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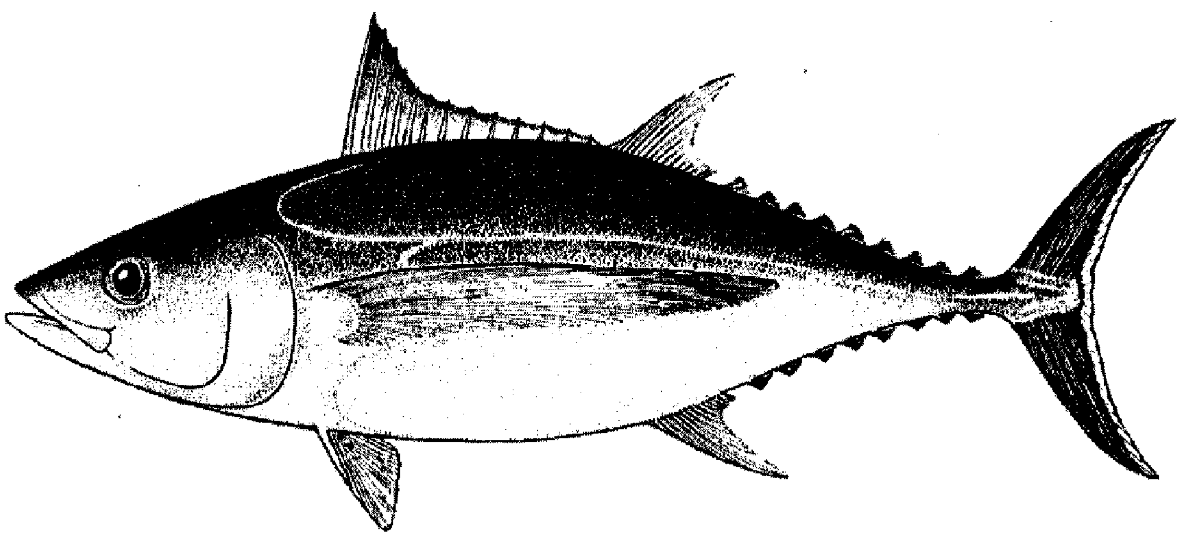
Two steps estimating the parameters *r*, *q* and *K* of South Pacific albacore stocks (*Thunnus alalunga*) based on surplus production model



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Title:

Two steps estimating the parameters *r*, *q* and *K* of South Pacific albacore stocks (*Thunnus alalunga*) based on surplus production model

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ABSTRACT

Based on catch and effort data of tuna longline fishery of the South Pacific albacore stocks, Schaefer model was used to estimate the intrinsic growth rate (*r*), catchability (*q*) and carrying capacity (*K*) by two steps. They are *r=1.89003, q=9.6217E-09 K=167,211 mt.*

Instantaneous net production rate m_t was induced and evaluated. During 1974-1998, they vary in the ranges of 0.8177-1.7620 with the average 1.1395. Correspondingly, fishing mortality rates F_t vary in the ranges of 0.7133-1.6777 with the average 1.1444. The differences defined by $d_t = m_t - F_t$ provide us the important information of fishery management. Positive d_t implies the increasing of biomass under fishing, hence increasing fishing intensity might be allowable. Negative d_t implies the decreasing of biomass under

fishing, hence regulation of fishing intensity should be required. Zero d_t means the stock in equilibrium, hence stable fishing intensity might be the most appreciable. In the case of South Pacific albacore stocks, they varied in the ranges of –0.303 to +0.235 with the average –0.033. Particular low values of d_t might be relative to the abnormal environmental conditions. At present status, keeping the stable fishing intensity might be the most appreciable.

Key words:

albacore, intrinsic growth rate, catchability, carrying capacity, net production rate

INTRODUCTION

South Pacific albacore stocks were mainly exploited by tuna longline fishery, especially by Taiwan (Wang 1984, 1988; Wang *et al.* 1988). Total catch was about 36,466mt in 1998 (Table 1). Numerous studies tried to assess the stocks (Skillman 1975; Wetherall *et al.* 1979; Wetherall and Yong 1984, 1987; Wang 1988; Yeh and Wang 1996). However, catchability (q), intrinsic growth rate (r) and carrying capacity (K) of this stock are still unknown. Wang (1999a, 2000) tried to estimate these parameters. Regretless, two points are not doubtful. Wang suggested that 1. due to incomplete information of the early stages of developing fishery, catch and effort data before 1974 should be deleted for estimating the parameters. 2. It was assumed that biomass is always having the maximum net production, i.e., $B_t = K/2$.

In order to rise the precision of the estimated K, q, and r, this paper tries to re-estimate these parameters based on the more complete considerations of Schaefer model.

MATERIALS

Long terms catch and effort data of Taiwanese tuna longline fishery operating in the South Pacific Ocean are used to estimate the effective fishing effort, and then catch per unit of effective fishing effort (CPUE). Effective fishing effort (*X*) and effective CPUE (*U*) are used to estimate the unknown parameters. All of the catch and effort data are the same as Wang (2000).

METHODS

Under exploitation, Schaefer model can be expressed as follows.

$$\frac{dB_t}{dt} = rB_t(1 - \frac{B_t}{K}) - F_tB_t \quad (1)$$

Here, F_t= *instantaneous fishing mortality rate,* B_t= *biomass,* r= *intrinsic growth rate,* K= *carrying capacity,* t= *time.* Set $\alpha = r - F$ and $\beta = r / K$, equation (1) becomes (2).

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

Integrated equation (2) for fixed fishing mortality, then biomass can be expressed as follows.

$$B_t = \frac{\alpha B_0 e^{\alpha t}}{\alpha + \beta B_0(e^{\alpha t} - 1)} \qquad (3)$$

During $t \sim t+1$, annual catch Y_t can be expressed as follows.

$$Y_t = \int_t^{t+1} FB_t dt = F\int_t^{t+1} \frac{\alpha B_0 e^{\alpha t}}{\alpha + \beta B_0(e^{\alpha t} - 1)} dt \qquad (4)$$

Integrating equation (4) and substituting $U_t = Y_t / X_t$ in it, then equation (5) can be obtained.

$$U_t = qK + \frac{qK}{r} ln(\frac{B_t}{B_{t+1}}) - \frac{q^2K}{r} X_t \qquad (5)$$

Here, *q= catchability, X= fishing efforts, U= CPUE by catch/hooks.* This is a linear function. It can be used to estimate the parameters *K*, *q*, and *r* by the method of the least squares (Wang 1999a, 2000). However, before estimating the parameters, some points should be noticed.

Equation (5) implies $U_t / qK = 1 + (1/r)(\, ln(B_t / B_{t+1})) - \text{q}\, X_t / r$

Since $U_t / q = B_t$ and set $a_t = B_t / K$ then

$$a_t = 1 + \frac{1}{r} ln(\frac{B_t}{B_{t+1}}) - \frac{q}{r} X_t \qquad (6)$$

This means that the relative biomass $a_t = B_t / K$ (relative to the carrying capacity) depends on the fishing intensity X_t and the relative biomass B_t / B_{t+1} (ratio of the biomass at beginning and ending of this year). It implies that only *q, r* and a_t can be obtained by this equation. In equation (5), *K* is an implicit parameter only.

Even if without fishing, biomass varied year by year in nature. If fishery is included, then fluctuation of biomass depends on both the environmental conditions and fishing intensity. Therefore, it can be expressed as follows.

$$B_{t+1} = B_t e^{m_t - F_t} \qquad (7)$$

Here, m_t is defined as the instantaneous net production rate. $a = 1$ if and only if $ln(B_t / B_{t+1}) = q\, X_t$, i.e., $m_t \equiv 0$, or constant environmental conditions. Therefore, unless it is assumed that the environmental conditions are always in constant and the initial biomass B_o just before the fishing entered is *K* ($a = 1$), *K* can not be obtained directly from equation (5). It needs to estimate the true *K* by $K = B_o / a$.

From equation (7), $B_t = B_{t+1}$ if only if $m_t = F_t = 0$ or $m_t = F_t$, otherwise $B_t \neq B_{t+1}$. It implies that a_t varies year by year in the real world. If sets $dB_t / B_t dt = m_t = r(1 - B_t/K)$ to be constant in unit time interval $t \to t+1$, then equation (7) is an approximate of the Schaefer model. m_t depends on the environmental conditions in nature, and independent on fishing intensity. $m_t \to 0$ if $B_t \to K$ and $m_t \to r$ if $B_t \to 0$, i.e., m_t varies in the ranges of $r > m_t \geq 0$ corresponding to the biomass relative to the carrying capacity. Since, $0 < B_t \leq K$, it implies that m_t can not be negative or larger than r. m_t could be considered as an **index of the status of the biomass,** i.e., an index corresponding to the goodness of the environmental conditions, larger m_t with better environmental conditions, and vise versa.

If $m_t > F_t$, then biomass increased under fishing. If $m_t < F_t$, then biomass decreased under fishing. If $m_t = F_t$, then biomass is in equilibrium. Therefore, the differences defined by $d_t = m_t - F_t$ could provide us useful and important information for decision making of fishery management. Positive d_t implies that continuous increasing fishing intensity might be allowable. Negative d_t implies that regulating fishing intensity is necessary. Zero d_t implies that stable fishing intensity might be the most appreciable case.

Substituting equation (7) in (6), then

$$a_t = 1 - \frac{m_t}{r} \qquad (8)$$

Clearly, a_t depends on m_t and r only. It is independent upon the fishing mortality. Therefore, the factor X_t in equation (6) might be an implicit factor only.

From equation (8), $a_t \to 0$ iff $m_t \to r$, and $a_t = 1$ iff $m_t = 0$. a_t varies in the ranges of $0 < a_t \leq 1$ implies m_t in $r > m_t \geq 0$. If $m_t \geq r$ then $a_t \leq 0$, this implies $B_t \leq 0$. It is meanless in nature. m_t can not be negative or greater than r implies that a_t can not be greater than 1 or negative. a_t depends on m_t and varied in the ranges of 0 to 1, it might be another index of the goodness of environmental conditions.

Generally, the assumption of constant environmental conditions is necessary for estimating the parameters, i.e., m_t =constant or a_t =constant. It needs to know constant in what level.

Equation (2) can be rewritten as follows.

$$\frac{dB_t}{dt} = -\frac{r}{K}[B_t - \frac{K}{2}(1-\frac{F_t}{r})]^2 + \frac{rK}{4}(1-\frac{F_t}{r})^2 \qquad (9)$$

It showed a set of parabola curves (Figure 1). For example, if $F = F'$ then parabola curve shifts from BAO-curve ($F = 0$) to B'A'O'-curve ($F = F'$). At the same time, maximum net production and the biomass with such production also shift from $f_t = rK/4$ to $f_t' = (rK/4)(1-F/r)^2$, and $B_t = K/2$ to $B_t' = (K/2)(1-F/r)$, respectively. If catch and effort data are used to estimate the parameters, then both, the initial biomass (*Bo*) and the catch curve, should be determined. For example, if $X_t = 0$ before 1967 and $B_{67}' = B_o < K/2$, then $\mathrm{B_oC}$ − curve is fitted, but if $B_{67}' = B_o' > K/2$, then $\mathrm{B_o'C}$ − curve is fitted. Moreovre, if $X_t \neq 0$, then $\mathrm{B_o''C}$ − curve is fitted.

If assuming that $B_o = K$, and $X_t = 0$, then OAB-curve is fitted. This is the equivalent surplus production model, and maximum sustainable yield $rK/4$ could be expected by managing the biomass at $B_t = K/2$. This is the basic concept of MSY (maximum sustainable yield).

If maintaining the biomass at the level of having the maximum net production, i.e.,

$a_t = 1/2$, is the first goal of the fishery management, then based on this idea, Wang (1996) developed the IPM-method (improved surplus production method). Set $B'_{74} = B'_o = K/2$ and $X_t = 0$ before 1974 for South Pacific albacore stocks, the parameters *K*, *q* and *r* are estimated (Wang 1999a, 2000).

However, in order to rise the reliability of the parameters, it needs to estimate the best estimation of the initial biomass, i.e., a of $B_o = aK$. Regretely, in the real world, it is not so easy to examine the environmental conditions whether or not they are in constant, i.e., to estimate a_t directly from the fluctuated environmental conditions. As shown above, constant environmental conditions implies constant a_t. Hnce, the average value of a_t with the minimum coefficient of variances might be considered as the best estimation of constant a_t. This is available by comparing the C.V. evaluated by deleting one of a_t, successively.

Therefore, if catch and effort data are used to estimate the parameters *K*, *q* and *r*, then first, the most likehood of the catch curve of equaion (5), and next, the best estimation of constant a_t, should be determined. By this two steps, more reliability of the parameters, *K*, *q*, and *r* could be obtained.

RESULTS AND DISCUSSIONS

For far distant fishing countries, catch and effort data might be the most important sources of the information providing the decision making of fishery management. Based on 1967-98's catch and effort data of Taiwanese tuna longline fishery, the effective fishing efforts operating in the South Pacific Ocean were estimated. The overalls of the South Pacific albacore catch and effective effort data of tuna long line fishery were listed in Table 1 (adopted from Table 1 of Wang 2000).

If effective CPUE (catch per unit of fishing effort) is defined as abundance index, then $U_t = catch/hooks$ represents the average biomass of t-year, $U_t^{'} = (U_{t-1} + U_t)/2$ and $U_{t+1}^{'} = (U_t + U_{t+1})/2$ represent the abundance index at the beginning and ending of that year, respectively. In equation (5), it is replaced by $\ln(B_t / B_{t+1}) = \ln(U_t^{'} / U_{t+1}^{'})$. U_t, X_t and $\ln(U_t^{'} / U_{t+1}^{'})$ are used to estimate the parameters by the method of the least squares. The results revealed that $q = 9.62169E-09$, $r = 1.89003$, and the initial biomass at the beginning of 1967 is about $B_{67}^{'} = 66331\ mt$. Now, it needs to estimate the constant a_t for getting the true K.

By equation (6), all of a_t can be calculated and shown in Table 2. As shown in Figure 2, before 1974, they show a clear decreasing trend. All of them are larger than 1/2. After 1974, although a_t varied year by year, most of them are lower than 1/2. It seems imply that South Pacific albacore tuna long line fisheries are still in developing before 1974. Biomass is still larger than *K/2*. After this year, sufficiently developed fisheries revealed that biomass is closing to or lower than *K/2*.

As shown in Figure 3a and 3b, C.V. evaluated by deleting one year successively revealed that the minimum C.V. is obtained by deleting those a_t before 1974. Average a_t in 1974-98 is about $a = 0.3967$. It is considered as the best estimation of the constant a_t. Hence, carrying capacity is estimated by $K = B_{67}^{'} / a = 167{,}211\ mt$.

As shown in equation (9), if fishery management is target on keeping the biomass to be having the maximum net production as suggested by Wang (1999a, 2000), then the biomass and net production are given as follows.

$$f_t = \frac{rK}{4}(1 - F_t / r)^2 \quad (10)$$

$$B_t = \frac{K}{2}(1 - F_t / r) \quad (11)$$

Since $Y_t = F_t B_t$, it implies that

$$Y_t = F_t B_t = F_t \frac{K}{2}(1 - \frac{F_t}{r}) \quad (12)$$

In equilibrium, it implies that

$$Y_t = F_t \frac{K}{2}(1 - \frac{F_t}{r}) = \frac{rK}{4}(1 - \frac{F_t}{r})^2 \quad (13)$$

Hence, $F_t = r/3$ is the unique solution of the equivalent status. In equilibrium, $F_e = r/3$ implies that

$$B_e = K/3,\ f_e = rK/9,\ Y_e = rK/9 \quad (14)$$

This is the basic concept of the improved surplus production method suggested by Wang (1996, 1999a, 2000). For South Pacific albacore stocks, theoretically equivalent catch point is evaluated as follows.

$$F_e = r/3 = 0.63001, \qquad B_e = K/3 = 55{,}737\ mt,$$

$$Y_e = F_e B_e = 36{,}786\ mt, \qquad X_e = F_e / q = 6.85949E07\ hooks \quad (15)$$

Clearly, almost all of the annual catches are still lower than the equivalent catch, except 1967's and 1973's, the early stage of the developing fishery. Noticeably, in 1998, it has been close to the equivalent point.

Even if under the assumption of constant catchability, fishing mortality rate varies year by year. The environmental conditions, and hence biomass, also fluctuated year by year. Therefore, setting fixed MSY or TAC (total allowable catch) to be the goal of fishery management could not reflect the fluctuations of the biomass. For assuring the success of fishery management, sufficient consideration of the environmental conditions might be necessary. Unfortunately, the information of fluctuations of environmental conditions is generally unavailable and/or insufficient. The alternative actions among each factor are generally unknown and/or very complicate with time delay. It is not so easy to examine the effects of biomass under environmental conditions directly. As stated above, Schaefer model provides us the useful index m_t and a_t responding to the goodness of environmental conditions.

For South Pacific albacore stocks, during 1967 to 1998, the average m_t is about 1.0131 with the ranges of 0.3164 to 1.7620. Correspondingly, the average a_t is about 0.4640, closing to 1/2, with the ranges of 0.0677 to 0.8326. Generally, they are rather stable. The particular low a_t with high m_t and F_t in 1994 may be relative to the particular high fishing efforts. During this year, over twenty new Taiwanese tuna long linners entered this area. In the next year, some shift to the Indian Ocean and some to Atlantic Ocean. Maybe it is relative to the quickly developing of the large size gill netters. Although this type of fishery ceased from 1993, their effects on the albacore recruitment might be lasting to this year.

For the South Pacific albacore stocks, m_t and F_t, both vary year by year (Figure 4). The differences defined by $d_t = m_t - F_t$ provide us the basic information of the status of the South

Pacific albacore stocks under exploitations. As shown in Figure 5, before 1974, all of d_t are negative. This is due to too small m_t. In this period, fishery is still in developing, biomass is in high level ($B_t > K/2,\ a_t > 1/2$). In 1968, $a_t = 0.8326$, it decreased to $a_t = 0.6189$ in 1973.

As shown in Figure 5, after 1974, d_t varied around zero with a horizontal tendency. It implies that F_t and m_t both are rather stable (Table 2). At present status, quickly increasing or decreasing fishing intensity in this area is not appreciable.

As shown in Figure 6, high correlation coefficient between F_t and m_t revealed that fishing mortality rate highly depends on the net production rate. This implies that South Pacific albacore tuna long line fishery has been a sufficient developed fishery. Maybe, this is the commom phenomenon of the sufficient developed fishery. Fishing condiitions has been reflected the net production rate, sufficiently.

Negative d_t appeared in 1978-81, 1983-84, 1987-89, 1993, 1996-97. During 1978 to 1984, there is a severe *El nino* event in 1982/83. After 1997, there is another severe *El nino* event in 1997/98. During 1987 to 1993, the influences of the strictly increasing of gill net are noticeable. Wang (1999b) showed that high correlation coefficients between the biomass and the environmental conditions; development of the large size gill nets and the distribution of the sea surface temperature, can be found. Although the alternative actions among them are not clear, at least, it implies that the relationships between the biomass and the fluctuated environmental conditions can not be neglected for successful fishery management.

Conclusively, the above results revealed that South Pacific albacore stocks are still in healthy conditions under long term exploitation.

CONCLUSIONS

1. Estimating the population parameters of *K*, *q* and *r* is important work for fishery management. This paper tried to estimate more reliable estimations of these parameters based on surplus production model. Two steps are necessary, one for fitting the best catch curve, one for estimating the best constant environmental conditions.
2. The instantaneous net production rate m_t was introduced. m_t is an indicator of the status of the biomass reflecting the goodness of the environmental conditions. $0 \le m_t < r$ implies $K \ge B_t > 0$. It implies that biomass is in equilibrium status or approaching the carrying capacity.
3. a_t is another indicator. It is the relative biomass ratio to the carrying capacity. It depends on m_t and *r*. $0 \le m_t < r$ implies $1 \ge a_t > 0$. $a_t = 0$ implies $B_t = 0$. It is meaning less in nature.
4. In assessing fish stocks, environmental conditions are commonly assumed to be constant. It corresponds to the constant net production rate m_t, hence the constant a_t. In assessing fish stocks, constant a_t could be found by setting the minimum coefficient of variances of a_t.
5. For the South Pacific albacore stocks, *r=1.89003*, *q=9.6217E-09* and *K=167,211 mt* are estimated by surplus production model based on the catch and effort data during 1967 to

1998.

6. If fishery management is target on maintaining the biomass to be having the maximum net production, i.e., $a_t \equiv 1/2$, then the unique equivalent catch point is given as: $F_e = r/3$, $B_e = K/3$, $Y_e = f_e = rK/9$, $X_e = F_e/q$. For the South Pacific albacore stocks, they are $F_e = 0.63001$, $B_e = 55{,}737\ mt$, $Y_e = f_e = 36{,}786\ mt$, $X_e = 6.85949E07\ hooks$.
7. The differences d_t between the net production rate m_t and fishing mortality rate F_t could be a useful index of the status of the fish stocks under fishing. It provides the important information for decision making of fishery management.
8. Target on fixed amount of annual catch, like as MSY or TAC, might be insufficient for assuring the success of the fishery management. It could be better by examine the status of the fish stocks year by year through the index of d_t. Because d_t seems reflecting the fishing intensity and the changes of the environmental simultanneously.
9. During 1974-1998, particular high values of net production rate and fishing mortality rate might be relative to the abnormal environmental conditions, like as severe *El nino* events and/or quickly developing of the large size gill nets in this area.
10. Due to small ranges of variations of net production rate, fishing mortality rate and the differences and high correlation between them, South Pacific albacore tuna long line fishery could have been a sufficient developed fishery. The present status of the fish stocks might be healthy and the most appreciable case.

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Table 1. Catch, effort and CPUE of the South Pacific albacore stocks, 1967-1998.

	total catch	total effort	CPUE: U_t=	U_t'=
Year	/10000 mt	/10^7	kg/100H	(Ut+Ut+1)/2
1967	4.0318	5.3673	75.1180	-
1968	2.9051	4.6268	62.7880	68.9530
1969	2.4360	4.1675	58.4520	60.6200
1970	3.2590	5.2290	62.3250	60.3885
1971	3.4708	8.1169	42.7600	52.5425
1972	3.3842	7.9004	42.8360	42.7980
1973	3.7649	10.6338	35.4050	39.1205
1974	3.0985	13.8400	22.3880	28.8965
1975	2.6131	11.3662	22.9900	22.6890
1976	2.4106	7.9521	30.3140	26.6520
1977	3.4849	11.1990	31.1180	30.7160
1978	3.4858	11.2405	31.0110	31.0645
1979	2.8739	11.8326	24.2880	27.6495
1980	3.1027	12.0395	25.7710	25.0295
1981	3.2632	17.4363	18.7150	22.2430
1982	2.8339	13.4442	21.0790	19.8970
1983	2.4303	10.0893	24.0880	22.5835
1984	2.0340	11.1605	18.2250	21.1565
1985	2.7138	12.5262	21.6650	19.9450
1986	3.2641	11.3297	28.8100	25.2375
1987	2.6877	11.5441	23.2820	26.0460
1988	3.1530	13.3777	23.5690	23.4255
1989	2.2247	12.8003	17.3800	20.4745
1990	2.2625	10.1144	22.3690	19.8745
1991	2.5000	11.7520	21.2730	21.8210
1992	3.0722	11.5034	26.7070	23.9900
1993	2.9901	12.9414	23.1050	24.9060
1994	3.3031	16.2068	20.3810	21.7430
1995	2.4369	7.4133	32.8720	26.6265
1996	2.5801	9.9660	25.8890	29.3805
1997	3.2784	12.3695	26.5040	26.1965
1998	3.6466	14.6015	24.9742	25.7391
mean	2.9686	10.8153	30.8891	30.2711
max	4.0318	17.4363	75.1180	68.9530
min	2.0340	4.1675	17.3800	19.8745

Table 2. Analysis of the South Pacific albacore stocks.

r=1.89003 q=9.62169E K=167,211 mt

Year	a_t =	mean a_t	C.V.=	m_t =	F_t =	$d_t = m_t - F_t$
1967	-	-	-	-	-	-
1968	0.8326	0.4637	0.0692	0.3164	0.4452	−0.1288
1969	0.7899	0.4509	0.0677	0.3972	0.4010	−0.0038
1970	0.8074	0.4388	0.0663	0.3639	0.5031	−0.1392
1971	0.6953	0.4252	0.0627	0.5759	0.7810	−0.2051
1972	0.6453	0.4148	0.0616	0.6703	0.7601	−0.0898
1973	0.6189	0.4056	0.0612	0.7202	1.0232	−0.3029
1974	0.4234	0.3967	0.0610	1.0898	1.3316	−0.2418
1975	0.3362	0.3955	0.0639	1.2546	1.0936	0.1610
1976	0.5201	0.3982	0.0661	0.9070	0.7651	0.1419
1977	0.4239	0.3924	0.0687	1.0888	1.0775	0.0113
1978	0.4894	0.3908	0.0725	0.9651	1.0815	−0.1165
1979	0.4503	0.3857	0.0763	1.0389	1.1385	−0.0996
1980	0.4495	0.3821	0.0809	1.0404	1.1584	−0.1180
1981	0.1713	0.3781	0.0861	1.5662	1.6777	−0.1115
1982	0.2486	0.3910	0.0815	1.4202	1.2936	0.1267
1983	0.5209	0.4005	0.0814	0.9055	0.9708	−0.0653
1984	0.4630	0.3919	0.0864	1.0149	1.0738	−0.0590
1985	0.2378	0.3865	0.0937	1.4406	1.2052	0.2354
1986	0.4065	0.3988	0.0930	1.1216	1.0901	0.0315
1987	0.4684	0.3981	0.1025	1.0047	1.1107	−0.1060
1988	0.3902	0.3911	0.1142	1.1525	1.2872	−0.1346
1989	0.3641	0.3912	0.1284	1.2019	1.2316	−0.0297
1990	0.4357	0.3946	0.1451	1.0666	0.9732	0.0934
1991	0.3516	0.3887	0.1707	1.2255	1.1307	0.0948
1992	0.3946	0.3949	0.2003	1.1443	1.1068	0.0375
1993	0.4130	0.3950	0.2501	1.1094	1.2452	−0.1358
1994	0.0677	0.3905	0.3367	1.7620	1.5594	0.2026
1995	0.5705	0.4981	0.2210	0.8117	0.7133	0.0984
1996	0.5533	0.4618	0.2836	0.8442	0.9589	−0.1147
1997	0.3796	0.3796	-	1.1725	1.1902	-0.0176
1998	-	-	-	-	-	-
mean	0.4640	0.4057	0.1156	1.0131	1.0459	−0.0328
max	0.8326	0.4981	0.3367	1.7620	1.6777	0.2354
min	0.0677	0.3781	0.0610	0.3164	0.4010	−0.3029

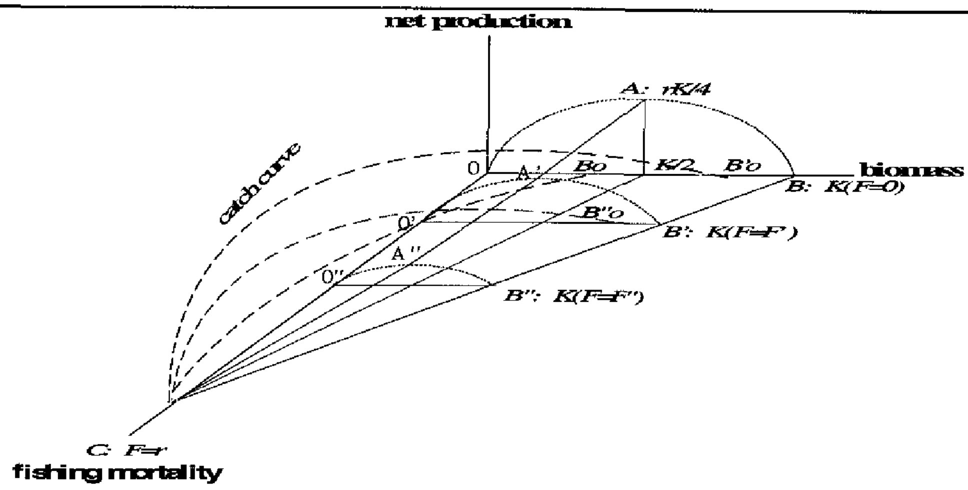

Fig. 1. Relationships among biomass, fishing mortality, net production and catch curves.

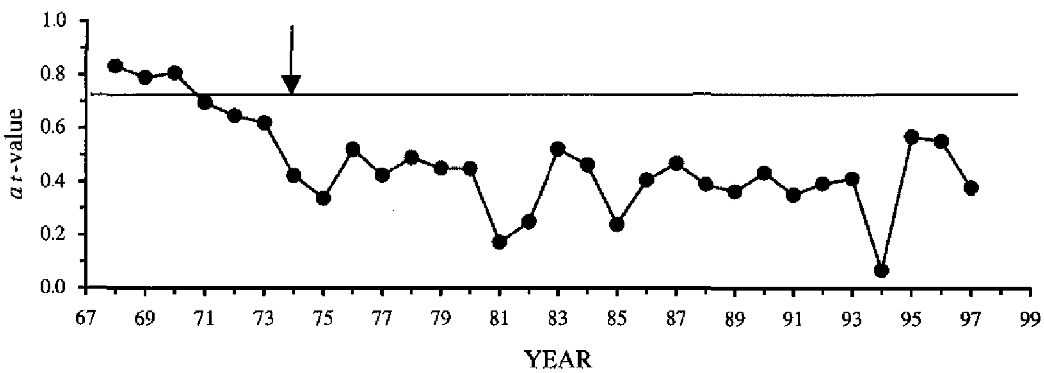

Figure 2. Variations of a_t.

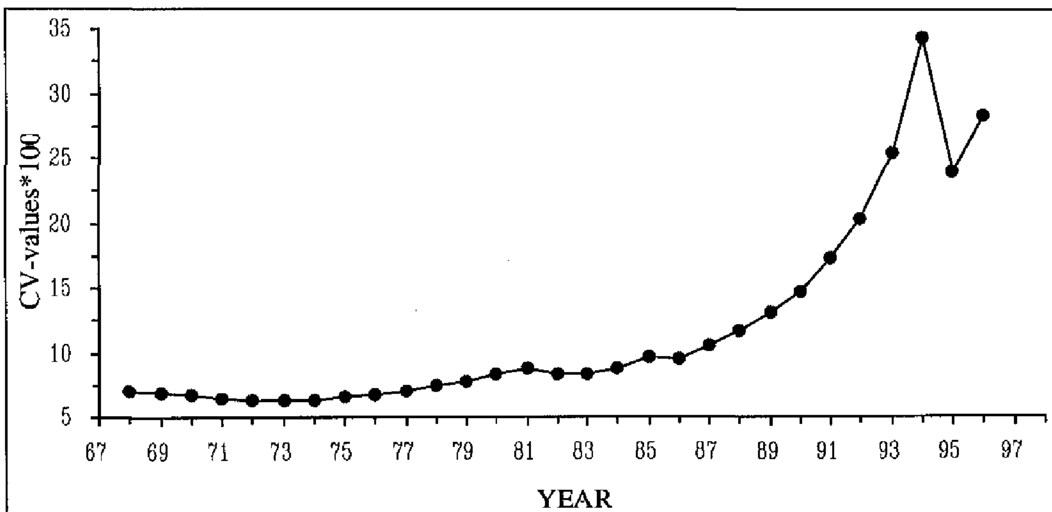

Figure 3a. Comparison of the coefficient of variances.

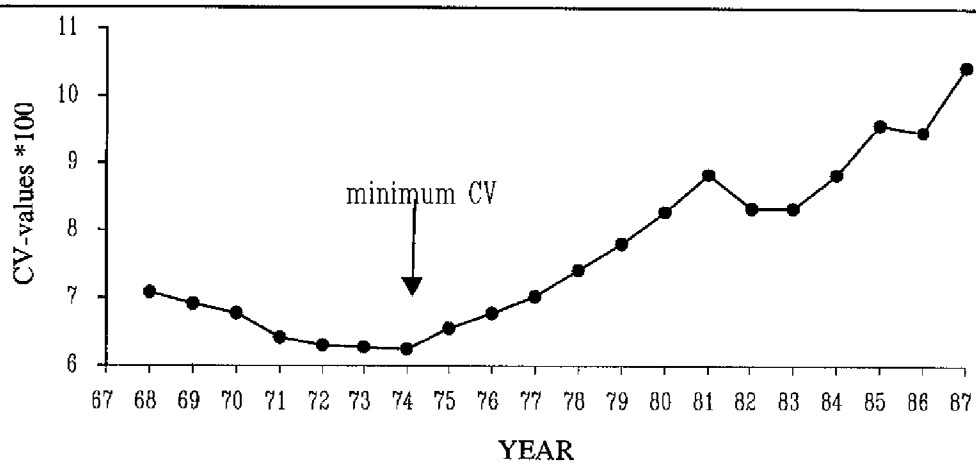

Figure 3b. Comparisons of the coefficient of variances.

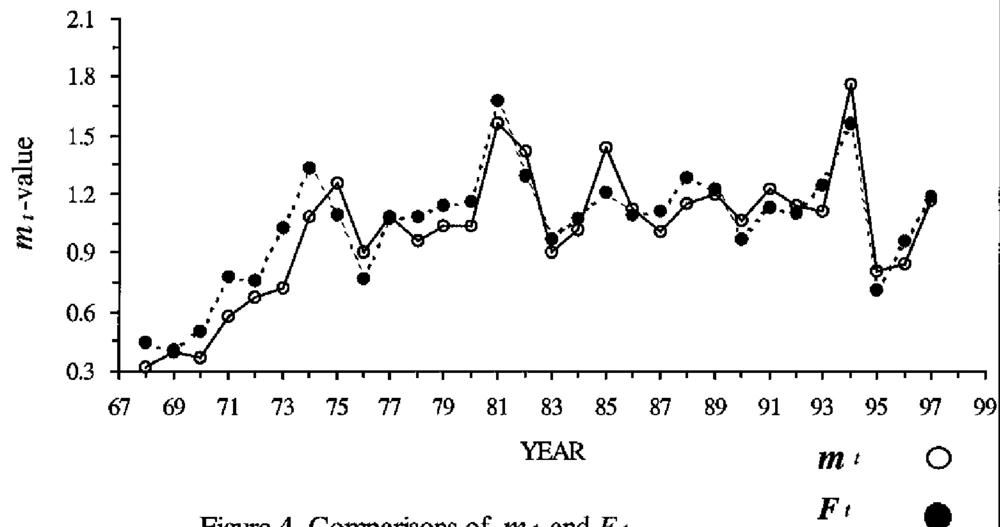

Figure 4. Comparisons of m_t and F_t.

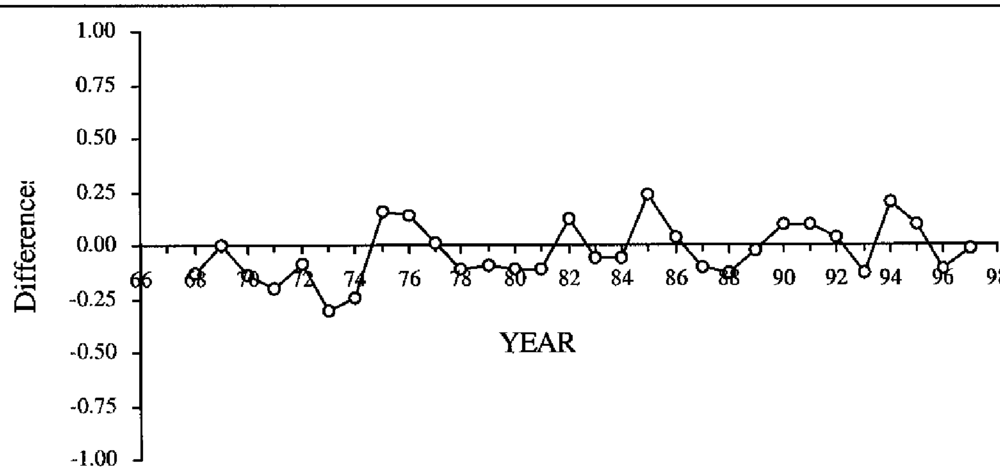

Figure 5. Variations of the differences: $d_t = m_t - F_t$.

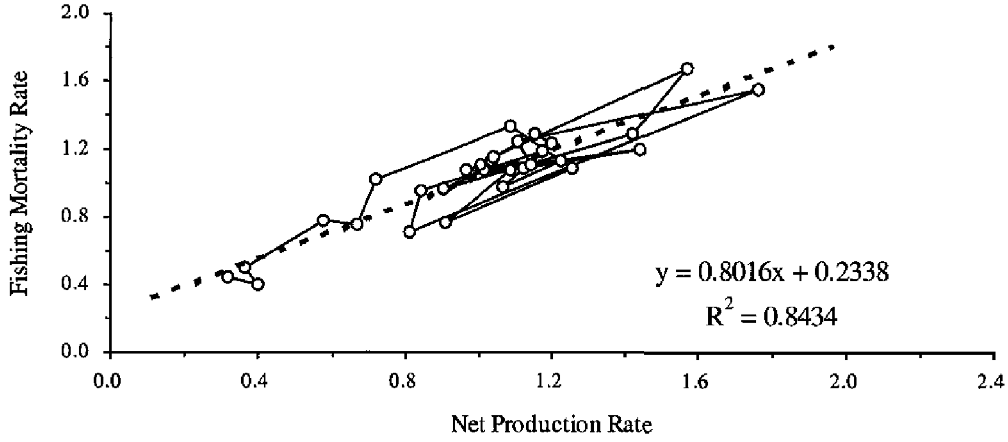

Figure 6. The relationships between the instantaneous net production rate and fishing mortality.