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AN INTRODUCTION TO DYNAMICAL SYSTEMS APPLIED TO EXPLOITED POPULATIONS

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ABSTRACT

Population dynamics is currently an interdisciplinary subject that aims at the mathematical representation, treatment and modeling of population growth processes, using a variety of applied mathematical techniques and tools. In this work, we present four dynamical models of an exploited population system describing the time evolution of the population. Assuming the natural growth of the population is logistic, we show the effects of predation on the population considering four types of Predatory function; Constant or Quota Yield, Holling Type I, Holling Type II and Holling Type III functional responses. The mathematical analysis of the models shows that under some assumptions, we obtain alternate stable equilibria in the population system using Holling Type II and Type III functions. We observe that using Holling Type III function a desirable situation occurs: the zero population is an unstable equilibrium for all levels of predation, thus, the population can be exploited without risk of extinction.

Keywords: Logistic model; population dynamics; predatory function; extinction; exploitation.

RESUMO

INTRODUÇÃO AOS SISTEMAS DINÂMICOS APLICADOS A EXPLORAÇÃO DE POPULAÇÕES. A dinâmica de populações é atualmente um tema interdisciplinar que busca representação matemática (modelagem) e analise dos processos de crescimento, usando uma variedade de técnicas e ferramentas da Matemática Aplicada. Nesse estudo são apresentados quatro modelos dinâmicos de sistemas populacionais sujeitos a predação ao longo do tempo. Partindo da premissa que o crescimento populacional é do tipo logístico, foram apontados os efeitos da predação na população considerando quatro tipos de função de predação: Constante ou por Quotas, Holling tipo I, II, e III. Quando se aplicam as funções Holling tipo II, e III a analise matemática do modelo aponta para estados de equilíbrios alternados na população, enquanto quando se implementa a função Holling tipo III temos que a população pode ser explorada sem risco de extinção, sendo essa, portanto, uma política de exploração desejável.

Palavras-chave: Modelo logístico; dinâmica populacional; função de predação; extinção; exploração.

RESUMEN

INTRODUCCION A LOS SISTEMAS DINAMICOS APLICADOS A POBLACIONES EXPLOTADAS. La dinámica de poblaciones es actualmente un tema interdisciplinario que busca representación matemática (modelación) y análisis de los procesos de crecimiento poblacional, haciendo uso de variadas técnicas y herramientas de las matemáticas aplicadas. En este estudio se presentan cuatro modelos dinámicos de sistemas de poblaciones explotadas a lo largo del tiempo. Partiendo de la premisa que el crecimiento poblacional es de tipo logístico, se muestran los efectos de la predación sobre la población considerando cuatro tipos de función de predación: constante o por cuotas, Holling tipo I, II y III. Cuando se aplican las funciones Holling tipo II y III el análisis matemático del modelo muestra que se obtienen estados de equilibrio estable alternado de la población. Cuando se implementa una función Holling tipo III la población puede ser explotada sin riesgo de extinción, siendo esta la situación deseable de explotación.

Palabras clave: Modelo logístico, dinámica poblacional, función de predación, extinción, exploración.

INTRODUCTION

Population dynamics has basic established principles (Berryman 2002, Berryman *et al*. 2002), but still has important questions to be answered (Rosenheim 2007, Hastings 2008); many of which could be addressed through mathematical modeling (Bravo de la Parra & Poggiale 2005). Mathematical tools can be employed over different principles underlying the dynamics of populations, especially those related with change in time and its rates. When these principles are expressed in mathematical terms, the relations are equations and the rates are derivatives.

Dynamical systems are an area of applied mathematics used to describe the behavior of complex systems over time. It deals with the long-term qualitative behavior of systems. It focuses not on finding precise solutions to the equations defining the system, but rather answers questions like “Will the system settle down to a steady state in the long term, and if so, what are the possible steady states?”, or “Does the long-term behavior of the system depend on its initial condition?”. Dynamical Systems approach has been used in Population Ecology since its beginning, as it studies short and long term changes in the size and age composition of populations in time, and the biological and environmental processes influencing those changes (Gotelli 2009).

Many researchers date the modern era of population studies to 1798 with the publication of “An Essay on the principle of Population” by Thomas Malthus; this “principle” is usually regarded as the exponential law of population (Malthus 1798). Malthusian growth predicted that human population grows exponentially while food supply grows algebraically, and Malthus was concerned about the implications for humankind to feed itself.

The early period of the dynamical systems applied to ecology was motivated by demographic studies, such as Benjamin Gompertz and Pierre François Verhulst works. In 1838, Pierre Verhulst proposed his logistic model of population growth, where population size is limited by a carrying capacity. This was a refinement and adjustment of the Malthusian demographic model to make it more realistic. This model did not call too much attention until Pearl retrieve it, and tried to announce a law in Ecology: thus, all populations will grown until reaches the carrying capacity (Kingsland 1995). Though the “Pearl law” could not be called a law, in the sense that it is called in the hard sciences, the logistic model offered a more realistic starting point for a deductive exploration in Population Ecology. From 1920 to 1932, there were some fundamental studies that until today influence our understanding of Population Ecology. From Lotka & Volterra´s work (Lotka 1925, 1932, Volterra 1928, 1931), Gause (1934) begun to explore mathematical models together with experiments, and one of the deduced concepts was the “Competitive Exclusion Principle” (Kingsland 1995)

Over the years, researchers including Holt (Beverton & Holt 1957), Berryman (1992), Royama (1992) and others (for example: Gause 1934, Allee *et al*. 1949, Hardin 1960, Rosenzweig & MacArthur 1963, Levins 1966, Rosenzweig 1971 e Turchin 2003) have developed theories that have improved understanding on population dynamics. All these authors, although some were not mathematicians, had to use the theory of dynamical systems to be able to fully understand previous studies, and to constuct new ideas and concepts for ecology.

In population ecology, the two types of dynamical systems used are: differential equations (also known as continuous-time dynamical system) and difference equations (also known as discrete-time dynamical system or iterative maps). Differential equations describe the evolution of the systems in continuous time, whereas difference equations arise in problems where time is discrete. Biologically, differential equations can represent taxa with generations overlapping - e.g., mammals and birds. Yet difference equations can be applied to taxa without overlapping of generations e.g., insects. Most concepts in dynamical systems have both differential equation and difference equation versions (Hastings 1997). The theory of differential equations and the methods used to study them are quite developed, and this makes them much more widely used in science, and some actual questions, like harversting and management of natural resources, are being adressed by those methods.

Harvesting and management has received considerable attention over the last decade. This has contributed to understanding the relationship between harvesting and extinction risk (Fryxell *et al*. 2005). Harvesting intensity may play an important role on exploited population, endangering around one-third of threatened species through the world (W.C.M.C 1992). Given the economic importance of many exploited population species, it is important to assess, among other factors, the effect that harvesting strategy and intensity has on prey population dynamics (Clark 2006).

In this paper we reviewed the dynamics of some population models that implemented predation functions (called functional responses). We discuss ecological process such as population extinction and sustainable yield. This allows for the identification of an efficient set of management measures which can be used as a tool in decisions concerning the maintenance of the population and the livelihoods of the predators as well as the sustainability of the ecosystem from which they are extracted.

It is possible to find written revisions on this topic in ecology literature (Hanski 1991, Getz 1998, Weisberg 2006), but none of them has been done by introducing the reader to dynamical systems concepts for a deeper and complete comprehension of the modeling process. We address the population models with rigor, with the goal to improve and motivate the reader to an interdisciplinary undertanding.

THE DYNAMICAL SYSTEM APPROACH: BASIC MATHEMATICAL CONCEPTS

Mathematical formalization is important because it adds accuracy to the process of deduction or modeling, links assumptions with results and makes it possible to follow the logic that guarantee better understanding and interpretation of the problem and solutions. For ecology, and population dynamics in particular, the understanding of the basic mathematical theory that underly the population models is vital for its comprehension. We can achieve this understanding by formalizing some concepts of dynamical systems.

Thus for a basic but still rigorous understanding of the concepts beneath population dynamics, we will introduce some formal concepts. A dynamical system can be defined in a more formal way, as an abstract phase space or state space X, a set of times t and a rule f for evolution, $f:(X, t)\rightarrow X$ that gives the consequent(s) to a state $x \in X$. Thus, a dynamical system on X tells us, for x in X, where x is at time zero, 1 unit time later, 2 units of time later and so on. We denote these new positions of x by x_0, x_1, x_2, respectively. Filling up the x-y plane with the time and corresponding positions i.e. (t, x_t), one obtains the trajectory x_t for all time t. The rule $R\rightarrow X$, which sends t into x_t, is a curve in X that represents the life history of x as it runs from $-\infty$ to ∞.

Different initial states result in different trajectories. The set of all trajectories forms the phase portrait of a dynamical system. Since it is usually impossible to derive an explicit formula for the solution of a nonlinear equation, the analysis of phase portraits provides an extremely useful way for visualizing and understanding qualitative features of solutions.

Additionally, two concepts, the equilibrium and the stability of the system have fundamental importance. To introduce them, the Existence and Uniqueness Theorem is considered:

Given the initial value problem

$$\frac{dx}{dt} = f(x) \qquad\qquad x(0) \tag{1.1}$$

Where x could be the abundance of a population, and so $\frac{dx}{dt}$ is how this population is varying in time.

Holding some important assumptations, there is a important theorem (Picard Theorem) saying that the initial value problem has a solution $x(t)$ on some time interval $(-\tau,\tau)$ about $t=0$, and the solution is unique. For proof of the theorem see Hirsch & Smale (1974).

To study dynamics of (1.1) and its dependence on initial condition, one does not need to solve it explicitly or even know the exact details of the function *f(x)*: it is apparent from the phase portrait. For one-dimensional systems, the state of the dynamical system can be specified by $x \in R^1$. A **phase line**, R^1 corresponds to physically meaningful states of the system. The phase line of a one-dimensional ordinary differential equation (ODE) is partitioned by the equilibria (points where $f(x) = 0$) and trajectories that connect the equilibria. The stability of the equilibria is determined by the directions of trajectories, which depend on the sign of the right-hand side function *f(x)* in (1.1). When $f(x)>0$, the direction of trajectories indicated by arrows on the phase line points to the right and to the left when $f(x) <0$.

The values of x for which $f(x) =0$ are called the **singular points or equilibria**. In other words, equilibria are the zeros of *f(x)* denoted x^*. Using linear stability analysis, the slope $f'(x)$ at x^* determines its stability. If $f'(x^*) <0$ then x^* is a stable equilibrium while when $f'(x^*)>0$ then x^* is an unstable equilibrium. However, when $f'(x)=0$, further analysis is needed to determine the stability since x^* can be stable, unstable or half stable (i.e the singular point is attracting from one side and repelling from the other side. Refer to Strogatz 1994 and Boyce & DiPrima 1999, for further discussion on dynamical systems and application to ecology). In order to simplify the qualitative analysis, graphical methods can be used, as we will see in the subsequent sections.

DYNAMICS APPLIED TO THE POPULATION

The dynamics of single species has been studied by several authors from different points of view (Quinn & Deriso 1999, Haddon 2001, Keshet 2005). The simplest models usually assume a logistic equation for the populations (Mchich *et al*. 2002). These populations, in general, depend on the natural food supply and space, so individuals compete for the limited resource, and consequently their growth is dependent on population density.

We could consider a population, whose biomass is n. The natural growth process of the population can be given by

$$\frac{dn}{dt} = f(n) \tag{2.1}$$

Here *f(n)* is a representation of the births and deaths of the species in absence of predation. We assume that the population is a closed system; so there is no migration to and from the population. We assume that the natural growth of the population is logistic, given by

$$\frac{dn}{dt} = f(n) = rn(1-\frac{n}{K}) \tag{2.2}$$

We solve (2.2) explicitly for *n(t)* by separation of variables subject to the initial condition $n(0) = n_0$. This gives the solution

$$n(t) \ = \frac{n_0 K}{n_0 + (K - n_0)e^{-rt}} \tag{2.3}$$

In particular, if $n_0 = 0$, then (2.3) requires that $n(t) = 0$ for all t. If $n_0 > 0$ and $t \to \infty$ then $\lim_{t\to\infty} n(t) = K$

Since K is the upper bound that is approached, but not exceeded, by growing populations starting below this value, it is referred to as the **saturation level**, or the **environmental carrying capacity** for the given population. The estimation of the carrying capacity is not a trivial work at the field, especially due to the continuous changes of the conditions of the environment. Still some new methods are being developed to estimate carrying capacities (Morris & Mukherjee 2007).

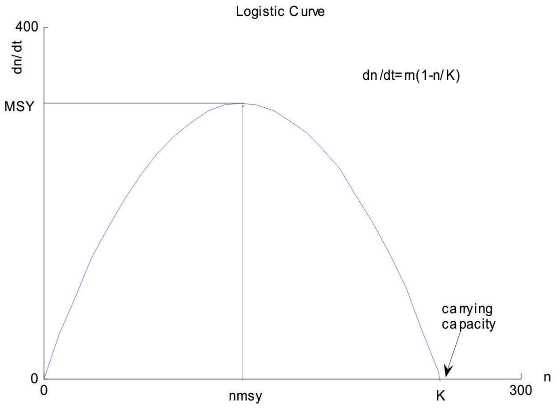

Figure 1. Corresponds to (2.2). The natural growth of the population, *dn/dt* is shown as a function of *n*. The growth of the population is positive whenever it is less than K ($dn/dt>0$ if $0<n<K$). *K* is the environmental carrying capacity and r the intrinsic growth rate. The parabola reaches its maximum value, MSY when n=nmsy. MSY = $rK/4$ and nmsy = $K/2$.

As indicated, the growth limit is *K*. Equating (2.2) to zero and solving the quadratic equation (i.e *dn/dt=0*), we confirm that the *K* is the zero of the function, as shown in the parabola of Figure 1. Thus, from this parabola we could begin the analysis of the population behavior. From the graph, it is clear that the growth function has a maximum point. When the biomass of the population is at n_{msy} , the growth rate of the population is at its maximum, and this maximum is referred to as the **Maximum Sustainable Yield (MSY)**, see Figure 1.

We compute the maximum point (n_{msy} , MSY) of the curve. This is done by differentiating *f (n)* and equating it to zero.

$$f^{'}(n) = rn(\frac{-1}{K}) + r(1-\frac{n}{K})$$

For *f' (n) =0*

$$-rn + r(K-n) = 0$$

Thus

$$n_{msy} = \frac{K}{2}$$

Hence,

$$f(\frac{K}{2}) = \frac{rK}{4}$$

Therefore, if the population is maintained at half its carrying capacity, the population growth is at a maximum and the sustainable yield is greatest. Thus, maximum sustainable yield of a population is reached when the biomass (stock level) is exactly half of its carrying capacity, K , as shown in Figure 1.

There are two biological equilibria; *n*=0* and *n*=K*. Any stock size above zero and below the carrying capacity, K will lead to positive growth and hence an increase in the stock. Any stock level above the carrying capacity will lead to excessive environmental resistance and hence to a decline in the stock.

DYNAMICS OF AN EXPLOITED POPULATION

Exploitation usually reduces population stability (Beddington & May 1977, May *et al.* 1978). To sustain a population requires harvesting strategies that maximize yield while accounting for uncertainty and risk of population collapse or extinction. If harvested populations become small, they are vulnerable to demographic stochasticity arising from chance events of individual mortality and reproduction (May 1974). Many mathematical models have been developed to describe and understand the dynamics of exploited populations. We follow earlier contributions (Beverton & Holt 1957, Goh 1977, Chau 2000, Reynolds *et al.* 2001, Jonzén *et al.* 2003, Fryxell *et al.* 2005, Costa 2007, Costa & Faria 2011).

Our work presents four models which could be considered as a general model of resource exploitation. Each model describes the evolution of the population which grows naturally and is exploited by one of the four forms of predation (i.e. Constant Yield, Holling Type I, II and III functional responses). We shall study the existence of positive equilibria (where the natural growth rate exactly balances the loss rate due to predation) and then investigate the local stability and bifurcation.

We consider the dynamical behavior of a population which is being exploited (for example, fisheries harvested by fishermen). Now, the net growth of the population is given by

$$\frac{dn}{dt} = f(n) - H(n) \tag{3.1}$$

$H(n)$ is the predatory function or functional response. When *f(n)>H(n)*, the net growth of the population is positive which means the population size is increasing. When *f(n)<H(n)*, the net growth of the population is negative with a decline in the population size. However, when *f(n)=H(n)*, the net growth is zero. There is no change in the population size and hence the population is at equilibrium.

Populations often are exploited using a constant yield or constant effort strategy, combined with a threshold or "escapement" level below which harvesting ceases. However, there are evidence of overexploited resources and population collapse (Ludwig *et al.* 1993, Hutchings & Myers 1994). In this work, we use graphical analysis to compare the performance of Holling Type II, III functional responses against Constant (Quota) yield and Constant effort (Holling Type I). A functional response in ecology is the amount of resources captured per unit of time and per unit of predator, as for example, in fishery context, the amount of fish caught per unit of fishing effort (Auger *et al.* 2009). Functional response brings information about basic mechanisms inherent in prey–predator dynamics (Lipcius & Hines 1986) – here assumed to be the amount of fish caught per unit of fishing effort, and is an essential component of prey–predator models (Jeschke *et al.* 2002). The functional response can also determine whether a predator is able to regulate the density of its prey when the response depends on density (Murdoch & Oaten 1975). Usually, the functional response is conveniently classified into three general types (Holling 1959) named I, II and III, which describe, respectively, linear, non-linear with saturation and sigmoid patterns. These three functional responses are common and reflect different types of hunting and feeding behavior of predators (Weiss 2009). However, there are several theoretically possible forms such as Type IV and Type V and functional response with predator interference (Hassell 1978, Abrams 1982, Taylor 1984, Turchin 2001). In this work we consider the following: Constant or Quota Yield, Holling Type I, II and III Function, as they are the most used as in theoretical or applied ecological studies (Holling 1959, Gotelli 2009, Weiss 2009).

CONSTANT OR QUOTA YIELD

This illustrates the case where a fixed quantity of the population is taken every time. The number taken, *H*, does not depend on the biomass present. Here (3.1) has the particular form;

$$\frac{dn}{dt} = rn(1 - \frac{n}{K}) \ - H \tag{3.1.1}$$

The equilibrium satisfy

$$\frac{dn}{dt} = f(n) - H = 0$$

$$f(n) = H$$

We therefore have,

$$H = rn(1 - \frac{n}{K}) \tag{3.1.2}$$

We solve (3.1.2) to find the population equilibrium. This represents sustainable yield. Geometrically, this can be found by plotting the line, H and the curve, $f(n)$ and finding where they intersect. The intersection points correspond to the equilibria for the system (see Figure 2). In the case of no harvesting i.e. $H = 0$, the species is in biological equilibrium. (3.1.1) then becomes (2.2) with $n^* = 0 \ and \ n^* = K$. Any population size above 0 and below *K*, will lead to positive growth and hence increase in the stock.

Calculating Equilibrium

The equilibrium of (3.1.2) is given by

$$rn - \frac{rn^2}{K} - H = 0$$

$$n^2 - Kn + \frac{KH}{r} = 0$$

We find *n* by using quadratic formula

$$n_{1,2} = \frac{K}{2} \pm \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})}$$

(i) If $K^2 - 4(\frac{KH}{r}) > 0$ then there are two distinct n-values, both of which are real numbers i.e.

$$n^*_1 = \frac{K}{2} - \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})} \ \ and \ \ n^*_2 = \frac{K}{2} + \frac{1}{2}\sqrt{K^2 - 4(\frac{KH}{r})}$$

(ii) If $K^2 - 4(\frac{KH}{r}) = 0$ then there is exactly one distinct real n-value, i.e. $n^* = \frac{K}{2}$

(iii) If $K^2 - 4(\frac{KH}{r}) < 0$ then there are *no* real roots.

Figure 2 illustrates these three situations better. The resulting dynamics of the population changes depends on the equilibrium points.

Graphical Analysis

We use graphical analysis to study the stability of the equilibria. We look at three possibilities.

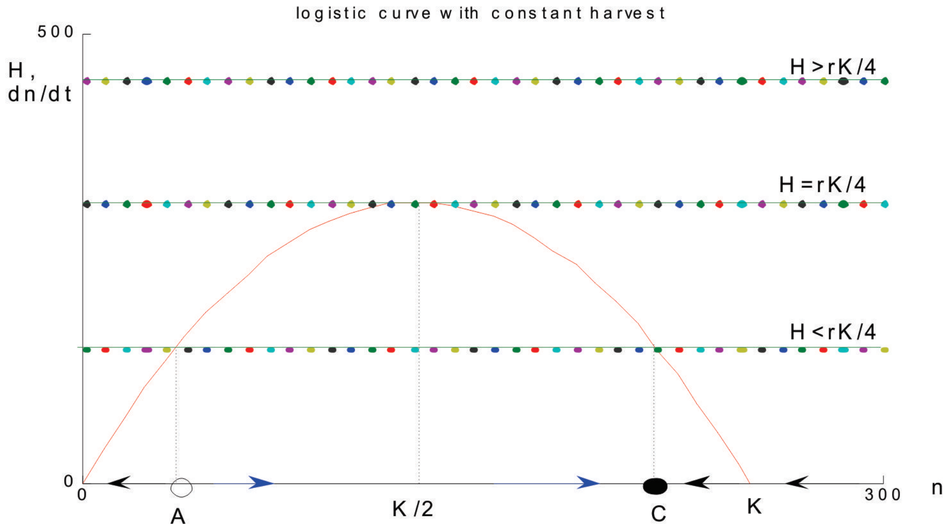

Figure 2. Corresponds to (3.1.1). The net growth of the population, *dn/dt* is shown as a function of *n*. *K* is the environmental carrying capacity and *r* the intrinsic growth rate. The parabola reaches its maximum when n= *K/2*. The parabola is the natural growth of the population while the horizontal lines are the constant yields, *H* at three different predating levels. Where the line lies above the parabola; the net growth rate is negative. Where the line lies below the parabola, the net growth rate is positive. The points of intersection correspond to possible equilibria and the arrows indicate the stability of the equilibria.

At predating level H above $\frac{rK}{4}$, which is the maximum sustainable yield, the net growth of the population is negative since $f(n) < H$. This means that, the population is being extracted faster than it can reproduce, potentially resulting in extinction.

At predating level H at the maximum sustainable yield, the population equilibrium is $n^* = \frac{K}{2}$. This means that, if the exploited population begins at the carrying capacity, K then there will be no growth in the population, instead will result in a decline in the population stock because $f(n) < H$. When the population declines to half the carrying capacity then the natural growth is matched by level of predating, and so its abundance can be sustained perpetually since $f(n) = H$. But the danger with this abundance level is that, if the population falls below $\frac{K}{2}$, then the rate of exploitation will exceed the natural population growth i.e. $f(n) < H$, and there will be a decline in the population, potentially resulting in extinction. Hence, the unique equilibrium $n^* = \frac{K}{2}$ is half-stable.

At predation level H below the maximum sustainable yield, there are two possible population equilibria; $n_1{}^* = A \text{ and } n_2{}^* = C$ which have been found algebraically in the earlier section. When $0 < n < n_1^*$ then $f(n) < H$ and the population will decline to extinction. If $n_1^* < n < n_2^*$ then $f(n) > H$ and so the population will increase until n_2^* is reached. Finally, if $n > n_2^*$ again $f(n) < H$, so the population will decline until it reaches n_2^*. From the observation, we conclude that n_1^* is a locally unstable equilibrium and n_2^* is a stable equilibrium.

It is observed that when $H < \frac{rK}{4}$, two equilibria are created. As H increases, the equilibria move towards each other. As $H = \frac{rK}{4}$, the equilibria collide into a half-stable equilibrium at $n = \frac{K}{2}$, as soon as, $H > \frac{rK}{4}$ the equilibria annihilate as shown in Figure 2. Therefore a saddle-node bifurcation occurs at $H = \frac{rK}{4}$ corresponding to the equilibrium $n^* = \frac{K}{2}$. Refer to Strogatz (1994) for further discussion on the types of bifurcations.

For an example of this practice, we refer to Brauer & Sanchez (1975) that considered a lake with the fish species harvested to give a constant yield. Their analysis corresponds to Figure 2. In natural situations, it is observed that constant harvesting does not make sense biologically when the population is small (Weiss 2009). For example, if there are only five tons of fish left in a certain area of the ocean, then harvesting ten tons per day makes no sense. There is a danger in operating at the MSY because the unique equilibrium (i.e., half the carrying capacity) which is half-stable can easily tend the fishery to extinction. The fishery can however operate below the MSY, by keeping a higher fish stock but low harvesting activities hence low productivity. Harvesting theory suggests that Constant harvesting strategy cause greater variation in stock density than other policies (May *et al*. 1978, Ludwig 1998). However, this policy was practiced by many fisheries in the past but it is no longer considered a safe management strategy due to the reasons shown above and others (Pascual & Hilborn 1995, Fryxell *et al*. 2005).

HOLLING TYPE I FUNCTIONAL RESPONSE

Here, the rate of predation increases linearly with the population size. It assumes the catch at time, t depends first on the population available, $n(t)$ and secondly, on the effort $e(t)$ expended by the predator (Schaefer 1957). Effort in this sense could be an index of all inputs commonly used for hunting (such as man-hours, trawlers, time spent at sea, nets, etc). This functional response is modeled by

$$H(n) = qen \qquad (3.2.1)$$

Where q denotes the technical efficiency (capturability) of inputs used for hunting. (3.1) now has the particular form,

$$\frac{dn}{dt} = rn(1 - \frac{n}{K}) - qen \qquad (3.2.2)$$

Calculating Equilibrium

The equilibrium of (3.2.2) is given by

$$rn(1 - \frac{n}{K}) = qen \qquad (3.2.3)$$

$$n_2^* = K(1 - \frac{qe}{r})$$

The population equilibria are $n_1^* = 0$ and.

(i) If $r < qe$, $n_2^* < 0$.

(ii) If $r > qe$, $n_2^* > 0$.

It is noticed that $n^* = 0$ is always a population equilibrium. However it is stable when $r < qe$, half-stable when $r = qe$ and unstable when $r > qe$. The non-zero equilibrium $n^* = K(1 - \frac{qe}{r})$ on the other hand, is locally unstable when $r < qe$, disappears when $r = qe$ and locally stable when $r > qe$. Hence the origin undergoes transcritical bifurcation as r is varied. Refer to Strogatz (1994) for furthur discussion on this bifurcation type.

We illustrate the case , $r > qe$, which has positive equilibrium in Figure 3.

Graphical Analysis

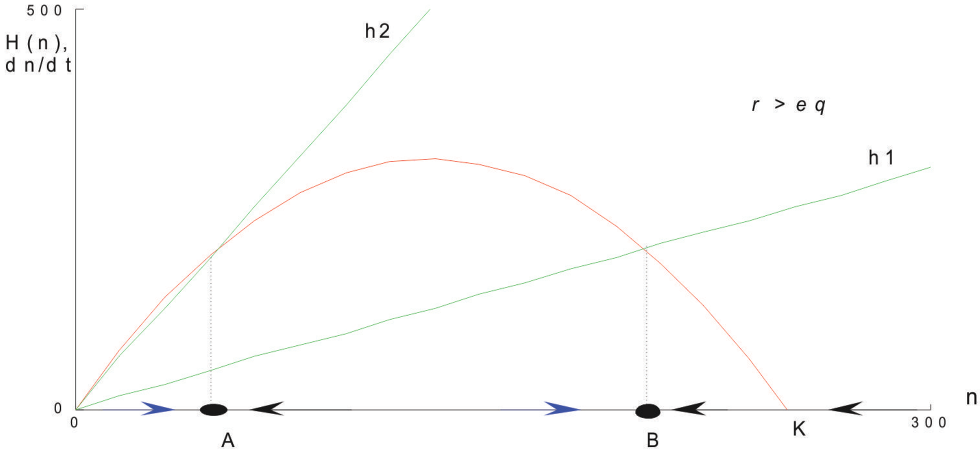

Figure 3. Corresponds to (3.2.2). The net growth of the population, *dn/dt* is shown as a function of *n*. *K* is the environmental carrying capacity, *r* is the intrinsic growth rate, *e* is the effort and *q* is the capturability. The parabola is the natural growth of the population while lines are loss due to predation using constant effort, $h=qe(t)n$. When $e(t)$ is increased, h_1 moves to the left to h_2. Where the line lies above the parabola; the net growth rate is negative. Where the line lies below the parabola, the net growth rate is positive. The points of intersection correspond to possible equilibria and the arrows indicate the stability of the equilibria.

At predating level h_1, there are two population equilibria. That is, $n_1{*}=0$ and $n_2{*}=B$ (which has been found algebraically). When the initial population is greater than zero, the net growth in the population is positive. Hence the population increases in size and grows away from zero. However, when population increases beyond the non-zero equilibrium B, the net growth in the population is negative. Predation exceeds reproduction. This results in a decline in the population size back to *B*. *B* is a locally stable equilibrium whiles $n=0$ is a locally unstable equilibrium.

From the graphical analysis, when effort *e(t)* is increased, the predating level h_1 moves to the left. This is represented by h_2. Still there are two equilbria just as in the case of h_1; the zero population and *A*. However, it is observed that $A<B$ as shown in Figure 3.

Also, when the population reproduces rapidly (i.e. $r>eq$), then any initial population, with the exception of zero, will grow away from extinction. However, increasing the effort extremely (i.e. to the left of h_2 as shown in Figure 3) will draw the population to extinction because then $r<eq$.

Under Holling Type I, predation can be done at the MSY without fear of local extinction if the natural growth exceeds the predation effort (i.e $r>eq$). This is because the non-zero equilibrium population is stable unlike the case of Constant Yield where the non-zero equilibrium population is half stable (Figure 2 and Figure 3). Hence this predation strategy is preferred over Constant Yield.

HOLLING TYPE II FUNCTIONAL RESPONSE

This assumes that at low population the predator is limited by prey availability, so that $H(n)$ increases with increasing prey population; at very high population, $H(n)$ saturates to some constant β, determined by the predators intake capacity or processing rate. It is identical to the Michaelis-Menten equation (Berryman 1992). This behavior is modeled by the function below;

$$H(n) = \frac{\beta n}{n_H + n} \qquad \beta>0 \text{ and } n_H>0 \tag{3.3.1}$$

n_H is the population where predation is half-saturated. (3.1) now has the particular form,

$$\frac{dn}{dt} = rn(1-\frac{n}{K}) - \frac{\beta n}{n_H + n} \tag{3.3.2}$$

Since the system has four parameters: r, K, β, n_H we non-dimensionalise it by introducing rescaled variables, in order to reduce the number of parameters and to simplify the analysis (Strogatz 1994).

Both n_H and K have the same dimension as n and so either n/n_H or n/K could serve as a dimensionless population level. We let

$$x = \frac{n}{K}, \quad \tau = rt, \; a = \frac{n_H}{K}, \; \text{and } \eta = \frac{\beta}{rK}$$

Then (3.3.2) becomes,

$$\frac{dx}{d\tau} = x(1-x) - \eta\frac{x}{a+x}$$

$$\eta > 0 \text{ and } a>0 \tag{3.3.3}$$

The slope of (3.3.3) is

$$f'(x) = 1 - 2x - \frac{\eta a}{(a+x)^2} \tag{3.3.4}$$

Calculating Equilibrium

The equilibrium of (3.3.3) is given by,

$$x(1-x) = \eta\frac{x}{(a+x)}$$

This gives $x_1^* = 0$ and $(1-x) = \eta/(a+x)$ whose roots give two additional equilibria.

The equilibrium x_1^* is an unstable equilibrium when $\eta < a$ and a stable equilibrium when $\eta > a$ since

$$f'(x_1^*) = 1 - \frac{\eta}{a}$$

The two roots of $(1-x) = \eta/(a+x)$ are given by

$$x^*_{1,2} = \frac{1}{2}((1-a) \pm \sqrt{(1-a)^2 - 4(\eta - a)} \tag{3.3.5}$$

This gives five possible cases:

(i) If $\eta < a$, there are two roots with opposite signs.

(ii)If $\eta = a$, there is at least one x-value which is zero. The other root is

(a) Positive when $a<1$.
(b) Negative when $a>1$.

(iii) If $a<\eta<\frac{(1+a)^2}{4}$, there are 2 roots with the same sign.

(a) For $a<1$ the roots are positive.
(b) For $a>1$ the roots are negative.

(iv) If $\eta=\frac{(1+a)^2}{4}$, then at least one root is zero. The other root is

(a) Positive when $a<1$.
(b) Negative when $a>1$.

(v) If $a<\frac{1}{4}(1+a)^2<\eta$ there are no real *x*-values.

We determine the stability of the equilibria of the five cases respectively using graphical method. Graphing (3.3.3), it is observed that for *a* >1, there is exactly one intersection since it has only negative equilibrium in addition to the zero equilirium. However, for *a* sufficiently less than 1, we can have one, two or three intersections (Figure 4) depending on the value of η.

We illustrate the five possibilities discussed above when *a<1* in Figure 4. Our interest is on the possible positive equilibria.

Observe that the two positive equilibria created when $a<\eta<\frac{(1+a)^2}{4}$, coalesce and create a one positive equilibrium when $\eta=\frac{(1+a)^2}{4}$. As η increases above $\frac{(1+a)^2}{4}$, all other equilibria disappear leaving $x^*=0$ as shown in Figure 4. Hence, a saddle –node bifurcation occurs at $\eta=\frac{(1+a)^2}{4}$.

Graphical Analysis

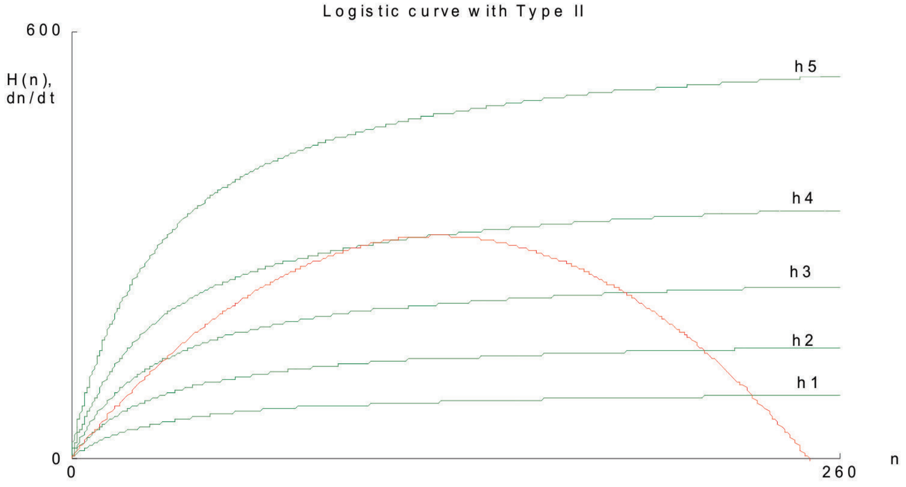

Figure 4. Corresponds to (3.3.2) and (3.3.3). The net growth of the population, *dn/dt* is shown as a function of *n. K* is the environmental carrying capacity and *H(n)* is Holling Type II functional response. The points of intersection correspond to the possible equilibria. Where the parabola is above the curve, the net growth rate is positive (the flow along the x-axis is to the right). Where the curve is above the parabola, the net growth rate is negative (the flow along the x-axis is to the left). *h(1),h(2),h(3),h(4),h(5)* are predation levels with *a* =0.12 and η =0.048, 0.136, 0.224, 0.312 and 0.48 respectively.

We observe from Figure 4 that the stability type alternates as we move along the x-axis.

At predation level h_1, we have two points of intersection: zero and a non-zero value slightly lower than K. The net growth of the population is positive when the population is smaller than the non-zero equilibrium. This means that, predation is relatively small, and the population is reproducing faster than being extracted. Therefore, there will be increase in the population size until the equilibrium (point of intersection) is reached. However, when the population is beyond the non-zero equilibrium, the net growth in the population is negative and as such, the population size will decline until it finally settles at the equilibrium. From Figure 4, the zero equilibrium is an unstable equilibrium whiles the non-zero equilibrium is a stable equilibrium.

At predation level h_2, we still have two points of intersection: zero and a non-zero value slightly lower than K. The zero equilibrium is unstable whiles the non-zero equilibrium is stable just as in h_1. However, the non-zero equilibrium in h_2 is smaller than that of predation level h_1.

At predation level h_3, there are three points of intersection: zero and two non- zero values.

The net growth of the population is negative when the population is between zero and the smaller of the two non-zero values. This means that, the population is being extracted faster than it reproduces. Hence, the population will decline to extinction. However, when the population is between the two non-zero values, the net growth is positive. Therefore there will be increase in the population size until the larger non-zero value is reached where it can be sustained forever. On the other hand, when the population size is above the larger non-zero value, then the net growth is negative and the population will decline until it reaches the non- zero value. The zero equilibrium and the larger of the two non-zero values are stable equilibria with their domain of attraction divided by the smaller non-zero equilibrium which is an unstable equilibrium. Therefore this unstable equilibrium acts as a breakpoint of the population.

At predating level h_4, predation saturates at the MSY. There are two points of intersection: zero and half the carrying capacity. This means that, if the exploited population begins at the carrying capacity, K, then there will be no population growth, but because the net growth is negative. When the population declines to half the carrying capacity then the natural growth is matched by level of predation, and so the population can be sustained perpetually. However, if the population falls below half the carrying capacity, then the rate of predation will exceed the natural population growth and there will be a decline in the population eventually resulting in extinction. Hence, the zero population is a stable equilibrium whiles $n^* = \frac{K}{2}$ is half-stable equilibrium.

At predating level h_5, predation saturates above the MSY. Here, there is a unique point of intersection: zero. The net growth is negative because predation is relatively large. The population is being extracted much faster than it can reproduce. Therefore, irrespective of the population size, the extinction will eventually occur.

From Figure 4, we observe that sustainability of the population can best be achieved if the predation level saturates below the MSY. Under Holling Type II, there is a danger operating at the MSY. This is because the non-zero equilibrium, $\frac{K}{2}$ is half- stable and therefore any environmental fluctuation can easily cause the population to fall below $\frac{K}{2}$ and this will eventually cause extinction.

HOLLING TYPE III FUNCTIONAL RESPONSE

It assumes that there is almost no predation when the population is scarce. However, once the population exceeds a certain critical level n_H, $H(n)$ increases faster than linearly (the predators are catching as much as they can) reaching the inflection point of the curve then behaves like Type II functional response and saturates to a constant β. This behavior is modeled by

$$H(n) = \frac{\beta n^2}{{n_H}^2 + n^2}$$

$$\beta > 0 \text{ and } n_H > 0 \qquad (3.4.1)$$

From (3.4.1), we observe that $H'(0)=0$.

The particular form of (3.1) becomes

$$\frac{dn}{dt} = rn(1 - \frac{n}{K}) - \frac{\beta n^2}{{n_H}^2 + n^2} \qquad (3.4.2)$$

We simplify the analysis by non-dimensionalising the system.

We let $x = \frac{n}{K}$, $\tau = rt$, $a = \frac{n_H}{K}$ *and* $\eta = \frac{\beta}{rK}$

(3.4.2) then becomes

$$\frac{dx}{d\tau} = x(1-x) - \frac{\eta x^2}{a^2 + x^2} \qquad (3.4.3)$$

The slope of (3.4.3) is

$$f'(x) = 1 - 2x - \frac{2\eta x}{(a^2 + x^2)}\left[1 - \frac{x^2}{a^2 + x^{2}}\right. \quad (3.4.4)$$

Calculating Equilibrium

The equilibrium of (3.4.3) is given by

$$x(1-x) = \eta \frac{x^2}{a^2 + x^2} \quad (3.4.5)$$

This gives $x_1^* = 0$ and $(1\text{-}x) = \eta \frac{x}{a^2 + x^2}$ whose roots give three additional equilibria.

The equilibrium $x_1^* = 0$ is always an unstable equilibrium since $f'(x_1^*) = 1$.

The three additional equilibria can be identified algebraically and classified using the discriminant of the cubic equation. However, we proceed using graphical analysis.

Graphing (3.4.2), it is observed that for a >1, there are exactly two intersections (see Figure 5). However, for a sufficiently less than 1, we can have two, three, or four intersections (see Figure 6) depending on the value of η .

Graphical Analysis

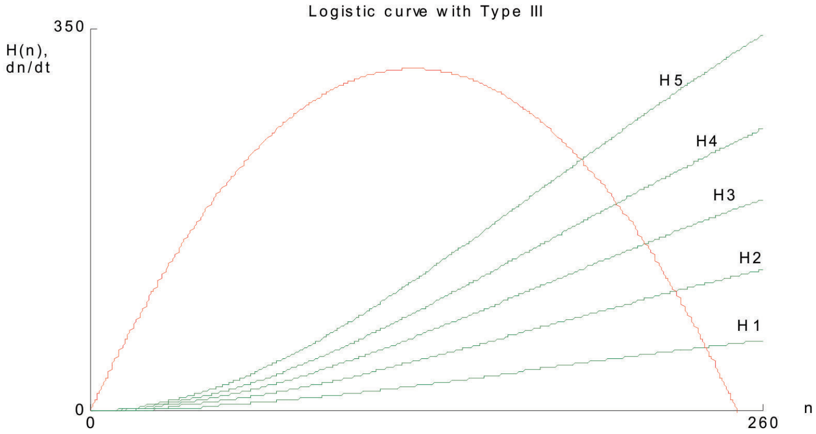

Figure 5. Corresponds to (3.4.2) and (3.4.3). The net growth of the population, *dn/dt* is shown as a function of *n*. *K* is the environmental carrying capacity and *H(n)* is Holling Type III functional response. The points of intersection correspond to the possible equilibria. Where the parabola is above the curve, the net growth rate is positive (the flow along the x-axis is to the right). Where the curve is above the parabola, the net growth rate is negative (the flow along the x-axis is to the left). *H(1),H(2),H(3),H(4),H(5)* are predation levels with a =1.2 and η =0.12, 0.24 , 0.36, 0.48 and 0.64 respectively.

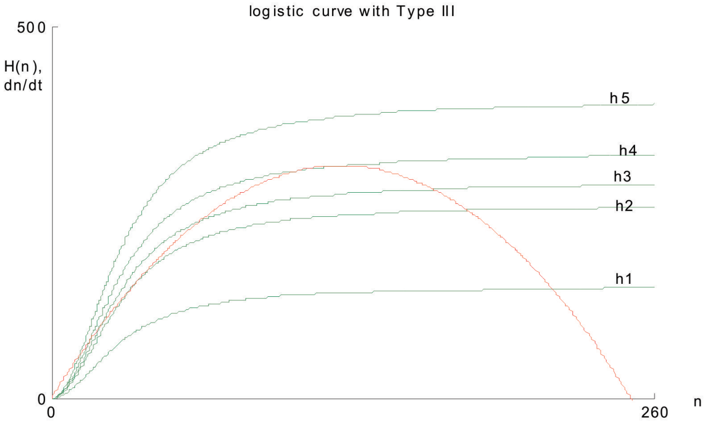

Figure 6. Corresponds to (3.4.2) and (3.4.3). The net growth of the population, *dn/dt* is shown as a function of *n*. *K* is the environmental carrying capacity and *H(n)* is Holling Type III functional response. The points of intersection correspond to the possible equilibria. Where the parabola is above the curve, the net growth rate is positive (the flow along the x-axis is to the right). Where the curve is above the parabola, the net growth rate is negative (the flow along the x-axis is to the left). *h(1),h(2),h(3),h(4),h(5)* are predation levels with a =0.12 and η =0.048, 0.136, 0.224, 0.312 and 0.48 respectively.

Figure 6 illustrates where $a<1$ i.e. where $n_H<K$. We observe that the stability type alternates as we move along the x-axis.

At predation level h_1, there are two points of intersection: zero and a non-zero value slightly below the carrying capacity, *K*. Here, predation is relatively unimportant. What happens is that the population reproduces at a rate much faster than it is extracted. This causes the population to increase until it reaches the non-zero value. However, when the population size is above the non-zero value, then the net growth is negative. This results in a decline in the population until it reaches the non-zero value. Therefore, zero is an unstable equilibrium whiles the non-zero value is a stable equilibrium.

At predation level h_2, there are three points of intersection: zero and two non- zero values.

The net growth of the population is positive when the population is between zero and the smaller of the two non-zero values. Hence, the population will increase until it reaches the non-zero value. However, when the population is between the two non-zero values, the net growth is positive. Therefore there will be an increase in the population size until the larger non-zero value is reached where the population can be sustained forever. On the other hand, when the population size is above the larger non-zero value, the net growth is negative and the population will decline until it reaches the larger non-zero value. Therefore, zero is an unstable equilibrium, the smaller non-zero value is a half stable equilibrium and the larger of the two non-zero value is a stable equilibrium.

At predation level h_3, there are four points of intersection: zero, in addition to three intersections. What happens here is that the population will tend towards either the second or fourth equilibrium depending on its initial size. For any initial population size greater than the third intersection, the net growth is positive. Hence, the population will increase until it reaches the fourth intersection. On the other hand, for any initial population smaller than the third intersection, the net growth is negative. Hence, the population will tend to decline until it reaches the second intersection. Therefore, the zero population is an unstable equilibrium, the second and fourth intersections are stable equilibria and their domain of attraction is divided by an unstable equilibrium which is the third intersection. The unstable equilibrium in the middle of the two stable equilibria therefore acts as the breakpoint.

At predation level h_4, predation saturates at the maximum sustainable yield. There are three points of intersection: the zero population, a small *n*-value and half the carrying capacity i.e. $n^*=K/2$. When the population is above half the carrying capacity, the net growth is negative. Therefore, the population declines until it settles at *K/2*. The danger is that if the population falls below $\frac{K}{2}$, then the net growth will be negative and there will be a decline in the population until it approaches the other non-zero equilibrium (small *n*-value) where it can be sustained forever. Finally, the net growth of the population is positive when the population is slightly above zero. Hence, the population will increase until the small n-value is reached and can be sustained perpetually. Therefore, the equilibrium at half the carrying capacity (*K/2*) is half-stable, the other equilibrium (small *n*-value) is stable while the zero population is an unstable equilibrium.

At predating level h_5, predation saturates above the MSY. Here, there are two points of intersection: zero and non- zero value which is slightly above zero. This means that the net growth is negative when predation is relatively large and the population is above the non-zero value. This will result in a decline in the population until it finally settles at the non-zero equilibrium which is slightly above zero. Hence, zero is an unstable equilibrium while the non-zero value is a stable equilibrium.

Figure 5 shows that two intersections which occur when $a>1$ are zero and a non-zero value. At all predation levels, zero is an unstable equilibrium whiles the non-zero value is a stable equilibrium. However, when predation is relatively large, H_5 then the non-zero value is smaller when predation is relatively unimportant, H_1.

Just as in Holling Type II, there is danger in operating at the Maximum Sustainable Yield. This is because any misjudgment when operating at the maximum sustainable yield can push the exploited population to collapse a very low size, although not to extinction. (see h_4 in Figure 6).

The essential feature that leads to two alternative stable states (see h_3 in Figure 6) is the assumption that $\boldsymbol{a=n_H/K}$ is significantly small. That is the exploited population has a large carrying capacity K and predation level is not extreme such that it saturates below MSY. It is observed that $x^*=0$ is always an equilibrium and in addition it is always an unstable equilibrium. Therefore, irrespective of the level of predation, the population will not decline to zero (extinction).

DISCUSSION

Different analyses addressed to exploited population have received significant attention trying to unfold the effects of management in theoretical and empirical studies (Reynolds *et al.* 2001, Jonzén *et al.* 2003, Fryxell *et al.* 2006, Costa & Faria 2011). Here we have considered predation as a kind of harvesting and analyzed the effects of different predation functions on long-term stability of prey populations. Specifically, we have demonstrated a variety of mathematical models of an exploited population. Each model considered the dynamics of the prey population given one predation function. We considered four different predatory functions; Constant Yield, Holling Type I, Holling Type II and Holling Type III and treated the predator population as a constant.

Predation is one important factor that influences the dynamics of many populations and it is sometimes overlooked, or covered in the simplest way (Wurts 1992). In the presence of predation, the loss rate due to predation, in general, depends both on the predation level and on the initial population size of the prey. Therefore the inadequate understanding of the predation processes could result in population management errors, like fishery management failures for example (Levhari & Mirman 1980).

Three kinds of harvesting policy are most employed worldwide: fixed quota, fixed proportion and fixed escapement (Fryxell *et al.* 2005). Here, the first two policies, fixed quota and fixed proportion – i.e., constant yield and Type I functional response, respectively - are analyzed in respect to prey population besides Type II and III functional response.

More importantly, the results have shown that continuous changes in predation rates can lead to discontinuous changes in the prey population, and also that, according to parameter values, one, two or three positive equilibria can coexist – i.e., multiple states of equilibrium (Scheffer 2009).

The existence of three positive equilibria could be observed in the population when Holling Type III is used. Indeed, the existence of three positive equilibrium occur when the condition $a<1$ holds. This condition occurs because predation saturates at a population size significantly below the carrying capacity of the prey population and in addition, the exploited population reproduces rapidly and has a large carrying capacity.

The case where two strictly stable positive equilibria can coexist with an unstable equilibrium in their middle for the same population is interesting. Chase (1999) observed that intermediate levels - i.e., prey abundance - in a predator-prey structured food web depicts also multiple alternative state of equilibrium and the initial conditions play an important role determining which equilibrium point the population will reach (see also Chase 2003 for more information about empirical corroboration). The possibility of two coexisting stable equilibria corresponds to: (*i*) over-exploitation; where the population can support large predatory activities but the size is maintained at a low size with risk of extinction, (*ii*) low predation pressure (“artisanal predation”); where the population is maintained at a large size, far from extinction, but can support small predatory activities. We noticed that the unstable equilibrium in the domain of attraction acts as a breakpoint or a threshold. Where a population will be in the immediate future depends on whether the initial condition is smaller or greater than the breakpoint value. Therefore, generally alternative stable states arise from a range of mechanisms, and usually, a positive feedback toward one of the states can be identified as the basic mechanism, and further, the strength of the positive feedback dictates which states will arise (Scheffer 2009).

The results have established that a sustainable population could be theoreticly achieved by imposing a Harvesting policy as modeled with Holling Type III functional response as, in this case, the population does not run the risk of local extinction since for all level of predation the zero population is an unstable equilibrium. This is so because predation is reduced or seized when the population size becomes relatively low, then the rate of reproduction exceeds the rate of predation allowing for the prey population to recover (grow) from the effect of predation. However, in the case of the other functions, zero alternates its stability with varying predation level (Figure 6). Interestingly, in more complex interactions, functional response Type III, displayed as a predator's prey preference, plays an important role stabilizing the dynamics and turning coexistence of species possible (McCann *et al.* 1998, Faria & Costa 2009).

Furthermore, these results caution against predation at the Maximum Sustainable Yield (MSY) when operating with Constant Yield and Holling Type II functional response. Here, the positive equilibrium which exists is half-stable. Therefore, any misjudgment or environmental fluctuation can easily carry the population to extinction. There is however a positive stable equilibrium when operating with Holling Type III but this value is slight greater than zero.

In addition, this analysis suggests that for a sufficiently small initial population, the effect of predation can be drastic in the short term but if the population reproduces rapidly and has a large carrying capacity then it could recover in the long term. Finally, the results discussed here can be employed for the estimation of important parameters like initial population for stocking and safer harvesting level, and also for reintroduction programs. This can prevent the risk of extinction and yield specific insights into the management of the system.

Modeling population dynamics as part of ecosystem management is frequently recommended but the associated complexity and uncertainty will always limit the extent to which the effects of predation can be predicted (Auger *et al*. 2009).

In conclusion, population dynamics – i.e., population density or abundance variation through time and space – may be treated in a formal and mathematical approach, to help understand the processes and mechanisms behind the dynamic behavior depicted by natural and exploited population species. Therefore, the interdisciplinary perspective between ecology and mathematical modeling is an important and useful approach to the challenge in understanding nature.

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