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# CONSIDERATION OF CARRYING CAPACITY IN RELATION TO LIMITS OF ARTIFICIAL STOCK ENHANCEMENT

by

Alec D. MacCall
NMFS/SWFSC Tiburon Laboratory
3150 Paradise Dr.
Tiburon, CA 94920

ABSTRACT

Hatchery-based enhancement of depleted marine fish populations often is guided by intuition more than by analysis. For example, so-called "carrying capacity" (i.e., the abundance of a natural population) is often thought to be an appropriate upper limit to enhancement efforts. Hatchery production is incremental to the status quo population, and therefore can be treated as a marginal value problem. Examination of the logistic model and related population models shows that knowledge of carrying capacity provides little guidance to optimization of enhancement. If the abundance of the receiving population is above the MSY level (one-half carrying capacity in the logistic model), the marginal value of hatchery-produced fish is less than unity. Even at carrying capacity this discount is not severe, each hatchery-produced fish being worth exp(-r) or approximately 1-r fish, where r is the intrinsic rate of increase.

## INTRODUCTION

Artificial enhancement of fish stocks by means of hatcheries is a proven though sometimes controversial tool of salmon and freshwater fishery management. In marine ecosystems hatchery-based attempts at stock enhancement also have a long history, but the tool cannot be considered proven. In most cases there has been little evidence that any benefit has been achieved (MacCall, 1989; Solemdal, 1984). Nonetheless, abundances of many natural marine fish stocks have been fished to low levels, and marine hatcheries are gaining popularity as an optimistic solution that may be politically preferable to closing fisheries. Whether marine fish hatcheries are economically worthwhile is subject to analysis (e.g., Hobbs et al., 1990). However, in cases where marine hatcheries are actually being constructed, hatchery management decisions become conditional on the assumption that they are in some sense effective. The important operational question is no longer whether to produce fish, but rather how many fish to produce.

There are few, if any, established demographic or ecological criteria for optimizing hatchery output. The concept of "carrying capacity" is sometimes invoked as an ad-hoc but seemingly reasonable limit to artificial enhancement. This criterion is appealing in that it intuitively relates to a presumed natural level of (or limit to) fish abundance, and that it would therefore appear to be undesirable (or impossible) to exceed that level. Unfortunately, that intuition is not supported by formal analysis of population growth dynamics, and "carrying capacity" may not provide a definitive reference point in management of efforts toward artificial enhancement.

## THE LOGISTIC MODEL

The term "carrying capacity" originally descibes a parameter in the logistic population growth model arising from the differential equation,

(1) $dN/dt = rN(K-N)/K$, where

- N is abundance,
- t is time,
- r is a maximum per capita rate of increase, and
- K is an asymptotic limit to abundance over time, also called the "carrying capacity."

Properties of this curve are well-known: Population growth or production (dN/dt) has a maximum (often associated with Maximum Sustainable Yield, MSY) at N=K/2, and falls to zero at N=0 and N=K. Population growth is negative at abundances above "carrying capacity" (N>K).

Equation (1) has a classic solution describing the trajectory of population growth over time (Figure 1). One parametrization of the solution, is given by Nisbet and Gurney (1983),

(2) $N_t = K/[1+N_o^{-1}(K-N_o)\exp(-rt)]$, where

$N_t$ is the abundance at time t, and

$N_o$ is the initial abundance at time t=0.

The asymptotic property of "carrying capacity" is easily seen in Figure 1. Importantly, Equation (2) describes the trajectory of population growth for initial population sizes above "carrying capacity" ($N_o$>K) as well as the more usually considered initial condition of $N_o$<K. Thus in the logistic growth model, "carrying capacity" is an upper limit to population size only if the initial condition is $N_o$<K. If initial abundance exceeds K, then the population size declines, and K is an asymptotic lower limit.

Another kind of solution to the logistic model of Equation (1) is a function that describes $N_{t+1}$ as a function of $N_t$ (known generically as a Ricatti function). This function can be derived algebraically from Equation (2) by writing a second equation for $N_{t+1}$, solving each equation for $N_o$, equating the two, and solving the resulting equation for $N_{t+1}$ as a function of $N_t$, giving

(3) $N_{t+1} = N_t\exp(r)/[1+N_t(\exp(r)-1)/K]$

This equation is of the form $y=Ax/(1+Bx)$ and describes a hyperbola, i.e., a shape similar to a Beverton-Holt stock-recruitment relationship (Figure 2). For values of $N_t<K$, the population grows, so $N_{t+1}>N_t$. For values of $N_t>K$, the population declines, so $N_{t+1}<N_t$. As expected, $N_{t+1}=N_t$ if $N_t=K$. Like Equation (2), Equation (3) shows that abundance approaches K whether initial values are above or below.

From the viewpoint of hatchery production, we would like to know the effect on the next year's abundance of a marginal increment in this year's abundance such as would result from release of hatchery-produced fish. This corresponds to the slope of the curve in Figure 2, and is given by the first derivative of Equation (3),

$$(4)\quad dN_{t+1}/dN_t = \exp(r)/[1+N_t(\exp(r)-1)/K]^2$$

which is shown in Figure 3. At very low initial abundance, the marginal population increase resulting from release of a unit quantity of hatchery fish ($dN_{t+1}/dN_t$) is $\exp(r)$, which is greater than 1 because $r>0$ and Equation (1) assumes the added fish immediately achieve functional equivalence to those already in the population. The marginal increase falls to unity (i.e., $dN_{t+1}/dN_t=1$) at $N_t$ very near $K/2$, where Equation (1) exhibits maximum surplus production. In the Ricatti equation maximum surplus productivion does not occur exactly at $N_t=K/2$, but rather at $N_t$ slightly below K/2 because Equation (3) incorporates an entire year of growth (MacCall, 1980). At $N_t$=K, the marginal rate falls to $dN_{t+1}/dN_t=\exp(-r)$, and continues to fall for $N_t$>K.

It is interesting to note that Equation (3) does have an asymptotic upper limit to $N_{t+1}$. This limit is K/(1-exp(-r)), or approximately K/r. In some ways, this limit corresponds more closely to the intuitive concept of "carrying capacity" as being the largest population size that can be achieved. Importantly, this limit is much larger than K. For example, if r=0.1 indicating that the maximum population growth rate would be about 10% per year, the upper limit to abundance is approximately 10K.

The logistic model does provide some guidance to hatchery optimization, but not of the sort originally envisioned by the use of "carrying capacity" as a limit. Assuming full viability, hatchery production is most effective when the abundance of the receiving population is below K/2. At population sizes above K/2, the marginal value of hatchery-produced fish is less than unity, or in other words, the introduced fish are subject to a discount. However, for low to moderate (i.e., typical) values of r, that discount is not severe, and other cost-benefit coniderations can readily compensate. From the viewpoint of this very simple bioeconomic model, hatchery production potentially can be advantageous at abundances substantially in excess of "carrying capacity."

## OTHER POPULATION MODELS

The logistic model is one of the simplest population models that can be applied to this problem. It is appropriate to consider how the results would change if a more complicated model were considered. The logistic model is a member of a differential equation family of growth models described by the Richards growth equation (Richards, 1959) and the generalized production model (Pella and Tomlinson, 1969),

(5) $dN/dt = rN[(K-N)/K]^m \qquad m>0,$ where

m is an exponent controlling skewness of the population growth curve.

The logistic model corresponds to the case of m=1. If m>1, the abundance producing MSY ($N_{MSY}$) is larger than K/2, and population growth rate drops sharply at higher levels of abundance. Because of this, the upper limit of $N_{t+1}$ is near K, even if r is small. This shape of population growth curve is often found in populations of whales and other large mammals (Fowler, 1987) that are unlikely candidates for artificial enhancement. In contrast, fish populations (i.e., typical candidates for hatchery production) often have a $N_{MSY}$ that is smaller than K/2, corresponding to the case of 0<m<1. Here the population growth rate declines more slowly as abundance increases, and the upper limit of $N_{t+1}$ is consequently even larger than would be predicted by the logistic model.

A popular alternative to differential equations is difference equations, where we consider an annual rather than instantaneous change in population size, i.e., $\Delta N/\Delta t$ (e.g., where $\Delta t$ is one year) rather than $dN/dt$. Theoretical population biology has explored the chaotic population behavior arising from high values of r in a difference equation analogous to the logistic model (May, 1975),

(6) $\Delta N/\Delta t = rN(K-N)/K$

where r is now a rate of increase associated with time interval $\Delta t$, in this case, annual. The equivalent Ricatti equation is simply

(7) $N_{t+1} = N_t + rN_t(K-N_t)/K$.

For the low values of r that are characteristic of fishes, difference Equation (6) does not exhibit peculiar properties, and behaves indistinguishably from differential Equation (1) in the range $0<N<K$ (Figure 2). The difference equation also has a maximum value of $N_{t+1}$, but it is not asymptotic and has a peak at $N_t=K(1+r)/2r$; $N_{t+1}$ declines at higher values of $N_t$. Except for very large values of $N_t$, the conclusions drawn from the

differential equation model are similar to those for the difference equation model.

More realistic population models would incorporate age structure, including a delay between when the hatchery fish are released and when those fish become reproductive. Unless there is a strong mechanism of population regulation (e.g., a limited number of recruitment sites that become saturated at high abundance of pre-recruits) operating during that period, it is unlikely that the previous model results will be invalidated.

## CONCLUSION

In conclusion, knowledge of "carrying capacity" provides little guidance to optimizing output of fish hatcheries. There may be a theoretical upper limit to stock abundance under artificial enhancement, but it is much larger than the natural equilibrium level or "carrying capacity." The marginal value of hatchery-produced fish declines slowly with the size of the receiving population, and remains high at and even above "carrying capacity." However "carrying capacity" may still be an appropriate target for the purpose of preserving ecosystem functioning (predator-prey relationships, etc.), but ecological aspects are beyond the scope of this discussion. Hatchery-related efforts to estimate "carrying capacity" with precision may be misguided; it is likely that a good guess may suffice for most purposes.

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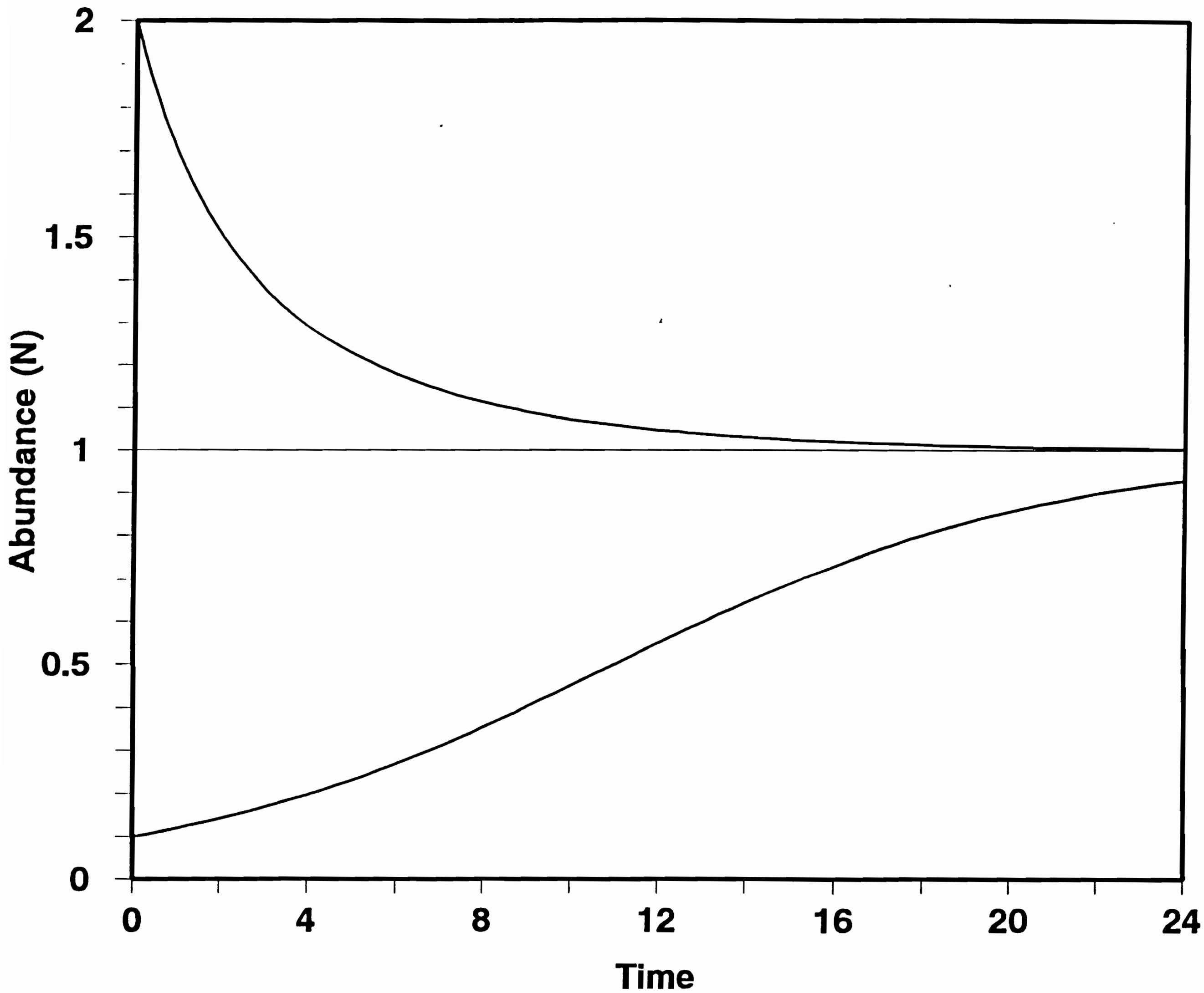
FIGURES:

1. Population growth characteristic of the logistic model. Lower curve is for $N_0<K$; upper curve is for $N_0>K$. (Parameter values: K=1, r=0.2/yr)

2. Ricatti curves for the differential (solid line) and difference (dotted line) forms of the logistic model. Parameter values as in Figure 1.

3. Slope of the Ricatti curves in Figure 2. Parameter values as in Figure 1.

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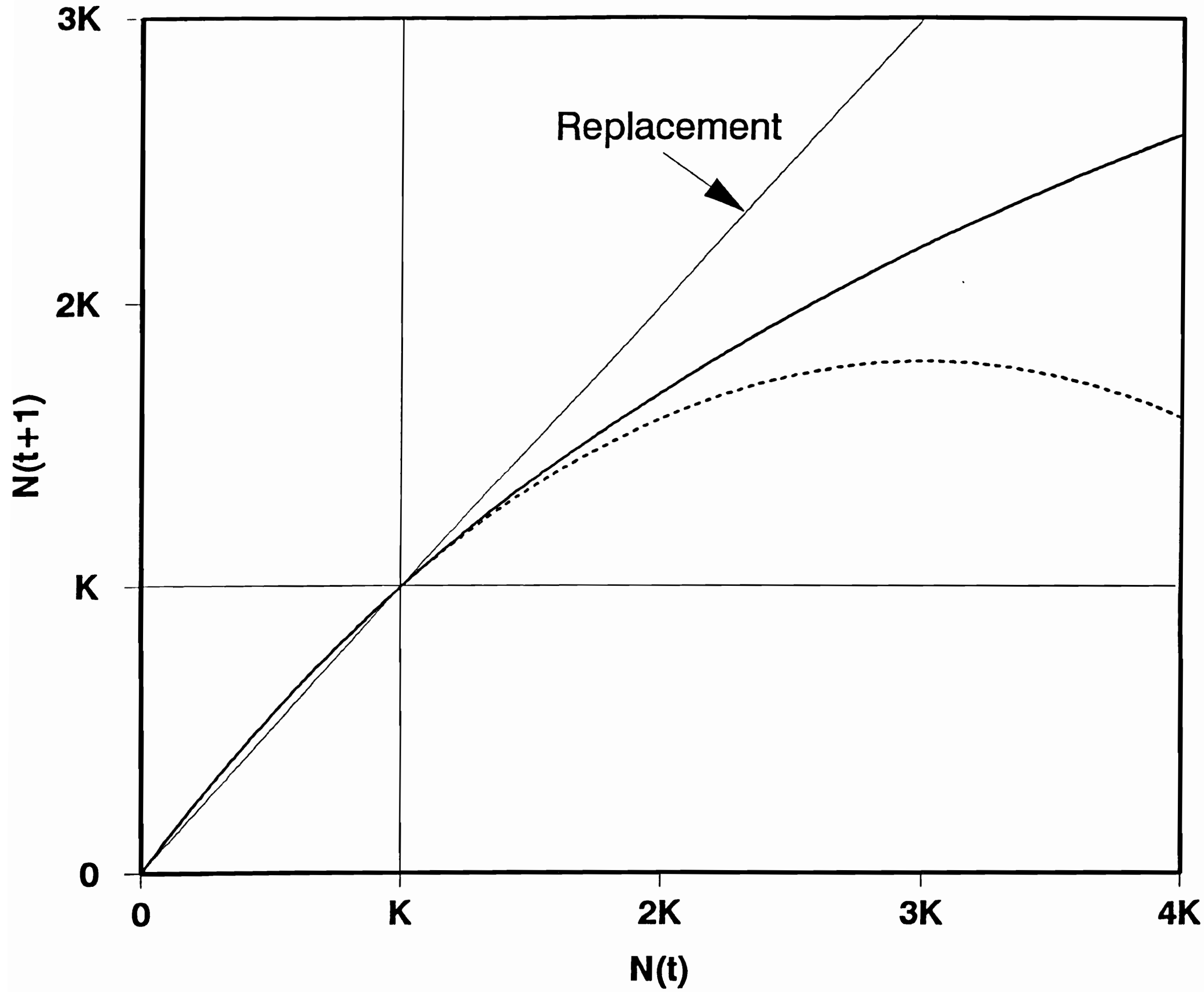


FIGURE 2. Ricatti curves for the differential (solid line) and difference (dotted line) forms of the logistic model. Parameter values as in Figure 1.

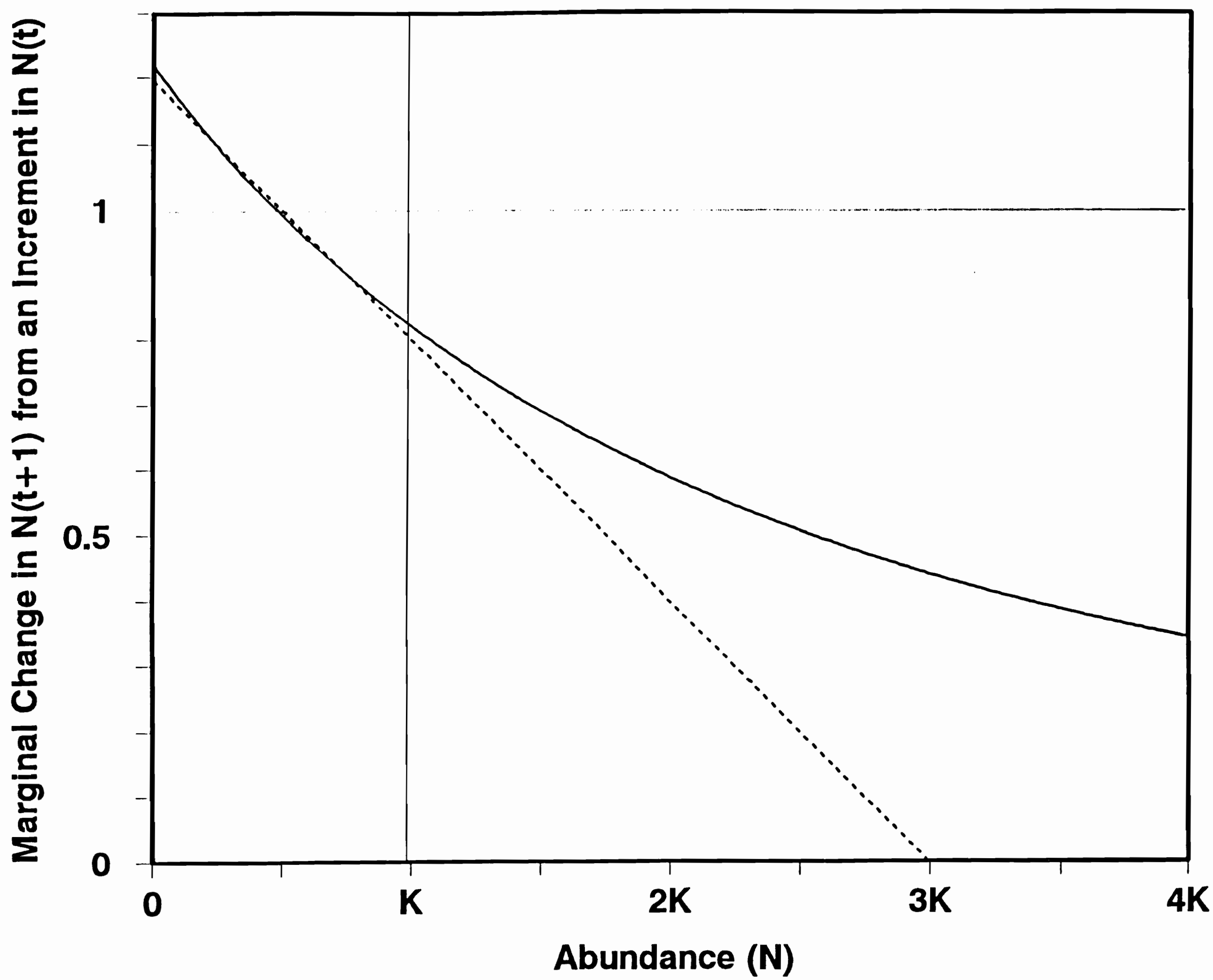


FIGURE 3. Slope of the Ricatti curves in Figure 2. Parameter values as in Figure 1.