ICES Journal of Marine Science, 54: 427–443. 1997

Stock and recruitment in Baltic cod (*Gadus morhua*): a new, non-linear approach

A. P. Solari, J. M. Martín-González, and C. Bas

Solari, A. P., Martín-González, J. M., and Bas, C. 1997. Stock and recruitment in Baltic cod (*Gadus morhua*): a new, non-linear approach. – ICES Journal of Marine Science, 54: 427–443.

The stock and recruitment (SR) relationship in Baltic cod is studied. In light of the field data, the authors suggest that the SR relationship oscillates at two levels of stability (cycles) due to the interaction between density-dependent compensation and depensation. Furthermore, density-independent transitions between equilibrium states are assumed due to fishing mortality and medium and long-term periodicities in the abiotic environment which may induce compensatory and depensatory effects upon stock and recruitment. These mechanics are related to concepts such as variable carrying capacity, multiple equilibria, minimum viable population and inverse density dependence. Carrying capacity is regarded as a critical threshold between different equilibrium states and the minimum viable population as an unstable equilibrium below which the SR relationship may not rehabilitate. A modelling approach is put forward where the SR-relationship is regarded as a system or summation of non-linear functions with dynamic features ranging from chaos (the ceiling, when external conditions are extremely benign), going through a range of relatively stable, converging cycles (as external stress increases), to a quasi-standstill state with no clear oscillations (when the minimum viable population is being approached) which may lead to inverse density-dependence (depensatory dynamics). This SR-system is considered as highly flexible as it has the capacity to, persistently, evolve and return within a range of equilibrium states. Also, it is proposed that the SR relationship is, at the present time, nearby the minimum viable population due to the combined effects from high fishing mortality and negative effects from external perturbations. However, a SR rehabilitation towards a low equilibrium state is expected, during the coming years likely due to positive trends in external perturbations. A simple numerical simulation is put forward where the SR system is perturbed by a sinusoidal external variable at three constant levels of mortality.

Key words: Baltic cod, stock-recruitment, dynamic system, variable carrying capacity, equilibrium states, compensation, depensation, minimum viable population, depensatory dynamics (inverse density-dependence).

Received 17 July 1995; accepted 6 August 1996.

A. P. Solari: Lund University (Sweden) at Fisheries Research Group, University of Las Palmas, E-35018, Las Palmas, Canary Islands. Email: solaris@searn.sunet.se. J. M. Martín-González: Department of Physics, University of Las Palmas, Las Palmas, Canary Islands. C. Bas: Institute of Marine Research—CSIC, E-08039, Barcelona, Spain.

Introduction

Two of the key assumptions underlying fishery theory are that (a) recruitment, considered as the influx of juveniles into the adult population, is a process of crucial importance for the continuity of the fish stock and (b) populations under exploitation are naturally limited in a way that will permit them to respond in a compensatory way to fishing (Beverton and Holt, 1957; Ricker, 1975; Clark, 1976; Cushing, 1977, 1983; Rothschild, 1986; Beyer, 1988; 1989).

The Beverton and Holt (1957) and Ricker (1954) functions are two widely accepted approaches for describing the theoretical relationship between parental stock and recruitment. These classical models, which established a general theoretical framework for modelling recruitment dynamics, consist of extinction curves where recruitment reaches either an asymptotic maximum (Beverton-Holt) or become low at high spawning stock sizes (Ricker).

Clark (1976), De Angelis (1988) and Fogarty (1993) suggested that the classical models provided important

1054–3139/97/040427+17 $25.00/0/jm960193

insights into SR dynamics but may not include key factors of specific situations. Also, Gulland (1989) observed that these models continue, to a very large extent, to be used in providing quantitative advice to fishery managers.

Recruitment involves multiple interacting population groups and extrinsic variables which are continuously perturbed from some approximately known state via human induced and/or natural phenomena (Atkinson, 1987). A particular SR relationship might imply multiple equilibria, variable carrying capacity, compensation and depensation phases at several levels of numbers and other dynamic features which should be addressed.

Recruitment failures in Baltic cod (*G. morhua*) during recent years (ICES, 1992, 1993; Larsson, 1994) may show the need for a greater insight into its specific dynamics. There is an increasing body of evidence indicating that recruitment success in Baltic cod may be affected by fluctuations in salinity, temperature and oxygen contents at depths where the cod eggs are deposited (Bagge, 1993; Bagge *et al.*, 1993; Plikshs *et al.*, 1993; Waller *et al.*, 1993). Also, Carlberg and Sjoeberg (1992) observed that the water volume in the Baltic basins in which the cod eggs can develop until hatching, defined as "reproduction volume" (RV), is very limited. Moreover, Kosior and Netzel (1989) pointed out that the abundance of Baltic cod depends mainly on environmental conditions during the spawning period. Baranova and Uzars (1986) observed that variations in growth and maturation were due to density-dependent mechanisms: mean length, weight and annual growth zones of otoliths in 2–7-year-old cod were lower due to the appearance of strong year classes.

Furthermore, the abiotic environment seems to follow, beyond seasonal variations, medium- and long-term periodicities. Kalejs and Ojaveer (1989a,b) suggested that 8-, 15- and 23-year periods in winter severity and fresh water inflow into the Baltic Sea could cause appreciable changes in salinity, oxygen and heat content, vertical exchange and hence in the reproduction conditions to fish.

Hence, the premises to approach the SR relationship in Baltic cod, as we see them, may be as follows: (a) density dependent, short-term and (b) density-independent medium- and long-term oscillations; (c) variable carrying capacity; (d) multiple equilibria and (e) external conditions during spawning. These terms should be coupled into a relationship which configures a relatively complex, non-linear, dynamic system. The purposes of this study were (i) to investigate the stock and recruitment dynamics in Baltic cod, in light of our criteria, attempting to model the SR relationship out of the field data; (ii) to compare the goodness-of-fit from our approach to those from the models proposed by Shepherd (1982) and Myers *et al.* (1995) which unified the dome-shaped and asymptotic SR approaches by Ricker (1954) and Beverton and Holt (1957) and modified the Beverton-Holt functional form to allow for depensatory dynamics, respectively; (iii) to raise further discussion on issues concerning features in this particular SR relationship, where dynamic systems and chaos criteria will be addressed (Cook, 1986; May, 1976; Schaffer and Kot, 1986; Kot *et al.*, 1988; Rietman, 1989; Conan, 1994). Furthermore, we aim to put forward a simple model which may be useful in fisheries management and, beyond the classical models, is sufficiently flexible to enable us to qualitatively explain stock and recruitment in Baltic cod.

Background to the model

Spawning stock and recruitment series in Baltic cod from ICES fishery areas 25–32, years 1972–1993 (ICES, 1993) are shown in Figure 1 and the SR relationship for the same field data, interpolated by a cubic spline, is shown in Figure 2. This SR relationship is assumed to turn around a low and a high equilibrium state described as A and B, respectively. Also, it is further assumed that there are density-independent transitions between these equilibria: C and D, which may imply compensatory and depensatory phases, respectively. During these transition phases, when parental stock either increase (C) or decreases (D), recruitment remains relatively stable. However, as the equilibria (A, B) are reached, parental stock remains relatively stable whereas oscillations in recruitment become high. Furthermore, we used the Welch method (after Oppenheim and Schafer, 1975) to estimate the spectral density of both series (Fig. 3). It appears the method detected two maxima around the periods of 16 and 4 years, respectively. Hence, we base our approach on the assumption that the SR relationship in Baltic cod may be determined by the following factors: (i) in absence of extreme external perturbations, oscillations around equilibria (A and B in Figs 1, 2) may be induced by density-dependent mechanisms and are limited by a particular carrying capacity operating in each equilibrium state, and (ii) transitions between equilibrium states (C and D in Figs 1, 2) which may be determined by medium- and long-term cycles in the abiotic environment and by high fishing mortality during depensation phases.

The model

The SR relationship in our model is proposed to consist of two coupled, cyclic phenomena which operate similarly but in two different temporal scales and are due to different causal mechanisms. The suggested criteria are as follows.

(1) Highly non-linear, short-term (4–8 years) oscillations which may exhibit behaviour ranging from limit

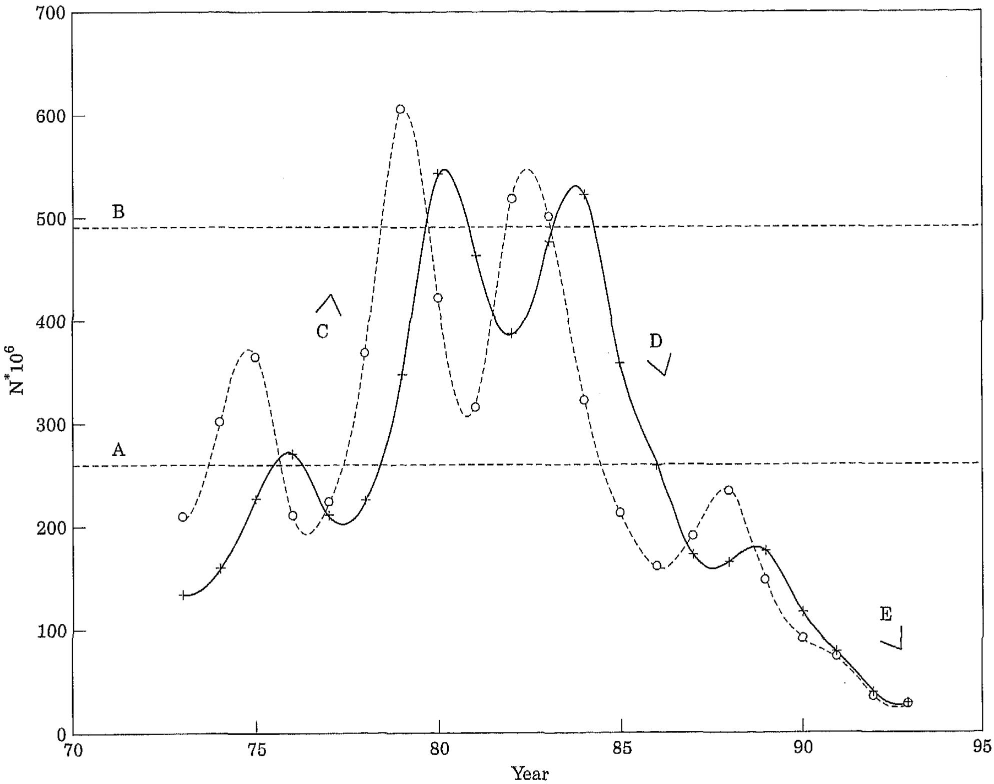

Figure 1. Spawning stock (dashed line) and recruitment (solid line) series in Baltic cod as estimated in fishery areas 25–32 for years 1973–1993 (after ICES, 1993). A and B describe the low and high equilibrium states, respectively. Density-independent compensation (C) and depensation (D) and inverse density-dependence (E) are indicated by the arrows. N=number of individuals.

cycles to chaos (A, B in Figs 1, 2). These are assumed to turn around stable, variable equilibria which are related to both variations in carrying capacity (K_i, i=1 ... m) and mean numbers in spawning stock and recruits. These oscillations within cycles may be induced by the interaction between population growth (compensatory phases) and density-dependent mortality (depensatory phases), the particular SR delay for Baltic cod (i.e. three years) and external short-term inputs. Also, a minimum viable population ($0<K_0$) is assumed under which stock and recruitment may not rehabilitate due to depensatory dynamics at low spawning stock sizes (E in Figs 1, 2), i.e. the SR relationship, being less sensitive to benign external conditions, may tend to zero (extinction of commercial fishery).

(2) A non-linear, medium-term (16 years), density-independent oscillation governed by the environment and by fishing mortality (C, D in Figs 1, 2). Due to cyclic environmental variations, carrying capacity is assumed to be variable allowing density-independent compensatory or depensatory effects between cycles towards higher and lower equilibria, respectively. As the SR relationship shifts to higher equilibria, the amplitude between maxima and minima may diverge. This divergence may, however, be limited by the maximum allowable carrying capacity (K_{max}), a threshold which may shift the SR relationship towards lower equilibria.

(3) During depensation phases, high fishing mortality and poor environmental conditions (henceforth referred to as negative perturbations) may affect the SR relationship by shifting the oscillations towards either lower equilibria or the minimum viable population (D, E in Figs 1, 2).

Also, dependence between stock and recruitment (SR dependence) is assumed to be stronger and less sensitive to external inputs while the relationship is either below the minimum viable population or when density-dependent mechanisms are operating. During transitions between equilibrium states, while $K_0<S<K_{max}$, the SR dependence may be weaker and more sensitive to

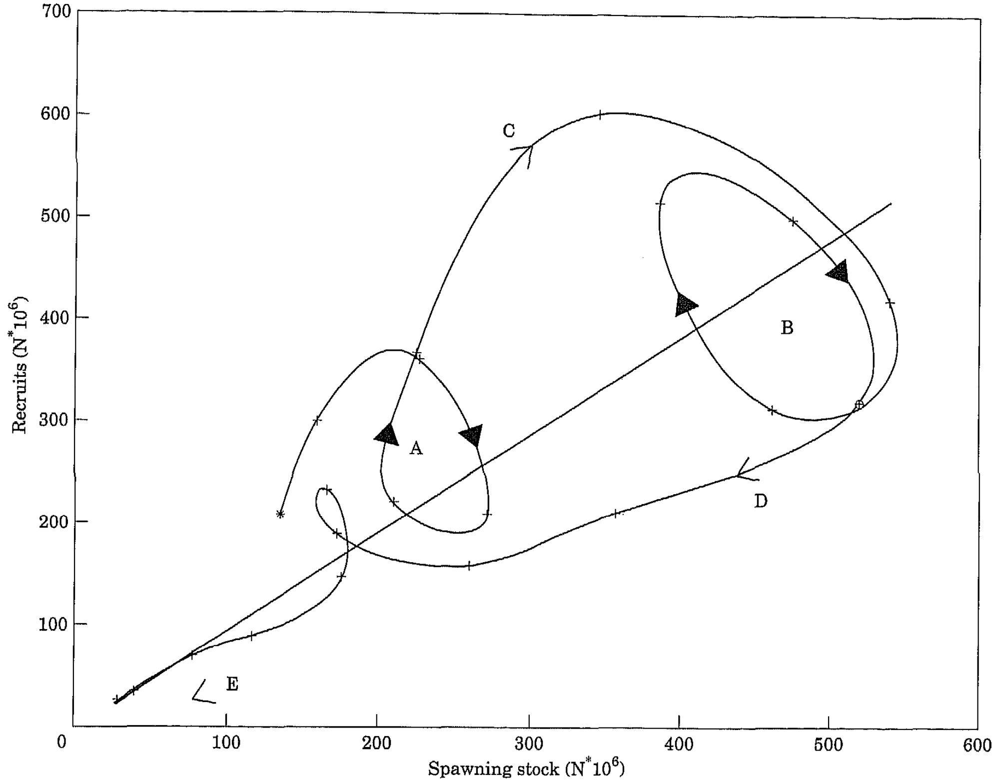

Figure 2. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25–32 for years 1973–1993 (after ICES, 1993) interpolated by a cubic spline. A and B describe the low and high equilibrium states (cycles), respectively. Density-dependent compensation and depensation within cycles are indicated by the closed arrows; density-independent compensation (C) and depensation (D) between cycles and inverse density-dependence (E) are indicated by the open arrows. The replacement line is given by a simple regression through the origin. N=number of individuals.

environmental variations. Furthermore, we should stress that K_{max} is considered, in our study, as a theoretical-only issue. We assume that the SR relationship will not tend towards K_{max} in a dynamic process permanently affected both by sinusoidally distributed external variables and relatively high fishing mortality.

A series of discrete equilibrium states may be induced by the interaction between spawning stock, recruitment and external variables which may affect the process. As external perturbations destabilize a particular equilibrium state shifting it either to its upper or lower limits, the SR relationship may evolve towards a new equilibrium. Thus, we consider that any particular equilibrium state in the SR relationship may be given by a maximum value of recruitment, an equilibrium point around which stock and recruitment oscillate and a critical stock density, K_i. Also, if the SR relationship either surpasses or shifts below any particular K_i, it may evolve towards a new equilibrium state with higher values of stock and lower values of recruitment. Furthermore, we assume that the SR relationship is limited by a ceiling or highest equilibrium state which bears both the maximum allowable recruitment, R_{max}, and carrying capacity, K_{max}. In this way, parental stock may increase until an equilibrium is reached whereby density-dependent depensation starts operating. Furthermore, shifts to higher equilibria (density-independent compensation) with higher carrying capacities may only occur when stock and recruitment increase due to benign external conditions. On the contrary, if external conditions (environment, fisheries) induce a density-independent depensatory effect, the SR relationship may shift to lower equilibria with lower carrying capacities.

To synthesize our criteria, recruitment, R, is defined in Equation (1) as the summation of non-linear functions of spawning stock, S, given by

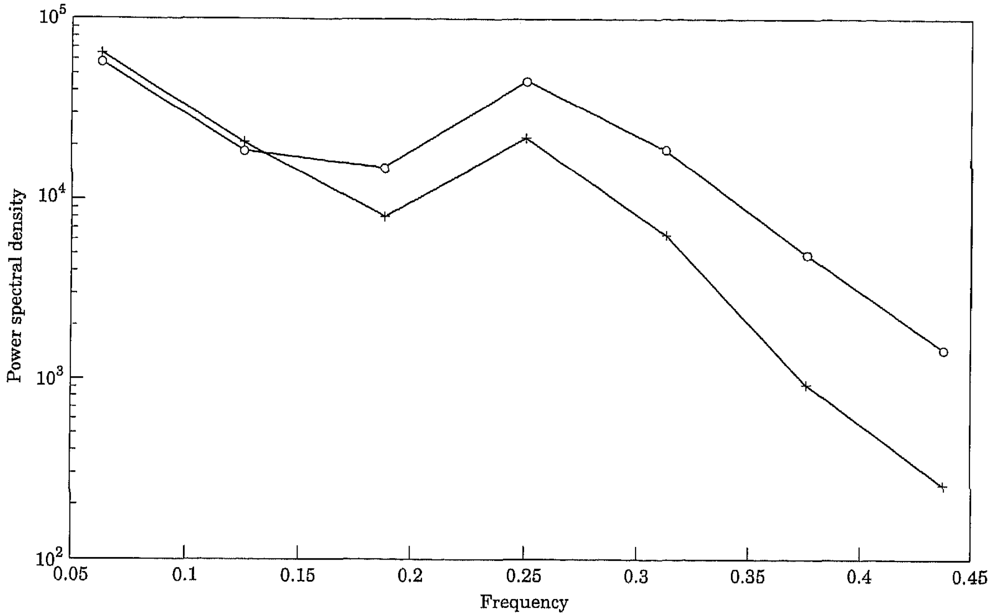

Figure 3. Estimated spectral density from spawning stock (+) and recruitment (O) series in Baltic cod as estimated in fishery areas 25–32 for years 1973–1993 (after ICES, 1993). Maxima were detected for periods of around 16 and 4 years, respectively.

$$R \cong \sum_{i=1}^{m} \frac{a_i \cdot (S)}{(S-b_i)^2 + c_i} \quad (1)$$

where the entries $i = 1 \ldots m$ represent the number of equilibrium states in the SR relationship and m is the highest equilibrium where the SR relationship reaches the ceiling or maximum allowable carrying capacity. Equilibrium states are controlled by the coefficients a_i (slope of the curve at the origin), with b_i and c_i being the density-dependent mortality entries. For instance, a_i fulfils a similar function to the natural rate of increase in the logistic equation. These coefficients will define each equilibrium state and their values may be fixed. Also, values of b_i will define the ranges of spawning stock for which equilibrium states may arise.

A case of Equation (1) with m equilibrium states is graphically represented in Figure 4. This case describes the SR relationship as a relatively complex dynamic system bearing several equilibrium states and which is characterized by the following features:

(1) K_m, K_{m-1}, K_{m-2}, which represent: (a) the minimum viable populations for the equilibrium states m, $m-1$ and $m-2$, respectively; (b) the values of spawning stock below which the relationship may shift towards lower equilibria; and (c) the carrying capacity for the immediate lower equilibrium state, respectively;

(2) E_m, E_{m-1}, E_{m-2}, E_0 which represent the equilibria around which the SR relationship turns in density-dependent compensation and depensation phases;

(3) K_{max} and K_0 are the ceiling and floor, respectively. K_{max} is the maximum allowable carrying capacity in the SR system and any values of stock surpassing this ceiling or upper limit will induce a shift towards lower equilibria. K_0 is the minimum viable population, a critical value and unstable equilibrium under which the SR relationship will tend to zero (extinction of commercial fishery);

(4) $R_{max} = R(K_{max})$ is the maximum allowable recruitment and any values surpassing this ceiling will either lead to lower equilibria or to extinction. Furthermore, $R_{m\,max}$, $R_{m-1\,max}$, $R_{m-2\,max}$ and $R_{0\,max}$ represent the ceiling in recruitment for their respective equilibria and the threshold above which the SR relationship may shift towards higher equilibrium states, $R_{m\,max} < R_{max}$. Also, as maximum recruitment values approach the replacement line, the SR relationship comes into a critical stage where perturbations may induce shifts to either higher or lower equilibria. In this way, the SR system defined by our functional form may allow for the continuity of stock and recruitment within a wide range of density-independent and density-dependent limits of variation. This flexibility to shift between equilibria allows the SR relationship both to evolve and return between higher and lower equilibrium states whereby the SR system may be persistent. Also, while the SR relationship is

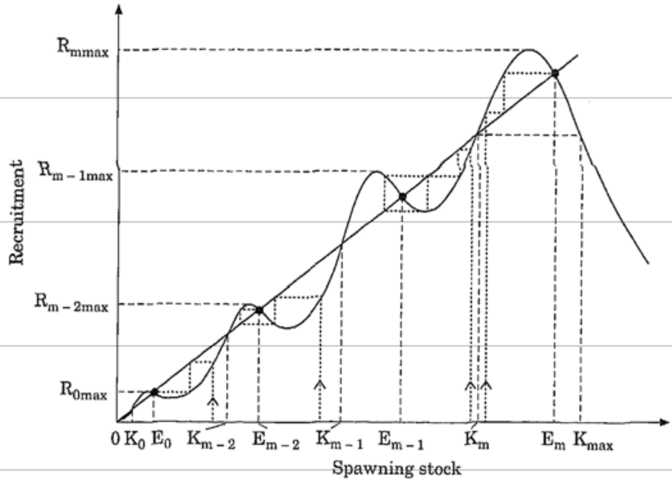

Figure 4. Graphical representation of the dynamic system with m equilibrium states (Equation 1) proposed for the SR relationship in Baltic cod in ICES fishery areas 25–32 for years 1973–1993 (after ICES, 1993). K_m, K_{m-1}, K_{m-2} represent both the minimum viable populations for the equilibrium states m, m − 1 and m − 2 and the carrying capacities for their immediate lower equilibria, respectively. E_m, E_{m-1}, E_{m-2}, E_0 represent equilibria around which the SR relationship may turn in density-dependent compensation and depensation phases. K_{max} is the maximum allowable carrying capacity and any values of stock surpassing this ceiling will induce a shift towards lower equilibria. K_0 is the floor or minimum viable population below which the SR relationship may tend to zero (extinction of commercial fishery). System persistence and local stability are shown in all three cases of stability analyses (dotted lines) while $K_0<S<K_{max}$ and $R(K_0)<R<R_{max}$. An m number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system.

below K_0, the extinction of the fishery, not of the stock, is invoked;

(5) Three cases of local stability analyses (dotted lines) are shown for the equilibrium states m, m − 1, m − 2 as well as the overall persistency while $K_0<S<K_{max}$ and $R(K_0)<R<R_{max}$.

To further analyse our model and to clarify the role of the coefficients a_i, b_i and c_i, a single equilibrium state (m=1) is described by Equation (2) (graphically represented in Fig. 5)

$$R \cong \frac{a \cdot (S)}{(S-b)^2+c} \quad (2)$$

where the numerator, or density-independent term, describes population growth when a>0, and the denominator describes the density-dependent mortality term for a particular carrying capacity. Furthermore, by making the right hand side of Equation (2) equal to zero, the intersection points with the replacement line, K_0 and E, become

$$K_0 = b - \sqrt{a-c} \quad (3a)$$

and

$$E = b + \sqrt{a-c} \quad (3b)$$

where a>c is the condition to allow the intersection. Also, adding expressions (3a) and (3b), the coefficient b, which is the middle point between the intersections, is given by

$$b = \frac{K_0+E}{2} \quad (4)$$

As the coefficient b is constant in the case described by Equation (2), the intersection points with the replacement line will be situated around b. Furthermore, the maximum value of spawning stock, S_{max}, for which there is maximum recruitment is obtained by making equal to zero the first derivative of function (2). Hence, S_{max} becomes

$$S_{max} = \sqrt{b^2+c} \quad (5)$$

which corresponds to the maximum recruitment given by

$$R_{max} = \frac{a}{2 \cdot (\sqrt{b^2+c}-b)} \quad (6)$$

As the parameter c tends to zero, recruitment will tend to infinity and S_{max} will tend to b. Also, R_{max} will increase with increments of both a (while b and c remain

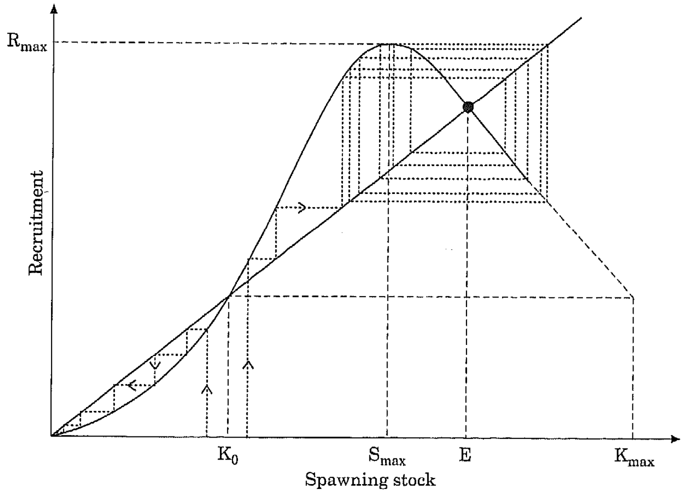

Figure 5. Graphical representation of an arbitrary single-equilibrium state (Equation 2). Stability analyses are shown by dotted lines. K_0=minimum viable population; E=equilibrium; K_{max}=maximum allowable carrying capacity; R_{max}=maximum recruitment. S_{max}=maximum spawning stock.

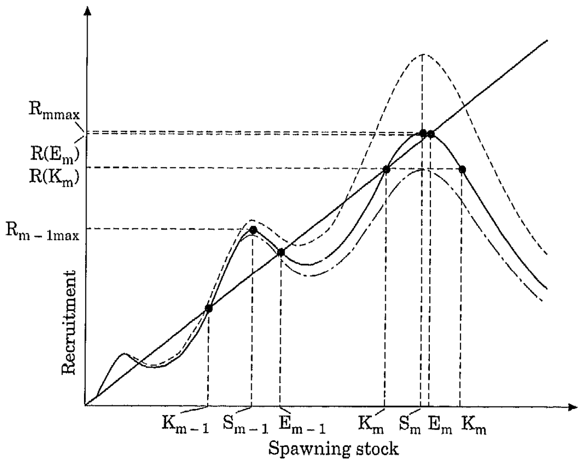

Figure 6. The SR relationship shaped by variations in the rate of increase a_m while the mortality parameters b_m and c_m are fixed. m and m − 1 are the equilibrium states; R=recruitment; max=maximum; E=equilibrium; K=carrying capacity; S=spawning stock.

either stable or constant) and with the difference between K_0 and E_m. Hence, while the slopes in an equilibrium state become steeper, the value of K_0 may either decrease or tend to zero whereas the maximum recruitment may increase. In this way, our functional form may include approximations to both Ricker's and the logistic approaches for high values of a, i.e. when recruitment success and carrying capacities are high due to extremely good external conditions and relatively low fishing mortality.

The functional form described in Equations (1), (2) formalizes some of our ideas about the SR relationship in Baltic cod. The function has clear maxima in stock and recruitment as well as a minimum viable population and allows for shifts between equilibria and complex behaviour.

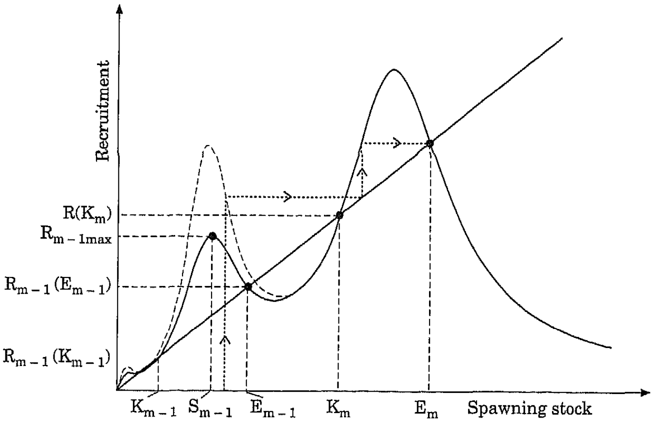

Figure 7. An example of transition between equilibrium states in the SR relationship. Increments of a_m over critical values may result in $R_{m-1\,max}>R(K_{m-1})$ followed by a shift to a higher equilibrium state. A case of transition is shown by the stability analyses (dotted lines). m and m − 1 are the equilibrium states; R=recruitment; max=maximum; E=equilibrium; K=carrying capacity; S=spawning stock.

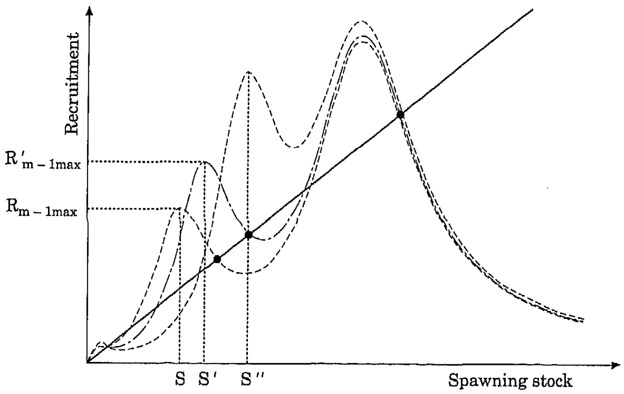

Figure 8. Example of transition in the SR relationship from the equilibrium state m − 1 (solid line) towards a higher equilibrium (m) through increments in both a_{m-1} and b_{m-1} (b, b′ . . . b″). R=recruitment; max=maximum; equilibria are indicated by the dots; S=spawning stock.

In Figures 6, 7 and 8, three cases of stock and recruitment are described for different values of the parameters a_i, b_i and c_i (Equation 1). Figure 6 shows three examples of how the SR relationship is shaped while a_m varies and b_m and c_m are fixed. An arbitrary value of a_m returned the SR relationship described by the solid line while variations of a_m for the other two cases were $a'_m=a_m+0.3*a_m$ (dashed line) and $a''_m=a_m-0.15*a_m$ (dotted-dashed line). For a'_m, $R_{m\,max}>R_{max}$ which causes spawning stock values to surpass K_{max} and be followed by a shift of the SR relationship towards the lower equilibrium state. For a''_m, $R_{m\,max}$ is below the replacement line which causes the equilibrium state m to disappear.

Figure 7 shows an example of transition in the SR relationship from the equilibrium state m − 1 (solid line) towards a higher equilibrium (m) through an increment in a_{m-1} (dashed line). The increment in a_{m-1} results in a $R_{m-1\,max}>R(K_m)$: This may imply that spawning stock values may surpass the carrying capacity (K_m) for the equilibrium state m − 1 and, hence, a shift towards the higher equilibrium, m, is induced. Furthermore, the model allows for situations of persistence within any one equilibrium state: the SR relationship may not shift towards higher equilibria if population increments are not sufficiently large. For instance, spawning stock values may range within the stability limits for a particular equilibrium state although there have been increments in recruitment (see the stability analyses in the figure).

Figure 8 shows another example of transition in the SR relationship from the equilibrium state $m-1$ (solid line) towards a higher equilibrium (m) through increments in both a_{m-1} and b_{m-1}. As external conditions allow sufficiently large increments in recruitment and spawning stock, a_{m-1} and b_{m-1} increase implying a shift towards a higher equilibrium. Also, the shift towards the higher equilibrium state may come about whenever spawning stock values have surpassed the replacement line. Furthermore, K_0 increases with the difference between K_0 and E_{m-1} whereby the SR system may shift from locally stable cycles to chaos.

We compared the goodness-of-fit from our approach (Equation 7) to those from the models proposed by Shepherd (1982, Equation 8) and Myers *et al.* (1995, Equation 9). We used the following functional form to fit the field data,

$$R \cong \frac{a_1 \cdot (S)}{(S-b_1)^2+c_1} + \frac{a_2 \cdot (S)}{(S-b_2)^2+c_2} \qquad (7)$$

where the entries R, S, a_i, b_i and b_i are those defined for Equation (1), assuming the SR series reflects two equilibria. Moreover, the Shepherd (1982) SR functional form is given by

$$R = \frac{\alpha \cdot S}{1+\left(\frac{S}{K}\right)^{\delta}} \qquad (8)$$

where R is recruitment, S is the spawning stock abundance, K the threshold abundance above which density-dependent effects dominate (i.e. the carrying capacity). The parameters α and δ are referred as the slope at the origin and degree of compensation involved, respectively. This approach could unify, within a single framework, both the classical dome-shaped (for $\delta>1$) and asymptotic (for $\delta=1$) functional forms proposed by Ricker (1954) and Beverton and Holt (1957), respectively.

Also, Myers *et al.* (1995) proposed an extension of the Beverton-Holt spawner and recruitment function modified to allow for depensatory dynamics. The functional form is given by

$$R = \frac{\alpha \cdot S^{\delta}}{1+\left(\frac{S^{\delta}}{K}\right)} \qquad (9)$$

where R is recruitment of new fish to the population; S is a metric spawner abundance; and α, K and δ are all positive parameters. Depensatory dynamics are characterized by $\delta>1$ and a sigmoidally shaped recruitment curve with an unstable equilibrium point at low spawning stock values.

The curve fittings on the spawning stock (age classes 4–9+"gr" or age classes>10) and recruitment (i.e. 3 year old cod) data (years 1973–1993) from fishery areas 25–32 in the Baltic (after ICES, 1993) are shown in Figure 9. Data values were fitted by least-squares according to Equations (7), (8) and (9). The replacement line is given by a linear regression through the origin. The Root Mean Square Error (RMSE) was used as a measure of the goodness-of-fit of the proposed models. Our approach fitted the SR data with a RMSE=93.12 while the functional forms proposed by Shepherd (1982) and Myers *et al.* (1995) showed RMSE=95.67 and RMSE=97.26, respectively. Furthermore, strong depensatory dynamics were detected on the SR series by the Myers *et al.* (1995) model which showed a $\delta=1.89$. This value of the δ parameter is similar to that reported by Myers *et al.* (1995) for stocks of *Culpea harengus* (spring spawners in Icelandic waters) for which depensatory dynamics were reported. Results are further summarized on Table 1.

Figure 9 shows the replacement line is crossed by density-dependent oscillations at two different levels of stock and recruitment (lower and higher equilibria). Also, the transition between the equilibrium states may be due to density-independent compensatory and depensatory effects induced by external inputs (environment and fishing mortality). In 1977, when the spawning stock was about to more than double, fishing mortality was higher (F=0.93) than during 1984 (F=0.90) when a shift to lower stock sizes followed. This may suggest both that higher fishing mortality is allowed during strong compensation (such as during 1977) and that a relatively minor reduction in the level of catches might not change the SR trend under density-independent depensation. Furthermore, fishing mortality had been relatively high during years 1980–1983 (≅3.8*10^5 Tn/year), when the SR relationship oscillated within the higher equilibrium state. The record annual catch (≅4.5*10^5 Tn) which followed in 1984 occurred during a period when the SR relationship was affected by two depensatory stages: (a) a density-dependent depensatory phase within the higher equilibrium state, and (b) a density-independent depensatory phase induced by negative trends in reproduction volume (RV), oxygen and salinity. Larsson (1994) reported a reduction of the reproduction volumes in the Bornholm, Gdansk and Gotland basins during years 1987–1993. According to our model, the combined effects from the negative perturbations may have induced a shift towards the lower equilibrium state which subsequently broke into a trend towards K_0.

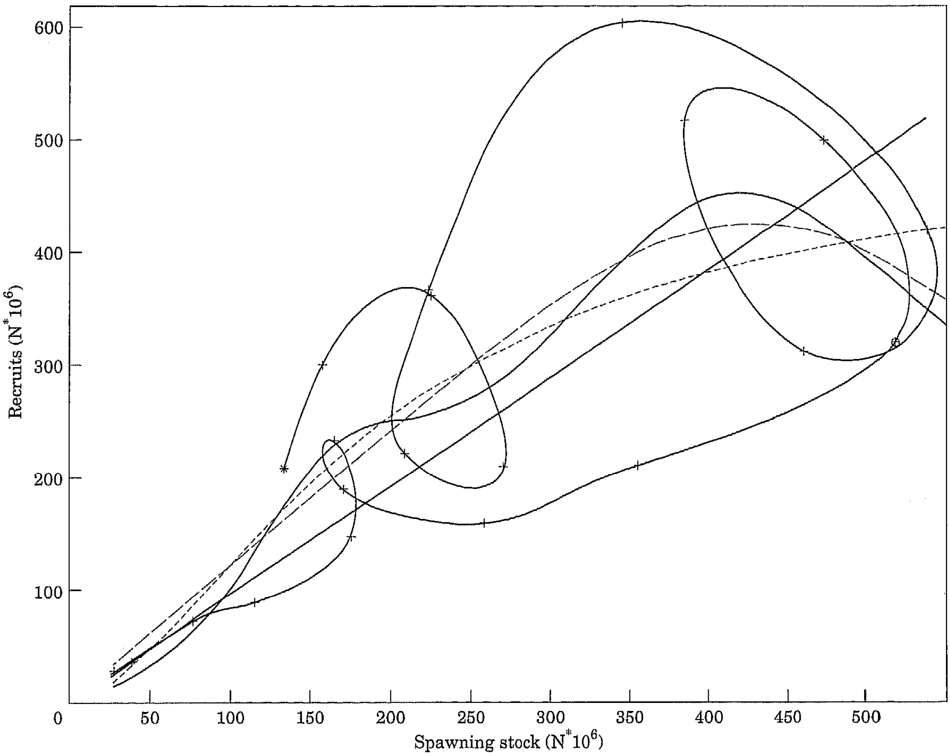

Figure 9. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25–32 for years 1973–1993 (after ICES, 1993) interpolated by a cubic spline and fitted by least-squares according to the functional forms proposed by the present model (solid line), Shepherd (1982, dashed line) and Myers *et al.* (1995, dotted line). Years of start of time series (1973) and record capture (1984, 4.5*10^5 Tn) are indicated by the asterisk and circle, respectively. The replacement line is given by a simple regression through the origin; N=number of individuals.

Simulation

In order to analyse the performance of our model, a simple numerical simulation is put forward. For simplicity, let consider the SR relationship as a two equilibrium system for which the parameters a_i, b_i and c_i are fixed and determine its stability limits. An external, sinusoidal perturbation will affect the SR relationship at three constant levels of mortality of spawning stock. To simulate these phenomena, we will use a delayed difference equation. In this way, the spawning stock at the beginning of any particular year, S_{t+1}, is given by

$$S_{t+1}=\sigma \cdot S_t+R(S_{t-\tau}) \tag{10}$$

where σ is the survivorship coefficient affecting the spawning stock, S_t, and recruitment is a function of the existing parental stock τ years before. Hence, recruitment is given by

$$R(S_t)=\frac{a_1 \cdot S_{t-\tau}}{(S_{t-\tau}-b_1)^2+c_1}+\frac{a_2 \cdot (1+P_t) \cdot S_{t-\tau}}{(S_{t-\tau}-b_2)^2+c_2} \tag{11}$$

where the entries a_i, b_i and b_i are those defined for Equation (1), τ is a fixed delay of three years (i.e. the age-at-maturity for Baltic cod) and P_t is a sinusoidal perturbation consisting of 20 values (graphically represented in Fig. 10). The iteration was carried out for 20 generations resulting in a time series of 400 values. The resulting SR relationships for $P_{t=1,\ 8,\ 13}$ (representing values around the mean (solid lines) as well as the lower (dashed lines) and upper (dashed-dotted lines) limits of the perturbation, respectively; circled in Fig. 10) and spawning stock trajectories for $P_{t=1}$ are shown in Figures 11 and 12.

Figure 11 shows the simulation output for a case where $\sigma=0.6$ (i.e. 40% of the spawning stock is harvested). The relatively low level of mortality of the spawning stock allows for high density-dependent

Table 1. Parameter estimates and goodness-of-fit as measured by RMSE (Root Mean Square Error) for the stock-recruitment functional forms proposed in our approach (Equation 7), Shepherd (1982), Myers *et al.* (1995) and a simple linear regression through the origin. Stock and recruitment series for Baltic cod from 1973–1993 in fishery areas 25–32 (ICES, 1993). All models were fit to the data using least-squares.

SR Model	Parameter estimates	RMSE
Equation (7)	a_1=6975.04, b_1=151.32, c_1=7042.91 a_2=6975.04, b_2=384.83, c_2=33 793.69	93.12
Shepherd (1982)	α=1.21, δ=5.43, K=564.87	95.67
Myers (1995)	α=0.026, δ=1.89, K=18 389.60	97.26
Regression	Slope (a)=0.96	101.94

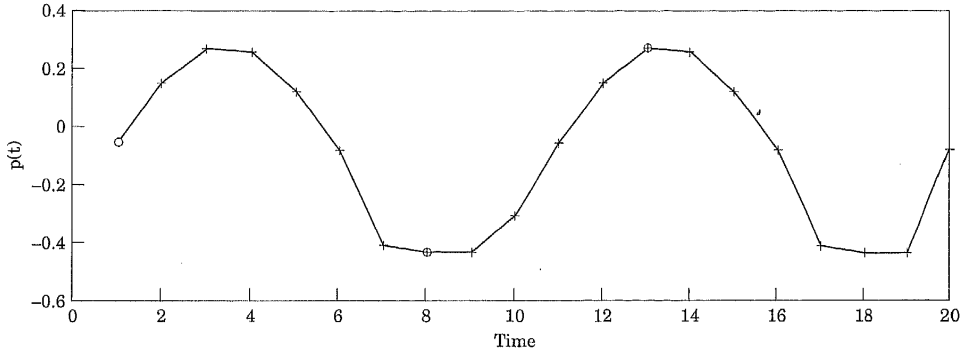

Figure 10. The sinusoidal perturbation P_t which affected stock and recruitment in the simulation. Circled values were chosen to plot simulation results (Figs 11, 12).

oscillations around a single, high equilibrium state. This simulation output could be approached by a classical dome-shaped SR model because the minimum viable population and possibility of depensatory dynamics become less clear and the high equilibrium state remains persistent while the SR relationship is affected by the lowest value of the perturbation (lower, dashed line).

Figure 12 shows the simulation output for a case where σ=0.3 (i.e. 70% of the spawning stock is harvested). The relatively high level of mortality of spawning stock combined to the effect of the perturbation returns the following limits for the SR relationship: (a) while the perturbation is positive, stock and recruitment turns around a higher equilibrium state (upper, dotted-dashed line) whereas the relationship turns around two equilibria (solid line) while the perturbation becomes less positive (i.e. when P_t approaches a value around the mean). The spawning stock trajectory shows the levels of stock which correspond to both of the equilibria. (b) Furthermore, while the perturbation becomes negative, the SR relationship turns around the lower equilibrium state (lower, dashed line) and the upper equilibrium state disappears. The situations described herein show a SR relationship which may shift to lower equilibrium states while harvests upon the spawning stock are relatively high and external perturbations become less benign. Moreover, the value of K_0 and likelihood of depensatory dynamics become more plausible under such conditions.

In Figure 13 the simulation output for the case where σ=0.05 (i.e. 99.5% of the spawning stock is harvested) is presented. The high level of mortality of the spawning stock implies the SR relationship turns around two equilibria (dotted-dashed and solid lines) at lower stock and recruitment levels. However, the SR relationship shifts to a lower equilibrium state with lower amplitude of variation while values of P_t become more negative (lower, dashed line) so that depensatory dynamics are more likely to occur.

The cases described in Figures 11–13 show a few of the possible outcomes of our model and how the combined effects from increasing fishing mortality as well as positive and negative environmental perturbations could affect stock and recruitment.

The present model may generate highly complex dynamics and, for simplicity, only the higher equilibrium state was perturbed as an example of a simple

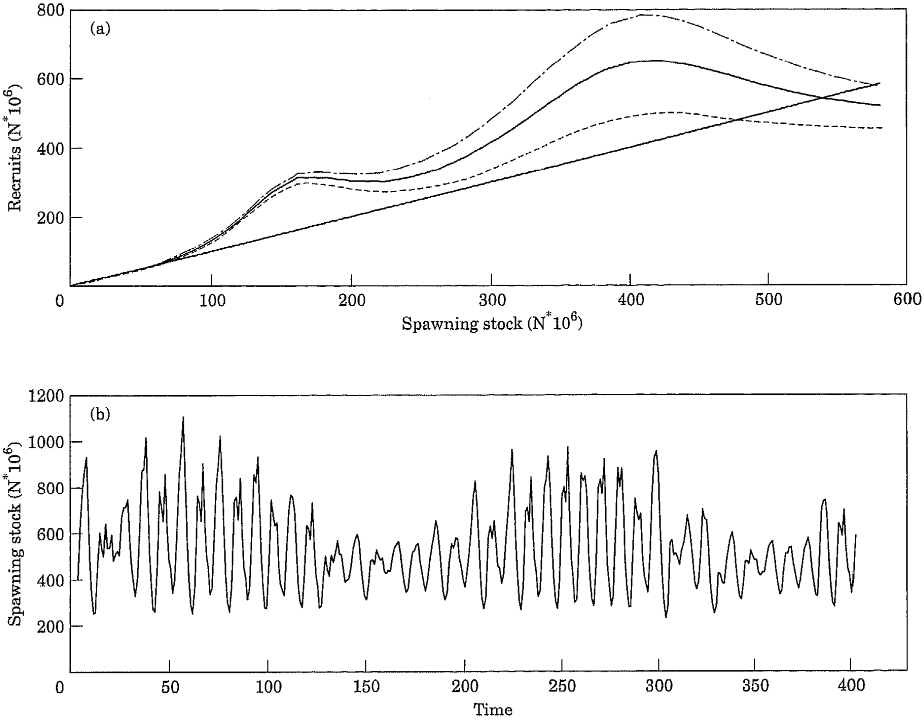

Figure 11. The stock-recruitment relationship (a) and spawning stock trajectory (b) in a simulation of a fish population which has survivorship $\delta=0.6$, age-at-maturity $\tau=3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (solid line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the solid line.

parametrization. However, it should be stressed that a parametrization to real world environmental perturbations may require that all parameters are affected by the external variables, subsequently increasing the degree of complexity of the output.

Discussion

Recruitment in Baltic cod may be considered as the final result of a three year long process which, we assume, may be mainly governed by external conditions and density-dependent mechanisms affecting age class 0.

Paulik (1973) described an overall spawner-recruit model which was formed from the concatenation of survivorship functions. This approach could exhibit multiple (stable) equilibria and complex dynamics and was the result of a multiplicative process where the initial egg production could be modified by non-linear functions specific to each life-stage and cohort-population size. In contrast, the model we put forward does not consider the underlying processes of mortality during the early life stages. This is due to the inavailability of 0-year class data on Baltic cod. However, our model may be justifiable on an ad hoc basis because of the flexibility it affords and should be considered from this standpoint. Also, it may offer some conceptual advantages over the model described by Paulik (1973) to approach the SR system in Baltic cod: (i) equilibria may be independent from each other; (ii) at any one moment, either a single equilibrium or several stable equilibria may operate for the overall stock-recruitment relationship; (iii) higher equilibria may disappear; (iv) transitions between equilibria may be more explicitly identified, described and mathematically controlled

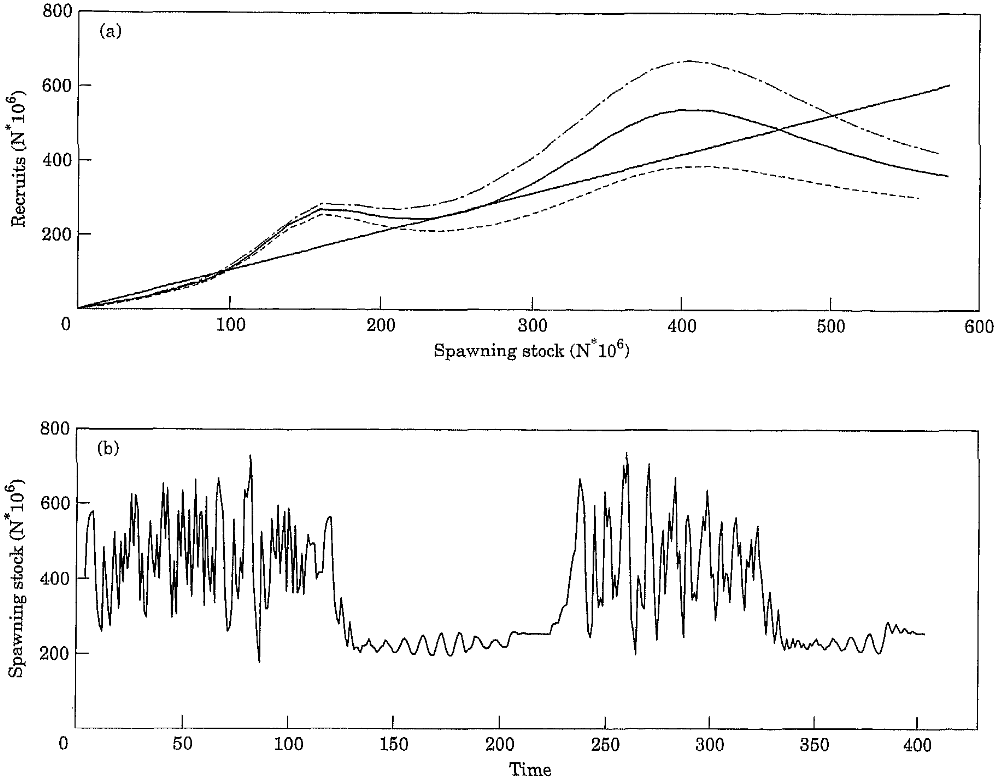

Figure 12. The stock-recruitment relationship (a) and spawning stock trajectory (b) in a simulation of a fish population which has survivorship $\delta=0.3$, age-at-maturity $\tau=3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (solid line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the solid line.

with regard to both density-dependent and density-independent inputs; (v) several maxima and minima may be described in the same relationship allowing for description of equilibrium states at different spatio-temporal scales, substocks and recruitment potential among different age classes; and (vi) depensatory dynamics are allowed.

Moreover, the functional form proposed by Shepherd (1982) could incorporate several (but not all) of the dynamic features identified in our study when extended to the following formulation

$$R=\frac{\alpha \cdot S \cdot e^{\varepsilon_t}}{1+\left(\frac{S}{K_t}\right)^{\gamma}} \tag{12}$$

where R, S and α are defined earlier and K_t is a time-varying, density-dependent parameter which can be related to the carrying capacity of the environment, c is a parameter controlling the degree of curvature of the function and ε_t is a random disturbance. Also, the time varying parameters could be expressed in a wave-like frequency domain. Within this framework, recruitment may display several (uncoupled) maxima and be related to varying carrying capacities and periodic environmental perturbations. However, the approach proposed by Shepherd (1982) and the above extension (Equation 12) could not incoporate either multiple stable equilibria or depensatory dynamics. Our model addresses dynamic features which, in part, may explain the phenomenology behind the SR relationship in Baltic cod.

Variable carrying capacity

This is, in our view, an important criterion in our approach: carrying capacity is regarded here as a critical

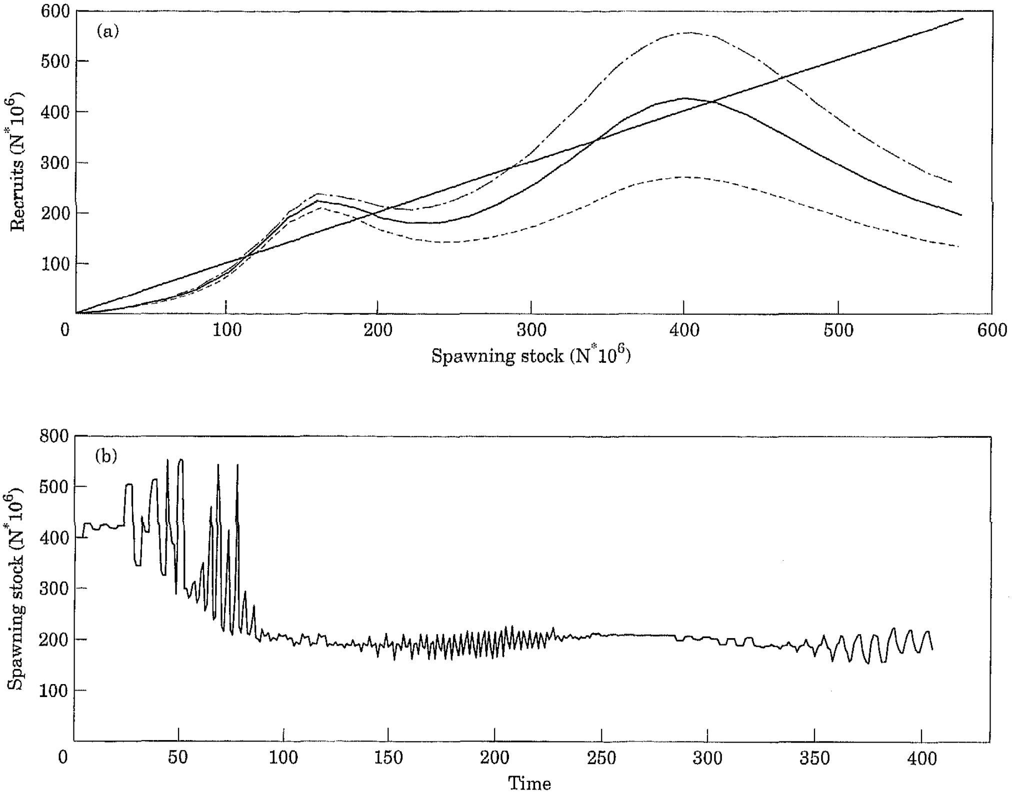

Figure 13. The stock-recruitment relationship (a) and spawning stock trajectory (b) in a simulation of a fish population which has survivorship $\delta=0.5$, age-at-maturity $\tau=3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (solid line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the solid line.

transition stage between different equilibrium states as well as a varying spatio-temporal parameter. As the particular carrying capacity for a given equilibrium state is reached, the SR relationship jumps on to the next equilibrium. Even the maximum allowable carrying capacity is assumed to allow for the transition to lower equilibrium states rather than shifting the SR relationship towards extinction. In our view, this is compatible both with the evident persistence in the SR relationship, dynamic features of external conditions (environment) and the barrier to spawning stock numbers imposed by high fishing mortality. Also, there are strong indications both in field studies on Baltic cod and oceanographic conditions suggesting that stock and recruitment may be affected by a variable carrying capacity; resource limitation may vary at several spatio-temporal scales during the time span of the SR series. Moreover, in light of how the SR series develops, we find indications to assume that each equilibrium state may be affected by a particular carrying capacity: density-dependent mechanisms may covary with environmentally induced effects upon spawning stock numbers and equilibrium states are expected to be related to different spatio-temporal ranges in resource utilization. For instance, there are two levels of maxima in recruitment at two significantly different levels of spawning stock numbers for which two carrying capacities may be invoked, respectively (Figs 1, 2). Also, the variable carrying capacity concept may become increasingly complex as we address spatio-temporal variations in stock and recruitment (fishery subareas) as well as different delays related to environmental conditions.

Multiple equilibria and chaos to cycles

In light of the classical models, the lack of causal relationships between stock and recruitment has led to the discussion on whether or not the recruitment process is deterministic (Kot *et al.*, 1988; Fogarty, 1993). In our view, stock and recruitment in Baltic cod may be a deterministic but highly complex phenomenon which is unpredictable in the long term. We propose the SR-system as a continuum ranging from chaos (the ceiling, when external conditions are extremely benign) going through a range of relatively stable, converging cycles (as external stress increases) to a quasi-standstill state with no clear oscillations (when K_0 is being approached). In this highly flexible approach, the SR relationship is allowed to evolve and return within a range of equilibrium states whereby it may be self-regenerated and persistent.

Conrad (1986), Schaffer and Kot (1986) and Kot *et al.* (1988) suggested that chaotic mechanisms would serve to maintain the adaptability of the population. Chaotic behaviour has earlier been proposed by May (1976) for laboratory and field populations of insects, by Powers (1989) for a two species system of fish and by Schaffer and Kot (1986) and Kot *et al.* (1988) for outbreaks of insects pests and of human diseases. Also, Berg and Getz (1988) suggested that stock and recruitment, in a sardine-like population, moved along a path or attractor in some higher dimension coordinate system and Conan (1994) observed that lobster and snow crab landings in Atlantic Canada may follow two orbits of stability or cycles.

Also, May (1974) showed that the logistic equation may produce highly variable outcomes when a simple deterministic feed-back over a time lag is introduced. In our approach, as delays and dependencies between age-classes are included, the (simulated) SR-system may become more sensitive to initial conditions and rapidly shift from relatively stable cycles into chaos. However, the SR data on Baltic cod may suggest that there are relatively wide tolerances for each of the proposed equilibrium states. This may be due to effects of "memory" both from density-dependent mechanisms and external inputs combined to delays. The concept of memory, in this context, refers to functions that describe inputs which may not jump but follow a relatively smooth, wave-like distribution pattern.

The proposed SR-system may, further, include all of the classical models. For instance, approximations to the Ricker and logistic approaches may be displayed by our model for high values of either or both a_i and/or b_i which may occur while environmental conditions are extremely benign. Also, while the SR relationship shifts to higher equilibria due to external, positive perturbations, oscillations may tend to become chaotic. We expect that a relatively high degree of variability in the SR relationship may reflect the dynamic process is healthy. Further, if the parameters of the model fall within the portion of phase-space leading to chaotic dynamics, the SR-system is allowed to rapidly shift between higher and lower equilibria. This implies an intrinsic feature in Equation (1) to describe several coupled cycles of different period length.

Also, there is no clear example of a chaotic pattern in the data, probably, due to actual stress conditions in the Baltic Sea and limited degrees of freedom in the time series. However, the amplitude of oscillations is higher for the high equilibrium state relative to the lower equilibrium. This could be regarded as an indication of a trend (from cycles) to chaos as external perturbations become more positive. Moreover, as external stress increases, stock and recruitment may develop towards lower equilibrium states with lower amplitudes of variation, approaching orbits of stability or limit cycles. In our view, the SR series analysed in this study may consist of two cycles and a depensatory trend towards K_0. In this case, further negative perturbations during depensation phases may imply that the SR system remains at excessively low equilibria, preventing the rehabilitation both of the stock and the commercial fishery.

Also, we assume that the SR-system is further affected by feedback mechanisms, multiple delays and non-linear relationships operating at several spatio-temporal scales, local and global stability and multiple memories related to the distribution of external perturbations. Bakun (1988) observed that recruitment does not reflect a single process but a large number of interacting processes. Our approach may be a flexible tool to allow the integration of such dynamic terms. Also, Conan (1994) pointed out that chaos theory applies to cases in which feedback mechanisms would affect the abundance of a species and that, in such cases, the oscillations of the system when it is affected by disturbances should be modelled.

Recruitment (overfishing), K_0 and depensatory dynamics

Models of population dynamics in which per capita reproductive success declines at low population levels (variously known as depensation, "Allee" effect, and inverse density dependence) predict that populations can have multiple equilibria and may suddenly shift from one equilibrium to another. If such depensatory mortality exist, reduced mortality may be insufficient to allow recovery of a population after abundancy has been severely reduced by harvesting (Myers *et al.*, 1995).

Beyond the classical models, our approach proposes a SR-system in which spawning stock may not rehabilitate if highly stressed during depensation phases. Sjöstrand (1989) reported that fishing mortality accounted for 3.8*10^5 Tn/year of Baltic cod during the years 1980–1983 followed by a record annual catch of 4.5*10^5 Tn in 1984. In our view, spawning stock was well rehabilitated during years 1980–1983. Oscillations around the higher equilibrium state seemed to fit and the system appeared to allow a fishing mortality which resulted in catches of around 3.8*10^5 Tn/year. However, the record catch in 1984 occurred under two depensatory phases: The higher cycle was under a density-dependent phase and spawning conditions were affected by negative trends in oxygen and salinity in the Baltic basins (for an overview on Reproduction Volume in the Baltic basins, refer to Larsson, 1994). This may have implied a shift to the lower equilibrium state. Thus, we suggest that due to the combined effects from negative perturbations (decrease of reproduction volume and high fishing mortality) during the depensatory phases, the lower cycle was broken, causing the SR relationship to shift towards the minimum viable population K_0. This situation, in our view, implies that stock and recruitment may have come to oscillate nearby K_0. However, if our criteria are theoretically correct, we may next expect a stock and recruitment rehabilitation to a low equilibrium state (similar to A, Fig. 1a,b) due to compensatory effects induced by the positive trends in reproduction volume, salinity and oxygen during the coming years. It is, however, important to stress that a fishery yielding a constant maximum may not be practicable on Baltic cod: while stock and recruitment comes into depensatory phases, the combined effect from high fishing mortality and environmental stress may come to either settle the SR relationship around lower equilibria or induce a shift towards K_0. This may negatively affect the outcome of the commercial fisheries once the stock becomes rehabilitated. Furthermore, it should be stressed that depensatory dynamics should not be assumed a priori in a general context for other species. Myers *et al.* (1995 suggested that estimates of spawner abundance and number of surviving progeny for 128 fish stocks indicated only 3 stocks with significant depensation. Moreover, the depensatory structure of the model is also dynamic. As the SR relationship tends to become chaotic at high equilibrium states, for instance when recruitment is high due to extremely benign external conditions, the value of K_0 will tend to zero. This implies a sufficiently wide tolerance to allow for perturbations (random or otherwise) which may be superimposed on the portion of phase-space describing the chaotic dynamics.

Acknowledgements

We would like to mention the following Senior scientists for their support: Dr Harry Dooley and Board of oceanographers from the International Council for the Exploration of the Seas (ICES, Copenhagen) who kindly provided the oceanographic data base for the Baltic Sea (years 1970–1993) for our preliminary and future studies on Baltic cod; Dr Per Olov Larsson (Institute of Marine Research, Lysekil, Sweden), Dr Gunnar Steffanson (Marine Research Institute, Reykjavik, Iceland), Dr José Castro (Fisheries Research Group, U. of Las Palmas, Canary Islands), Dr Fernando Fernandez (Non-linear mathematics, U. of Las Palmas) and both of the Anonymous referees for their useful comments and encouragement. Dr Henrik Sparholt (ICES, Copenhagen) is acknowledged for providing data on the Baltic cod. Special thanks to Systems Manager Dr Antonio Ocon and Dr Enrique Rubio-Royo (CICEI, U. of Las Palmas) for providing high quality electronic communications and computer support. Further, Eng. Eugenio Torres (School of Superior Eng., U. of Las Palmas) is acknowledged for programming routines to the early parametric approach to stock and recruitment in Baltic cod. This study was supported both by the Swedish National Board of Student Aid (CSN) and the U. of Las Palmas.

References

Atkinson, C. A. 1987. A nonlinear programming approach to the analyses of perturbed marine ecosystems under model parameter uncertainty. Ecol. Modelling, 35: 1–28.

Bagge, O. 1993. Possible effects on fish reproduction due to the changed oceanographic conditions in the Baltic Proper. ICES CM, P/J: 31.

Bagge, O., Bay, J., and Steffensen, E. 1993. Fluctuations in abundance of the Baltic cod (*Gadus morhua*) stock in relation to changes in the environment and the fishery. NAFO Scientific Council Studies, 18: 35–42.

Bakun, A. 1988. Recruitment in fishery resources and its relationships to environment: accessible pathways to greater insight. Memorias del Simposio Internacional de los Recursos Vivos y las Pesquerías en el Pacífico Sudeste. Viña del Mar (Chile) 1988.

Baranova, T., and Uzars, D. 1986. Growth and maturation of cod (*Gadus morhua callarias* L.) in the eastern Baltic. ICES Council Meeting, P/J: 7.

Berg, M., and Getz, W. 1988. Stability of discrete age-structured and aggregated delay-difference population models. J. Math. Biol., 26: 551–581.

Beverton, R. J., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food (London). Fisheries investigation series 2 (19).

Beyer, J. 1988. The stock and recruitment problem. Early life history symposium. ICES CM/P: 86.

Beyer, J. 1989. Recruitment stability and survival- simple size-specific theory with examples from the early life dynamics of marine fish. Dana, 7: 45–147.

Carlberg, S., and Sjoeberg, S. 1992. Is the reproduction of Baltic cod governed by oceanographic factors? ICES Marine Science Symposium, 195: 487.

Clark, C. 1976. Mathematical Bioeconomics: the optimal management of renewable resources. John Wiley and Sons Inc.

Conan, G. 1994. Can simple linear correlation satisfactorily detect environmental or interspecific effects on fisheries landings in a chaotic oceanic universe? ICES CM, P: 8.

Conrad, M. 1986. What is the use of Chaos? *In* Chaos: nonlinear science, theory and applications, pp. 1–14. Ed. by Arun V. Holden. Manchester University Press, UK.

Cook, P. 1986. Nonlinear dynamic systems. Prentice Hall International Series in Control Engineering. Prentice-Hall, UK.

Cushing, D. H. 1977. The problems of stock and recruitment. *In* Fish population dynamics, pp. 116–133. Ed. by J. A. Gulland. John Wiley and Sons Inc.

Cushing, D. H. 1983. Key papers on fish populations. IRL Press, Oxford, WA.

De Angelis, D. L. 1988. Strategies and difficulties of applying models to aquatic populations food webs. Ecol. Modelling, 43: 57–73.

Fogarty, M. 1993. Recruitment in randomly varying environments. ICES Journal of Marine Science, 50: 247–260.

Gulland, G. A. 1989. Fish populations and their management. J. of Fish Biol., 35 (Supplement A: 1–9). Ed. by C. E. Hollingworth and A. R. Margetts. The Fisheries Society of the British Isles.

ICES. 1992. ICES Cooperative Research Report. Reports of the ICES Advisory Committee on Fishery Management. 193, Part 2.

ICES. 1993. Report of the Working Group on the Assessment of Demersal Stocks in the Baltic. ICES CM/Assess: 16.

Kot, M., Schaffer, W. M., Truty, G. L., Graser, D. J., and Olsen, L. F. 1988. Changing criteria for imposing order. Ecol. Modelling, 43: 75–110.

Kalejs, M., and Ojaveer, E. 1989a. Long-term fluctuations in environmental conditions and fish stocks in the Baltic. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 190: 153–158.

Kalejs, M., and Ojaveer, E. 1989b. Major regularities in changes of environmental conditions and commercial fish stocks in the Baltic Sea. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 190: 250–262.

Kosior, M., and Netzel, J. 1989. Eastern Baltic cod stocks and environmental conditions. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 190: 159–162.

Larsson, P. O. 1994. Recent development of the cod stocks around Sweden and possible reproduction disturbances. *In* Report from the Uppsala Workshop on Reproduction Disturbances in Fish, 20–22 Oct. 1993. Ed. by L. Norrgren. Swedish Environment Protection Board, Report. 4346, pp. 26–34.

May, R. 1976. Simple mathematical models with very complicated dynamics. Nature, 261: 459–467.

Myers, R. A., Barrowman, N. J., Hutchings, J. A., and Rosenberg, A. A. 1995. Population dynamics of exploited fish stocks at low population levels. Science, 269: 1106–1108.

Oppenheim, A. V., and Schafer, R. W. 1975. Digital Signal Processing. Prentice-Hall, 556 pp.

Paulik, G. J. 1973. Studies of the possible form of the stock-recruitment curve. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 164: 302–315.

Plikshs, M., Kalejs, M., and Grauman, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. ICES CM, P/J: 22.

Powers, J. E. 1989. Multispecies models and chaotic dynamics. ICES CM P: 21.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559–623.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada., 191: 382 p.

Rietman, E. 1989. Exploring the geometry of nature: computer modeling of chaos, fractals, cellular automata and neural networks. Advanced programming technology series. Windcrest books, USA.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, USA.

Schaffer, W. M., and Kot, M. 1986. Differential systems in ecology and epidemiology. *In* Chaos: nonlinear science, theory and applications, pp. 158–178. Ed. by Arun V. Holden. Manchester University Press, UK.

Shepherd, J. G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. Journal du Conseil International pour l'Exploration de la Mer, 40: 67–75.

Sjöstrand, B. 1989. Information från Havsfiskelaboratoriet. Sammanställning över fiskbeståndens tillstånd i våra omgivande hav baserad på uppskattningar gjorda inom Internationella Havsforskningsrådet. Fiskeristyrelsen 1989: 2. Report from the Institute of Marine Research, Lysekil (Sweden). In Swedish.

Waller, U., Wieland, K., and Schnack, K. 1993. The survival of eggs and the hatching of larvae of cod (*Gadus morhua*) at different oxygen levels. ICES CM P/J: 21.