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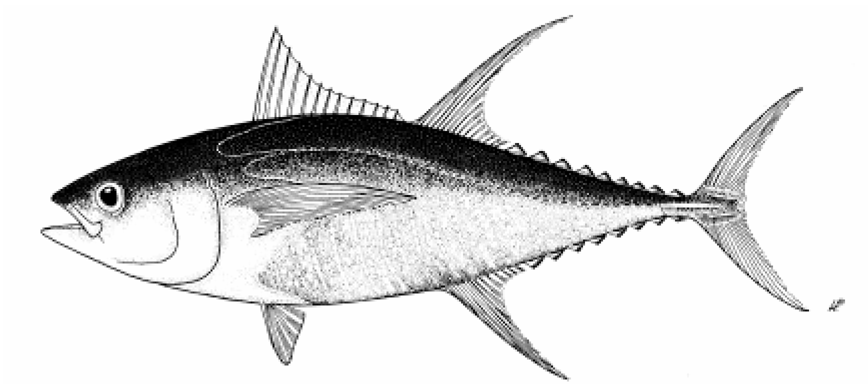
Theoretical development of Schaefer model and its application



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(2 Figures, 3 Tables, 9pp text)

Title:

Theoretical development of Schaefer model and its application.

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ABSTRACT

A general type of catch curve can be derived from Schaefer model based on mathematical development of this model. This curve provides an useful tool for estimating the intrinsic growth rate and carrying capacity. In order to get the more precise estimations, a conversion factor and iterative calculation are necessary. As a numerical example, catch and effort data of South Pacific albacore stocks exploited by

tuna longline fisheries were used to fit this method. Without conversion factor, the results revealed that $K=97,985$ metric tons and $r=1.28374$. Based on the best estimation of the conversion factor $\delta=0.409768$, the results revealed that $K=166,081$ metric tons and $r=2.17591$.

Keywords: stock dynamics, Schaefer model, carrying capacity

Population dynamics

In nature, population growth of any species should be sigmoid curve. It can not be a decay equation or this species will approach extinction. Also, it can not be an increasing equation, or the species will growth infinitely. This is the common sense. Hence, the relationships between net production and biomass should be a dome shape curve (Figure 1) under the same environmental conditions. This dome shape curve might be symmetric or non-symmetric. There is unique peak where biomass is B_{MNP} with the maximum net production (*MNP*). Figure 1 also reflects the mechanism of self regulations of the species as follows.

Without disturbance, no fishing with stable environmental conditions, the stock dynamics is purely depending on the current status of biomass. When the current biomass is greater than B_{MNP}, then the stock is still in better conditions. Hence, the crisis of life is correspondingly lower. Due to loose the competition and to avoid the infinite growth, the stock will reduce the net production. Hence, the greater biomass always implies the less net production.

Contrary, when the current biomass is less than B_{MNP}, then the stock has been in worse conditions. Hence, the crisis of life is correspondingly higher. Due to strengthen the competition and to avoid the collapse of the species, the stock will increase the net production. Hence, the greater biomass always implies the greater net production. As stated above, any species is endowed such common characteristics. They try to avoid the collapse and approach the stable status. They try to approach the carrying capacity, i.e., commensurate with the environmental conditions (Figure 1).

If there is any disturbance, exploitation or any changes of the environmental conditions, they also reflect the similar characteristics. However, the stock dynamics will depend on both of the current status of biomass and the strength of the disturbance. When the current biomass is greater than B_{MNP}, the stock is still in better conditions. In this case, no matter how strength of the disturbance is, the biomass will converge to the disturbance. The species tends to adjust itself to adapt the disturbance. It seems implying that there is some sluggishness of the species in nature. When biomass is still in better conditions, the species tend to go with tide or to adapt itself to circumstance only.

Contrary, when the current biomass is less than B_{MNP}, it means that the stock has been in worse conditions. If the disturbance is greater than the net production of the current biomass, then the biomass will decrease continuously and approaching collapse. Contrary, if the disturbance is less than the net production, then the biomass will increase continuously till greater than B_{MNP} and then converge to the disturbance. Clearly, the response of the species is quite different and depending on the strength of the disturbance. The crisis of life will stimulate the growth ability of the species. If the growth ability of the species can not cover the coming disturbance, then the stock will approach collapse. Contrary, if the growth ability can cover the disturbance, then the species will increase continuously over B_{MNP} and converge to the disturbance.

As stated above, without any mathematical model, Figure 1 revealed the clear life strategy of the species. The different strategies are depending on the current biomass and the strength of the disturbance. When the biomass is greater than B_{MNP}, then no matter how large the disturbance is, the biomass tends to converge to the disturbance. It means that the species tends to adapt itself to circumstance. Contrary, when the biomass has been less than B_{MNP}, then the biomass is divergent and depending on the strength of disturbance. If the disturbance is greater than the net production, then the biomass is approaching collapse. If the disturbance is less than the net production, then the biomass will increase continuously and into the convergent status. It means that the species will face the elimination through selection or competition.

Schaefer model

Schaefer model (Schaefer 1954; 1957) is a simple, useful and convenient method for assessing fish stocks. Generally, it is written as follows.

$$\frac{dB_t}{B_t dt} = r(1 - \frac{B_t}{K}) \qquad .....(1)$$

Where, B_t= *biomass at time t, r= intrinsic growth rate, K= carrying capacity, t= time*.

Integrated equation (1), then following equation can be obtained.

$$B_t = \frac{KB_0 e^{rt}}{K + B_0(e^{rt} - 1)} \qquad .....(2)$$

This is a sigmoid curve of population growth. Set the net prodution as follows.

$$f_t = \frac{dB_t}{dt} = rB_t(1 - \frac{B_t}{K}) \qquad .....(3)$$

Equation (3) can be rewritten as follows.

$$f_t = -\frac{r}{K}(B_t - \frac{K}{2})^2 + \frac{rK}{4} \qquad .....(4)$$

This is the dome shape curve with the peak equal to *rK/4* at $B_t=B_{MNP}=K/2$. Hence, Schaefer model might be the simplest model representing the population dynamics. This model includes two parameters only. One is the intrinsic growth rate combining all growth ability including the reproduction and growth. Another one is the carrying capacity combining all outer limitations including all biotic and non-biological factors. These two parameters provide the basic information of the population dynamics; the growth ability of the species and the constraint of the population growth. In ecology, r-selection and K-selection were extensively discussed (MacArthur and Wilson 1967; Pianka 1970; Stearns 1980; 1992). The problem is how to estimate these two parameters.

In fishery science, Schaefer model and its improvements was extensively used in assessing fish stocks (Pella and Tomlinson 1969; Fox 1970; Schnute 1977; Walters and Hilborn 1976; Yeh and Wang 1996). Under fishing, it can be rewritten as follows.

$$\frac{dB_t}{B_t dt} = r(1 - \frac{B_t}{K}) - F_t \qquad \text{.....(5)}$$

Where, *F_t=fishing mortality rate at time t.* Applied it in assessing fish stocks, generally it needs to assume that catch is at equilibrium or not.

General type of catch curve

Under exploitation, set *F=constant* and $\alpha = r - F$ and $\beta = r / K$ during the unit time period *t~t+1*, then

$$\frac{dB_t}{dt} = rB_t(1 - B_t / K) - FB_t = \alpha B_t - \beta B_t^2 \qquad \text{.....(6)}$$

Integrated equation (6), following equation can be obtained.

$$B_{t+1} = \frac{\alpha B_t e^{\alpha}}{\alpha + \beta B_t (e^{\alpha} - 1)} \qquad \text{.....(7)}$$

Where, *B_t= biomass at the beginning of this time period and B_{t+1}= biomass at the end of this time period*. Expressing the initial biomass by B_o then the biomass at time *t* can be expressed as follows.

$$B_t = \frac{\alpha B_0 e^{\alpha t}}{\alpha + \beta B_0 (e^{\alpha t} - 1)} \qquad \text{.....(8)}$$

Hence, the catch Y can be obtained as follows.

$$Y = \int_t^{t+1} FB_t dt = F\int_t^{t+1} \frac{\alpha B_0 e^{\alpha t}}{\alpha + \beta B_0 (e^{\alpha t} - 1)} d = FK[1 + \frac{1}{r}\ln(\frac{B_t}{B_{t+1}}) - \frac{F}{r}] \qquad \text{.....(9)}$$

Set this time period to be one year, then annual catch can be expressed as follows.

$$Y_i = F_i K[1 + \frac{1}{r}\ln(\frac{B_{i,t}}{B_{i,t+1}}) - \frac{F_i}{r}] \qquad \text{.....(10)}$$

If catch is at equilibrium then $B_{i,t} = B_{i,t+1}$, it implies that

$$Y_i = F_i K(1 - \frac{F_i}{r}) \qquad \text{.....(11)}$$

Hence, equation (10) is the general type of catch curve derived from Schaefer model. It is an useful tool for estimating the parameters.

Approximate estimation

Set $U_i = Y_i / X_i$, then equation (10) can be rewritten as follows.

$$U_i = qK[1 + \frac{1}{r}\ln(\frac{B_{i,t}}{B_{i,t+1}}) - \frac{q}{r}X_i] \qquad (12)$$

Where, *q= catchability, X= fishing efforts, U= CPUE= catch per unit of fishing effort.*

At equilibrium then biomass will be stable, hence $B_{i,t} = B_{i,t+1}$ implies follows.

$$U_i = qK(1 - \frac{qX_i}{r}) \qquad \text{.....(13)}$$

Base on catch at equilibrium, equation (13) is always used to estimate the maximum sustainable yield (MSY). No matter catch is at equilibrium or not, equation (12) can be used to estimate the parameters *r, q and K*, directly.

Approximately, $B_{i,t} = (U_{i-1} + U_i)/2$ and $B_{i,t+1} = (U_i + U_{i+1})/2$ are adopted and rewritten equation (12) as follows.

$$U_i = A_1 + A_2 \ln(\frac{U_{i-1} + U_i}{U_i + U_{i+1}}) + A_3 X_i \qquad \text{.....(14)}$$

Where $A_1 = qK$, $\mathrm{A}_2 = qK/r$, $A_3 = -q^2 K/r$. If catch and effort data are available, then the coefficients A_1, A_2 and A_3 can be estimated. Hence, the parameters *r, q and K* can be obatined by $r = A_1/A_2$, $q = -A_3/A_2$, $K = -A_1 A_2/A_3$, respectively.

More precise estimation

Generally, the biomass at the beginning and the end of the time period is unknown. Approximately, they are replaced by the average of CPUE of two successive years. In order to get more precise estimations, it needs a conversion factor δ to adjust it. That is set

$$\frac{B_{i,t}}{B_{i,t+1}} = \delta(\frac{U_{i-1} + U_i}{U_i + U_{i+1}})$$

Hence, equation (14) becomes follows.

$$U_i = qK\{1 + \frac{1}{r}\ln[\delta(\frac{U_{i-1} + U_i}{U_i + U_{i+1}})] - \frac{q}{r} X_i\} \qquad \text{.....(15)}$$

This is equal to follows.

$$U_i = qK[1 + \frac{1}{r}\ln\delta + \frac{1}{r}\ln(\frac{U_{i-1}+U_i}{U_i+U_{i+1}}) - \frac{q}{r}X_i] \qquad .....(16)$$

The problem is how to estimate the conversion factor δ and to get the best estimation of the parameters.

As shown in equation (15), over estimation of δ impies under estimation of K, and *vice versa*. Hence, the best solution of δ can be obtained as two successive estimations of δ are equal. If they are unequal, then searching work should be kept going on. On the other hand, equation (16) can be rewritten as follows.

$$Z_i = \frac{U_i}{q'K} = 1 + \frac{1}{r}\ln\delta + \frac{1}{r} * \ln(\frac{U_{i-1}+U_i}{U_i+U_{i+1}}) - \frac{q}{r} * X_i \qquad .....(17)$$

Theoretically, *q'* and *q* should be equal. Hence based on equation (17), *q* can be estimated by given *q'*. By the iterative calculation, they will converge to the same value of *q'=q*. By iterative calculation, the estimated δ and *q* will converge to the best solutions. Hence, the best estimation of δ and *q* can be obtained as follows.

1. **Start of iterative calculation.**
2. Set $\delta=1$ in equation (15) to get the initial estimation of *r, q* and *K*.
3. Set *q'=q* and substituted *q'* and *K* in equation (17) to get Z_i .
4. Fitting catch and effort data to equation (17) to get the new estimation of *r*, *q* and δ.
5. If *q* is unequal to *q'*, it needs back to step-3 to get the new estimation of *r*, *q* and δ. until they are equal.
6. If *q* is equal to *q'*, then the new estimation of δ can be obtained and expressed by δ'.

7. If δ' is not equal to δ, then set $\delta=\delta'$ and substituted it in equation (15) to get the new estimation of *r; q* and *K* and back to step-3.
8. If δ' is equal to δ, then $\delta'=\delta$ might be the best estimation of the conversion factor δ.
9. Substituted the best estimation of the conversion factor δ in equation (15), the best estimation of *r; q* and *K* can be obtained.

10. End of iterative calculation.

As stated above, the best estmation of the conversion factor δ and hence the parameters *r; q and K* can be obtained.

Time varied carrying capacities

If carrying capacity is time-varied, then equation (10) should be rewritten as follows.

$$U_i = qK_i[1+\frac{1}{r}\ln(\frac{B_{i,t}}{B_{i,t+1}})-\frac{q}{r}X_i] \qquad \text{.....(18)}$$

It means that

$$K_i = \frac{U_i}{q[1+\frac{1}{r}\ln(\frac{B_{i,t}}{B_{i,t+1}})-\frac{q}{r}X_i]} \qquad \text{.....(19)}$$

By the above improved Schaefer model, if the parameters *r; q* and δ can be obtained, then the time-varied carrying capacity can be evaluated year by year as follows.

$$K_i = \frac{U_i}{q[1+\frac{1}{r}\ln[\delta(\frac{U_{i-1}+U_i}{U_i+U_{i+1}})]-\frac{q}{r}X_i]} \qquad .....(20)$$

Since q is available, the fishing mortality rate *Fi* can be evaluated year by year by *Fi=qXi*. If the relationships between *Fi and Ki* are good enough, then empirically the carrying capacity of the virgin stock can be evaluated by set *Fi=0*. This is the virgin stock of this species; biomass just before the fishery entered.

Numerical example

Catch and effort data of South Pacific albacore stocks (*Thunnus alalunga*) are used to fit above methods. Table 1 showed the catch, standardized effort and catch per unit of fishing effort of tuna longline fishery operating in the South Pacific Ocean. As shown in Table 2, *K=97,985* metric tons and *r=1.28374* without the adjustment of the conversion factor δ=1. Based on the best estimation of the conversion factor *δ=0.409768*, then *K=166,081* metric tons and *r=2.17591*. They have the same estimation of q=6.02115E-09 (Table 2).

The time-varied carrying capacities are shown in Table 2. Without the adjustment of conversion factor, the estimated carrying capacities are varied in the ranges of 73,734 ~ 266,732 metric tons. Mean of the carring capacities is about 101,807 metric tons with MSY=32,673 metric tons. MSY is closing the results estimated by other researches (Skillman, 1975; Wetherall *et al*, 1979; Wetherall and Yong, 1984, 1987;

Wang *et al*, 1988; Yeh and Wang, 1996). However, they are based on constant carrying capacity and without the adjustment of conversion factor. Based on the conversion factor, the best estimations of the carrying capacity are varied in the ranges of 124,976 ~ 452,103 metric tons. Mean of the carrying capacities is about 172,560 metric tons with MSY=93,869 metric tons. Clearly, the current catch is still far less than the MSY, even if all of other fisheries are included.

As shown in Figure 2, the relationships between the estimated carrying capacities and fishing mortality rates are good enough for estimating the virgin stocks. The correlation coefficient is about 0.8579. Without the adjustment of conversion factor, it is about 218,667 metric tons. With the adjustment of conversion factor, it is about 370,633 metric tons. Based on the virgin stocks, MSY is about 70,178 and 201,616 metric tons, respectively.

Conclusions

Commonly, population growth can be expressed by a sigmoid curve. The relationships between biomass and net production of any stock revealed a dome shape curve. Peak of this curve implies the biomass with the maximum net production. Before the peak or biomass less than that having the maximum net production, any disturbance will cause the biomass to be divergent. After the peak or biomass greater than that having the maximum net production, any disturbance will cause the biomass to be convergent.

General type of catch curve can be derived from Schaefer model based on the mathematical development of this model. This curve provides a useful tool for estimating the intrinsic growth rate and carrying capacity. A conversion factor and iterative calculation are necessary to get the more precise estimation. This curve also provides a useful tool for estimating the time-varied carrying capacities. They are useful and helpful in the fields of ecological researches.

As a numerical example, catch and effort data of South Pacific albacore stocks were used to fit this curve. Without conversion factor, the results revealed that $K=97,985$ metric tons and $r=1.28374$. Based on the best estimation of the conversion factor $\delta=0.409768$, the results revealed that $K=166,081$ metric tons and $r=2.17591$.

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Dear Editor:

As you know, the influences of the changes of environmental conditions are not negligible in many fields of biological researches. Unfortunately, how to get the indicator of the environmental conditions is still a problem.

Really, Schaefer model is too simple to provide sufficient information of the fish stocks. However, it includes K, an index of the environmental conditions. Hence, I think Schaefer model might be a useful tool for estimating K, evenly the time-varied K. As shown in this paper, a general type of catch curve can be obtained from Schaefer model directly. This curve is a useful tool for estimating the parameters.

In this manuscript, I try to show the simplest model of the population dynamics (Figure) to the most complicated model (estimating the time-varied carrying capacities).

I hope it is valuable to acceptable by your Journal

With my best regards

Chien-Hsiung Wang
March 24 2005.

Figure

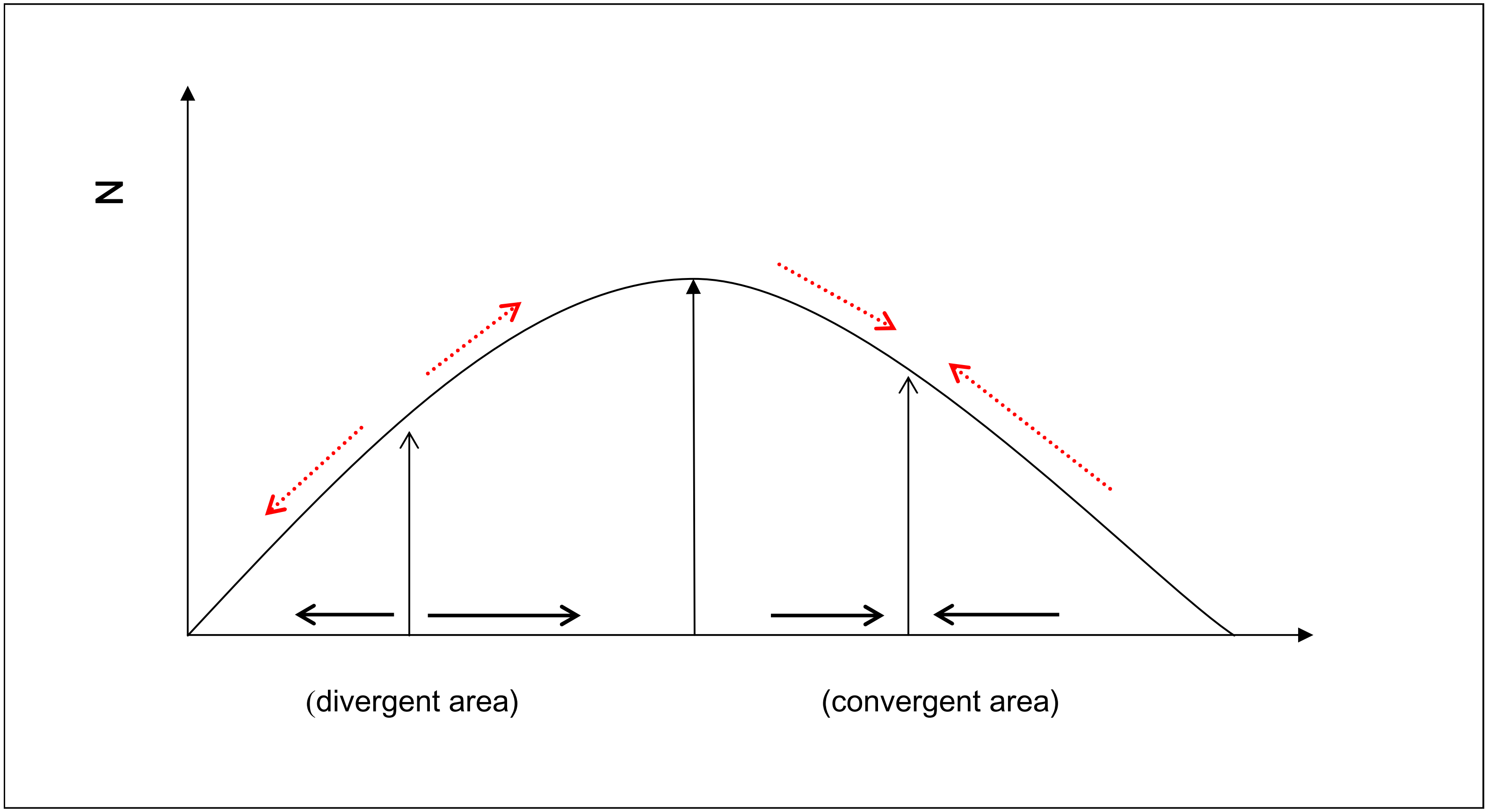

Figure 1. Theoretical considerations of the relationships between biomass and net production.

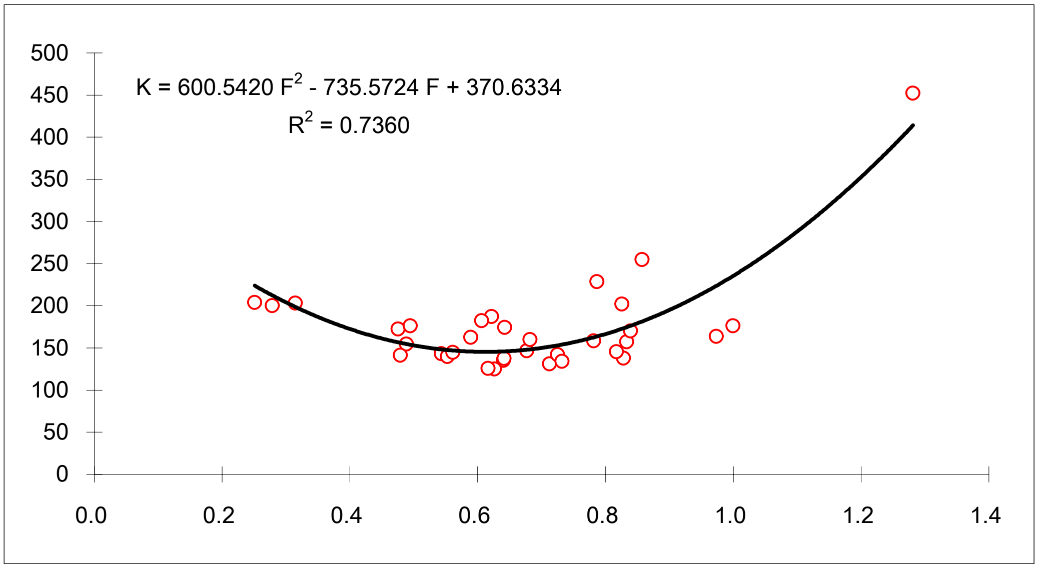

Figure 2. Empirical relationships between carrying capacities and fishing mortality rates.

Table

Table 1. Catch, standardized effort and catch per uint of fishing effort of South Pacific albacore exploited by tuna longline fishery.

	tuna longline fishery only			including other fisheries
YEAR	U (kg/100 hooks)	X (million hooks)	Y (metric tons)	Y (metric tons)
1967	75.118	53.673	40318	40323
1968	62.788	46.268	29051	29065
1969	58.452	41.675	24360	24360
1970	62.325	52.290	32590	32740
1971	42.760	81.169	34708	34808
1972	42.836	79.004	33842	34232
1973	35.405	106.338	37649	38274
1974	22.388	138.400	30985	32692
1975	31.829	82.098	26131	26877
1976	30.314	79.521	24106	24231
1977	33.734	103.307	34849	35570
1978	31.011	112.405	34858	36644
1979	24.288	118.326	28739	29653
1980	25.771	120.395	31027	32596
1981	19.651	166.060	32632	34722
1982	20.657	137.186	28339	30780
1983	23.365	104.013	24303	25086
1984	19.865	102.390	20340	24704
1985	27.731	97.861	27138	32328
1986	23.735	137.523	32641	36590
1987	19.808	135.689	26877	29950
1988	22.626	139.356	31531	41110
1989	18.288	121.601	22238	52576
1990	25.077	90.218	22624	37382
1991	23.188	106.548	24706	34014
1992	26.707	113.259	30248	36902
1993	23.105	129.786	29987	34427
1994	25.440	130.638	33235	40555
1995	27.941	91.811	25653	33604
1996	25.889	93.167	24120	31673
1997	32.158	100.728	32392	37225
1998	28.194	142.372	40141	46531
1999	33.766	106.684	36023	39626
2000	24.634	161.719	39838	45947
2001	21.560	212.826	45886	51689
2002	17.410	264.032	45969	50858
mean	30.828	113.898	31113	35565

Table 2. Estimated population parameters.

	δ=1.00000	δ=0.40977
K =	97,985 mt	166,081 mt
r=	1.28374	2.17591
q=	6.02115E-09	6.02115E-09
K_v =	218,667 mt	370,633 mt

Table 3. Estimated time-varied carrying capacities.

	approximate solution	precise solutions
	(1000 metric tons)	(1000 metric tons)
YEAR	Ki as δ=1.00000	Ki as δ=0.40977
1968	118.0537	200.0975
1969	120.2185	203.7668
1970	119.9204	203.2616
1971	91.1538	154.5030
1972	101.7142	172.4026
1973	79.7613	135.1930
1974	92.8121	157.3138
1975	103.9261	176.1517
1976	83.4222	141.3982
1977	110.4968	187.2888
1978	86.4697	146.5636
1979	77.1921	130.8383
1980	83.7530	141.9589
1981	103.8818	176.0765
1982	119.1711	201.9916
1983	73.7336	124.9763
1984	74.1710	125.7176
1985	95.9278	162.5948
1986	81.2425	137.7036
1987	85.7436	145.3328
1988	100.2625	169.9420
1989	79.0253	133.9456
1990	84.4006	143.0565
1991	81.1797	137.5971
1992	94.3584	159.9348
1993	93.2906	158.1249
1994	134.8649	228.5920
1995	82.4448	139.7416
1996	85.2654	144.5223
1997	107.4145	182.0645
1998	150.2035	254.5905
1999	102.7621	174.1787
2000	96.4635	163.5029
2001	266.7318	452.1025
maximum	266.7318	452.1025
minimum	73.7336	124.9763
mean	101.8068	172.5596