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CONSIDERATIONS OVER A NEW RECRUITMENT MODEL FOR EXPLOITED FISH POPULATIONS.

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CONSIDERATIONS OVER A NEW RECRUITMENT MODEL FOR EXPLOITED FISH POPULATIONS.

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Abstract. The stock and recruitment (SR) relationships in both Baltic and Icelandic cod are studied. In light of the field data, the relationships are assumed to turn around two orbits of stability or equilibrium states due to the interaction between density-dependent and density-independent compensation and depensation. A general framework is proposed where the SR relationship is considered as as multiple steady-state system which is described as a summation of non-linear functions allowing for stable, periodic and chaotic dynamics. The SR system is considered as a dynamic continuum, limited by a maximum allowable carrying capacity (K_{max}) and a minimum viable population (K_0) and may consist of multiple equilibrium states and carrying capacities: stock and recruitment may, persistently, evolve and return between the ceiling and floor of the system allowing for the description of highly complex dynamics. The conceptual advantages of the new framework are discussed.

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

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(1) INTRODUCTION.

What is recruitment ? It is a process which results in spawning stock increments due to reproduction activity. In the dynamics of fish populations, recruitment is a dependent variable which is directly influenced both by external and internal situations. The total biomass of the spawning stock depends on the temporal evolution and success of the recruitment process. Both of these aspects are highly relevant to fishery management and to the research of the correct model to describe the stock and recruitment relationship. Several periods are considered between the eclosion of eggs and recruitment of individuals to the population or fishery. At early life, the alevine is strongly influenced both by the environment and density dependence. However, the effect of external influences may decrease as the alevine grows. Environmental temperature, salinity and oxigen contents are external factors directly influencing the egg eclosion success. Also, the availability of adequate food items - quantity and size - is basic to survival during the early life. Other critical moments before recruitment are the vitellum exhaustion, methamorphosis and ossification stages as well as habitat changes.

(2) PREVIOUS RECRUITMENT MODELS.

Ricker (1954 and 1975) and Beverton and Holt (1957) proposed very simple, general stock-recruitment (SR) models: they established a general, theoretical framework for modelling recruitment dynamics and consist of extinction curves where recruitment becomes either low (Ricker) or reaches an asymptotic maximum (Beverton-Holt) at high spawning stock sizes. Furthermore, other authors have proposed models in a more exploratory context: Shepherd (1982) allowed several uncoupled equilibria and a variable carrying capacity. However, the model did neither allow linked equilibria nor inverse-density-dependence (decline of per capita reproductive success at low population levels). Also, Paulik (1973) described a general 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. However, the Paulik (1973) approach was not sufficiently flexible due to the interdependency between the functions in the multiplicative model and that it did not allow for inverse-density-dependence. Also, Myers et al. (1995) modified the Beverton-Holt functional form to allow for depensatory dynamics although the approach could not allow for multiple equilibria.

(3) PURPOSES.

The purposes of the present study were (i) to analyze whether the proposed framework is adequate to both Baltic and Icelandic cod; (ii) to examine whether there are any conceptual advantages over the classical models and (iii) to raise further discussion on the dynamic qualities of stock and recruitment.

(4) GENERAL FUNCTIONAL FORM OF THE PROPOSED MODEL.

In our approach, 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. The system is suggested to have the capacity to, persistently, evolve and return within a wide range of equilibrium states allowing for multiple carrying capacities and replacement lines as well density-dependent, density-independent and inverse-density-dependent coupled mechanics (Solari et al., 1997). (García, 5. 1998, Sharp, G. et al. 1983).

The proposed criteria may be described by the general functional form (Equation 1) where recruitment, R, is defined as the summation of non-linear functions (f_i) of spawning stock (S_i) given by

$$R \cong \sum_{i=1}^{m} f_i^{(g)}(S_i) \qquad (1)$$

where i = 1 ... m is the number of equilibrium states in the SR relationship, being m the highest allowed equilibrium where the SR system is limited by K_{max} and g represents the base function, $f_i^{(1)}$, proposed below.

(5) PREVIOUS CONSIDERATIONS.

To put forward the basic aspects of the new framework, data on both Baltic and Icelandic cod is considered.

(5.1) Study case: Baltic cod.

Spawning stock and recruitment series in Baltic cod from ICES fishery areas 25-32, years 1972-1993 (Anon, 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 increases *(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 (Figure 3): it appears the method detected two maxima around the periods of 16 and 4 years, respectively. Hence, we intend to base our approach in 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 Figure 1-2) may be induced by density-dependent mechanisms and are limited by a particular carrying capacity operating in each equilibrium state; (ii) Transitions between equilibrium states (*C* and *D* in Figure 1-2) which may be determined by medium- and long term cycles in the abiotic environment and by high fishing mortality during depensation phases.

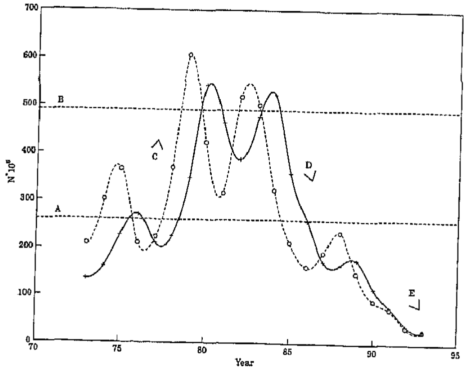

Fig. 1. Spawning stock (dashed line) and recruitment (unbroken line) series in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after ICES, 1993). A and B describe the low and high equilibrium states, respectively. Density-independent compensation (C) and depensation (D) and inverse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

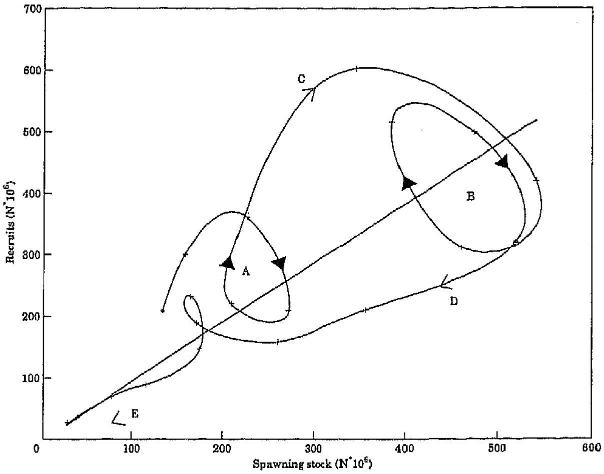

Fig. 2. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993) interpolated by a cubic spline. A and B describe the low and high equilibrium states (cycles), respectively. Density-dependent compensation and depensation within cycles 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.

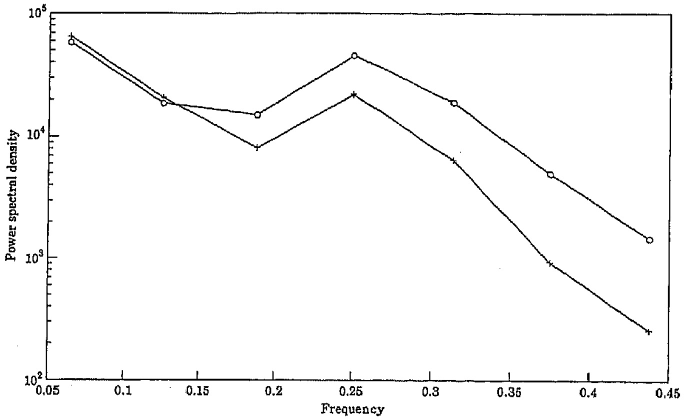

Fig. 3. Estimated spectral density from spawning stock (+) and recruitment (o) series in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993). Maxima were detected for periods of around 16 and 4 years, respectively.

(5.2) Proposed model.

The 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 mechanims:

(i) Highly non-linear short-term oscillations (4-8 years) which may exhibit behaviour ranging from limit cycles to chaos (A and B in Figure 1-2). Also, it is assumed that cycles turn around stable, variable equilibria which are related to both variations in the carrying capacity of the system (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 SR delay (which is three years in Baltic cod) and external short term inputs. Also, a minimum viable population ($0 < K_0$; E, Fig 1-2) under which stock and recruitment may not rehabilitate and the commercial fishery may tend to zero is assumed;

(ii) A non-linear, medium-term (16 years), density-independent oscillation governed by the environment and by fishing mortality (C, D in Figure 1-2). Due to cyclic environmental variations, carrying capacity is assumed to be variable allowing for density-independent compensatory and depensatory effects between cycles towards higher and lower equilibria, respectively. As the 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;

(iii) During depensation phases, high fishing mortality and poor environmental conditions may affect the SR relationship by shifting the oscillation towards either lower equilibria or the minimum viable population. Furthermore, we 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. We consider that any particular equilibrium state in the SR relationship may be given by a maximum value of recruitment, an equilibrium point (E_i) 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, respectively lower values of stock and recruitment. In this framework, each equilibrium or point in oscillation may be considered as an attractor.

In summary, recruitment, R, is defined in Equation 2 as the summation of non-linear functions of spawning stock, S, given by

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

where the entries i = 1 ... m represent the number of equilibrium states in the SR relationship, being m 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, related to the growth capacity), being b_i and c_i the density-dependent mortality entries. For instance, a_i fulfills 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:

(i) 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; (c) the carrying capacity for the immediate lower equilibrium state, respectively;

(ii) 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;

(iii) 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 (extintion of commercial fishery);

(iv) $R_{max} = R(K_{max})$ is the maximum allowable recruitment and any values surpassing this ceiling will either lead to lower equilibria or to extintion. 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 as 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 below K_0, the extinction of the fishery -not of the stock - is assumed;

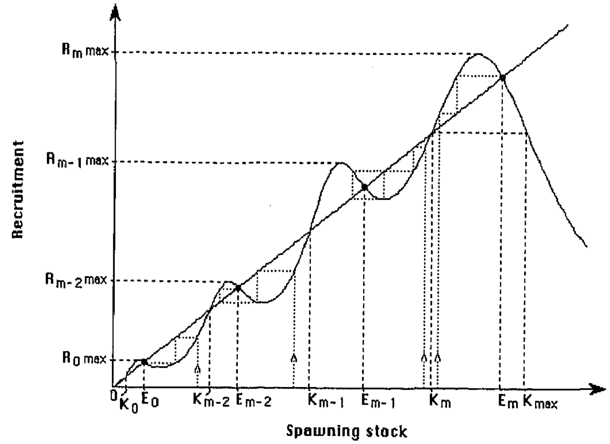

Fig. 4. Graphical representation of the dynamic sistem with *m* equilibrium states proposec for the SR relationship in Baltic cod in ICES fishery areas 25-32 for years 1973-1993. K_m, K_{m-1}, K_{m-2}, represent both the minimum viable populations for the equilibrium states m, m-1 and m-2 and the carrying 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 surpasing this ceiling will induce a shift towards lower equilibria. K_0 is the floor or minimum viable population below which the SR relationship may either cease to oscillate or then to zero (extintion fo commercial fishery). Sistem 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 sistem. After Solari et al., 1997.

(5.3)

To further analyze 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 3 (graphically represented in Figure 5)

$$R \cong \frac{a \cdot (S)}{(S-b)^2 + c} \qquad (3)$$

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

$$K_0 = b - \sqrt{a-c} \qquad (3\ \text{a.})$$

and

$$E = b + \sqrt{a-c} \qquad (3\ \text{b.})$$

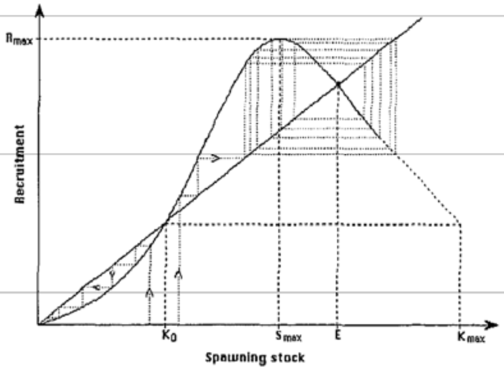

Fig. 5. Graphical representation of an arbitrary single-equilibrium state. Stability analyses is shown by dotted lines. K_0 = minimum viable population; E = equilibrium; K_{max} = maximum allowable carrying capacity; R_{max} = maximum recruitment.

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

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

As the coefficient b is constant in the case described by Equation 3, 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

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

which corresponds to the maximum recruitment given by

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

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 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 the Rickerian and 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 Equation 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. Also, our global functional form to fit the field data is given by

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

where the entries R, S, a_i, b_i and c_i are those defined for Equation 1, assuming the SR series reflects two equilibria.

On Figure 6, we may observe 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 (enviroment and fishing mortality). During the considered period, the SR relationship was affected by two depensatory stages: (i) A density-dependent depensatory phase within the higher equilibrium state and (ii) a density-independent depensatory phase induced by negative trends in oxygen and salinity. 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. In all oscillations, stock and recruitment will be found between $K_0<S<K_{max}$ and $R(K_0)<R<R(K_{max})$. Furthermore, the Root Mean Square Error (RMSE) was considered

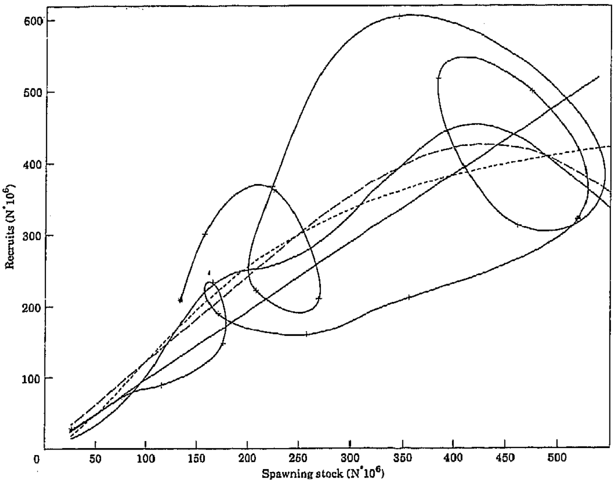

Fig. 6. Spawing stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (aster ICES, 1993) interpolated by a cubic spline and fitted by least-squares according to the functional forms proposed by the present model (unbroken line), Shepherd (1982, dashed line) and Myers (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.

as a measure of the goodness-of-fit of the proposed models. Our approach fitted the SR data with a RMSE = 93.1218 while the functional forms proposed by Shepherd (1982) and Myers et al. (1995) showed RMSE = 95.6728 and RMSE = 97.2648, respectively. Furthermore, strong depensatory dynamics were detected on the SR series by the Myers et al. (1995) model which showed a ä = 1.886. This value of the ä 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.

(6) STUDY CASE:

Icelandic cod. Spawning stock and recruitment series in Icelandic cod (numbers-at-age), years 1956-1997, are shown in Figure 7 (after ICES, 1997). We used the Welch method (after Oppenheim and Schafer, 1975) to estimate the spectral density of the smoothed SR series (Figure 8): although degrees of freedom were limited, peaks corresponding to periods of approximately 10 years were detected for both of the series. Also, the SR relationship from the field data, both interpolated by a

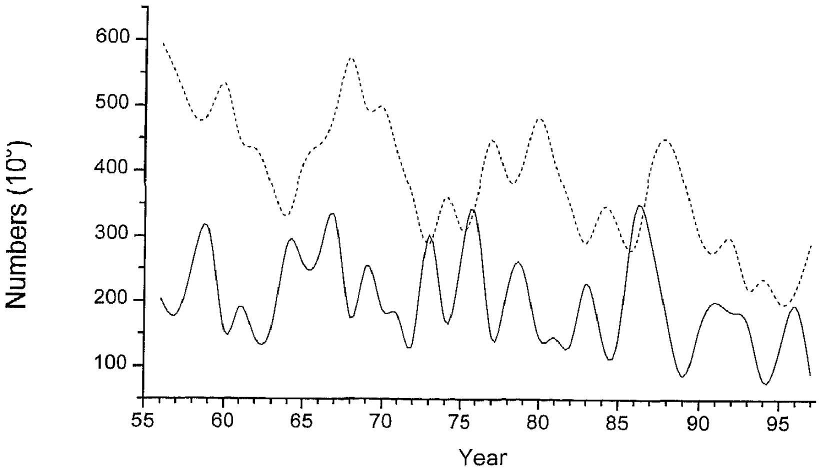

Fig. 7. Spawning stock (dashed line) and recruitment (continuous line) series in Icelandic cod (numbers-at-age), years 1956-97 (after ICES, 1997).

cubic spline and smoothed, is shown in Figure 9 where the following dynamic features are proposed: the present SR system is assumed to turn around two equilibria; a high equilibrium state (A) both at large and intermediate spawning stock levels and a low equilibrium (B), which arises during the late 1980's, with significantly lower numbers in both spawners and recruits. Furthermore, it is assumed that (i) each equilibrium state is limited by a particular carrying capacity which will variate as a function of external perturbations; (ii) oscillations, within equilibria, are due to density-dependent compensation (↑) and depensation (↓) as numbers increase and decrease, respectively; (iii) equilibria are linked through density-independent transitions due to compensatory (D, →) and depensatory (E, ←) mechanisms which arise when the external environment is either benign or disturbances increase, respectively. As the spawning stock either increases (D) or decreases (E), recruitment remains relatively stable. However, as the SR relationship settles onto new equilibria (A, B), recruitment variability becomes relatively high. Moreover, it is further assumed that (i) shifts towards lower equilibria may be induced by fishing mortality; (ii) the combined effects from both fishing mortality and environmental medium term disturbances may shift the SR system towards the low equilibrium state, observed at the present time and (iii) any additional disturbances, while depensatory mechanisms are operating, may imply further shifts towards the minimum viable population and, hence, the extinction of the commercial fishery.

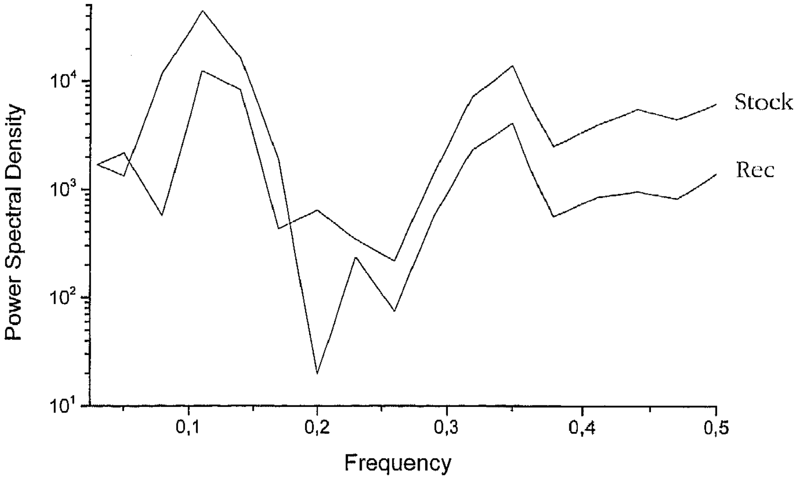

Fig. 8. The spectral density of the somoothed stock-recruitment series in Icelandic cod, years 1956-1997. The highest peaks correspond to periods of approximately 10 years. Stock = spawning stock; rec = recruitment.

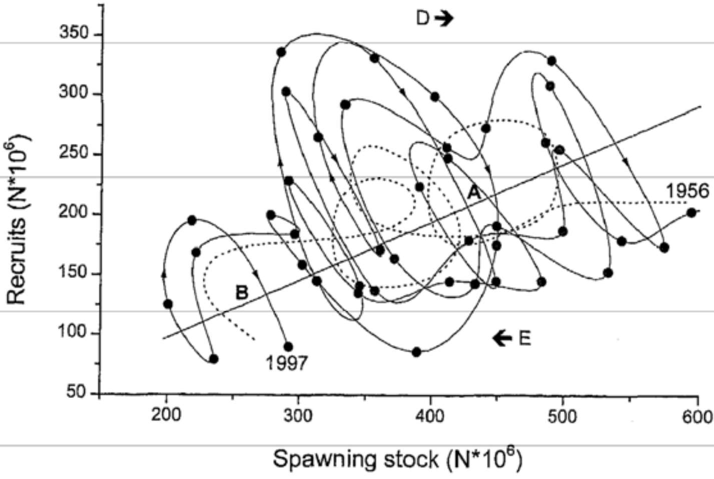

Fig. 9. The stock-recruitment relationship in Icelandic cod both interpolated by a cubic spline and smoothed (dotted line). a and B represent the high and low equilibrium states, respectively. Density-dependent compensation (↑) and depensation (↓) are represented by the arrows on the spline. Also, D (→) and E (←) represent density-independent compensatory and depensatory transitions; the 1956 and 1997 labels are the start and end year of the series, respectively.

(6.1) PROPOSED MODEL.

The SR system in this particular case, is proposed to consist of two kinds of coupled, cyclic phenomena which operate similarly, within the same temporal scale, but are due to different causal mechanisms. The suggested criteria are as follows:

(I) Highly non-linear, density-dependent medium term (≅ 10 years) oscillations which may exhibit behavior ranging from limit cycles to chaos (A-C in Figure 9): this kind of regular fluctuation is assumed to (i) turn around stable, variable equilibria (E_i, $i = 1 \dots m$) which are related to both variations in carrying capacity (K_i, $i = 1 \dots m$) and mean numbers in spawning stock and recruits; (ii) keep similar geometric distances in relation to the equilibrium state SR values are turning around, making up orbits of stability and (iii) be due to the interaction between density-dependent population growth (induces compensation), mortality (induces depensation) and delays between short and medium term external disturbances and recruitment. Also, a variable 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, a mechanism which may imply the extinction of commercial fishery;

(II). Compensatory and depensatory, density-independent transitions (≅ 3-5 years on either phase) between equilibria which make up medium term, non-linear oscillations, governed by both the environment and fishing mortality (D, E in Figure 9). As the time length of these regular variations may be shorter than that of density-dependent oscillations, we may propose either that different orbits of stability overlap or there is a single attractor operating over high and intermediate SR values which may shift due to fishing mortality. Furthermore, K_i is assumed to variate due to external cyclic, quasi-cyclic or random-shock perturbations inducing such density-independent transitions: as the external environment becomes either benign or more stressed, stock and recruitment may shift towards higher and lower equilibria, respectively. Also, fishing mortality is considered as an external perturbation limiting the carrying capacity of an equilibrium: as numbers decrease due to fisheries, the SR relationship may shift towards lower equilibria with lower carrying capacities. However, any shifts towards the ceiling of an equilibrium and, hence, towards higher equilibria may be limited by fishing.

Both of the described mechanisms are coupled due to the development of the dynamic system: the SR relationship may evolve and return within a wide range of stable, variable equilibria which are dynamically linked and partially dependent on each other. Both links and dependencies between equilibria may arise due to (i) the plasticity of individuals and the cohort-population to, gradually, adjust to external perturbations within a dynamic continuum; (ii) the interaction between critical thresholds allowed in each equilibrium state and (iii) dependencies due to the effects of past disturbances.

Also, as the SR relationship shifts towards the ceiling or carrying capacity (K_i) of a particular equilibrium state (E_i), the later switches from attractor to repellor allowing the shift to the upper equilibrium (E_{i+1}) which, now, becomes the new attractor. Furthermore, a similar mechanism may apply as the SR relationship shifts towards the floor of an equilibrium: as the carrying capacity (K_{i-1}) of the preceding equilibrium state is approached, E_i becomes a repellor and E_{i-1} an attractor allowing the shift towards the lower equilibrium state. Attractor-repellor switches may be caused both by the intensity and degree of external changes such as variations in K_i and levels of fishing mortality.

In the Icelandic situation is very possible the influence of the very important changes in the environmental conditional collision of the Inminguer current and polar current -soure hare important causeguencies in the reproduccion paterrns and recornitment ancly. This sitmetrive is in the other han strongly related with the intensity of fiwhing- figning sustralety. The combined sitrietiony explane the complexity of the model in Icelandic S/R relationship.

On Figure 10, we may observe two curve fittings representing the present, low and high (dashed line) equilibrium states. Each equilibrium incoporates it's own replacement line. We chose to represent both of the regimes separately due to the overlapping between the equilibrium states. In our view, the data may show the SR system in Icelandic cod is under K_{max} and governed by fishing mortality.

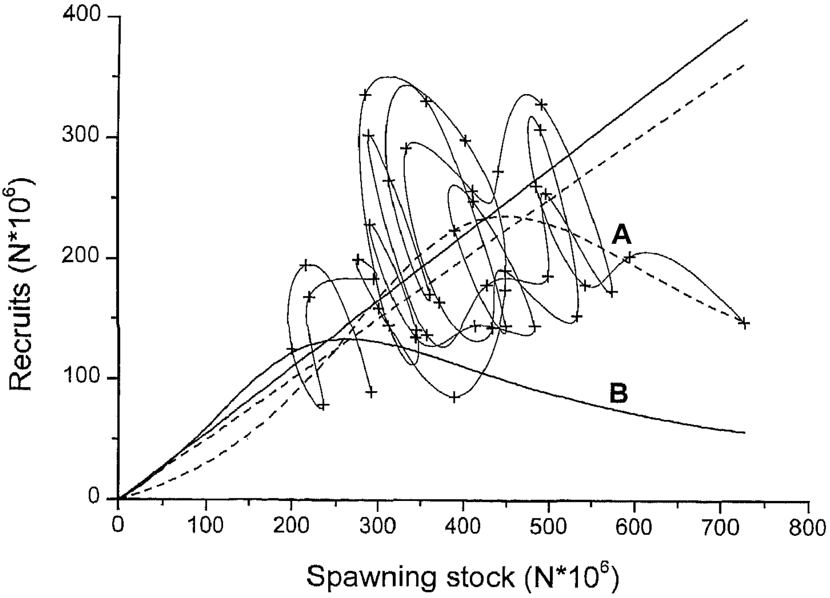

Fig. 10. The stock-recruitment relationship in icelandico cod both interpolated by a cubic spline and fitted by least squares on each equilibrium state with corresponding replacement line. A and B represent the high and low equilibrium states, respectively.

Within our framework, the carrying capacity in each equilibrium state is regarded both as a critical threshold allowing transitions between equilibria and a link between attractors and repellors. Also, the attractor is defined as a particular situation controlling each equilibrium level. Moreover, as the SR relationship shifts towards either higher or lower equilibria, the amplitude between maxima and minima may diverge and converge, respectively. Different orbits of stability may show different degrees of stretching (divergence) or shrinking (convergence) due to density dependence at higher and lower numbers, respectively. Also, stretching may be limited by K_{max} or highest allowed ceiling in the SR system, a threshold which will shift the SR relationship towards lower equilibria. Furthermore, shrinking may be limited by K_0 which is a critical threshold where density-dependent oscillations may cease, implying the extinction of the commercial fishery due to sustained low catches per unit of fishing effort. Moreover, K_0 is variable: while disturbances are low, it may tend to zero allowing a logistic kind of development within the lowest equilibrium state of the SR system whereas it will increase and become an unstable equilibrium as external stress increases. Hence, at low spawning stock and recruit numbers, our approach allows a minimum viable population which may either be relatively low while the external environment is benign or high as external stress increases. Also, K_0 may become an unstable equilibrium if the intensity of external disturbances (environment and/or fisheries) increase, upon the remaining of the spawning stock, implying a shift of the SR relationship towards zero. Otherwise, the combined effect from both fishing mortality and environmental stress may shift the SR system towards low equilibria implying the collapse of the fishery. Hence, it is, further, suggested both that (i) delays affecting stock and recruitment should be considered; (ii) high fishing mortality may be allowed during the late stages of strong compensation and (iii) a relatively minor reduction in the level of captures might not change the SR trend under density-independent depensation.

(7). GENERAL DISCUSSION.

The proposed general framework is similar for both of the case studies on Baltic and Icelandic cod and may be sufficiently general to describe stock and recuitment in several situations. The additive approach is flexible and may be appropriate to describe SR systems where the following is observed: (i) equilibria are clearly defined and orbits of stability either do or do not overlap; (ii) time span of the density-independent oscillations is relatively longer than that of the density-dependent; (iii) spawning stock and recruitment numbers are strongly or weakly related; (iv) recruitment remains at similar levels across several intermediate and high spawning stock densities, decreasing significantly once the SR system settles onto low equilibria at low spawning stock numbers; (v) the time spans of both density-independent and density-dependent oscillations are similar. Furthermore, the proposed framework allows to describe SR systems in (i) semi-enclosed areas such as minor seas, estuaries and lakes where K_i may be the main control factor. For instance, stock and recruitment may be governed by environmental perturbations such as changes in salinity, oxygen (the so "called reproduction volume" in the Baltic basins) and temperature as well as other variables which may significantly affect the dynamic process (winds, ice, nitrogen run-off among others). This might be the case for Baltic cod where salinity and oxygen-temperature may be limiting factors both for recruitment success, shifts towards higher equilibria and the rehabilitation of the spawning stock; (ii) in open areas where fisheries may limit shifts towards both K_i, upper equilibria and K_{max}. For instance, stock and recruitment may shift towards lower equilibria due to high and intense fishing mortality; however we may not know whether there are several overlapping equilibria or there is a single attractor operating at several levels of numbers until either a low equilibrium state or depensatory dynamics occur. This may be the case for Icelandic cod, a system whose orbits of stability are less discrete and which appear to be, mainly, controlled by fishing mortality rather than by changes in K_i.

Our model addresses dynamic features which, in part, may explain the phenomenology behind the SR relationship in both Baltic and Icelandic cod:

Variable carrying capacity. On the one hand, all components of an ecosystem may be interrelated and biomasses of populations may be limited by a global ceiling or global carrying capacity. Such a global ceiling is difficult to define as it may include an undetermined number of limiting factors of environmental and biological nature which may be interrelated in several scales or dimensions. A parameter which could describe the global carrying capacity might be the energetic or carbon flux through the system. However, these may be difficult to measure. On the other hand, each population or system, such as the stock and recruitment system, may be assumed to have a particular carrying capacity. This is a key concept in our approach. In general, carrying capacity may be regarded as a determining factor for different aspects of the dynamics of populations: growth, natural mortality, and, particularly, the level of recruitment are affected by external perturbations. The pre-recruitment period may be, specially, affected by negative perturbations. A complex problem is related to both the identification and values of this parameter. Possibly, the maximum biomass of the population could be a good indication. However, such values are obtained a posteriori and it would be useful to have a forecast of the carrying capacity of the system. In our approach, carrying capacity is regarded as a critical 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 onto the next equilibrium. Even the maximum allowable carrying capacity is assumed to allow for the transition to lower equilibrim states rather than shifting the SR relationship towards extintion. 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 in field studies suggesting that stock and recruitment may be affected by a non-steady 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 in Baltic cod for which two carrying capacities may be invoked, respectively. Also, the variable carrying capacity concept may become increasingly complex as we address spatio-temporal variations in stock and recruitment (fishery subareas and other spatial locations) as well as different delays related to environmental conditions. The new carrying capacity concept we put forward may be useful both to observe and describe different ecological aspects and their interrelationships in fish population dynamics. As far as field data is concerned, there is no reason to believe there is a single and steady carrying capacity governing the dynamics of fish populations.

Multiple equilibria and chaos to cycles. In light of the classical models, the lack of causal relationships between stock and recruitment has lead to the discussion on whether the recruitment process is deterministic (Kot et al. 1988, Fogarty 1993). In our view, stock and recruitment in both of the case studies may be a deterministic but a highly complex phenomenon which is unpredictable in the long term: We propose the SR-system as a dynamic 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. Rothschild (1992) suggested that populations reduced by fishing or antropogenic substances which compensate for reductions in vital rates may easily transit among stable, periodic and chaotic population dynamics. Garcia (1998) and Sharp et al. (1983) suggested that the Hokaido sardine series were characterized by loops and proposed an oscillating system consisting two strange attractors, linked by some transitional shifts, operating at two different levels of spawners and recruits. Conrad (1986), Schaffer (1986) and Kot et al. (1988) suggested that chaotic mechanisms would serve to maintain the adaptability of the population. Also, chaotic behavior has been proposed by May (1976) for laboratory and field populations of insects, by Powers (1989) for a 2 species system of fish and by Schaffer and Kot (1986) and Kot et al. (1988) for outbreaks of insects pests and of human diseases. Moreover, 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, Conan (1994) observed that lobster and snow crab landings in Atlantic Canada may follow two orbits of stability or cycles and Tyutyunov et al. (1993) demostrated cycles of different period and chaos in population dynamics of perch from 10 lakes. Furthermore, Caddy (1998) pointed out several other cases, in semi-enclosed areas, where SR dynamics could be linked to oscillatory phenomena: (i) an apparent 9-18 year periodicity for the Bay of Fundy scallop stocks (Caddy, 1979); (ii) a 12 year, fishing-effort-independent periodicity in the landings of both hake and red mullet at the island of Mallorca in the Mediterranean Sea (Astudillo and Caddy, 1986) and (iii) a 12-13 year oscillatory pattern in the catches of the Adriatic sardine.

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 sensible to initial conditions to rapidly shift from relatively stable cycles into chaos. However, the SR data on Baltic cod may suggest that there may be 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 which describe inputs which may not jump but follow a relatively smooth, wave-like distribution pattern.

Furthermore, the proposed SR-system may 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 instrinsic feature in the model to describe several coupled cycles of different period length. Moreover, there is no clear example of a chaotic pattern in the data, probably, due to actual stress conditions (environmental and high fishing mortality) 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 or quasi-cycles to chaos as external perturbations become more positive. Also, as external stress increases, stock and recruitment may develop towards lower equilibrium states with lower amplitudes of variation, approaching orbits of stability such as limit cycles, quasi-cycles or even a standstill point with no clear density-dependent oscillations. In our view, the SR series analyzed in this study may consist of two cycles and a depensatory trend towards K_0 in Baltic cod. A similar but less clear situation may occur in Icelandic cod where the influence of environmental conditions such as changes in the Irminger and other currents may be key factors affecting both the reproduction pattern and recruitment success. Also, the SR system in Icelandic cod may be strongly affected by the intensity of fishing mortality during the past 10-15 years. In both of these cases, further negative perturbations during depensation may imply that the SR system remains at excesively low equilibria, preventing the rehabilitation both of the stock and the commercial fishery. Also, we assume that the SR-system is further affected by feed back 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 feed-back 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.

It is, however, important to stress that a fishery yielding a constant maximum may not be practicable on either cod stock: while stock and recruitment comes into depensatory phases, the combined effect from high fishing mortality and environmental stress may come either to settle the SR relationship around lower equilibria or induce a shift towards K_0. This may affect negatively the outcome of the commercial fisheries once the stock becomes rehabilitated since the SR system may settle onto low equilibria with no clear density-dependent oscillations. Furthermore, it should be stressed that depensatory dynamics should not be assumed a priori in a general context for other species but it should be allowed in the theoretical framework as it can neither be ruled out a priori. 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 dynamic as well: as the SR relationship tends to become chaotic at high equilibrium states, for instance when recruitment is high due to extremely beningn 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.

In summary, our approach allows for the incorporation of different environmental and fishing situations into a relatively simple and highly flexible model. For some situations, K_i and K_{max} are key parameters as the SR system may be governed by the environment. For other situations, K_i may shift from "right to left" in the phase space due to either fisheries impact or the combined effect of high fishing pressure and negative environmental perturbations. Also, the proposed model is characterized by three important features: (a) It allows to explain changes in the SR relationship in agreement with different situations which may arise in the marine system. In each situation, the equilibrium point functions as a local attractor around which the density-denependent oscillations may become limited by a particular carrying capacity; (b) Denso-independent oscillations are assumed to be caused by either or both strong environmental or/and fishing impacts; (c) Due to external stress, the model allows the SR system to reach K_0 and, hence, the collapse of the commercial fishery. However, the SR system may become rehabilitated as the external environment becomes more benign. Moreover, the framework proposed by the model is compatible with previous, classical Beverton-Holt and Ricker approaches and allows a highly flexible system to evolve and return within a wide range of dynamical situations: these may include chaos, cycles, quasi-cycles down to a near-standstill situation with no clear oscillations as the system approaches K_0. Such dynamic features were not possible in earlier approaches.

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RESUMEN

Se estudia la relación entre el estoc reproductor y el reclutamiento (S/R) en la población de bacalao del Báltico y en la de Islandia. De acuerdo con los datos disponibles, se asume que esta relación está representada por dos órbitas de estabilidad como consecuencia de la interacción entre compensaciones y depensaciones denso-dependientes y denso-independientes. En el modelo propuesto la relación S/R es considerada como sistema múltiple de diferentes equilibrios, como suma de funciones no lineales que permiten situaciones dinámicas estables, periódicas o de dinámica caótica. El sistema S/R es considerado como un proceso dinámico contínuo limitado por una máxima capacidad de carga (Kmax) y una población mínima viable (Ko). Pueden existir múltiples estados de equilibrio unidos a diferentes capacidades de carga. Reproductores y reclutas pueden oscilar entre máximos y mínimos de un sistema con muy complejos procesos dinámicos. Las ventajas del modelo propuesto son consideradas.

RESUM

S'analitza la relación entre l'estoc reproductor i el reclutament (S/R) en les poblacions de bacallà del Bàltic i d'Islàndia. Les dades disponibles permeten considerar que aquesta relació està representada per dues òrbites d'estabilitat, resultat de la interacció entre compensació u depensació denso-dependents i denso-independents. En el model proposat la relació S/R es considerada com un sistema múltiple de diferents equilibris; suma de funcions no lineals que permeten situacions dinàmiques estables, periódiques o de dinàmica caòtica. El sistema S/R% es acceptat com un procés dinàmic continu limitat per una capacidad màxima de càrrega (kmax) i una població mínima viable (ko). Es podenm presentar varis estats d'equilibri així com diferents valors de la capacitat de càrrega. Reproductors i reclutes poden oscil·lar entre màxims i mínims en un sistema dinàmic molt complex. Les aventatges del nou model són examinades.