ABSTRACT

We study the combined effects of periodically varying carrying capacity and survival rates on the fish population in the ocean (sea). We introduce a new delay differential equation model with a control parameter which describes how fish are harvested.

We consider a predation function as the function of the delayed estimate of the true population. It is important to be able to model this delay because it has serious implications for the long term behavior of populations.

We study the existence of global solutions for the initial value problem, extinction and persistence conditions, and the existence of periodic solutions.

Along with qualitative studies we use numerical simulations to discuss some general models and the weekly tow-by-tow data for Pacific ocean perch (POP), obtained by the Pacific Biological Station (Nanaimo, BC) in 1995-2004.

Keywords: Population models, Delay Differential Equations, Harvesting, Fisheries, Dynamic Carrying Capacity, and Periodic Solutions, Parameter Estimation, Fisheries Data

INTRODUCTION
Ecosystem effects and environmental variability are very important factors, and mathematical models cannot ignore [1-4] for example, year-to-year changes in weather, habitat destruction and exploitation, the expanding food surplus, and other factors that affect the population growth.

Traditional Population Ecology is based on the concept that carrying capacity does not change over time, even though it is known that the values of carrying capacity related to the habitat areas might vary, e.g., the more biodiverse a system, the greater the carrying capacity and hence also the productivity. Some scientists [5-7] have recognized carrying capacity as problematic, and it is not a species concept, it is a system concept.

The effects of a periodically varying environment [8-10] are also an important factor in laboratory ecosystems, where the feeding pattern may influence the population. It goes on to say that abrupt climate change is likely to stretch carrying capacity well beyond its already precarious limits.

The introduction of delays into existing population ecology equations is supported by general arguments [1] that the interacting species somehow rely on resources and harvesting that have been accumulated in the past. It is now a well-known fact that small delays may be a cause of some otherwise inexplicable periodic oscillations.

We will modify the Beverton-Holt type difference [1,11] equation and extend it to include varying carrying capacity, fecundity and natural mortality rates and periodic harvesting rate. We study the existence of positive global solutions for the initial value problem, persistence conditions, and the existence of periodic solutions.

Along with qualitative studies we use numerical simulations to compare some general models with the weekly tow-by-tow data for Pacific ocean perch (POP), obtained by the Pacific Biological Station (Nanaimo, BC) in 1995-2004.

The interior-reflective Newton method was used to efficiently estimate the parameters of discussed models.

1. BASIC FISHERIES MODELS

Consider the following standard differential equation which is widely used in Population Dynamics [ 1,3 ]

$$\frac{dN}{dt} = G(t, N)N(t) - F(t)N(t)$$

where $N = N(t)$ is the population biomass, $G(t, N)$ is the per-capita intrinsic rate, and $F(t)$ is the per-capita depletion rate.

According to M. Hassell, models in Population Dynamics in a limited environment are based on two fundamental premises; that populations have the potential to increase exponentially and there is a feedback that progressively reduces the actual rate of increase. We assume that function $G(t,N)$ is satisfying the following conditions:
A1. \( G(t,N) > 0 \), \hspace{1em} A2. \( G(t,N) \) is continuously differentiable with \( \frac{\partial G}{\partial N} < 0 \), and
A3. \( G(0^+) > F(t) > G(\infty) \).

Prototypes of \( G(t,N) \) satisfying A1-A3 are well-known in Fisheries Dynamics functions.

\[
G(t, N) = \exp \left[ r \left( 1 - \frac{N}{K} \right)^\theta \right] \hspace{1em} \theta - \text{Ricker Model}
\]

\[
G(t, N) = r \left[ 1 - \left( \frac{N}{K} \right)^\theta \right] \hspace{1em} \theta - \text{Logistic Model}
\]

\[
G(t, N) = r \left\{ \ln \frac{K}{N} \right\}^\theta \hspace{1em} \theta - \text{Fox Production Model}
\]

\[
G(t, N) = \frac{r}{K^\theta + N^\theta} \hspace{1em} \theta - \text{Beverton-Holt Model}
\]

\[
G(t, N) = \frac{r}{(K+N)^\theta} \hspace{1em} \theta - \text{Hassell Model}
\]

\[
G(t, N) = r \frac{K^\theta - N^\theta}{K^\theta + N^\theta} \hspace{1em} \theta - \text{Food-Limited Model}
\]

In this paper we consider some classical models and compare the obtained results with the actual Fisheries data.

Let us study biological motivation for the modified Beverton-Holt model.

Let \( G(t,N) \) be a Hill’s type function

\[
G(t, N) = \frac{r(t)}{1 + \left( \frac{N(t)}{K(t)} \right)^\gamma}
\]

Parameter \( \gamma > 1 \) is referred to by W. Getz [11] as the “abruptness” parameter.

Consider the following differential equation

\[
\frac{dN}{dt} = \frac{rN}{1 + \left( \frac{N}{K(t)} \right)^\gamma} - F(t)N = Q(t,N)N \hspace{1em} (1)
\]

3
Remark: equation (1) is an alternative to the $\gamma$–logistic model.

\[
\frac{dN}{dt} = rN \left[ 1 - \left( \frac{N}{K} \right)^\gamma \right] - FN \quad (2)
\]

Clearly, from equation (1)

\[
\Phi(N) = \frac{d}{dN} Q(t, N) = - \frac{r\gamma N^{\gamma-1} K^{-\gamma}}{\left( 1 + \left( \frac{N}{K} \right)^\gamma \right)^2} = 0.
\]

It is obvious that $\Phi(0) = 0$, $\Phi(N) < 0$ and $\Phi(N) \to \infty$. Function $\Phi(N)$ has a maximum not at the origin (compare with logistic, Ricker, and Hassell models), but at the point

\[
N^* = \left[ \frac{\gamma-1}{\gamma+1} \right]^\frac{1}{\gamma} K.
\]

The value of $N^*$ is depending on the value of $\gamma > 1$, that is why the parameter $\gamma$, that controls how rapidly density dependence sets in, can be regarded as an abruptness parameter.

2. TIME LAGS IN FISHERIES MODELS

**Biological Motivation**

In order to model processes in nature and engineering it is frequently required to know system states in the past. Depending on the phenomena under study the after-effects represent duration of some hidden processes. In general, DDE's exhibit much more complicated dynamics than ODE's since a time lag can change a stable equilibrium into an unstable one and make populations fluctuate, they provide a richer mathematical framework (compared with ordinary differential equations) for the analysis of biological systems.

Introduction of complex models of Population Dynamics, based on nonlinear DDE's, has received much attention in the literature in recent years [2].

The application of delay equations to biomodelling is in many cases associated with studies of dynamic phenomena like oscillations, bifurcations, and chaotic behavior. Time delays represent an additional level of complexity that can be incorporated in a detailed analysis of a particular system.
The introduction of delays into existing population ecology equations is supported by general arguments that the interacting species somehow rely on resources and harvesting that have been accumulated in the past. It is now a well-known fact that small delays may be a cause of some otherwise inexplicable periodic oscillations [2, 3].

Consider a logistic-like equation with a harvesting (hunting) strategy, we do not know the population at the exact time. However, we need it to determine the hunting quota. There is always a delay in processing and distributing field information. The quota must be set long before the hunting season begins.

The time lags in ecological systems one could justify as a discovery time: predator requires time to discover the prey is very abundant. In a case of metapopulation time lags can be the result of the situation where prey population becomes sufficiently rare that the predator switches to alternative prey or an alternative source of prey (different island).

It might be reasonable to consider a predation function as the function of the delayed estimate of the true population. It is important to be able to model this delay because it has serious implications for the long term behavior of populations. Time lags yield specific insights into the management of complex ecological systems.

It is considered [2] that the major effect of delays is to make them less stable than the analogous models without delays.

Recently [12] we have considered the modified delay logistic form of Pella and Tomlinson or Richards' growth delay equation

\[
\dot{N}(t) = r N(t) \left[ 1 - \left( \frac{N(t-\tau)}{K} \right)^m \right].
\]

**Beverton-Holt non-autonomous differential equation with delay.**

Generally, models with the delay in the reproduction term recognize that for real organisms it takes time to develop from newborns to reproductively active adults. If we take into account that delay, then we have the following time-lag model based on equation (1)

\[
\dot{N}(t) = \left[ \frac{r(t)}{1 + \left( \frac{N(g(t))}{K(t)} \right)^g} - m(t) \right] N(t) - F(t)N(t), t \geq 0. \tag{3}
\]

Here \( r(t) > 0 \) is a fecundity factor, \( m(t) > 0 \) is a natural mortality factor, \( F(t) > 0 \) is a harvesting factor, \( K(t) > 0 \) is a carrying capacity, \( g(t) \) is the time to develop from newborns to reproductively active adults, \( 0 \leq g(t) \leq t \).
For \( F(t) \equiv 0 \), \( r(t) \equiv r \), \( g(t) = t \), \( m(t) \equiv m \), \( K(t) \equiv K \), equation (3) is the Beverton-Holt type differential equation that describes dynamics of the fish population.

If we denote \( M(t) = m(t) - F(t) \), then equation (3) has the following form

\[
\dot{N}(t) = \frac{r(t)N(t)}{1 + \left( \frac{N(g(t))}{K(t)} \right)^\gamma} - M(t)N(t), \quad t \geq 0,
\]

with the initial function and the initial value

\[
N(t) = \phi(t), \quad t < 0, \quad N(0) = N_0,
\]

under the following conditions: (a1) \( \gamma > 0 \);

(a2) \( r(t) \), \( M(t) \), \( K(t) \) are continuous on \([0, \infty)\) functions, \( r(t) > 0 \), \( M(t) \geq m > 0 \), \( K(t) \geq k > 0 \);

(a3) \( g(t) \) is a continuous function, \( g(t) \leq t \);

(a4) \( \varphi: (-\infty, 0) \to R \) is a continuous bounded function, \( \varphi(t) \geq 0, N_0 > 0 \).

We proved the following theorems.

**Theorem 1.** Suppose (a1)-(a4) hold and

\[
r(t) > M(t), \quad \sup_{t \geq 0} \int_{g(t)}^t [r(s) - M(s)]ds < \infty, \quad \sup_{t \geq 0} \int_{g(t)}^t M(s)ds < \infty.
\]

Then problem (3) has on \([0, \infty)\) a unique positive solution \( N(t) \) such that

\[
\min \left\{ N_0, \inf_{t \geq 0} K(t) \left( \frac{r(t)}{M(t)} - 1 \right)^{\frac{1}{\gamma}} \exp \left\{ -\sup_{t \geq 0} \int_{g(t)}^t M(s)ds \right\} \right\} \leq N(t)
\]

\[
N(t) \leq \max \left\{ N_0, \sup_{t \geq 0} K(t) \left( \frac{r(t)}{M(t)} - 1 \right)^{\frac{1}{\gamma}} \exp \left\{ \sup_{t \geq 0} \int_{g(t)}^t (r(s) - M(s))ds \right\} \right\}.
\]
Periodic harvesting is used frequently as a tool by fishery managers to protect a stock during a spawning season for a defined period of time [4,5,9].

Consider equation (4). Now we assume that r, K, and M are all positive continuous T-periodic functions. Function \( g(t) \) is defined as \( g(t) = t - \theta(t) \) where \( \theta(t) \) is a T-periodic function.

**Theorem 2.** Let \( M(t), K(t), \theta(t) \) and \( r(t) \) be T-periodic functions. Suppose \( M(t) \geq m > 0, r(t) - M(t) \geq r > 0 \) for some positive constants \( m \) and \( r \).

If at least one of the following conditions hold:

\[
\inf_{t \in [0, T]} \left( \frac{r(t)}{M(t)} - 1 \right) K''(t) > 1 \quad \text{or} \quad \sup_{t \in [0, T]} \left( \frac{r(t)}{M(t)} - 1 \right) K''(t) < 1
\]

then equation (4) has at least one periodic positive solution \( N_0(t) \).

### 3. NUMERICAL SIMULATIONS AND PARAMETER ESTIMATION

Here we used records of tow-by-tow data for Pacific ocean perch (POP), obtained every week for 9 years from 1996 to 2004 by the Pacific Biological Station (Nanaimo, BC).

For the rest of this paper, the amount of fish being caught is referred to as *catch* data.

To make our program runs smoothly, we make the following changes to the data: firstly, there are around 10 missing data. We filled in the blank with the average of the same week in other 8 years; Secondly, for week 52 in 2001 and week 1 in 2002, the catches were like 2.7. All other catches are in a magnitude of \( 10^3 \) at least.

The modified Beverton-Holt model has four different parameters: \( r = r(t), K = K(t), M = M(t) \) and \( g = g(t) \). We assumed that all four functions are periodic functions, however, that periods have a lowest common multiple, which defines the period for the system. Each periodic function that modeled functions \( r(t), K(t), M(t) \), and \( g(t) \) has a form \( f(t) = A[1+B\sin(\pi(t-\tau)/T)\] where \( A, B, T, \) and \( \tau \) are constant parameters.
Parameters’ estimates were calculated using Matlab function LSQNONLIN which solves nonlinear least-squares (nonlinear data-fitting) problems. By default LSQNONLIN chooses the large-scale algorithm. This algorithm is a subspace trust region method and is based on the interior-reflective Newton method in [13].

Each iteration for the approximate solution of a large linear system was obtained by using the method of preconditioned conjugate gradients (PCG).

**Parameter estimation for the logistic model (equation (2)).**

![Figure I. Logistic Model](image)

Note that this model doesn’t pick up different peaks for different years.

**Parameter estimation for the Modified Beverton-Holt Model (equation (4)).**

The parameters were fitted using the first two years of data only. Then catches for 1999-2004 were estimated using ODE with these parameter values (see Figure II)
This model seems to fit the original the best among the three models we tried. In a long run catches eventually stabilize after a few years (see Figure III).
Findings in the Modified Beverton-Holt Model.

Looking at the original data, we see that there are two general patterns: the first 4 years (1996-1999) look more alike and the latter 5 years (2000-2004) look alike to each other. The first 3 years look like bimodal, and the latter years look like unimodal. Thus, if data from all 9 years are used to estimate parameters, the results will contain complex numbers. To avoid this, first, data from 1996 to 1999 were used to estimate parameters.

For cross-validation purposes, this set of estimates was estimated by using data from 1996 to 1999, we use them to estimate catches for 9 years, and plotted against 9 years of original data.

For cross-validation purposes, even those this set of estimates was estimated by using data from 2000 to 2003, we use them to estimate catches for 2000 to 2004, and plotted against these 5 years of original data. The model doesn’t hold for a long period of time with these estimates. To get more accurate results, the years with different catch patterns should be separated.
SUMMARY
In closing, we would like to summarize by saying that even simple one-dimensional models with harvesting, may exhibit a wide variety of dynamical behaviors.

Periodic environment causes periodic orbits that is consistent with the weekly tow-by-tow data for Pacific ocean perch (POP), obtained by the Pacific Biological Station (Nanaimo, BC) in 1995-2004.

If the harvesting rate is based on the size of the population some time ago, then for the survival of the population it is important that the field data on the population size is collected at the time when the population is not abundant.

Periodic harvesting in stable environment produces larger yield in comparison with the proportional harvest. By changing periods of harvesting we anticipate an increase in the total yield. That result might be useful in rotational use of resource areas.

References