Studies on Estimating Parameters of a Fish Population Supplied by Sequential Recruitment—I. The Effect on Estimates for Pacific Yellowfin Tuna

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In studying the dynamics of fish populations, it is necessary to estimate various parameters, such as the natural mortality coefficient (M) and the catchability coefficient (q). Several methods of estimation of these parameters have been presented by previous authors (BEVERTON and HOLT¹⁾, WIDRIG²⁾, PALOHEIMO³⁾, RICKER⁴⁾, and there are many examples of application (e.g. CUSHING⁵⁾). For the application of these methods, it is necessary to assume that recruitment does not occur within the exploited phase of a population. If it does occur, and this is rather common, the range of age to be used must be limited to the age groups after recruitment is completed.

From the studies of Pacific yellowfin tuna, *Thunnus albacares* (BONNATERRE), caught by tuna longline, by previous authors (KAMIMURA and HONMA⁶⁾), in which the population abundance index was calculated from the size and age compositions of tuna longline catch and fishing effort, it seems that the population is not fully exploited at the younger ages and recruitment takes place even at ages 3 and 4 which constitute the main part of the catch. In such a population, which the population parameters are estimated for ages at which recruitment is not finished by the method mentioned above, the results will be significantly biased.

The purpose of this paper is to evaluate the effect of sequential recruitment on estimated values of natural mortality coefficient and catchability coefficient for Equatorial Pacific yellowfin tuna.

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Model of recruitment system and method of calculation

Notation: The following notations will be used:

i : subscript, refer to year i , $i=49-79$

j : „ „ subarea j , $j=1-6$

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- k : subscript, refer to the k -year-old fish, $k=1-9$
 l : „ „ the l th line* of recruitment, $l=1-5$
 h : „ „ the h year class
 N_{ijkl} : Numbers of the k -year-old fish of the l th line of recruitment at the end of the year i in the subarea j
 C_{ijk} : Numbers of k -year-old fish caught during the year i in the subarea j
 f_{ijk} : Total effective fishing intensity against the k -year-old fish during the year i and the subarea j
 p'_{ijk} : Population index of k -year-old during the year i in the subarea j
 p'_{sijk} : Population index obtained by simulation of k -year-old during the year i in the subarea j
 q : Catchability coefficient
 M_k : Natural mortality coefficient of the k -year-old fish
 F_{ijk} : Fishing mortality coefficient of the k -year-old fish during the year i in the subarea j
 T_{jk} : Transfer coefficient of the k -year-old fish in the subarea j into the subarea $j+1$
 Z_{ijk} : Total decrease coefficient of the k -year-old fish during the year i in the subarea j
 r_l or r_k : The proportion of recruits in the l th line of recruitment or at k th age to the total
 R_{jh} : Total number of recruits in h year class in the subarea j
 R'_{jk-hl} : Number of recruits of which the unit is the same as that of p' in the l th line of recruitment of h year class in the subarea j
 $\hat{M}, \hat{q}$: Estimates of M, q

Dynamic process of population For basic formulae of the decrease of a year class, the model described by BEVERTON and HOLT¹⁾ is used. That is,

$$N_{ijk} = N_{i-1,j,k-1} e^{-Z_{ijk}}, \quad (1)$$

$$C_{ijk} = \frac{F_{ijk}}{Z_{ijk}} N_{i-1,j,k-1} \{1 - e^{-Z_{ijk}}\}, \quad (2)$$

$$F_{ijk} = q f_{ijk}, \quad (3)$$

$$Z_{ijk} = q f_{ijk} + M_k + T_{jk}. \quad (4)$$

In this paper both M and T are assumed to be constant and independent of age. It is also assumed that f_{ijk} is common to all age groups. The factor of transfer is taken into consideration in this paper, because it has been suggested that yellowfin tuna gradually move eastward as they grow older.

Recruitment system As analysis of the relation between the sequential recruitment

* See section of Recruitment system.

and the bias of population parameter estimated from catch samples requires knowledge of the process of recruitment into exploited fish population. Unfortunately, relatively little is known about the process due to the difficulties of measurement. Here, a theoretical model for recruitment is set up as illustrated in Fig. 1. Young fish are

Fig. 1. The population curve of each line of the recruitment in the sequential recruitment.

R : The size of the year class.

$r_1 \sim r_5$: The proportion of recruits of each line among total.

-----: Ages in which only M is included in the decreasing factor for population.

—: Ages in which both F and M are included.

divided into five groups at the beginning of their second year (Age 1), and each of these groups will be recruited into exploited population successively every year at the beginning of the year starting from Age 1. The process of recruitment of each group may be called line here, and the relative size of each line is given by r_i . The flow chart of recruitment system is indicated in Fig. 2.

Fig. 2. The network of the sequential recruitment and the proportion of recruits obtained from the normal distribution.

$(r_i R)$: The number of recruits in each line of recruitment.

(C_k) : Catch in each age.

$[M]$: The process in which M acts on the population.

$[F]$: " " " " " " " "

—: The route of population.

-----: The route of catch in each age.

Fig. 3. The structure of the population which has sequential recruitment.

▨: Population index (p') which is obtained from the catch data.

Estimation of the pattern of recruitment on the proportion of recruits in each line Two types of data were used for calculating r_i . One is purely hypothetical and the other is derived from actual data. In the first case the hypothetical pattern of recruitment derived from the normal distribution was applied. These values of r_i are obtained from the following formulae;

$$\left. \begin{aligned} r_1 &= P_r[u < -1.5] \\ r_2 &= P_r[-1.5 \leq u < -0.5] \\ r_3 &= P_r[-0.5 \leq u < 0.5] \\ r_4 &= P_r[0.5 \leq u < 1.5] \\ r_5 &= P_r[1.5 \leq u] \end{aligned} \right\} \quad (5)$$

where $P_r[a \leq u < b] = \int_a^b \frac{1}{\sqrt{2\pi}} e^{-u^2/2} du$.

These values are given in Fig. 2. The same values are applied to all subareas and all year classes. In the second case, r_i was calculated for each subarea and year class by solving formulae (6) in which observed values of p' and assumed values of M and q were substituted. (Fig. 3)

$$\left. \begin{aligned} p'_{t+1,j,1} &= p'_{t+1,j,1,1} = \left[\frac{1}{qf_{t+1,j} + M} \{1 - \exp(-qf_{t+1,j} - M)\} \right] R'_{j,t,1} \\ p'_{t+2,j,2} &= p'_{t+2,j,2,1} + p'_{t+2,j,2,2} = \left[\frac{1}{qf_{t+2,j} + M} \{1 - \exp(-qf_{t+2,j} - M)\} \right] \\ &\quad \times [R'_{j,t,1} \exp(-qf_{t+1,j} - M) + R'_{j,t,2} \exp(-M)] \\ &\quad \dots \dots \dots \\ p'_{t+5,j,5} &= \sum_{i=1}^5 p'_{t+5,j,5,i} = \left[\frac{1}{qf_{t+5,j} + M} \{1 - \exp(-qf_{t+5,j} - M)\} \right] \\ &\quad \times [R'_{j,t,1} \exp(-4M - q \sum_{i=t+1}^{t+4} f_{i,j}) + R'_{j,t,2} \exp(-4M - q \sum_{i=t+2}^{t+4} f_{i,j}) \\ &\quad + R'_{j,t,3} \exp(-4M - q \sum_{i=t+3}^{t+4} f_{i,j}) + R'_{j,t,4} \exp(-4M - qf_{t+4,j}) \\ &\quad + R'_{j,t,5} \exp(-4M)] \end{aligned} \right\} \quad (6)$$

where $h=t, i=t+1, \dots, t+5$. The values of r_i were obtained by averaging the values of r_{ih} according to years to give one mean pattern of recruitment or two if the pattern did not seem to be common for all year classes. The results will be presented sepa-

rately for each of the two cases.

Procedure of the analysis The procedure of this analysis is to compute*, for given values of r_i , R_{jk} , M , q and F_i , catches in each subarea from the model population described above, and then to estimate* the natural mortality coefficient and catchability coefficient from the catch data based on the assumption that the recruitment is completed at Age 1.

Two methods were used for calculating M and q . One is that presented by BEVERTON and HOLT, and the formula is

$$Z'_{ijk} + \log_e \left\{ \frac{(qf_{ij} + M)(1 - e^{-(qf_{i+1,j} + M)})}{(qf_{i+1,j} + M)(1 - e^{-(qf_{ij} + M)})} \right\} = qf_{ij} + M, \quad (7)$$

where

$$Z'_{ijk} = \log_e \left(\frac{p'_{sijk}}{p'_{s,i+1,j,k+1}} \right).$$

For the first approximation the second term of the left side of formula (7) was neglected. The number of iterations was fixed at three times in every case. In the other one (TANAKA⁸⁾, PALOHEIMO⁹⁾ the mean of f_{ij} and $f_{i+1,j}$ is substituted for f_{ij} and formula (7) is approximated by

$$Z'_{ijk} = q \left(\frac{f_{ij} + f_{i+1,j}}{2} \right) + M. \quad (8)$$

The area which is considered in this paper is located in the Equatorial Pacific (12°N–16°S, 120°E–100°W) and consists of six subareas. (Fig. 4)

Division of the subarea and calculation of effective fishing intensity are entirely research contributions of the staff of Nankai Regional Fisheries Research Laboratory.

Fig. 4. Designation of subareas.

Result

The results are presented below in two cases which were divided according to the methods to derive the pattern of recruitment.

Case I The hypothetical pattern of recruitment derived from the normal distribution was applied. Further it is assumed that the total number of recruits (R_k) to each subarea is constant (10^8) and the natural mortality coefficient (M) is independent of age and subarea. The transfer coefficient is given by the following formula,

$$T = (6-j) \times [0.01 + \{0.001 \times (k-1)\}]$$

j : Subarea number j : 1–6
 k : Age k : 1–9

* An OKITAC—5090C computer was used.

T increases by 0.001 with each year's growth and decreases from west to east. In Subarea VI, T is zero for all ages. The assumption on T is derived from the information obtained so far.

I-1) Effective intensity (f) and catchability coefficient (q) are put as follows.

$$\begin{array}{lll} i=49\sim 62 & f_i=0.05 (i-48) & q=1 \\ i=63\sim 79 & f_i=0.70 & q=1 \end{array}$$

The value of M given ranges from 0 to 0.8 in the step of 0.1 ($M=0(0.1)0.8$). The relation between the true value of M and its estimates $\hat{M}$ in Subarea I is shown in Fig. 5 for example. Except $M=0.7$ and 0.8 $\hat{M}$ was not calculated for Age 1 and Age

Fig. 5. The relation between M and $\hat{M}$ when M varies from 0 to 0.8 in Subarea I.

- : BEVERTON and HOLT method.
- : The estimated value by the approximation method.
- ⊙: The estimated value when the two values are about same.

Age 1 2 3 4 5 6 7 8
 ○ ○ ○ ○ ○ ○ ○ ○

Fig. 6. The relation in each subarea between the value of $\hat{M}-M$ and age. Average for $M=0.1\sim 0.8$.

Subarea I II III IV V VI
 ○ □ ◇ △ ▽ ▹

2 because $p_k' < p_{k+1}'$, and so Z was negative. For $M=0.7$ and 0.8 , through $\hat{M}$ was calculated, the difference between M and $\hat{M}$ is extremely large. For the ages larger than three, parameters were estimated in each case and these estimated values by the two methods practically coincided with each other. The value of $\hat{M}-M$ was variable in each age and subarea, but these values seemed to be independent of the value of M . (Fig. 6)

It was recognized that the absolute value of $\hat{M}-M$ in Age 2 and Age 3 were very large. The value for Age 3 being about -0.22 can not be disregarded though this

age group dominated in the catch and 69% of the recruitment had been completed. In Subarea I, $\hat{M}-M$ of higher ages, Ages 5–8, were 0.07–0.09 and this bias was derived from the transfer effect. On the other hand, in Subarea II–V, the range of $\hat{M}-M$ was from -0.02 to 0.01 .

I—2) The value of effective fishing intensity (f_{ij}) was calculated from the actual

Fig. 7. The variation of effective fishing intensity in each subarea and year.

Fig. 8. The relation between $\hat{M}$ and M of each age and method in Subarea II when M varies from 0.3 to 0.7. Values of effective fishing effort (f) were calculated from the catch data. The marks are the same as those in Fig. 5.

Fig. 9. The relation between $\hat{M}-M$ and age of each subarea when $M=0.4$.

○: BEVERTON and HOLT method.
●: The estimated value by the approximation method.

Subarea I II III IV V VI
○ □ ◇ △ ▽ ▹

statistical data, and $q=0.02$ (Fig. 7). All other conditions and methods are the same as those in I-1.

The results of I-2 were similar to those in I-1. The relation between $\hat{M}$ and M is shown in Fig. 8 taking Subarea II for example. Fig. 9 shows the value of $\hat{M}-M$ of each age and subarea when M is 0.3. $\hat{M}$ of Age 3 was smaller by about 0.25 than M . The variation of $\hat{M}$ between subareas was larger than that of I-1, and the difference between $\hat{M}$ by two methods was not as small as that of I-1, especially in Age 3 and 4.

Case II Values illustrated in Fig. 7 were applied to f_{ij} and it is assumed that $q=0.045$ and $T=0$ or no transfer between subareas. M was varied from 0 to 0.8 at intervals of 0.1. This range of M is considered to be sufficiently large.

For the pattern of recruitment, the value of recruitment in each age (R'_{jhl}) was calculated from formula (6) for various combinations of subareas and year classes (Table 1) on the basis⁷⁾ of $M=0.4$ and $q=0.045$. These are the values which seem to be reasonable. The pattern was not symmetrical and R'_{j44} and R'_{j45} were negative in many cases (Table 2). To avoid negative values R' , the right side of the peak of R' curve was assumed to be symmetrical to the left side. For Subareas I and IV two patterns of recruitment were calculated because there is obvious difference of the pattern between years. The results are summarized in Fig. 10. It being not possible

Table 1. Combination of subarea and year class, for which r_l was calculated.

Subarea	'48	'49	'50	'51	'52	'53	'54	'55	'56	'57
I			0	0	0	0	0	0	0	0
II	0	0	0	0	0	0	0	0	0	0
III		0	0	0	0	0	0	0	0	0
IV			0	0	0	0	0	0	0	0
V							0	0	0	0

Table 2. The value of recruitment, which was calculated from the actual catch data for year class in Subarea I under the assumption that $M=0.4$ and $q=0.045$. Unit of R'_l is the same as that of population index (p').

Year class	R'_1	R'_2	R'_3	R'_4	R'_5
1950	48.0	2708.7	4232.1	-351.6	-696.4
1951	52.5	1339.4	2842.8	-421.7	-559.1
1952	82.3	656.9	2242.5	31.8	-399.8
1953	58.9	654.2	2440.9	-347.8	-505.8
1954	27.9	1744.8	2513.0	-792.7	-317.4
1955	97.4	906.8	3116.4	952.1	-63.6
1956	83.9	1359.0	6219.5	829.9	-216.3
1957	33.9	4792.6	4951.2	968.8	-498.1

to obtain r_i in Subarea VI, values in Subarea V were substituted.

Number of fish in population and catch were calculated by formulae (1)–(4) for each subarea and year class under the assumption mentioned above. The value of $\hat{M}-M$ and q which were calculated for $M=0.3$ are illustrated by ages in Fig. 11 and Fig. 12 respectively. As the population index increases upto Age 3 the estimation of parameter was not done for Ages 1 and 2. In ages older than 4 the value of $\hat{M}-M$ was nearly equal to zero and q was nearly equal to 0.045 in each subarea. For both parameters, estimated values in Ages 3 and 4 were very variable, and those values in Age 3 were obtained only for Subareas I–IV. The difference between values estimated by two methods was large. Particularly it is very large in Subarea I and IV where the pattern of recruitment was not same for all year classes.

Fig. 10. The pattern of recruitment r_i calculated from the catch data in each subarea.

Fig. 11. Variation of $\hat{M}-M$ by age in each subarea in two methods of estimation when $M=0.3$. The marks are the same as those in Fig. 9.

Fig. 12. Variation of $\hat{q}$ by age in each subarea when $M=0.3$. The marks are the same as those in Fig. 9.

Discussion

When the natural mortality coefficient and catchability coefficient are estimated in fish populations, where the age composition of the catch is similar to that of Pacific yellowfin tuna caught by longline, by the method assuming that recruitment is completed, only a small part of the total catch data is useful and it is not possible to estimate these parameters in the age group which occupies the main part of the total

catch. If it is tried to estimate these parameters in those young ages where recruitment is not completed by the ordinary method, it is feared that the estimated value of each parameter will have significant bias. If this bias is not so serious, it may be useful to utilize the data of the young ages in the viewpoint of effective usage of available data. So, it is very important to estimate the value of this bias in each parameter.

It was found that the effect of the sequential recruitment on the estimated value of M by ordinary methods could not be neglected in younger age groups including age 3 of which data is generally most abundant in this species. By these methods the value of M was underestimated by about 0.2 in Age 3, but if the pattern of recruitment varies by year classes the variation of estimated value is remarkable. Here, only a few examples among possible cases were examined. However, the results show very clearly that if the ordinary method is applied directly to the data of this species, the bias is unavoidable for ages younger than 5 and even a negative value of M would often be obtained. Any model which provides age structure of the catch similar to the one observed for yellowfin tuna, gradual change of q with age for instance, would present the same result. Therefore, it is necessary to formulate a new method for estimating parameters taking into account sequential recruitment.

Summary

- 1) In tuna longline fishery, yellowfin tuna seems not to be recruited fully at a certain age, but sequentially over some years.
- 2) The bias of estimated value of parameters by two ordinary methods, especially of the natural mortality coefficient (M), in age at which the recruitment is not completed is evaluated by simulation.
- 3) When the rate of recruitment is derived from the normal distribution assuming that the fish recruits from Age 1 to Age 5 and the mode of recruitment is at Age 3, $\hat{M}$ in Ages 1 and 2 was impossible to obtain, and $\hat{M}$ in Ages 3 and 4 are smaller than M in each case. The bias of $\hat{M}$ in ages older than 4 is negligible.
- 4) When the rate of recruitment calculated from the catch data and given values of M and q are used, $\hat{M}$ in Ages 3 and 4 are different from the given value, and that bias of $\hat{M}$ varies in each subarea. Especially in the subarea where the rate of recruitment changed, the variation is remarkable.
- 5) In a fish population which has sequential recruitment, it is necessary to formulate a new method of estimating population parameters.

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