruitment function as number of metamorphosing larvae given the density of first feeding larvae and the density of prey organisms n (m^{-3})
lo	number of first feeding larvae (m^{-3})
lm	number of larvae at metamorphosis (m^{-3})
lc	number of first feeding larvae (m^{-3}) – parameter used in approximating the larval stock-recruitment model
M	instantaneous rate of adult natural mortality (per year)
Me	instantaneous rate of egg natural mortality (per day)
Mj	total natural mortality rate from metamorphosis to age one
n	the initial number of copepod prey (m^{-3})
pm_i	proportion mature at age i
SSB_t	biomass of the mature population in year t (thousand tonnes)
Se	proportion of eggs suriving to first feeding larvae
Sj	proportion of metamorphosed larvae surviving to age one
s_i	selectivity at age i
S_i	proportion of adults surviving annually
ti	incubation time of eggs (days)
tf	time from hatching to first feeding (days)
V	volume of water holding haddock larvae on Georges' Bank (m^3)
w_i	mass at age i (kg)
$X_{i,t}$	numbers of haddock age i at the beginning of year t (millions)
Z_i	total instantaneous mortality rate on adult age i (per year)
α	parameter of the larval stock-recruitment model
β	parameter of the larval stock-recruitment model
γ	parameter of the larval stock-recruitment model

'0-groups'. The post-metamorphosis mortality rate (M_j) is still high, and survival to age-1 recruits (Sj), at the beginning of year $t+1$, is given by $Sj = \exp(-M_j)$, and therefore,

$$X_{1,t+1} = h(lo).V.Sj = h(1/2.SSB_t.f.10^9.Se/V).V.Sj.$$

The shapes of the function $h(lo\,|\,n)$, the survival conditional on prey density n, can be seen in figure 1. Over some initial density of lo the survival rate of feeding larvae (S_l) is constant. The shape is then sensitive to the value of n. It has proved difficult to express the family of curves with a single relation dependent upon lo and n. Consequently, a set of curves was obtained that fit well to those constructed by Cushing & Horwood (1994). For $n = 5000\ \mathrm{m}^{-3}$, a single exponential and power function provided a reasonable approximation ($lm = \alpha.lo.\exp(-\beta.lo.^{\gamma})$). For initial food levels of $n = 10000$ and $15000\ \mathrm{m}^{-3}$, this function was used only after a larval density l_c. At lower densities a constant survival rate, S_l, was used. For higher food levels, even this function was inadequate to represent $h(lo\,|\,n)$ and, above l_c, the function $lm = -(\alpha - \beta.lo.^{\gamma})^{-1}$ was used. The parameters for the six curves are given table 2.

3. MODEL PARAMETERS AND SCALING

This completes the model, but the values of the parameters have to be obtained, and they are given in table 3. The adult age-specific parameters (pm, wm, s) and the natural mortality rate (M) were taken from Gabriel *et al.* (1989), and they are consistent with the later assessment by Gavaris & Eeckhaute (1994). The value of the specific fecundity (f), of 500 eggs g^{-1}, is from North Sea haddock (Hislop 1988).

The incubation time of the eggs is temperature dependent, and spawning in waters of about 7 °C gives an incubation time (ti) of 14 days (Russell 1976). The time to first feeding (tf) is two days (Lawrence 1974). The mortality rate of fish eggs and larvae was reviewed by Bailey & Houde (1989), and the 70% daily survival for haddock eggs implies a mortality rate (Me) of 0.35 day^{-1}.

The remaining parameters are the volume of water inhabited by the population of haddock larvae on Georges' Bank (V) and the 0-group mortality (M_j). For V, a value of $2.33.10^{10}$ has been used, which is consistent with the size of Georges Bank. For M_j, a value of 1.945 has been used, which is similar to the 0-group mortality estimated for North Sea haddock (Anon. 1993). Although appropriate, the values were actually obtained so as to scale the model to give results consistent with the observed sizes of adult and larval populations. Hence, any imprecision in the above larval mortality rates and fecundity is not important.

The haddock recruitment is very variable but over the past 50 years the average recruitment, at age 1, has been about 50.10^6 (Gabriel *et al.* 1989). The adult model gives an unexploited spawning stock biomass per recruit (SSB/X_1) of 10.17 kg per recruit, and hence an unexploited spawning biomass of about 500 kt. The values for V and M_j were set, for a larval food level (n) of 15000 m^{-3}, such that the unexploited SSB gave a

Table 2. *Values of the parameters for the functions approximating $h(lo\,|\,n)$ for various food levels (n) in 1000 m^{-3}*

food level	l_c	S_l	α	β	γ
n					
5	n/a	n/a	0.04283	0.64349	0.61891
10	2.43889	0.0453518	253.099	7.35869	0.17837
15	4.26051	0.0453518	$3.187.10^{11}$	26.19	0.0840
20	6.69215	0.0453518	135.7	88.8	0.2357
30	10.2982	0.0453518	102.335	34.543	0.4746
40	13.88020.	0.0453518	326.56	173.67	0.2419

Table 3. *Parameter values for the model*

age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+
pm	0.00	0.30	0.81	0.91	0.98	0.98	0.99	0.99	0.99	1.0	1.0	1.0	1.0	1.0	1.0
w	0.098	0.49	1.11	1.79	2.43	2.79	3.41	3.76	4.02	4.21	4.36	4.46	4.54	4.60	4.64
s	0.06	0.50	0.90	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
f	500														
ti	14														
tf	2														
M	0.2														
Me	0.35														
Mj	1.945														
V	$2.3336.10^{10}$														

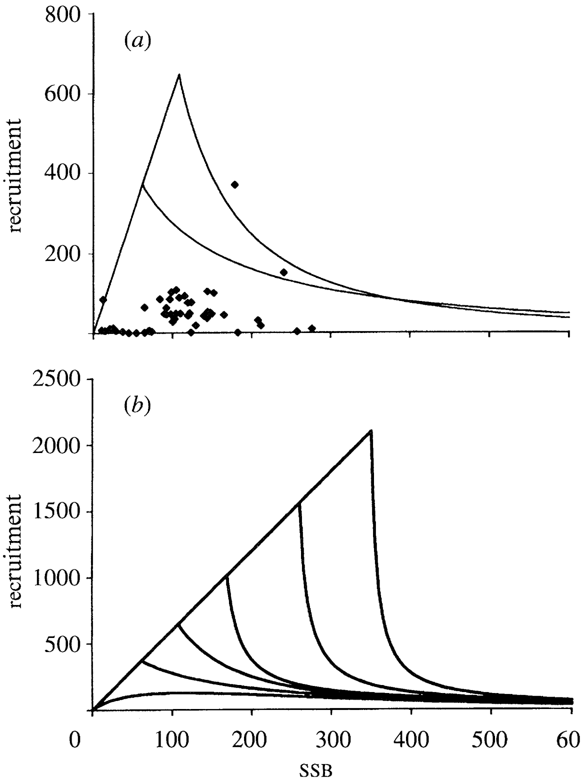

Figure 2. The relation between recruitment (10^{-6}), at age 1, and spawning stock biomass (*SSB*) in kt of Georges Bank haddock, derived from the model. (*a*) gives the data points and the curves for initial copepod densities of 10 and 15 10^3 m^{-3}; and (*b*) gives the curves for densities of 5, 10, 15, 20, 30 and 40 10^3 m^{-3}.

density of first feeding larvae (*lo*) of 20 m^{-3}, giving a density of metamorphosing larvae (*lm*) of 0.015 m^{-3}. Hence, $V = 50.10^6/(0.015.Sj)$. The only flexibility this has given is to choose, within limits, the equilibrium density of the first feeding larvae in the unexploited stock.

Figure 2*a* shows the resulting stock and recruitment curve for initial copepod densities of 10 and 15 10^3 m^{-3}, and the data points from Gabriel *et al.* (1989). The points are typically below the lines. Within the context of the model, this suggests that copepod densities may be generally lower than 15 10^3 m^{-3}, or that the unobserved and unexploited stock may have had recruitments lower than the assumed 50000000. Figure 2*b* shows the stock and recruitment curves for the initial copepod densities of 5, 10, 15, 20, 30 and 40 10^3 m^{-3}.

4. THE STATIC EQUILIBRIUM

The above equations can be solved to give the static equilibrium spawning stock biomass, as the fishing mortality rate is increased, for each of the copepod food densities. The results are shown in figure 3. For the copepod density of 15000 m^{-3}, the unexploited spawning biomass is 500 kt, as designed. For the other densities, the unexploited biomass ranges from 500–600 kt depending upon the details of the function *h*(*lo*).

The behaviour of the equilibrium at high fishing rates could be anticipated. Fishing occurs before the onset of maturity and first spawning. This alone will reduce the spawning biomass to low levels and combined with a normal density dependent function is likely to lead to extinction at some finite fishing rate. It can also be anticipated that the choice to fit a continuous curve to the plankton model, for $n = 5000$ m^{-3}, allows the trajectory to extinction to be smooth. Conversely, the use of a constant survival rate, below a threshold larval density, means that extinction will occur abruptly. These behaviours can be recognized in figure 3. For $n = 5000$ m^{-3}, the spawning biomass is smoothly reduced to zero at about $F = 2.1$ y^{-1}, whereas for the other models, with higher copepod densities, the reduction is abrupt at a similar value of about $F = 2.65$ y^{-1}.

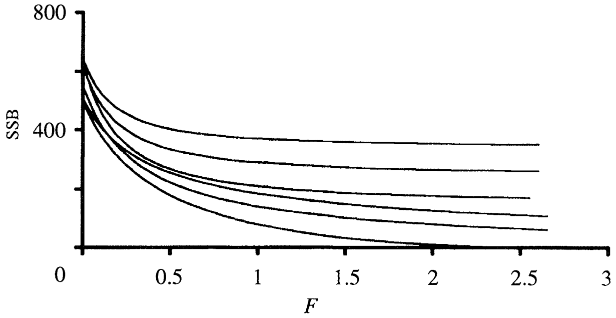

Figure 3. The static equilibrium spawning stock biomass (*SSB*) in kt, against the instantaneous fishing mortality rate (*F*), for the models with the six initial copepod densities.

Although extinction occurs at the same level of fishing mortality, it occurs at different levels of spawning stock biomass. From about the same unexploited levels, the model predicts much higher spawning biomasses when copepod densities are high. The equilibrium behaviour indicates that, as fishing increases, there is an initial rapid decrease in the spawning biomass. With further increases in fishing mortality the biomass declines only slowly, as the decrease in biomass by fishing is almost compensated for by increased recruitments. The traditional picture from yield per recruit plots (Beverton & Holt 1957) generally suggest a low optimal fishing rate, and for the Georges Bank haddock $F_{0.1}$ is 0.26 y^{-1} (Gabriel *et al.* 1989). The current model predicts that yields will increase rapidly as the fishing rate increases to critical levels. With the spawning biomass stable and recruitment and yields increasing, the collapse is sudden and unexpected. However an examination of the dynamics is required to give the full picture, especially the time over which the collapse can be observed.

5. BIFURCATION PLOTS

The shape of the stock and recruitment relations imply that chaotic or limit cycle dynamics might exist. In fact, some of the earliest observations of such dynamic behaviour were noted by fisheries dynamicists (Ricker 1954; Beverton & Holt 1957). However, the model is of a multi-cohort nature, and it is easily possible for the biomass in the cohorts to dampen and dispel potential cyclic behaviour. On the other hand, the age-structure *per se* introduces an increased time delay into the system which is intrinsically destabilizing. Whether the stability of increased age classes outweighs the effects of the time-delays depends on the precise

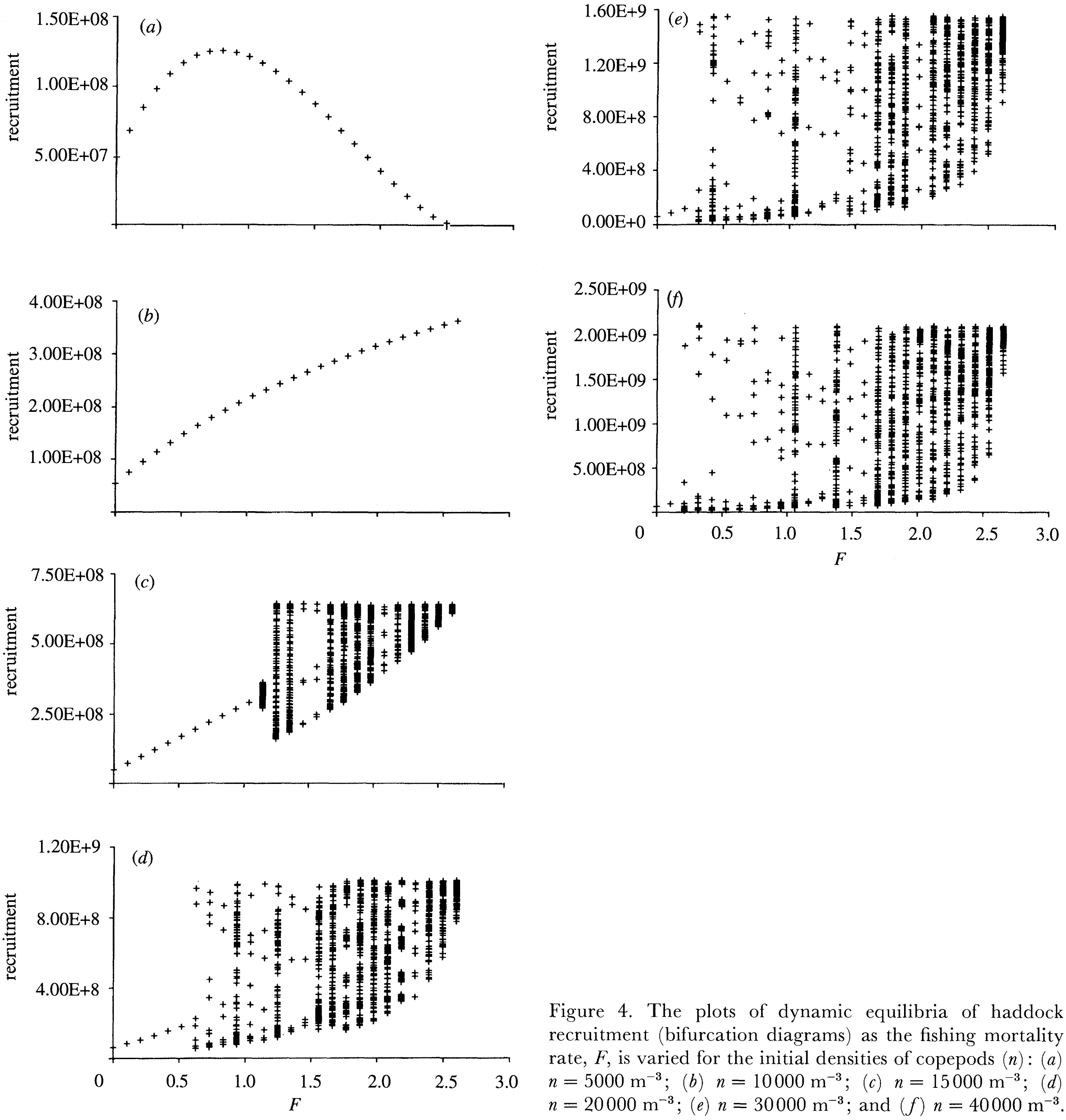

Figure 4. The plots of dynamic equilibria of haddock recruitment (bifurcation diagrams) as the fishing mortality rate, F, is varied for the initial densities of copepods (n): (*a*) $n = 5000\ \mathrm{m}^{-3}$; (*b*) $n = 10\,000\ \mathrm{m}^{-3}$; (*c*) $n = 15\,000\ \mathrm{m}^{-3}$; (*d*) $n = 20\,000\ \mathrm{m}^{-3}$; (*e*) $n = 30\,000\ \mathrm{m}^{-3}$; and (*f*) $n = 40\,000\ \mathrm{m}^{-3}$.

character of the model (e.g. May *et al.* 1978; Levin 1981; Nisbet & Gurney 1982; Bergh & Getz 1988). In practice, the stock and recruitment models estimated for fisheries generally do not give rise to cyclic or aperiodic behaviour at reasonable fishing mortality rates.

However, *n*-point limit cycles and chaotic-like behaviour is a feature of this deterministic model. The dynamic models were run for 1500 years, for the range of fixed fishing mortality rates and started from near to their equilibrium. The last 100 years of recruitments ($X_{1,t}$) were obtained. Figures 4*a–f* show the resulting bifurcation diagrams plotted against *F*.

Figure 4*a* gives the results for $n = 5000$ m^{-3}. The maximum value for *F* is as described above. There is a single stable equilibrium solution for all *F* below the maximum, and recruitment declines smoothly to zero at the maximum *F*. Figure 4*b* gives the results for $n = 10\,000$ m^{-3}. There is also a single stable equilibrium solution for all *F* below the maximum, but the recruitment increases until the maximum *F*.

Figure 4*c* gives the results for $n = 15\,000$ m^{-3} and a change in the character of the results occurred. There is a single, stable equilibrium for values of $F \leqslant 1.1$ y^{-1}. At higher values a complex pattern is seen. For most values of *F* there are no repeated points in the 100 examined, and the system appears chaotic. There are intervals where periodicity returns. At about $F = 1.5$ y^{-1} six-point cycles can be seen, with the points occurring in pairs. At $F = 2.05$ y^{-1} there is an eleven-point cycle. The transitions from chaos to periodic behaviour and back are frequently encountered in highly non-linear systems (e.g. Bolker & Grenfell 1993). The shape of the plot shows the range of the recruitments encountered. Initially the recruitments steadily increase. As the single equilibrium disappears, the trajectory covers lower recruitments than the last stable equilibrium recruitment, and a maximum recruitment. The maximum recruitment is near the peak of the stock-recruitment curve seen in figure 2. As *F* increases, the values of recruitment become more restricted to the top of the stock-recruitment curve. The points are mainly on the descending right limb of the curve, only occasionally visiting the top of the linear section of the curve.

A similar behaviour is seen for $n = 20\,000$ m^{-3} (see figure 4*c*). The bifurcations start at a lower value of *F* of about 0.6 y^{-1}. Periodic behaviour is most common for *F* less than about 1.5 y^{-1}. Cycles of 7, 8, 13 and 15 years can be seen, with the occasional aperiodic region. For higher values of *F*, the system is generally aperiodic, but there can be considerable pattern to the recruitments encountered. Similar-sized recruitments can be regularly visited. The lower bound of the recruitments is lower than before, and the linear section of the stock-recruitment curve is more regularly visited.

Figures 4*d* and 4*e* give the results for $n = 30\,000$ and $40\,000$ m^{-3}, respectively. A similar behaviour to that described for $n = 15\,000$ m^{-3} is seen. The bifurcations occur at lower values of *F*, the patterns of periodic and aperiodic behaviour are similar, and a fuller range of recruitments are encountered.

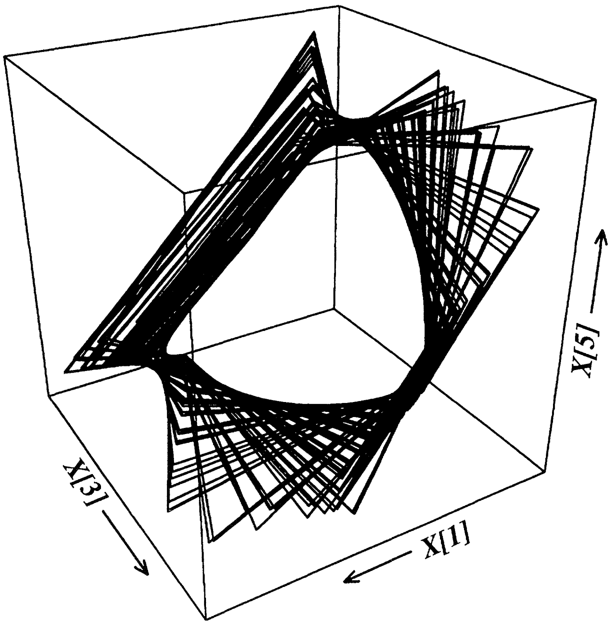

Figure 5. The three dimensional 500-year trajectory of age classes 1 (scale 0–10^9), 3 (scale 0–4.10^8) and 5 (scale 0–4.10^7) for the deterministic model of a prey density of $20\,000$ m^{-3} with a fishing mortality of $F = 0.936$ y^{-1}, comparable with the results for age-class 1 of figure 4*d*.

The above is by no means a full description of the dynamic properties of the model, which has not been attempted in this study. The requirements for a more complete non-linear deterministic (e.g. Levin & Goodyear 1980; Guckenheimer & Holmes 1990) and stochastic (e.g. Engbert & Drepper 1994) analysis are demanding. It at least requires the expression of recruitment as an appropriate single function of prey density (*n*); this alone has proved difficult and separate functions have been used in this study. The details given in here should enable anyone to carry forward such analyses but if not the author can be contacted for assistance. Figure 5 suggests the complexity to be encountered. It is a plot of the three dimensional trajectory of age classes 1, 3 and 5 for 500 years, after an initial 1500 years, from one starting position. It is for the deterministic model of a prey density of $20\,000$ m^{-3} with a fishing mortality of $F = 0.936$ y^{-1}, comparable with the results for age-class 1 of figure 4*d*. As anticipated there is a richness of the dynamics and an indication of quasiperiodic behaviour and precession. Analyses of similarly structured models have been reported by Guckenheimer *et al.* (1977), Levin & Goodyear (1980) and Wikan & Mjølhus (1995).

6. A DYNAMIC REALIZATION

As an illustration of the temporal dynamics that would be apparent in such a model world, a single stochastic simulation was carried out. The current fishing mortality on the Georges' Bank haddock is about unity and has risen over the past two decades (Gavaris & Eeckhaute 1994). The model was run for 50 years, starting at $F = 0.2$ y^{-1}, and increasing it exponentially so as to be at $F = 1.0$ y^{-1} after 50 years; an approximation to the exploitation of the Georges Bank

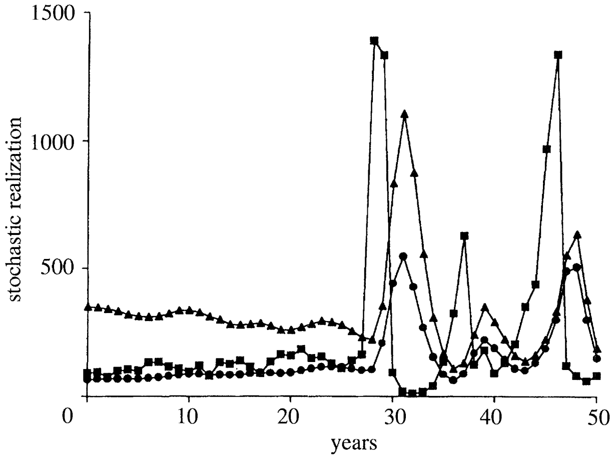

Figure 6. A stochastic realization of: recruitment (10^{-6}) denoted by filled squares; mature population size (kt) denoted by open triangles; and yield (kt) denoted by filled circles.

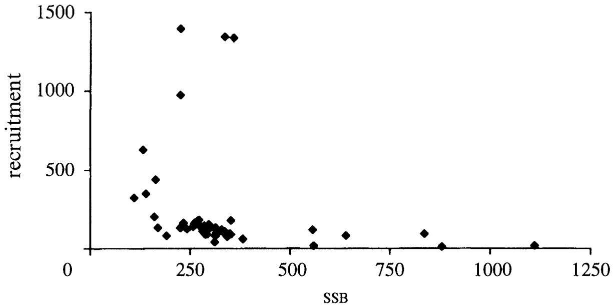

Figure 7. The resulting plot of recruitment (10^{-6}) against spawning stock biomass (kt) for the time series of figure 5.

haddock from 1945 to the present day. The model was started from equilibrium with the copepod density of 15000 m^{-3}. A copepod food level was chosen at random each year, with 0.4 probability of it being 15000, a 0.2 probability of it being either 10 or 20000, and a 0.1 probability of it being 5 or 40000. Figure 6 shows the outcome of this single trial.

The system is well behaved for the first 25 years. Fishing is slowly increasing to reduce the spawning stock biomass and recruitments and yield are relatively stable or increasing. At years 28 and 29, the copepods are at high level of 40000 m^{-3}, and two high recruitments result, sending up the biomass and subsequent yields. A further high recruitment is seen in year 37, but this is due to the peak of the stock-recruitment curve being attained under normal food conditions. At year 46, another high recruitment occurred with a high copepod density. The large increase in recruitments has an important impact on the stock, returning it to levels of low recruitment and setting up a cyclic behaviour.

Such a system would be manageable if the underlying dynamics could be ascertained from the outputs. Figure 7 shows the plots of recruitment against spawning stock biomass. It has all the features of real fisheries data. There is great variability and little structure. We may see an increased variability at intermediate stock sizes, and we may see reduced recruitments at the lowest stock sizes. The data allow little insight into the dynamics, except the important point that at least at the observed levels the stock has been maintained.

7. DISCUSSION

Various methods have been proposed to identify chaotic dynamics from output data (Blythe & Stokes 1988; Sugihara & May 1990; Casdagli 1992). However, even with long time series, the ability to distinguish between chaotic and stochastic forces in biological populations and diseases is inadequate (Casdagli 1992; Godfray & Grenfell 1993). There are indices and records of catches of marine fishes for periods of a few hundreds of years (Wyatt & Larraneta 1988), but the insights they give into the abundance of the populations tend to be unrefined. In many cases the catches fluctuate because of changes in fishing effort and market forces. The information from scale deposits (Soutar & Isaacs 1974) lacks the required temporal resolution. In any case, the population is a compound unit comprised of many age classes. Detailed data from stock assessments rarely provides as much as 50 years of data on the strength of year-classes. It is therefore almost impossible to distinguish between chaotic dynamics or stochastic events or some combination as being the driving mechanism for the highly variable time-series of recruitments. Furthermore, the interactions between stochasticity and chaotic dynamics can be the dominant factor in the dynamics in some systems (Rand & Wilson 1991; Engbert & Drepper 1994).

From the observations of stock and recruitment we cannot conclude one way or the other whether chaotic dynamics are involved. Shepherd & Cushing (1990) argued that single-species deterministic chaos was unlikely as the underlying shape of the density dependence would still be exposed in the stock-recruitment plots. That may be true if only deterministic dynamics were involved, but the introduction of some stochastic elements into the above model shows that the underlying structure is quickly hidden (see figure 7). Even if it were not affected by random events the underlying model might easily be unrecognized, as described below.

The lack of ability to determine the existence of chaos allows prejudice to take a part. Along with Berryman & Millstein (1989), I considered that chaotic dynamics were unlikely to be at all general in population dynamics because of the difficulty, at the population and evolutionary levels, of coping with the variability. However, counter arguments are many (e.g. Nisbet *et al.* 1989), and this prejudice was particularly weakened by the studies of Allen *et al.* (1993) who showed that ensembles of populations could be less prone to extinction under chaotic conditions. With little empirical basis to recognize the dynamic mechanisms from the data one has to look to the mechanisms to predict the dynamics. This is very difficult in the case of marine fisheries and the Cushing & Horwood (1994) model was one approach.

The above demonstration of chaotic-like dynamics is only as valid as the model. But the model cannot be regarded as exceptional. It has parallels in entomology with the recognition of 'scramble' competition. The model essentially says that circumstances can exist that allow the build up of large biomasses of a predator, but too favourable conditions will then cause this biomass to wipe out its prey and cause a collapse of the predator. The fortunes of prey and predator are closely linked. In northern waters we do see the development of recognizable cohorts of copepods over scales of 50–100 km, and these cohorts can persist for months (Cushing & Tungate 1963; Horwood & Cushing 1978). Fish larvae exist at similar scales (Lough & Bolz 1989). The distribution is such that fish larvae must take advantage of the patches or starve. In areas such as the northern North Sea or Georges' Bank there is only space for a limited number of such patches, and little option to switch between patches. The model extends the behaviour of the larvae observed in the laboratory to provide a plausible reality. Nevertheless, a weakness with the model is the lack of spatial structure. The number of patches of copepods may be finite, but recent studies have revealed that some stability can be regained with migration and dispersal amongst patches (Stone 1993; Ruxton 1994). McCallum (1992) has also shown that immigration or refuges can have a stabilizing effect on populations subject to scramble competition, and most of the large populations of marine fish might better be described as metapopulations.

A chaotic dynamics of fish populations was postulated by Wilson *et al.* (1991). Here there was a community dynamics, but essentially the concept is similar to that described for the single species. There is a build up of biomass that cannot be sustained and predator and prey collapse. The deterministic chaotic dynamics of a model of the Hudson River striped bass was investigated by Levin & Goodyear (1980). They show that a region of chaotic dynamics exists for at least high values of fish recruits per parent and high exploitation rates, but it is not clear whether such parmeter values are encountered.

The greatest annual variability in fish recruitment is seen in the gadoid stocks. These occur in the northern waters, rich in calanoid copepods and euphausids and where single species of larval prey predominate. In more coastal areas, such as the Southern Bight of the North Sea or the Bristol Channel, the zooplankton are smaller, more diverse and with smaller variations in time and space. The flatfish are common in these areas and, although an occasional abundant year-class is seen, the recruitments are much less variable (Garrod 1983; Horwood 1993). This is supportive of the general applicability of the Cushing & Horwood model.

A major natural phenomenon has been the 'gadoid outburst' in the North Sea. From about 1962, all the gadoid stocks had increased recruitments and probably increased variability. The size of the stocks increased enormously: cod numbers increased threefold. A short time later the pelagic stocks, especially the herring, declined. The reasons have not been resolved and they are unlikely to be simple. They include a greater production of *Calanus* (at a later time of the year), and a decrease in *Pseudocalanus* (food released for the gadoids by over-fishing of the herring) after the initial increased recruitments; and changes in the energy pathways favourable to the gadoids and unfavourable to the herring (Anderson & Ursin 1977; Hempel 1978; Cushing 1984). The above model suggests another linkage. The extra availability of calanoids is described by Cushing (1984). At intermediate stock sizes, the model suggests greatly increased and more variable recruitments, consistent with the gadoid story. At higher food levels the larval biomass can become great and can easily remove the copepod population. At lower food levels, the interaction between fish and copepod is more balanced. At lower food levels the copepods survive and at higher food levels their existence is more precarious. The adult herring will feed upon the copepodite and adult stages of *Calanus*, as well as *Pseudocalanus*, and their subsequent cohorts. Consequently, the food available to the adult herring may have been more erratic and precarious. The decline of the herring was predominantly caused by over-fishing, but this decline may have been accelerated, and maintained at a low level, by adverse feeding of the adults, and subsequent abundance and fitness of their eggs, larvae and recruitment. The recent reversal in the fortunes of the gadoids is consistent with the current increase in herring, which was started by improved recruitments, and a lower level of *Calanus* is implied. Corten (1990) argued that a simple stock-recruit relation was not the explanation for the increase in the herring, but this more complex path, driven by the gadoid stock-recruit-copepod relation could be.

There is still an immense gap between the speculation of the model and observations in the sea. The problem is obviously one of fisheries but it is also an opportunity for marine life-science. The population dynamics of the marine ecosystem are very poorly understood, for reasons of logistics and expense. The massive fluctuation in gadoid recruitments offers a focus to explain a major event and to learn how the middle trophic layers work in the sea. Until we can conduct series of observations, at time and space scales appropriate to copepods and fish larvae (Steele 1978; Levin 1992) we will make no progress in this area.

Fisheries managers need advice on the size of fish stocks and potential yields. Recently they have needed to know how low stocks can be driven before they collapse. In waters around the U.K., The Internation Council for Exploration of the Sea (ICES) determined that more than half of the populations of commercial finfish are near or below safe levels. One approach has been to fit stock and recruit relations to the data. The models are simple, for with few points a highly parameterized model is not credible. The variation about the simple model is treated as 'noise'. It can be appreciated from figure 7 how misleading such an exercise can be. It not only misrepresents the situation to managers it misrepresents the biology of the fish. At present, the only suitable statistic to characterize the maximum fishing rate would appear to be 'F-high' (Anon. 1983; Sissenwine & Shepherd 1987; Jakobsen 1993). This is obtained by drawing a line through the origin of figure 7, leaving 10% of the points to the left. From this line a 'maximum' fishing rate can obtained.

Even with the above model, this would return a reasonable estimate of the maximum rate of fishing that the stock could withstand.

Finally, this is a caricature of the Georges' Bank haddock. Its use is to demonstrate the potential existence of chaotic-like dynamics rather than to assert a specific mechanism and its presence. But progress to seeking the mechanisms can only be made with more sampling in the sea.

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