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LOCAL STABILITY AND MAXIMUM NET PRODUCTIVITY LEVELS FOR A SIMPLE MODEL OF PORPOISE POPULATION SIZES

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National Oceanic and Atmospheric Administration
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Southwest Fisheries Center

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FOR A SIMPLE MODEL OF PORPOISE POPULATION SIZES

by

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I. INTRODUCTION

A ratio of current population size to pre-exploitation population size of porpoise involved in the Eastern Tropical Pacific tuna fishery has been used to evaluate the status of the stocks (NMFS, 1976¹; Smith, 1976²). The method of estimating pre-exploitation population size is complex and involves accounting for several variables. The most recent estimates are based on the following discrete model of density-dependent population growth:

$$N_{t+1} = (N_t - 0.5 K_t) \left[1 + r \left(1 - \frac{N_t z}{N_p z} \right) \right] - 0.5 K_t, \quad (1)$$

where

N_t = the population size in year t

K_t = the kill in year t

r = the maximum net reproductive rate

N_p = the pre-exploitation or equilibrium population size

z = a shape parameter for the density-dependent response.

¹NMFS. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. (July 27-31, 1976, La Jolla, California). SWFC Administrative Report No. LJ-76-29.

²Smith, T. (ed). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). SWFC Administrative Report No. LJ-79-41.

Two aspects of the model are considered here. These are 1) the stability properties of the model and 2) the calculation of the maximum net productivity level (M.N.P.L.).

II. STABILITY OF THE PROJECTION MODEL

Discrete time models can exhibit unstable behavior especially when the reproductive rates are high and/or there is marked nonlinearity in the density-dependent response. The local stability characteristics of a discrete time model or difference equation can be determined from its eigenvalue at equilibrium. If the model is of the simple one-dimensional form

$$N_{t+1} = F(N_t)$$

where N_t is of a single dimension, then the eigenvalue of F (λ_F) is the partial derivative of F with respect to N evaluated at equilibrium value of N (i.e., $\partial F / \partial N | N^*$). The following conditions hold for the behavior of a one dimensional model near its equilibrium (N^*). If $-1 < \lambda_F < 0$, then the model will have monotonic damping near N^* . If $0 < \lambda_F < 1$, then the model will exhibit oscillatory damping near N^* . If $1 < \lambda_F$, then the model will be repelling near N^* and will exhibit either stable limit cycles or, for sufficiently large values of λ , chaotic behavior (i.e. there exist a finite number of periodic points plus an uncountable number of points whose trajectories are totally aperiodic but bounded). The above conclusions are taken directly from May and Oster (1976).

These criteria can be used to evaluate the behavior of the projection model used in estimating porpoise abundance. The density-dependent model (ignoring the kills) is:

$$N_{t+1} = F_1(N_t) = N_t(1+r(1-(N_t/N_p)^z)) \quad (2)$$

and the

$$\frac{\partial F_1}{\partial N_t} = 1+r-r(z+1) (N_t/N_p)^z \quad (3)$$

which reduces at the equilibrium (i.e. $N=N_p$) to

$$\lambda_{F_1} = (\partial F / \partial N | N^*) = 1 - rz \quad (4)$$

Thus, the stability characteristics of the basic model are dependent on the product of rz and can be summarized as follows:

If $0 < rz < 1$, then monotonic damping,
 if $1 < rz < 2$, then oscillatory damping,
 if $2 < rz$, then repelling.

Table 1 lists some combinations of the critical values of r and z corresponding to the above criteria. It can be seen there that for the values of r and z that have been considered reasonable for porpoise stocks (e.g. $r < 0.04$ and $z < 20$; Smith, 1979²) population projections will exhibit smooth monotonic damping as the population approaches equilibrium.

The question of the effect of a fixed quota on the above stability properties can be analyzed in a similar fashion. The case where the quota is taken after the annual net reproduction will be considered first. The case where the quota is taken before annual net reproduction is considerably more complicated. In the case where the quota is taken after net reproduction, the model is

$$N_{t+1} = F_2(N_t) = N_t(1+r(1-(N_t/N_p)^z)) - Q, \quad (5)$$

and

$$\frac{\partial F_2}{\partial N_t} = 1+r(1-f^z(1+z)), \quad (6)$$

where

Q = a fixed annual quota

$f = N_t/N_p$.

Note that the value of f at equilibrium is a function of the annual quota relative to the unexploited population size (N_p). The value of f can range anywhere between the ratio of M.N.P.L. to N_p and one. If Q is greater than the potential yield at M.N.P.L., no positive equilibrium value exists for the model. If one lets

$$\begin{aligned} W &= -(1 - f^z (1+z)) \\ &= f^z (1+z) - 1 \end{aligned} \quad (7)$$

then the stability requirements of this model are the same as those for

the basic model (F_1), with W replacing z . Since, in general $W < z$ (i.e. $f^Z < 1$), this fixed quota model will be more stable than the basic model. However, unlike z , W can be less than zero (if f is small enough) which would mean that $\lambda F_2 < 0$ and the model would be unstable. For W to be less than zero, it would mean that

$$f < \frac{1}{(1+z)^{1/z}} \quad (8)$$

The right-hand side of equation 8 is the same as the proportion of N_p at which maximum net productivity occurs (see Part III below) and is the lower limit for f at which a positive equilibrium for this model can exist. Therefore, if the quotas are not so large as to drive the population to extinction, this fixed quota model will be more stable than the basic model.

The situation in which the kills are taken prior to the net reproduction is more complex. In this situation, the model is

$$N_{t+1} = F_3(N_t) = (N_t - Q) (1 + r - r(N_t/N_p)^Z) \quad (9)$$

and

$$\begin{aligned} \frac{\partial F_3}{\partial N_t} &= 1 + r(1 - (z+1)f^Z + Qz \frac{N_t^{z-1}}{N_p^z}) \\ &= 1 + r(1 - (z+1-pz)f^Z) \end{aligned} \quad (10)$$

where

$$p = Q/N_t$$

and

$$f = N_t/N_p.$$

By letting

$$\begin{aligned} Y &= -(1 - (z+1-pz)f^Z) \\ &= (z+1-pz)f^Z - 1 \end{aligned} \quad (11)$$

the stability requirements are the same as for the basic model F, but with Y replacing Z. Similar to the situation with F₂, Y is less than Z since $f^2 < 1$ and $P > 0$. Thus, this fixed quota model (F₃) in general will be more stable than the basic model.

Similar to the situation with F₂, Y can be less than zero but again only when f is below the proportion of N_p at which maximum net productivity occurs. This is shown in Appendix I. Thus, if the quotas are not so large as to drive the population to extinction, this model will also be more stable than the basic model.

The projection model that has been used for calculating porpoise abundances is actually a mixture of models F₂ and F₃. Since both of these models are more stable than the basic projection model F₁, the values in Table 1 should provide a guide to the combinations of critical values for r and z for which the models bifurcates and changes its stability behavior. For the range of values for r and z that have been used to project porpoise population sizes, the model exhibits monotonic damping as the population approaches an equilibrium.

III. CALCULATING MAXIMUM NET PRODUCTIVITY LEVELS

In Smith (1979²), M.N.P.L. for various porpoise stocks was calculated by

$$\text{M.N.P.L.} = N_p \left(\frac{1}{1+z} \right)^{1/z} \quad (12)$$

where N_p was estimated from calculations based on equation 1. The above expression for M.N.P.L. was derived by finding the maximum value for the net population growth curve for the basic density-dependent model (equation 2). This method of deriving M.N.P.L. fails to account for the timing of the kills relative to the timing of reproduction and results in a technically incorrect expression for M.N.P.L. for equation 1. Equation 12 is actually the correct expression for M.N.P.L. for the situation in which the kills occur after reproduction (equation 5).

An explicit expression for M.N.P.L. for the model represented by equation 1 is

$$\text{M.N.P.L.} = N_p \left(\frac{(r+z+1) - \sqrt{(r+z+1)^2 - 2r - r^2}}{r} \right)^{1/z} \quad (13)$$

A derivation of this expression is provided in Appendix 2. Note that in equation 13, M.N.P.L. is not solely a function of the shape parameter z but is also a function of the maximum net reproductivity. This contrasts with many

common density-dependent models in which harvesting is assumed (either explicitly or implicitly) to occur after reproduction. Table 2 provides calculations of M.N.P.L. as a proportion of N_p based on equation 13. Also presented in this table are the corresponding calculations based on equation 12 for comparison. As illustrated in this table, equation 12 is a lower bound for the actual M.N.P.L. calculated by equation 13. Also, M.N.P.L. is still primarily dominated by the shape parameter z , at least for reasonably small values of r . The magnitude of the differences in M.N.P.L. as calculated by equations 12 and 13 increases with increases in r and with decreases in z . However, the actual differences tend to be small for values of r and z considered reasonable for porpoise population (i.e. $r < .10$ and $z > 1$). As such, equation 12 represents a close approximation to the actual expression (equation 13) for M.N.P.L. for the projection model represented by equation 1.

LITERATURE CITED

May, R. M. and G. F. Oster. 1976. Bifurcation and dynamic complexity in simple ecological models. Am. Nat. 110:573-599.

Table 1. Critical combinations of r and z at which the stability behavior of equation 2 changes.

Value of r	Corresponding critical value of Z so that	
	$rz=1$	$rz=2$
.01	100.0	200.0
.02	50.0	100.0
.03	33.3	66.7
.04	25.0	50.0
.05	20.0	40.0
.06	16.7	33.3
.08	12.5	25.0
.10	10.0	20.0
.20	5.0	10.0
.30	3.3	6.6
.40	2.5	5.0
.50	2.0	4.0
.60	1.7	3.3
.70	1.4	2.9
.80	1.2	2.5
.90	1.1	2.2
1.00	1.0	2.0

Table 2. Comparison of M.N.P.L. as a proportion of N_p for equations 12 and 13 for a range of values for the shape parameter (z) and maximum net reproductive rate (r).

Value of Z	M.N.P.L. for Equation 12	M.N.P.L. for Equation 13					
		Value of r					
		.02	.04	.06	.10	.20	.30
1	.500	.501	.502	.504	.506	.512	.517
2	.577	.579	.580	.581	.584	.590	.595
3.5	.651	.652	.653	.654	.656	.661	.666
6.0	.723	.724	.725	.726	.727	.731	.745
11.5	.803	.803	.804	.805	.806	.808	.811
20.0	.859	.859	.860	.860	.861	.862	.864

Appendix 1. The relationship between the critical value of N_t/N_p for stability and M.N.P.L. for a fixed kill occurring after reproduction.

M.N.P.L. for F_3

For F_3

$$N_{t+1} [N_t - Q][1 + R]$$

where

$$R = r \left(1 - \left(\frac{N_t}{N_p} \right)^z \right)$$

and at equilibrium

$$Q = \frac{NR}{1+R}$$

M.N.P.L. will be achieved when

$$\begin{aligned} 0 &= \partial Q / \partial N \\ &= [NR / (1+R)] / \partial N \\ &= [1 / (1+R)] \frac{\partial NR}{\partial N} - \frac{NR}{(1+R)^2} \frac{\partial [1+R]}{\partial N} . \end{aligned}$$

Then

$$\frac{\partial NR}{\partial N} = r - (z+1)hr$$

where

$$h = \left(\frac{N}{N_p} \right)^z$$

and

$$\frac{\partial 1+R}{\partial N} = -zr N^{z-1}/N_p^z .$$

Thus

$$\begin{aligned} 0 &= \frac{r-(z+1)hr}{1+R} - \frac{NR}{[1+R]^2} \left(-z r N^{z-1}/N_p^z \right) \\ &= r - (z+1)hr + \frac{(r-rh)}{1+r-rh} z r h \\ &= rh^2 - (1+z+2r) h + (1+r) , \end{aligned}$$

and

$$h = \frac{(1+z+2r) \pm \sqrt{(1+z+2r)^2 - 4r(1+r)}}{2r} \quad (1)$$

Note only the negative square root term yields a value of h less than 1.

Therefore at M.N.P.L., h must equal the negative root of equation 1.

Value of h for which Y<0

From Equation 11 in Part II

$$Y = (z+1-P)f^z - 1 = (z+1-Pz)h - 1$$

where

$$\begin{aligned} P &= Q/N \\ &= \frac{NR}{(1+R)} \frac{1}{N} = \frac{R}{1+R} \end{aligned}$$

Thus

$$\begin{aligned} Y &= \left[z+1 - \frac{Rz}{1+R} \right] h - 1 \\ &= \left[z+1 - \frac{rz - rhz}{1+r-rh} \right] h - 1 \end{aligned}$$

For $Y=0$ means

$$0 = \left[z+1 - \frac{rz - rhz}{1+r-rh} \right] h - 1$$

$$= - rh^2 + (1+z+2r)h - (1+r)$$

Thus

$$h = \frac{(1+z+2r) \pm \sqrt{(1+z+2r)^2 - 4zr(1+r)}}{2r} \quad (2)$$

Thus, for $Y < 0$, h must be greater than the positive root of 2 or less than the negative root. Only the negative root is less than 1 and is of interest (i.e., allows for a positive kill). Since equations 1 and 2 are identical, the critical value of h for which $y < 0$ equals the value of h at which M.N.P.L. is achieved.

Appendix 2: An Expression for the Population Level Giving Maximum Net Productivity for Equation 1.

If
$$N_{t+1} = (N_t - 0.5K) (1+R) - 0.5K$$

where

$$R = r (1 - N_t^z / N_p^z)$$

at equilibrium $N_{t+1} = N_t$, thus

$$0 = (N_t - 0.5K) (1+R) - 0.5K - N_t$$

$$0 = N_t R - K (1+0.5R)$$

$$k = N_t R / (1+0.5R)$$

Dropping the subscript t, then

$$\frac{\partial K}{\partial N} = \frac{\partial(NR)}{\partial N} \frac{1}{1+0.5R} - \frac{NR}{(1+0.5R)^2} \frac{\partial(0.5R)}{\partial N}$$

Expressions for the two partial derivatives in the above equation are:

$$\begin{aligned} \frac{\partial NR}{\partial N} &= r - r(z+1) N^z / N_p^z \\ &= r - r(z+1)h \end{aligned}$$

where

$$h = N^z / N_p^z$$

and

$$\frac{\partial(0.5R)}{\partial N} = -0.5r z \frac{N^{z-1}}{N_p^z}$$

Thus

$$\begin{aligned} \frac{K}{\partial N} &= \frac{r-r(z+1)h}{1+0.5R} - \frac{NR (-0.5rz N^{z-1}/N_p^z)}{(1+0.5R)^z} \\ &= \frac{r-r(z+1)h}{1+0.5R} + \frac{0.5Rrzh}{(1+0.5R)^2} \end{aligned}$$

For K to be a maximum, $\frac{\partial K}{\partial N} = 0$; therefore multiplying by $(1+0.5R)/r$ yields

$$0 = (1-(z+1)h)(1+0.5R) + 0.5Rzh$$

which can be reduced to

$$0 = (1+0.5r) - h(r+z+1) + h^2(0.5r)$$

Thus

$$h = \frac{(r+z+1) \pm \sqrt{(r+z+1)^2 - 2r - r^2}}{r}$$

Note only the negative square root term yields a value of h less than 1.

Also, since $h = (N/N_p)^z$ then

$$\begin{aligned} \text{M.N.P.L.} &= N_p (h)^{1/z} \\ &= N_p \left(\frac{(r+z+1) - \sqrt{(r+z+1)^2 - 2r - r^2}}{r} \right)^{1/z} \end{aligned}$$

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