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On the Harvesting of Age Structured of Fish Populations

Research Article

H. Behncke¹ and Sadiq Al-Nassir^{1,2,*}

¹*Fachbereich Mathematik, Universität Osnabrück, Osnabrück, Germany*

²*Department of Mathematics, College of Science, University of Baghdad, Baghdad, Iraq*

***Corresponding author:** sadiq.naji@scbaghdad.edu.iq

Abstract. The yearly cycle of marine fish suggests to describe such populations by a discrete time dynamical Leslie model. The only nonlinear input into this model is the recruitment functions. Its influence on the stability of equilibria is investigated. We show that a monotone recruitment function leads to globally stable equilibria. Harvesting is introduced as fishing mortality so that the structure of the underlying model remains the same. The impact of the recruitment function is also discussed.

Keywords. Marine fish; Age class population model; Stability; Harvesting

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1. Introduction

Fish could be one of the most important sources of food for mankind, if properly managed. Now many fish stocks have been driven to low levels by overfishing, inadequate gear and mismanagement [11, 17, 18]. Mathematical models could make a great deal to derive optimal sustainable harvesting policies. An all encompassing model, which takes into account several species and economic as well as political aspects would be too demanding and complex. For

this reason we restrict ourselves to a simple but flexible model of a single fish stock. This is analyzed numerically in particular for populations of cod. However, the model is so general as to be applicable to other fish species. In [32] the authors have tested the model in extensive calculations of other fish stocks and species.

Mathematical models of fish have a long tradition, ranging from simple biomass, to rather detailed multi-class models [1, 3, 4, 30, 31, 33, 34]. Some of these papers study essentially only the properties of the underlying dynamical system [21, 40, 41], while others concentrate on harvesting and the maximum sustainable yield [14]. Excellent surveys can be found in the book of Clark [3], or the articles by Tahvonen [36] or Wilen [42]. Here we will mostly refer to the more recent papers by Li *et al.* [24], Diekert *et al.* [9, 10, 12] and by Tahvonen [38], Tahvonen *et al.* [39], and Quaas *et al.* [29]. They have developed specific age class models. But these apply only to the Norwegian or Baltic cod stocks.

The yearly cycle of marine fish suggests to describe such populations by a discrete time Leslie type model. Such matrix models have always been used in describing biological systems. See for example the books of Caswell [2] or Cushing [7] or the articles by Levin *et al.* [21] or Tahvonen [37–39]. Our plan is to develop a flexible Leslie type matrix model, which depends only on a few biological meaningful parameters. Even though it is applied to cod mostly, the model can easily be adapted to other fish populations for example herring, plaice or haddock. A key ingredient in this system is the recruitment function, which describes the development of fish from an egg to a first year adult. The recruitment function is the only nonlinear component of this model with profound effects on the dynamics and position of the equilibria. In the literature the Beverton-Holt or Ricker recruitment function are commonly used because of their mathematical simplicity. Other forms can easily be found.

This paper is designed as follows: In Section 2, the recruitment function is presented and the model is formulated. In Section 3, the stability of the model is investigated. It is shown that monotone increasing bounded recruitment functions give rise to a unique stable equilibrium. In Section 4, harvesting is introduced as harvesting intensity, which is a measure for the number of boats, size of gear and man hours which are employed in fishing. Thus, it can also be interpreted as fishing mortality [3], so that the underlying structure of the model remains the same. Also we discuss for the first time the impact of the recruitment function. A study of the equilibrium model is necessary in order to investigate the impact, range and sensitivity of the parameters.

Here the costs are linear function of the harvesting intensity or effort h . Finally, the numerical simulations for cod population illustrates our results.

2. The Recruitment Function and the Model

2.1 The Recruitment Function

The growth of fish is best described by the Bertalanffy growth equation, which gives the length $L(t)$ and by scaling the weight $W(t)$ as a function of the age t ,

$$L(t) = L_{\infty}(1 - e^{-K(t-t_1)}), \quad W(t) = W_{\infty} \left(\frac{L(t)}{L_{\infty}} \right)^3. \quad (2.1)$$

Here t is measured in years. L_∞, W_∞ are the maximum length and weight of the fish respectively. The parameters K and t_1 depend on the particular species of fish. More details about K and t_1 can be found in [1]. We assume that we have the age classes $1, 2, \dots, k$, and that $x_i(t)$ gives the number of fish in class i at time t . The parameter t will always be measured in years. While we allow a juvenile period of T_1 years, we will always assume the other age classes to be of one year only. Thus the maximum age of the fish species is $T_1 + k - 1$. We assume that the fertility begins with class 2. Then $x(t) = (x_1(t), x_2(t), \dots, x_k(t))$ gives the age distribution of the population at time t . For convenience we also assume that the sex ratio is 1 : 1 in the eggs. Thus, it was focused on the females only. The number of eggs $E(t)$ in year t is given by

$$E(t) = \sum_{i=2}^k F_i x_i(t), \tag{2.2}$$

where F_i denotes the average fecundity (number of eggs) per females of class i .

Fecundity is one of the most important aspect of fish reproductive biology. The number of eggs produced by a mature female is most likely proportional to its weight, because the gonads are heavily convoluted [1]. Thus we use proportionality to the weight as this is commonly done. But actual data of the striped bass in paper of Levin *et al.* [21] and cod in Diekert *et al.* [9] indicates that young fish are comparatively less fertile than their weight would indicate. This is probably due to the fact that the gonads take time to develop or that eggs of the young fish are less viable. We model this by the mitigating factors, p_i with

$$p_i = \begin{cases} \frac{i-1}{\tilde{s}} & : 2 \leq i < \tilde{s} \\ 1 & : i \geq \tilde{s} \end{cases} \tag{2.3}$$

where \tilde{s} is about one quarter of the maximum age of the fish species, $\tilde{s} \approx \frac{k+T_1-1}{4}$. Where \tilde{s} is chosen ad hoc for convenience, but leads to an adequate fit with actual fecundity data. Thus if there are no actual data on the fecundity available we write

$$F_i = c_1 p_i W_i, \quad i = 2, \dots, k, \quad W_i = W(i + T_1 - 1). \tag{2.4}$$

Here c_1 is a proportionality constant, which measures the number of viable eggs per unit weight of fish. W_i is the average weight for fish of age $i + T_1 - 1$ as given by the Bertalanffy formula (2.1) in class i . Of course if actual data on W_i or F_i are known, one should use these values. The general conclusions of this paper, however, are not affected by this. With this the number $E(t)$ of eggs produced by the entire stock is

$$E(t) = \sum_{i=2}^k c_1 p_i W_i x_i(t).$$

These eggs are put into the sea and fertilized. From the eggs larvae hatch, which metamorphose into juvenile fish. Most of the eggs, larvae or young fish are eaten, die of starvation or sickness. We express this through a factor c but also through the depensation function r , which measures the decrease of the larval and juvenile population caused by competition, starvation and sickness

at higher densities. The number of recruits for the following year is thus given by

$$\sum_{i=2}^k c c_1 p_i W_i x_i(t) r(E(t)) = c E(t) r(E(t)) = R(E(t)). \quad (2.5)$$

The function R is called the recruitment function, while r denotes its depensation part. It describes the development process from egg to juvenile fish, and young adult fish, respectively. Thus c can be interpreted as the probability of a viable egg to develop into young adult fish. Here we will define recruitment as recruitment into the adult class when fertility begins. Despite its importance the recruitment process is as yet poorly understood. So far it is generally described by the recruitment function $R(E)$, where $R(E)$ gives the number of adult fish which develop out of E eggs. The most commonly used forms are

$$R(E) = cE \left(1 + \frac{E}{E_0}\right)^{-1} \quad (\text{Beverton-Holt}) \quad (2.6)$$

$$R(E) = cE e^{-\frac{E}{E_0}} \quad (\text{Ricker})$$

Other forms are also possible for e.g. [16, 35]

$$R(E) = cE \left(1 + \left(\frac{E}{E_0}\right)^\alpha\right)^{-1}, \quad \alpha \geq 1 \quad (\text{Shepherd}) \quad (2.7)$$

$$R(E) = cE \left(1 + \frac{E}{E_0}\right)^{-\alpha}, \quad \alpha \geq 1 \quad (\text{Hassell})$$

while many other versions have been proposed for a global description of this rather complicated process. Here E_0 is a scaling parameter, which measures the depensation at higher level densities. Nevertheless a detailed analysis of the recruitment process is absolutely necessary. This also means that stability is independent of E_0 . It has the dimension of population and measures the onset of depensation. By scaling the dynamical properties of this model will be independent of E_0 . Even though the recruitment process is the fundamental importance for fish populations very little has been done yet to analyze it or to derive accurate forms of the recruitment function. In fact this paper seems to be the first in which the impact of the recruitment function on the equilibria, harvest etc is analyzed. A thorough understanding of R , however, is necessary for any serious modeling of fish populations. At the moment there are good indications that R is nearly linear for small E i.e. depensation at low population levels has not been observed [26, 27]. This is probably due to the fact that marine fish move in swarms or schools. That there is a depensations at higher populations levels is likewise accepted generally. This depensations is due competition among larvae, predation and to cannibalism against eggs or larvae. Even though the study of Cushing and Horwood [5] gives good discussions for a dome shaped curve, this is not conclusive yet, because there are too few high density catch data. In addition these data are scattered seriously. For this see e.g. the book by Cushing [6] the article by R. Myers in the Handbook of Fish Biology and Fisheries [19]. Note that the Ricker model leads to a dome shaped recruitment functions. So do the Hassell or Shepherd functions for $\alpha > 1$. In addition climate variations, piracy and the bycatch make catch data difficult to analyze. Here we shall mainly employ the Ricker version, because it is plausible and mathematically easy to handle. This of course applies to the Beverton-Holt function likewise. In fact it is mainly

their simplicity that leads to their general acceptance. As we will see later the choice of the recruitment function has a considerable influence on the population dynamics, equilibria and optimal harvesting. Nevertheless most modelers use either the Beverton-Holt form or Ricker form without much comment or justification. The choice of a realistic recruitment function, however, is impeded by a lack of high density data or realistic models of the recruitment process.

In order to complete the model we need to specify the mortality μ . Here μ is generally considered constant in contrast to well known mortality laws, e.g. the Gompertz law, used in biology elsewhere. Density dependence of μ has not been observed yet with marine fish, but it could easily be incorporated into the model. It is advantageous to express mortality in an exponential form because this permits a better description of harvesting so the survival goes through the factor $e^{-\mu} = \tilde{\tau}$.

2.2 The Model

With these preparations the model can be specified by

$$x_1(t + 1) = \tilde{\tau} \left(1 - \frac{1}{T_1} \right) x_1(t) + R(E(t)), \quad \tilde{\tau} = e^{-\mu}. \tag{2.8}$$

Here the number of recruits $R(E(t))$ is given by (2.5) and T_1 is the duration of juvenile stage. The first term $\sigma_1 = \tilde{\tau} \left(1 - \frac{1}{T_1} \right)$ represents the young fish that survive and remain in class 1.

For class 2 we have

$$x_2(t + 1) = \frac{\tilde{\tau}}{T_1} x_1(t) \tag{2.9}$$

because the part $\frac{\tilde{\tau}}{T_1}$ moves from class 1 to class 2.

For the remaining classes one has

$$x_i(t + 1) = \tilde{\tau} x_{i-1}(t) \quad i = 3, \dots, k \tag{2.10}$$

because all surviving class i fish are in class $i + 1$ after one year. This model is thus of the generalized Leslie [20] form and can be written as

$$x(t + 1) = A(x)x(t) \tag{2.11}$$

with

$$A(x) = \begin{bmatrix} \sigma_1 & r_2(x) & r_3(x) & \cdots & r_k(x) \\ \tilde{\tau}_1 & 0 & 0 & \cdots & 0 \\ 0 & \tilde{\tau} & \ddots & \vdots & 0 \\ \vdots & 0 & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & \tilde{\tau} & 0 \end{bmatrix}. \tag{2.12}$$

$\tilde{\tau} = e^{-\mu}$, $\tilde{\tau}_1 = \frac{\tilde{\tau}}{T_1}$ and $\sigma_1 = \tilde{\tau} \left(1 - \frac{1}{T_1} \right)$, $r_{i+1} = cF_{i+1}r(E)$, $i = 1, 2, \dots, k - 1$. Models like (2.11), (2.12) have been discussed in great details in [2, 7]. For the moment assume the r_i to be constant i.e. we are considering the population at low density. The matrix A is nonnegative, so that the Perron Frobenius theory can be applied [23]. The matrix A is primitive [2, 7]. In this case the spectral radius λ_A of A is an eigenvalue, which dominates all other eigenvalues λ , $\lambda_A > |\lambda|$. The associated eigenvector x_A has positive components only. If the r_i would not depend on E

the population would eventually grow with the factor λ_A and the population profile would be given by x_A . The λ_A is difficult to compute. In [7] Cushing has introduced the concept of net reproduction number n . To define it, one writes $A = \widehat{T} + F$, where \widehat{T} is the transition part and F the fertility part, all r_i 's of the matrix. Then $N = (1 - \widehat{T})^{-1}F$ is well defined, because $0 \leq \sigma_1 < 1$. It is nonnegative and of rank one and its Perron Frobenius eigenvalue is n . Cushing *et al.* [8] have shown.

Lemma 1. *The eigenvalue n of $N = (I - \widehat{T})^{-1}F$ satisfies $1 < \lambda_A < n$ iff $n > 1$, and $\lambda_A = 1$ iff $n = 1$. For $\lambda_A < 1$ one has $n < \lambda_A < 1$.*

Remark. The importance of the net reproduction value lies in the fact that it can be computed directly. In fact

$$n = (1 - \sigma_1)^{-1} \sum_{i=2}^k r_i L_i, \quad r_i = cF_i r(E), \quad L_i = \bar{\tau}_{i-1} \dots \bar{\tau}_1. \tag{2.13}$$

Thus n represents the number of offspring an adult generates throughout its lifetime, because L_i gives the probability to reach the age i while the r_i measures the number of eggs produced by a female of age i . The notations n goes back to [7].

It is advantageous to replace the above model by an equivalent one, which is more transparent and easier to handle. Let C denote the diagonal matrix

$$C = \text{diag}(1, L_2, L_3, \dots, L_k).$$

Then for $y = C^{-1}x$ we get

$$y(t + 1) = C^{-1}x(t + 1) = C^{-1}A(x)x(t) = C^{-1}ACy(t) = \tilde{A}y(t) \tag{2.14}$$

with

$$\tilde{A} = \begin{bmatrix} \sigma_1 & \tilde{r}_2 & \tilde{r}_3 & \dots & \tilde{r}_k \\ 1 & 0 & 0 & \dots & 0 \\ 0 & 1 & \ddots & \vdots & 0 \\ \vdots & 0 & \ddots & \ddots & \vdots \\ 0 & \dots & 0 & 1 & 0 \end{bmatrix} \tag{2.15}$$

and $\tilde{r}_i = cF_i L_i r(E)$, $i = 2, 3, \dots, k$. Thus \tilde{r}_i is the expectation value of the number of eggs coming from age class i . The following proposition summarizes the main properties of the above Leslie-Usher model (2.11), (2.12). The model (2.14), (2.15) will be called the standardized model.

For the standard form(2.15) the equilibrium vector is given by $\bar{y} = \bar{y}_1(1, \dots, 1)$ so that $1 = \sigma_1 + \sum_{i=2}^k cF_i L_i r(\bar{E})$ where $\bar{E} = \sum_{i=2}^k F_i L_i \bar{y}_1$ with $B_1 = \sum_{i=2}^k cF_i L_i$. This can be rewritten as

$$1 = \sigma_1 + B_1 r(\bar{E}) \quad \text{and} \quad \bar{E} = r^{-1} \left(\frac{1 - \sigma_1}{B_1} \right) = c^{-1} B_1 \bar{y}_1. \tag{2.16}$$

At this point one has to fix the recruitment function. In most cases we will use the Ricker function with

$$r(E) = e^{-\frac{E}{E_0}}. \tag{2.17}$$

E_0 appears as the maximum of R and in concrete cases this would be the means to determine it. This form of the Ricker recruitment thus separates the two properties, fecundity at low density as measured by the natural reproductive number (2.13) and depensation at high densities expressed through E_0 , in a product form. This of course also holds for the other recruitment functions likewise. With r as in (2.17) we get for the equilibrium values

$$\bar{E} = E_0 \ln\left(\frac{B_1}{1-\sigma_1}\right), \quad \bar{y}_1 = \left(\frac{cE_0}{B_1}\right) \ln\left(\frac{B_1}{1-\sigma_1}\right). \tag{2.18}$$

It follows from (2.16) that depensation functions with a faster decay will result in smaller equilibrium values \bar{E} and \bar{y} . The corresponding values for the Beverton-Holt function are $\bar{y}_1 = \frac{\bar{E}c}{B_1}$, $\bar{E} = E_0 \left(\frac{B_1}{1-\sigma_1} - 1\right)$. A Beverton Holt model will thus always predict higher catches than its Ricker counter part, if both are based on the same natural reproduction number n . For this see also Figure 1. From work of R. Myers [27] n can be determined well. The high density behaviour of R is extremely insecure as can be seen from the data of Cushing [6] or the article of R. Myers [27]. Thus we are far from determining the recruitment function from actual data. Even though E_0 acts as a scaling parameter, it is an important invariant for the particular stock. Whereas a large E_0 describes favourable environmental condition for the larvae. In as much as there is a large variation of n , we can also expect a similar large variation in E_0 . Ultimately E_0 and more generally the recruitment function can only be determined from the actual catches.

3. Stability Analysis

The most important property for an equilibrium \bar{x} in a dynamical system is its stability. Natural populations are always subject to external perturbations. Thus stability is important for concrete applications. In particular stability is relevant if the analysis is mainly restricted to equilibrium solutions. For local stability of the equilibrium one uses the Jacobi matrix at the equilibrium. For this we refer to the book of Cushing [7]. The problem with the Jacobian's is that they do not permit to determine the domain of attraction. For this the method of the Lyapunov function would be better suited. Here such functions, however, are difficult to come by with this model. Local stability holds if the spectral radius of the Jacobian is strictly less than 1. The simplest result for our model is

Lemma 2. *Assume we have $\frac{dR}{dE}(\bar{E}) \leq 0$, and $\sum_{i=2}^k (2r(\bar{E}) + \bar{E}r'(\bar{E}))cF_iL_i > 0$, then the equilibrium value is locally stable.*

Proof. Assume $-\sum_{i=2}^k \left(2r(\bar{E}) + \bar{E} \frac{dr(\bar{E})}{dE}\right) cF_iL_i < 0$. Together with the equilibrium condition

$$1 = \sigma_1 + \sum_{i=2}^k cF_iL_i r(\bar{E}).$$

This gives $-\sum_{i=2}^k \bar{E} \frac{dr(\bar{E})}{dE} cF_i L_i < 2(1 - \sigma_1)$, and $2\sigma_1 - \sum_{i=2}^k \bar{E} \frac{dr(\bar{E})}{dE} cF_i L_i < 2$. Then

$$\sigma_1 - \sum_{i=2}^k cF_i L_i r(\bar{E}) - \sum_{i=2}^k \bar{E} \frac{dr(\bar{E})}{dE} cF_i L_i < 1$$

so that

$$\sigma_1 - \left(r(\bar{E}) + \bar{E} \frac{dr(\bar{E})}{dE} \right) \sum_{i=2}^k cF_i L_i < 1$$

but $\frac{dR}{dE}(\bar{E}) = c \left(r(\bar{E}) + \bar{E} \frac{dr(\bar{E})}{dE} \right) \leq 0$, hence $\sigma_1 + \sum_{i=2}^k |V_i| < 1$, and the result follows because all eigenvalues are strictly less than 1. □

The next lemma on local stability can be found in [21].

Lemma 3. *For the Ricker recruitment function the nontrivial equilibrium value is locally stable if $0 < \ln(n) < 2$.*

We conjecture that these conditions for local stability also result in global stability. These propositions underline again the importance of the recruitment function for the dynamics, and the stability (2.16).

For $n = 1$, the following results are new and underlines again the importance of the recruitment function.

Theorem 1. *Assume the recruitment function R is bounded and continuous such that $r(E)$ decreases to 0 strictly monotonically. Then all solutions are bounded. If the net reproduction number at zero density (2.13) satisfies $n \leq 1$ the trivial equilibrium is globally stable. This holds also for the model with density dependent transmission coefficients \tilde{r}_i , if $\partial_{x_i}(\tilde{r}) \leq 0$.*

Proof. It follows from the first equation in (2.11) that $x_1(t)$ is uniformly bounded. Since the transmission coefficients are bounded, all $x_j(t)$ are uniformly bounded.

Now use the standardized model. Assume the zero density natural reproductive number n , which given by (2.13) with $r(0) = 1$, satisfies $n \leq 1$. Then all rows in \tilde{A} have a sum less or equal to 1. Let $y(0)$ be in arbitrary initial state and let Ω be its ω -limit set. Ω is compact and $E(t)$ is a continuous function on Ω . Let E_1 be its minimal value on Ω . $E_1 = 0$ would imply $y_2 = y_3 = \dots = y_k = 0$. Such states, however, are not in the range of \tilde{A} . Thus $E_1 > 0$ and the sum of the first row in \tilde{A} , $\sigma_1 + \sum_{i=2}^k cF_i L_i r(E) < 1$. Thus there exists a $\delta > 0$ such that with $C = \text{diag}(1, (1 + \delta)^{-1}, \dots, (1 + \delta)^{-(k-1)})$, the matrix $C\tilde{A}C^{-1} = B$ has a row sum of less than one in each row. Thus there is a matrix norm $\|\cdot\|$ with $\|B\| < 1$. Hence $B^n \rightarrow 0$ and $\tilde{A}^n \rightarrow 0$ and Ω consists only the trivial solution, because Ω is \tilde{A} invariant. □

Remark. Theorem 1 states the stability of the trivial equilibrium, $x_i = 0$, also for $n = 1$, which is plausible, but not obvious. It applies to all recruitment functions.

Theorem 2. Consider a general fisheries model (2.8) with a smooth monotone increasing bounded recruitment function $R(E) = cEr(E)$ for which depensation part r converges monotonically to 0. Assume the natural reproduction number n satisfies $n > 1$ then the unique nontrivial equilibrium is globally asymptotically stable i.e. all nontrivial solutions in the positive cone converge to this equilibrium.

The proof is based on a result of Hautus and Bolis as presented on the book of Elaydi [13, Theorem 5.17].

We use the standard representation and have

$$x_1(t + 1) = \sigma_1 x_1(t) + R(E(t)) \quad \text{with} \quad E(t) = \sum_{i=2}^k L_i F_i x_i(t)$$

and

$$x_i(t + 1) = x_{i-1}(t), \quad i = 2, \dots, k.$$

For $t > n$ this can be written as

$$x_i(t + 1) = x_{i-1}(t) = \dots = x_1(t - i + 1)$$

and with $y(t) = x_1(t)$ this gives

$$y(t + 1) = f(y(t), y(t - 1), \dots, y(t - k + 1)) = \sigma_1 y(t) + cE(t)r(E(t)), \tag{3.1}$$

where $y(t) = x_1$ and $E(t) = \sum_{i=2}^k L_i F_i y_i(t - i + 1)$. By assumption we have $\sigma_1 + c \sum_{i=2}^k L_i F_i > 1$

and the equilibrium $\bar{x} = \bar{x}_1(1, 1, \dots, 1)$ is defined uniquely by $1 - \sigma_1 = c \sum_{i=2}^k L_i F_i r(\bar{E})$ with $\bar{E} = \bar{x}_1 \sum_{i=2}^k L_i F_i = \bar{y} \left(\sum_{i=2}^k L_i F_i \right)$. The function defined by (3.1) is monotone, because $R(E(t))$ is.

Now let $u > \bar{y}$ then with $E_u = u \sum_{i=2}^k L_i F_i$ we have

$$\begin{aligned} f(u, u, \dots, u) - u &= (\sigma_1 - 1)u + u \left(c \sum_{i=2}^k L_i F_i \right) r(E_u) \\ &< (\sigma_1 - 1)u + (1 - \sigma_1)u = 0. \end{aligned}$$

This shows(ii)in the theorem for $u > \bar{y}$. The same proof also works for $u < \bar{y}$. Now apply the theorem.

Remark. By continuity one would expect global asymptotic stability also for recruitment functions with a wide dome. This will be illustrated by Figure 1 where only the Ricker function leads to periodic solutions [21]. Periodic solutions can only be expected for models in which high fertility, large n , is combined with a high mortality large μ . Thus a Ricker model is globally stable if $\ln(n) < 2$. None-monotone recruitment functions, however, will lead to oscillatory convergence to equilibrium. In [32], this has been checked with extensive numerical calculations. The present

cod model with $\mu \approx 0.2$ for example is globally stable for Ricker recruitment even for $n(0)$ as larger as 20, otherwise, the plots look rather similar.

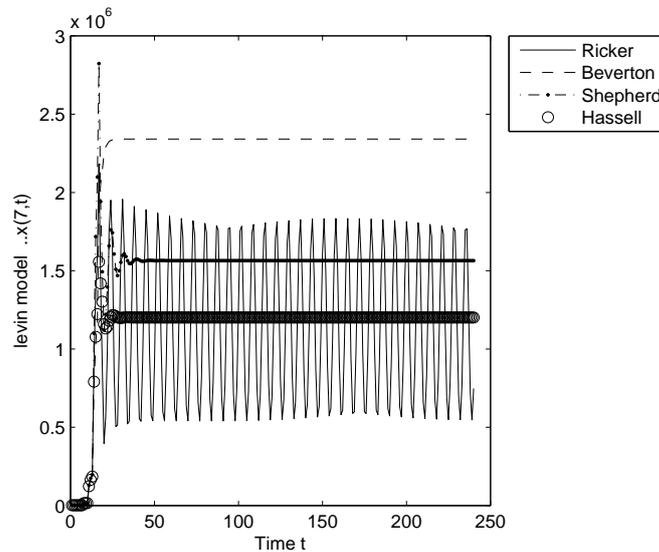


Figure 1. The striped bass model for different recruitment functions which is based on model of Levin and Goodyear [21]. $n = 15$. Hassell and Shepherd recruitment functions with $\alpha = 2$. $E_0 = 400$ (B.H), $E_0 = 1000$ (R.H.S). Note the fast convergence for Beverton-Holt systems and its size compared to the other recruitment functions.

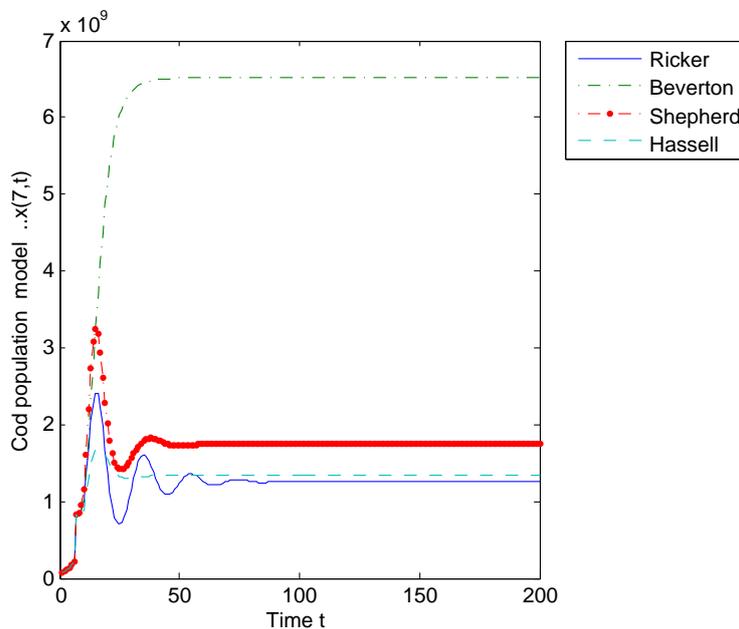


Figure 2. Stability for cod population model based on model (2.11). The cod population model for different recruitment functions. $n = 15$. Hassell and Shepherd recruitment functions with $\alpha = 2$. All functions have the same parameter E_0 . Note that Ricker recruitment leads to a more oscillatory behavior and a lower equilibrium level. This plot also indicates that Beverton-Holt recruitment leads to more rapid convergence with larger equilibria.

4. Harvesting

4.1 The Modeling of Harvesting

Harvesting can be represented as impulse harvesting at the end of the year with an escape factor $(1 - h)$ as in [15]. Such an approach is unrealistic for several reasons such a description makes it difficult to interpret h as a harvesting intensity and to assign costs to h . $h = 1$ would imply that all fish are caught. This is unrealistic because fishing becomes more difficult as the sea is depleted [5]. In addition it neglects the interaction of fishing mortality and natural mortality. For these reasons we choose a description which has been employed in differential equation models. The present form was introduced by Getz [14]. It is based on a no harvest season $[0, t_c]$ just after spawning, and constant h harvesting thereafter. Here h stands for the harvesting intensity or effort, for example the number of boats, people employed, etc. We will usually take $t_c \approx 0.3$ to 0.4 year. If $x(t)$ denotes the number of fish in a population class and if h is the harvesting intensity, one has

$$\frac{dx(t)}{dt} = \begin{cases} -\mu x & : 0 \leq t \leq t_c \\ -(\mu + h)x & : t_c < t \leq 1 \end{cases} \tag{4.1}$$

This results in

$$x(t + 1) = x(t)e^{-\mu - h(1 - t_c)}. \tag{4.2}$$

This expression also shows, why it is advantageous to express survival in an exponential form. Let h_i denote the fishing effort in class i . Then the model becomes

$$x(t + 1) = A(t)x(t) \tag{4.3}$$

with

$$A(x) = \begin{bmatrix} \sigma_1 & r_2(x) & r_3(x) & \cdots & r_k(x) \\ \tilde{\tau}_1 & 0 & 0 & \cdots & 0 \\ 0 & \tilde{\tau}_2 & \ddots & \vdots & 0 \\ \vdots & 0 & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & \tilde{\tau}_{k-1} & 0 \end{bmatrix}.$$

$\tilde{\tau}_i = e^{-\mu_i - (1 - t_c)h_i}$, $i = 2, \dots, k - 1$. The harvested amount in class i is then

$$H_i = \int_{t_c}^1 x_i(t)h_i W_i dt = \frac{h_i W_i x_i(t)e^{-\mu_i t_c}}{\mu_i + h_i} (1 - e^{-(\mu_i + h_i)(1 - t_c)}).$$

This shows that in the model only the mortality has changed. In particular all previous results on equilibria and stability carry over. For a given harvesting vector $\vec{h} = (0, h_2, h_3, \dots, h_k)$ we will therefore write $n(h)$, $\bar{x}(h)$, $y(h)$, $\bar{y}_1(h)$ for the corresponding quantities. Fishing with seines has the consequence that all fish of a size less than ℓ_1 (in length) escape, while all fish above the size ℓ_2 are caught. Gear selectivity as described in [9, 10] is based on the normal distribution function of the length of fish in the various age classes. It can best be described by a linear

interpolation of the harvesting intensities between the age class s_1 with length ℓ_1 and class s_2 with length ℓ_2 .

Here we will only use the knife edge harvesting with

$$h_i = \begin{cases} 0 & : i < s \\ h & : i \geq s \end{cases} \quad (4.4)$$

because gear selectivity with $s = (\ell_1 + \ell_2)/2$ does not alter all results seriously.

We shall speak of an (h, s) fishing strategy in this case. For an equilibrium value \bar{x} respectively $\bar{y} = \bar{y}(h, s)$ this means for the harvested amount

$$H(h, s) = \sum_{i=s}^k (\mu_i + h)^{-1} W_i h L_i(h, s) \bar{y} e^{-\mu_i t_c} (1 - e^{-(\mu_i + h)(1 - t_c)}). \quad (4.5)$$

If the price of one unit fish in class i is q_i , one will have to replace W_i above by $q_i W_i$. Older and larger fish usually give a higher price because they have considerably more meat. Unfortunately it is not so easy to get the price per kilogram of an ungutted fish. The following data have been extracted from [9, 28]. Regression gives in relative units that

$$q_i = \begin{cases} 0.18 + 0.09i & : 2 \leq i \leq 9 \\ 1.08 & : i \geq 10 \end{cases} \quad (4.6)$$

A higher price of large fish will clearly move the optimal mesh size s up and more young fish will be saved.

4.2 The Effect of Costs

Harvesting incurs a considerable amount of costs. These are fixed costs in terms of boats, gear and processing factories. The cost proportional to the harvesting intensity arises from fuel, wages and depreciation of boats and gear. In addition there are costs arising from processing the fish. These are proportional to the harvested amount and can be taken care of through the price. Thus we write

$$C(h) = a + bh \quad (4.7)$$

for the cost. This is slightly more general than the approach in the book of Clark [6]. Here a describes the fixed cost and b is the cost parameter of the harvesting effort h . In order to determine the parameters a and b , we assume that the cost amount to a fixed percentage of the maximal yield. In general we would expect the cost to be to about 60% to 80% of the total yield. This based on the paper of Froese [11]. It will be very difficult to determine the real cost because of subsidies, taxation, different currencies and other economic factors, which even vary from country to country. Further aspects are discussed in the book of Clark [6]. In [37] Tahvonen chooses an even more general approach via a utility function. The cost analysis is even more complicated because in reality fishing is not of the sole owner type as the model suggests. It is obvious that for the optimization only the term bh is relevant. Since $H(h, s)$ increases only

little for larger h , the effect of harvesting cost amounts to a decrease of the optimal h . We will always assume that the non fixed cost are proportional to the maximum yield and we write $bh_{\max} = k_1 H_{\max}$, with $k_1 = 0.3$ or 0.4 . For simplicity we will set $a = bh_{\max}$. Thus k_1 is the appropriate factor to relate the maximal harvest H_{\max} with the cost. This restricts k_1 to less than 0.5 . If bh amounts to fixed percentage of $H(h, s)$, b is defined only implicitly and has to be determined by a fix-point algorithm. For the moment this seems the most reasonable way to fix the cost parameters. The choice of a 30 to 40 percent gain based on the paper of Froese [11]. It seems to be a reasonable estimate of what could be attained. The results, however, would not change dramatically with other values. This was checked for cost factors between 50 to 90 percent. The net gain as a function of h is then the difference between the yield $H(h, s)$ and the total cost $C(h)$ i.e.

$$NH(h) = H(h, s) - C(h). \quad (4.8)$$

This also shows that subsidies for fuel or wages, which decrease b , will lead to a larger optimal harvesting intensity. This has already been observed with single class model [3]. This effect is stronger if the cost term bh is larger. The importance for this is that it keeps the harvested populations more stable. Subsidies for fuel and wages will decrease b and thus increase the optimal fishing mortality. Thus all in all subsidies have a detrimental effect on the stock in particular on a severely depleted stock.

4.3 The Influence of the Recruitment Function

The Beverton-Holt recruitment function leads to higher equilibrium values than the Ricker function. This is also hold for other recruitment functions. This will clearly hold for the harvested amount and net profit likewise. Since the Beverton-Holt function describes less competition for higher densities the optimal net parameters will be larger. This can be seen from the data in Table 1. All in all the Beverton-Holt recruitment function leads to the higher equilibria and harvests. Let us thus summarize the major results on the influence of the recruitment functions. For simplicity we compare only the Beverton-Holt function and the Ricker model.

Beverton-Holt: Larger equilibrium values which are globally stable, fast convergence to the equilibrium, and large harvests.

Ricker: For a high mortality μ and high fertility n periodic solutions are possible. Hardly for realistic values though. Slow oscillatory convergence to the equilibrium, which is lower.

5. Numerical Results

These ideas will now be checked for a cod population. We emphasize again that calculations for other marine fish give similar results. We use the standard parameters of Table 1.1 in [32], and values from the paper of Law *et al.* [22].

The values are: maximum age = 30, $T_1 = 3$, $W(t) = 17(1 - e^{(-0.12t)})^3$, scaling parameter $E_0 = 4.1 \times 10^{14}$, mortality $\mu \approx 0.2$ and $t_c = 0.25$. In actual computations it turns out that for small s , $s = 2$ or 3 , the equilibrium value $\bar{y}(h) = 0$ is reached too quickly for rather moderate harvesting intensities. So $s = 2, 3$ will never be optimal and will therefore not be considered. If we use prices increasing with weight in (4.6) this will be even more pronounced so that actually only $s > 3$ will be relevant. Similarly net parameters s larger than 9 are inefficient, because they spare too many fish of weight 9 or 10 kg.

As noted before gear selective harvesting has little effect. So it will not be considered any more. In extensive calculations we have seen that different n leads to different equilibria, however, the underlying dynamics is not changed seriously.

A typical plot for $H(h, s)$ is shown in Figure 3.

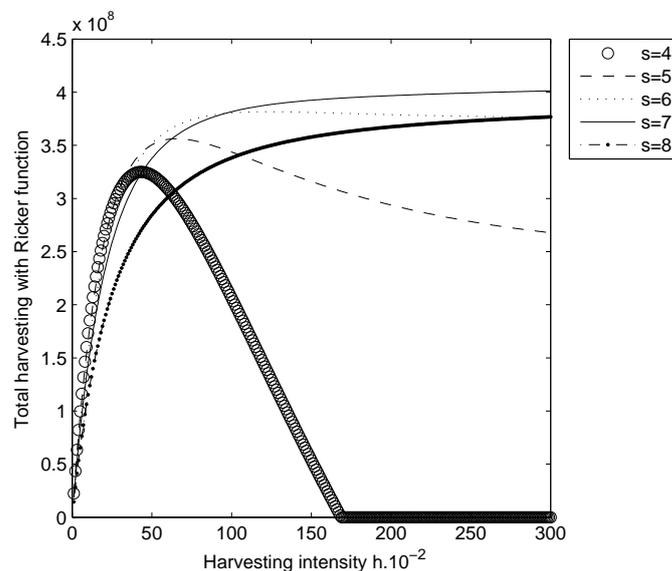


Figure 3. The total harvest as a function of $h \times 10^{-2}$, $n = 10$.

For small s an increasing h will have a strong effect on $n(h, s)$, $\bar{y}_1(h)$, and the the total harvest H . The harvested amount will initially increase rapidly, until $\bar{y}_1(h)$ decreases. As $\bar{y}_1(h)$ hits 0 the total harvest becomes 0 likewise because here we are dealing with an equilibrium model. For large s the remaining small classes preserve $\bar{y}_1(h)$ and it may never tend 0. Thus the total harvest may stay at a nonnegative level. Most likely such an increasing $H(h, s)$ is responsible for the optimal pulse fishing or periodic solutions if costs are neglected. Finally let us stress again the importance of the recruitment function on the MSY. Depensation functions with a slower decay will result in larger harvests. This effect is larger than a modified mortality or different harvesting pattern. A typical plot for $NH(h)$ is presented in Figure 4. For other values of n or other fish species, the corresponding plots are rather similar.

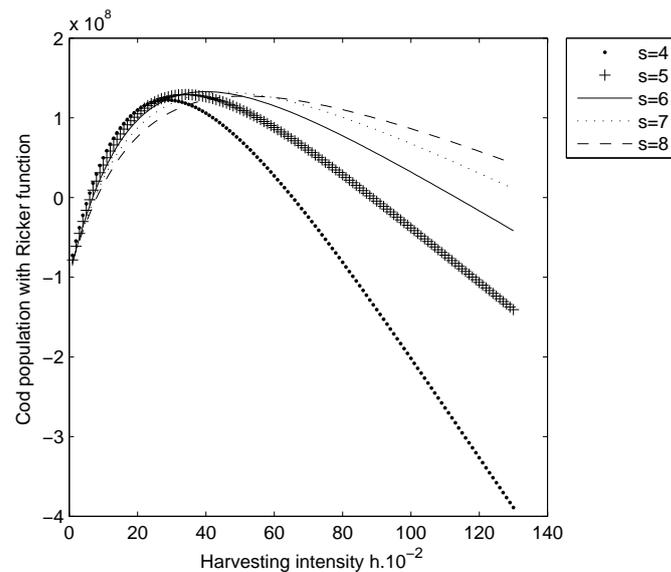


Figure 4. The net gain as a function of $h \times 10^{-2}$. The cost parameters are $a = 0.3H$ and $bh_{op} = 0.3H$ with $n = 10$.

A larger cost parameter b will lead to a lower harvesting intensity. Typical optimal fishing mortality will be about 0.4. The average fishing mortality, however, is $(1 - t_c)h_{opt}$. It is obvious that a higher price for larger fish will shift the net parameter to higher values. Optimal harvesting intensities have to be determined numerically.

Table 1 shows the influence of the recruitment function.

Table 1. The results of optimal harvesting based on cod population for different recruitment functions with the same other parameters

n	Ricker function				Beverton-Holt function			
	h_{opt}	s_o	H	$NH(h_{opt})$	h_{opt}	s_o	H	$NH(h_{opt})$
5	0.391	8	1.78×10^8	7.13×10^7	0.314	9	3.03×10^8	1.21×10^8
7	0.395	7	2.48×10^8	9.91×10^7	0.345	9	4.87×10^8	1.95×10^8
10	0.401	6	3.32×10^8	1.33×10^8	0.309	8	7.66×10^8	3.065×10^8
15	0.421	5	4.46×10^8	1.78×10^8	0.326	8	1.24×10^9	4.96×10^8

6. Conclusion

In this paper it has been analyzed the impact of the recruitment function on the position and stability of the equilibrium. It is obvious that monotone recruitment function lead to a globally stable equilibrium. Monotone functions also lead to a faster decay will result in lower equilibria and thus to lower harvests. The effects exceed 50% (Table 1) when comparing the Ricker and

Beverton Holt model. Thus fishery scientists will need a much better understanding of the recruitment process.

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Competing Interests

The authors declare that they have no competing interests.

Authors' Contributions

All the authors contributed significantly in writing this article. The authors read and approved the final manuscript.

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