

**Note:** Dr. Harold Ornes is the editor of *Ecology* 101. Anyone wishing to contribute articles or reviews to this section should contact him at the Department of Biology and Geology, University of South Carolina–Aiken, 171 University Parkway, Aiken, SC 29801; phone (803) 641-3299; fax (803) 641-3631; e-mail haroldo@aiken.sc.edu.

*This section's first article by Mangel, Mulch, Mullan, Staub, and Yasukochi presents good examples of how economics and population biology can be linked to understand population dynamics typically studied in ecology or conservation biology courses. Dr. Joel Snodgrass, Savannah River Ecology Laboratory, Aiken, South Carolina was good enough to review this article and make helpful suggestions to the authors.*

*In the second article, Professor Lloyd Goldwasser has contributed a number of grammatical points that complement Ken Lertzman's "Notes on writing papers and theses" (ESA Bulletin 76:86–90, June 1995). Professor Goldwasser's grammatical points focus on details that can derail an otherwise well-written sentence. I promise you a good read.—Ed.*

## A GENERALLY ACCESSIBLE DERIVATION OF THE GOLDEN RULE OF BIOECONOMICS

It is generally agreed that many of the world's fisheries are in crisis (Vincent and Hall 1996) and that both ecological and economic understanding are required to resolve the crisis (Roberts 1997). The "Golden Rule of Bioeconomics" melds the harvest of a renewing resource, such as a stock of fish, with the economic concept of discounting future returns (explained below and in Clark 1985, 1990, Henderson and Sutherland 1996). It does this by comparing the income lost from not harvesting the stock now with that gained in the future after the stock has grown, and explains, for example, why under conditions of open access, certain slow-growing stocks, such as whales, were fished to virtual extinction.

Previous derivations of this important result relied on optimal control theory (Clark 1990) or on integration by parts in special cases (Clark 1985). Here, we present a novel derivation of the Golden Rule of Bioeconomics that can be done using only elementary algebra and spreadsheets, thus making the ideas broadly accessible. The novel aspect of this derivation also shows in a very

transparent manner how biology and economics interact.

We imagine a stock that grows according to the logistic dynamics

$$X(t+1) = X(t) + rX(t)(1 - [X(t)/K]) \quad (1)$$

where  $X(t)$  is the biomass of the stock (e.g., measured in tons) at the start of time period  $t$ ,  $r$  is the maximum per capita reproduction, and  $K$  is the carrying capacity, in the sense that if  $X(t) = K$ , then the population does not change. Thus,  $K$  can also be viewed as the stock biomass before exploitation starts.

We now harvest the stock in a two-stage process (Clark 1973). In the first stage, assuming that the stock is at  $K$ , the stock is "fished down" to a level  $X_s$ , after which a steady harvest is removed in each year. The steady harvest,  $h$ , is the biological production at the level  $X_s$ . It is found from the "reproductive" component of the logistic growth curve, which is the second term on the right side of Eq. 1. Thus

$$h = rX_s(1 - [X_s/K]). \quad (2)$$

Note that we focus on the stock, rather than the harvest itself. Such a shift from a focus on yields to a focus on stocks is essential for effective

conservation (Mangel et al. 1996).

In general, solving Eq. 2 for  $X_s$  results in two stock sizes,  $X_1$  and  $X_2$ , that are steady states because all growth is harvested, leaving  $X(t+1) = X(t)$  if  $X(t) = X_1$  or  $X_2$ . We assume that  $X_1 < X_2$ ; the smaller steady state is dynamically unstable, and the larger is dynamically stable (Fig. 1); also see Neher (1990:22). Thus, one "passes through"  $X_2$  while harvesting down to  $X_1$ . If  $X_1 = X_2 = K/2$ , the steady harvest is at its maximum value, called the Maximum Sustainable Yield (Hilborn and Mangel 1997) and which is dynamically metastable: perturbations to the right lead to a return to  $K/2$ , but perturbations to the left lead to further declines in the population.

We assume the goal of harvest actions is to maximize a long-term measure of the benefits from harvest. (Other elaborations, such as including price and cost, are discussed below.) Future benefits are discounted to reflect the idea that returns received in the future are less valuable than those received in the present because if they were invested now they would

earn a return  $\delta$ . In particular, a benefit obtained  $t$  years in the future is worth a fraction  $(1 + \delta)^{-t}$  of the same benefit obtained today (Henderson and Sutherland 1996). For simplicity, we assume that benefits are directly equal to harvests, although this is easily changed (see Eq. 8).

The Present Value (PV) of fishing the stock down to a level  $X_s$  when the discount rate is  $\delta$  thus consists of two terms: the value of the harvest obtained in the current year from fishing the stock down to  $X_s$ ,  $K - X_s$ , and the sum of the discounted steady future harvests at the stock level  $X_s$ :

$$PV(X_s) = K - X_s + \sum_{t=1}^{\infty} (1 + \delta)^{-t} h. \quad (3)$$

Since the harvest,  $h$ , after fishing down is independent of time, we remove it from the summation and substitute Eq. 2 to obtain

$$PV(X_s) = K - X_s + rX_s(1 - [X_s/K]) \sum_{t=1}^{\infty} (1 + \delta)^{-t}. \quad (4)$$

We next replace the summation by

the following, which is not obvious, but which can be verified numerically or checked in Gradshteyn and Ryzhik (1980):

$$\sum_{t=1}^{\infty} (1 + \delta)^{-t} = 1/\delta \quad (5)$$

to obtain

$$PV(X_s, \delta) = K - X_s + 1/\delta(rX_s[1 - (X_s/K)]). \quad (6)$$

Note that Present Value increases as the discount rate  $\delta$  decreases.

This equation shows how the biological parameters ( $r$ ,  $K$ ), the socially chosen economic parameter ( $\delta$ ) and operational parameter characterizing harvest ( $X_s$ ) interact in determining the present value of the combined current and future harvests. It also maintains a focus on stock, rather than yield, by concentrating on the steady level to which the stock is fished.

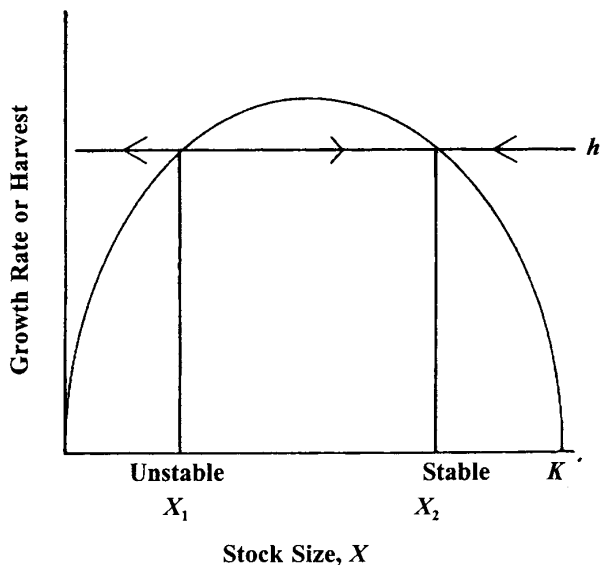
Individuals who are not facile with calculus can determine the maximum value of  $PV(X_s, \delta)$  by making a matrix in which columns are labeled by the value of  $\delta$ , rows are labeled by  $X_s/K$ , and the entry of matrix is  $PV(X_s, \delta)$ . Table 1 shows such results given the biological parameters of the three different species (Clark 1990): Antarctic fin whale:  $r = 0.08$ ,  $K = 400,000$  whales; Pacific halibut:  $r = 0.71$ ,  $K = 17.5 \times 10^6$  kg; yellowfin tuna:  $r = 2.61$ ,  $K = 134 \times 10^6$  kg.

Examination of how  $PV(X_s, \delta)$  varies in Table 1 for the different species allows one to study the interaction between  $r$  and  $\delta$  in determining the optimal level  $X_s$ . In particular, the economic optimality of extinction, for large values of the discount rate, is immediately seen in Part a of this table.

Using calculus (or the solver associated with a spreadsheet such as EXCEL) one can determine the optimal value of  $X_s$  by differentiating Eq. 6 with respect to  $X_s$  and setting the result to 0. Thus, if there is an internal optimum, it occurs at

$$X_s^* = K/2(1 - [\delta/r]) \quad (7)$$

and this again allows one to understand how the discount rate and maxi-



**Fig. 1.** When harvest is constant, there are generally two steady states. The lower value,  $X_1$ , is dynamically unstable in the sense that if the population is perturbed from  $X_1$ , it will continue to move away from the steady state. The higher value,  $X_2$ , is dynamically stable: if the population is perturbed from  $X_2$ , it will return to  $X_2$ . The two steady states coalesce at  $X_1 = X_2 = K/2$ . This point is dynamically metastable: perturbations to the right lead to a return to  $K/2$ , but perturbations to the left lead to further declines in the population.

**Table 1.** Present value of harvesting down to  $X_s$  for different values of  $\delta$ . For each value of  $\delta$ , the optimal value of  $X_s/K$  (to within 10% of  $K$ ) is shown in bold. Note that if  $r < \delta$ , as in the case of fin whales, the maximum value of present value is obtained by harvesting to  $X_s = 0$ , or extinction.

$X_s/K$	$\delta$					
	0.01	0.05	0.09	0.13	0.17	0.21
a) Antarctic fin whale						
0.0	400	400	<b>400</b>	<b>400</b>	<b>400</b>	<b>400</b>
0.1	648	417.6	392	382.1	376.9	373.7
0.2	832	<b>422.4</b>	376.8	359.3	350.1	344.3
0.3	952	414.4	354.6	331.6	319.5	312
0.4	<b>1008</b>	393.5	325.3	299	285.1	276.5
0.5	1000	360	288.8	261.5	247	238
0.6	927.9	313.5	245.3	219	205.1	196.5
0.7	792	254.3	194.6	171.6	159.5	152
0.8	592	182.4	136.8	119.3	110.1	104.3
0.9	328	97.6	72	62.1	56.9	53.7
b) Pacific halibut						
0.0	17.5	17.5	17.5	17.5	17.5	17.5
0.1	127.5	38.1	28.1	24.3	22.3	21
0.2	212.8	53.7	36	29.2	25.6	23.4
0.3	273.1	64.4	41.2	32.3	27.5	24.6
0.4	308.7	70.1	<b>43.6</b>	<b>33.4</b>	<b>28</b>	<b>24.6</b>
0.5	<b>319.3</b>	<b>70.8</b>	43.2	32.6	27	23.5
0.6	305.1	66.6	40.1	29.9	24.5	21.1
0.7	266.1	57.4	34.2	25.3	20.5	17.6
0.8	202.2	43.2	25.5	18.7	15.1	12.9
0.9	113.5	24.1	14.1	10.3	8.3	7
c) Yellowfin tuna						
0.0	136	136	136	136	136	136
0.1	3317	761.3	477.3	368.1	310.3	274.5
0.2	5788.1	1244.6	739.8	545.6	442.8	379.2
0.3	7549.3	1586	923.4	668.5	533.6	450.1
0.4	8600.6	1785.4	1028.1	736.9	582.7	487.2
0.5	<b>8942</b>	<b>1842.8</b>	<b>1054</b>	<b>750.6</b>	<b>590</b>	<b>490.5</b>
0.6	8573.4	1758.2	1000.9	709.7	555.5	460
0.7	7494.9	1531.6	869	614.1	479.2	395.7
0.8	5706.5	1163	658.2	464	361.2	297.6
0.9	3208.2	652.5	368.5	259.3	201.5	165.7

mum per capita growth rate interact. For example, one could plot a table of  $X_s/K = \max(0, 1/2(1 - \delta/r))$  as a function of the two parameters  $\delta$  and  $r$ .

More complicated biology and economics can be included in a straightforward manner. For example, if the population growth rate at size  $X$

is  $g(X)$ , the cost of harvesting down to  $X_s$  is  $c_1(X_s)$ , the cost of a steady harvest is  $c_2(X_s)$ , and the price received for the resource is  $p$ , the generalization of Eq. 6 is

$$PV(X_s, \delta) = (K - X_s)(p - c_1[X_s]) + (1/\delta)g(X_s)(p - c_2[X_s]). \quad (8)$$

Differentiating Eq. 8 gives the generalized golden rule of bioeconomics that Clark (1985, 1990) previously obtained by the use of optimal control theory; this rule is now generally accessible.

There are a number of ways that this result can be used in the classroom. First, it is an example accessible to lower level students of how economics and population biology interact. Second, instructors can use the mathematical methods here to set up spreadsheets and hands-on computer demonstrations of the results in lower level courses. Third, the mathematical methods themselves can be taught in higher level ecology, conservation, and fisheries courses. At each level student assignments could include literature searches to estimate  $r$  and  $\delta$  for different species (the results apply equally to terrestrial organisms such as elephants), investigations of what happens if different biological dynamics are assumed (once the spreadsheet is set, this is straightforward), and investigations of what happens when additional complications, such as those described in Eq. 8, are included.

#### Acknowledgments

We thank Edgar Beccera, Michael Billet, Erin Dodd, Natalie Hooner, Michael Johnson, Matthew Schutz, and Astrid Terry for various discussions about this material and Colin Clark, Richard Howarth, and Joel Snodgrass for comments on previous versions of the manuscript.

#### Literature cited

- Clark, C. W. 1973. The economics of overexploitation. *Science* **181**:603–634.
- . 1985. *Bioeconomics and fisheries management*. Wiley, New York, New York, USA.
- . 1990. *Mathematical bioeconomics*. Second edition. Wiley, New York, New York, USA.
- Gradshteyn, I. S., and I. M. Ryzhik. 1980. *Table of integrals, series and products*. Academic Press, New York, New York, USA.
- Henderson, N., and W. J. Sutherland. 1996. *Two truths about discount-*

- ing and their environmental consequences. *Trends in Ecology and Evolution* **11**:527-528. Ensuing correspondence: *Trends in Ecology and Evolution* **12**:193-194; 230.
- Hilborn, R., and M. Mangel. 1997. The ecological detective. Confronting models with data. Princeton University Press, Princeton, New Jersey, USA.
- Mangel, M., and 42 co-authors. 1996. Principles for the conservation of wild living resources. *Ecological Applications* **6**:338-362.
- Neher, P. 1990. Natural resource economics: conservation and exploitation. Cambridge University Press, New York, New York, USA.
- Roberts, C. M. 1997. Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* **12**:35-38.
- Vincent, A. C. J., and H. J. Hall. 1996. The threatened status of marine fisheries. *Trends in Ecology and Evolution* **11**:360-361.

*Marc Mangel, Allen Mulch, Anne Mullan, Wendy Staub, and Emily Yasukochi  
Department of  
Environmental Studies  
University of California  
Santa Cruz, CA 95064*