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Estimation of the Abundance of the Southern Bluefin Tuna (*Thunnus maccoyii* (Castlenau)) Subpopulation Exploited by the Australian Fishery

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ESTIMATION OF THE ABUNDANCE OF THE SOUTHERN BLUEFIN TUNA (*Thunnus maccoyii* (Castlenau)) SUBPOPULATION EXPLOITED BY THE AUSTRALIAN FISHERY

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Abstract

The abundance of the southern bluefin tuna (*Thunnus maccoyii* (Castlenau)) subpopulation exploited by the Australian surface fishery is estimated on the basis of tagging data. A specific method of analysis is developed to suit the available data and the features of the population. The calculated numbers of fish at age 2, 3, and 4 years in the subpopulation vary from cohort to cohort between (in millions) 3.56 and 8.93 (mean: 6.14 ± 0.10 (standard error)), 3.47 and 16.70 (mean: 7.33 ± 1.54), and 2.12 and 8.63 (mean: 4.74 ± 1.98), respectively. The estimated yearly rates of exploitation fluctuate between 0.024 and 0.076 (mean: 0.056 ± 0.01), 0.019 and 0.074 (mean: 0.037 ± 0.006), and 0.031 and 0.060 (mean: 0.048 ± 0.009) for fish at age 2-3, 3-4, and 4-5 years, respectively. The assumptions associated with the analysis are discussed. Insufficient mixing of tagged and untagged fish on a large geographical scale is detected. The numbers of fish at age 2, 3, and 4 years calculated in this paper are different from those evaluated (with the aid of cohort analysis) for the global population of southern bluefin tuna by -30% to +40%, -83% to +74%, and -46% to +60%, respectively. When only the two cases for which a high degree of mixing is likely to be present are considered, the estimates from the tagging data are slightly smaller (by 6% and 12%) from those obtained with the aid of cohort analysis. However, it cannot be concluded on this basis that the fraction of fish which does not enter the Australian fishing grounds is much smaller than that passing Australia because (i) the abundance estimates derived on the basis of tagging data are very sensitive to one highly uncertain input parameter used, (ii) the estimates are based on very small numbers of tagged fish, (iii) full test of mixing could not be executed due to the lack of the data from the log book system and the result of the preliminary test implemented could be incidental, and (iv) uncertainties in the results of cohort analysis are not fully evaluated. Suggestions are made for redesigning the tagging program to overcome difficulties encountered in the present analysis.

INTRODUCTION

Southern bluefin tuna (*Thunnus maccoyii* (Castlenau)) is difficult to manage rationally due to its world-wide migration, international exploitation, and continuously increasing market prices (see review in Murphy 1977; Shingu 1978). The biological state of the population (see Murphy and Majkowski 1981) and the latest developments and expansion of the Australian southern bluefin tuna fishery (see Majkowski *et al.* 1981) necessitate gaining further knowledge of this population for its rational management.

A question which requires an answer is concerned with the fraction of the global southern bluefin tuna population which is passing through the Australian fishing grounds. There is accumulating evidence that a large number of young fish spawned south of Java make their way into the Japanese longline population without passing through the Australian fishing grounds (Hynd 1969; Hynd and Lucas 1975; Murphy 1977). The knowledge of the subpopulation which is vulnerable to the Australian fishery is essential for any rational management of this subpopulation, as well as of the global population.

One possible approach for answering the above-mentioned question is to analyse the results of the Australian southern bluefin tuna tagging program for the purpose of estimating the abundance of the subpopulation exploited by the Australian fishery. If this estimation is successful, the fraction of the global southern bluefin tuna population which is passing Australia can be evaluated by comparing the abundance estimates of the subpopulation with those of the global population derived on the basis of cohort analysis (Murphy and Sutherland submitted).

TAGGING PROGRAM

The Australian southern bluefin tuna tagging program was initiated in the late fifties (for details see Hynd 1965; Shingu 1978; Kirkwood 1981; Williams in press; Murphy and Sutherland submitted). The fish caught (mainly by pole and line but also by trolling) by Australian fishermen were tagged in three areas of their operation: off the coasts of Western Australia, South Australia, and New South Wales. The locations of fish releases were arbitrary (incidental in respect to this analysis). The number of tagged fish fluctuated up to several thousands of fish per year. Nearly all fish were double tagged using standard tuna dart tags. The following information regarding each tagged and released fish was recorded: (i) date and geographical position of release, (ii) name of the commercial boat used, (iii) length of fish, and (iv) tag numbers (Williams in press). Similar information concerning each recapture of tagged fish was collected. The data stored on computer tapes were carefully compared with the original documentation and edited in a few cases where this was desirable (for details see Hearn in press). The fish (caught by trolling) tagged without the supervision of CSIRO staff and those for which the above information was not available and could not be estimated were excluded from the analysis.

METHOD OF ANALYSIS

Estimation of abundance

The analysis of tagging results for the purpose of estimating the abundance of the subpopulation exploited by Australian fishermen is based on the well-known Petersen method (cf. Seber 1973; Ricker 1975). According to this method, the rate of exploitation of the subpopulation, u, during the period τ can be approximately determined on the basis of the formula

$$u = R/T, \tag{1}$$

where R is the number of fish recaptured with attached tags by the Australian fishermen from the subpopulation during the period τ and T is the number of tagged fish within the subpopulation at the beginning of period τ. The abundance of the subpopulation, N, at the beginning of period τ can be approximately evaluated with the aid of the formula

$$N = C/u = TC/R, \tag{2}$$

where C is the Australian catch (in number) from the subpopulation during the period τ. The coefficient of variation for N is approximately equal to $1/\sqrt{R}$ (Seber 1973).

Assumptions

The assumptions associated with the method are (Seber 1973; Ricker 1975): (i) the tagged fish are randomly mixed into the subpopulation during the period τ (i.e. uniformly distributed through the subpopulation); (ii) the subpopulation is not joined by any new fish during the period τ* (however, the fish belonging to the subpopulation can leave the subpopulation during the period τ); (iii) tag shedding does not take place or is accounted for in the procedure; (iv) tagged fish are not subject to death caused by tagging; (v) all the tags recovered are reported to the tagging authority; and (vi) both fishing and natural mortalities (and emigration rates if fish are subject to emigration) are the same for tagged and untagged fish.

The southern bluefin tuna subpopulation fished by the Australian fishermen consists of surface schools. The knowledge of the rate of fish exchange among the schools is poor and, therefore, it is difficult to predict what is the effect of schooling upon mixing of untagged and tagged fish. If this exchange is small, schooling can interfere with mixing, especially if fish from only a few schools were tagged. Therefore, the validity of assumption (i) should be examined in detail.

Since the subpopulation harvested by the Australian fishermen occupies a relatively large area around the southern and eastern coast of Australia (Majkowski *et al.* 1981), the period τ has to be chosen with a delay sufficient to allow mixing of the tagged and untagged fish. However, this delay cannot be too long since the rate of recaptures of tagged fish by the Australian fishermen decreases as the delay increases. Hence, the calendar year following the year of tagging is chosen as the period τ. (Choice of a longer period was impossible due to a much smaller number of recaptures). The degree of compliance with assumption (i) (mixing) under these circumstances is discussed later.

The validity of assumption (ii) is very difficult to verify with the existing data (especially because of the lack of an effective log book system for the Australian fishery) and the method of their analysis. The latter is determined by the available data collected during the

* This assumption is not essential if only the rate of exploitation is being estimated (Ricker 1975).

tagging program which was not designed particularly for the purpose of this analysis. However, it is frequently claimed that fish inhabit areas close to the coasts when they are small and move gradually offshore when older rather than a reverse situation. This is also thought to be true of the southern bluefin tuna migration pattern around the Australian coast. Since the tagged fish were young (up to four years old) relative to their life-span (about twenty years), it seems that assumption (ii) is satisfied to a high degree.

Tag shedding will be accounted for in the procedure. The analysis performed by Hearn and Murphy (unpublished) suggests that the tagged fish recover from the effects of tagging within a few weeks. This allows us to presume that these effects are not drastic and consequently, that the tagging mortality, if present, is very small. The direct observations of fish behaviour during tagging confirm this (K. Williams, pers. comm.). The tagging program organisers are confident that all (or at least, the majority of) tags recovered by the Australian fishermen are reported (K. Williams, pers. comm.). Since the tagged fish recover from the effects of tagging within a few weeks of tagging, it seems that the tagged and untagged fish are subject to similar fishing and natural mortalities.

Determination of T

The age of a fish at tagging is determined on the basis of its length and the age-length relationship (Murphy and Sutherland submitted)

$$t = t_0 - \frac{1}{K} \ln(1 - \frac{L}{L_\infty}) \qquad (3)$$

where t is the age (years), L is the length (cm), and t_0(t_0 = -0.41 ± 0.08 (standard error) years), K(K = 0.122 ± 0.004 year^{-1}) and L_∞ (L_∞ = 211.6 ± 3.0cm) are constants. (An effective method of direct age determination such as scale or otolith reading has not been developed for this species.) The date of birth of the tagged fish is calculated by subtracting the age at tagging from the date of tagging. Since the spawning period of this species is between September-October and March (Serventy 1956; Shingu 1978), inclusion in the appropriate cohort is determined by finding the calendar year associated with the smallest time interval between the calculated date of birth and the first of January. It is assumed then, for further considerations, that the fish was born on the 1st January of this calculated calendar year (the same assumption is applied by Murphy and Sutherland (submitted) during fish age determination).

Each cohort is separately considered. The number of tagged fish alive at the beginning of period τ is estimated in three ways:

(a) as the number of tagged fish released reduced by the number of tagged fish recaptured during the calendar year of tagging,

(b) under the assumption that each tagged fish is subject to the yearly rate of total mortality and emigration, Z, of 0.7 (Murphy and Sutherland submitted) which is uniformly distributed throughout the calendar year, and

(c) under the assumption that the rate of total mortality and emigration cumulated over the period between the date of release and the beginning of period τ is equal to 0.7 (i.e. the number of tagged fish within the subpopulation at the beginning of period τ is equal to the number of released fish (tagged) · decreased by the factor of $e^{-0.7}$). The yearly rate of total mortality and emigration of 0.7 was estimated as an average rate over the period following the tagging and for the subpopulation harvested by the Australian fishery (Murphy and Sutherland submitted); this estimate was made using a semi-graphical method (Gulland 1969). The real number of tagged fish at the beginning of period τ should be between those estimated under assumptions (a) and (c), and is likely to be close to that evaluated under assumption (b).

Determination of R

Double tagging, in addition to increasing the number of returns, allows us to estimate the rate of tag shedding. A new method (Kirkwood 1981), which allows the rate of tag shedding to decrease with time (instead of the generally utilized and unrealistic assumption of being time-independent), is used to account for tag shedding. The number of tagged fish which would be recaptured if the tags are not shed is estimated on the basis of the number of fish recaptured in reality and the expected fraction of fish unrecaptured due to tag shedding during the period $\bar{t}$, between the tagging operation and the recapture. This expected fraction, $E(p_{\bar{t}})$, for single tagged fish is determined according to the statistical model developed for southern bluefin tuna by Kirkwood (1981):

$$E(p_{\bar{t}}) = \Theta\left[1 - \left(\frac{b}{b+\lambda\bar{t}}\right)^{b}\right] \quad (4)$$

where $1 - \Theta$ is the fraction of tagged fish with tags permanently affixed, $\Theta(= 0.61 \pm 0.11$ (standard error)), $b(= 2.92 \pm 6.3)$ and $\lambda(= 0.97 \pm 0.19)$ are the parameters of a gamma distribution describing the tag shedding process. This fraction for double tagged fish is equal to the square of $E(p_{\bar{t}})$. Due to different dates of tagging within the calendar year as well as dates of recaptures, each recaptured fish is considered separately to account properly for tag shedding.

Determination of C

The catch, C, which appears in equations (1) and (2), is estimated in the following way. Fish landings (in number of fish) are sorted in 1 cm length classes on the basis of length-frequency samples (for details see Hampton in press; Williams in press) and ages associated with these length-classes are determined on the basis of formula (3). A length-class is allocated to the appropriate cohort by finding the calendar year associated with the smallest time interval between the calculated date of birth for the size class (i.e. the date of landing reduced by the estimated age) and 1st January. It is assumed then for further consideration that the fish belonging to the length-class were born on 1st January of that calendar year.

Those age-groups for which the number of fish recaptured with tags during the period τ was smaller than 10 were excluded from the analysis since the coefficients of variation for N associated with these age-groups were very large. Also, the evaluation of u and N was not carried out for the calendar years for which length-frequency samples of the Australian catch were lacking, since it was impossible to estimate C for these years.

RESULTS

The results of the analysis are presented in Tables 1-3. Since the estimates derived under assumption (b) are most likely to be closest to the real values, only they will be discussed in full detail. The calculated (under assumption (b)) rates of exploitation (only the Australian fishery taken into account) of the subpopulation fluctuate from cohort to cohort between 0.024 and 0.076 (standard deviation: 0.022, mean: 0.056 ± 0.01 (standard error)), 0.019 and 0.074 (standard deviation: 0.018, mean: 0.037 ± 0.006), and 0.031 and 0.060 (standard deviation: 0.015, mean: 0.048 ± 0.009) for fish at age 2-3, 3-4, and 4-5 years, respectively. The calculated (under assumption (b)) number of fish at age 2, 3, and 4 years (on 1st January) fluctuates between (in millions) 3.56 and 8.93 (standard deviation: 2.23, mean: 6.14 ± 0.10), 3.47 and 16.70 (standard deviation: 4.36, mean: 7.33 ± 1.54),and 2.12 and 8.63 (standard deviation: 3.43, mean: 4.74 ± 1.98), respectively. If a single cohort is analysed (cohort 1962 - compare N at age 2 and 3 years; cohort 1966 - compare N at age 2 and 3 years; cohort 1961 - compare N at age 3 and 4 years and cohort 1963 - compare N at age 3 and 4 years), it can be noticed that the number of fish for certain cohorts increases when the fish age increases. In both cases when an increase in the abundance of older fish occurs (cohorts 1961 and 1963), the abundance estimates of these age-groups are much higher than the calculated average one and presumably too high.

If assumption (i), associated with the estimation method is satisfied, the ratio of the number of recaptured fish with attached tags to the corresponding catch (in number) should be the same for each area of fishing ground (these areas and associated fishing periods should be chosen to be relatively large and long, respectively, to avoid random fluctuations). Due to lack of an effective log book system for the Australian fishery, the locations of various catches cannot be determined accurately (only the areas off the coasts of WA, SA, and NSW associated with the catches can be identified). The analysis of the number of recaptured fish with attached tags off the coasts of WA, SA, and NSW in respect to the catches in these areas (see Tables 1-3) provides evidence that the mixing of tagged fish with untagged ones, at least in certain cases, is not sufficient (this can be clearly observed for fish in cohorts: 1974 and 1977 in Table 1 and 1962-5 and 1971 in Table 2).

Sensitivity of the results to changes in assumption (b) were investigated by replacing it with its extreme equivalents, namely, assumptions (a) and (c). It can be concluded that the results are sensitive to these changes. For example, the number of fish at age 2 years calculated under assumption (a) and (c) fluctuates between 4.77 and 11.52, and 2.35 and 5.73 (in millions), respectively.

DISCUSSION

The estimates derived in this paper can be compared with those calculated for the global population of southern bluefin tuna (Murphy and Sutherland submitted). The number of fish at age 2, 3, and 4 years estimated under assumption (b) is different from those evaluated by cohort analysis by -30% to +40%, -83% to +74%, and -46% to +60%, respectively.

According to the comments made in the Introduction it is expected that the estimates of abundance obtained on the basis of tagging data should be, in all cases, smaller than those from cohort analysis. This is not observed and can be caused by various factors. One of them, which is evident, is limited mixing of the tagged and untagged fish.

The effect of limited mixing on the estimates makes prediction difficult. It can lead either to the under - or over-estimation of the subpopulation depending on geographical distribution of the tagged fish within the subpopulation and its relationship to the locations and associated magnitudes of catches. If the distribution of fishing effort within the subpopulation is proportional to the number of fish in different parts of the fishing grounds (which is presumably not the case, although it is difficult to prove this due to unknown locations of catches), limited mixing would have a very weak effect on the degree of estimation accuracy (Ricker 1975).

As discussed, other assumptions associated with this analysis seem to be satisfied; nevertheless, their potential effects upon the estimates will be discussed. If the subpopulation is joined by new fish during the period τ, the abundance is over-estimated (Ricker 1975). Over- or under-estimation of tag shedding will cause under- or over-estimation of the subpopulation, respectively. If tagged fish are subject to death caused by tagging or not all recovered tags are reported to the tagging authorities, the abundance is over-estimated. Higher natural mortality of tagged fish than that of untagged fish would also cause over-estimation of the subpopulation. It is unlikely that the natural mortality of tagged fish is lower than that of untagged ones. Higher or lower fishing mortalities of tagged fish in comparison to that of untagged fish would cause under- or over-estimation of the subpopulation, respectively.

The results obtained from cohort analysis are also likely to be in error, because many of the input parameters required for that analysis are uncertain to some degree. These are (i) the instantaneous rate of natural mortality assumed to be independent of fish age and calendar year, (ii) the so-called terminal rate of fishing mortality assumed to be independent of the cohort under consideration, and (iii) the catch-matrix evaluated in a way similar to that used for estimation of C assuming that the changes in the fish growth rate from year to year, caused by environmental factors, are negligible. Verification of these assumptions and the values associated with them is necessary before the question raised in the Introduction can be answered with a high degree of confidence.

The performed examination of mixing indicates that only for cohorts 1962 in Table 1 and 1966 in Table 2 is the degree of mixing likely to be very high. (In the light of poor mixing for other cases, one may suspect that the results of the performed mixing test are incidental and further tests concerning smaller areas should be implemented for the last two cases. As discussed earlier, this is not possible at present.) When only these cases are considered, the estimates from the tagging data are smaller (by 6% and 12%, respectively) from those obtained on the basis of cohort analysis. However, it cannot be concluded on this basis that the fraction of fish which does not enter the Australian fishing grounds is much smaller than that passing Australia for the various reasons *mentioned earlier*. Namely, (i) the abundance estimates derived on the basis of tagging data are very sensitive to one highly uncertain input parameter (Z) used, (ii) the estimates are based on very small numbers of tagged fish, (iii) full test of mixing could not be executed due to the lack of the data from the log book system and the results of the preliminary test could be incidental, and (iv) uncertainties in the results of cohort analysis are not fully evaluated.

The present analysis suggests that the tagging program should be redesigned in a way that would suit a new method of analysis avoiding the difficulties encountered in the present analysis, namely, insufficient mixing of the tagged and untagged fish on a large geographical scale and the uncertainty around assumption (b). Mixing of the tagged fish with the untagged population seems to be an assumption which can be questionable in many other analyses. This basic condition associated with any quantitative analysis of tagging data is rarely checked, although examination of its validity is simple when the locations of various catches are known.

RECOMMENDED FEATURES OF REDESIGNED TAGGING PROGRAM

The difficulties encountered in this analysis could be overcome if fish belonging to the same age-group were tagged each calendar year (let us assume for the period of 3 years) in all three areas, i.e. off the coasts of WA, SA, and NSW. If the fish were tagged at the beginning of the fishing season in each area (e.g., in the first month of fishing activities), the abundance in each area could be estimated on the basis of the Peterson method using the number of recovered tags during the fraction of the fishing season for which mixing within the area is achieved. This fraction could be determined if the locations associated with various catches were known (this knowledge could be derived on the basis of a log book system for the Australian fishery if such an effective system was introduced). The degree of mixing could be increased if fish from many schools distributed over the entire area were tagged. Gaining a better knowledge of the rate of fish exchange among schools would be helpful in designing the tagging program.

The natural and fishing mortalities for the subpopulation exploited by the Australian fishery are low, particularly in comparison with the rate of fish emigration from the areas exploited by the Australians (Majkowski *et al.* 1981; Murphy and Sutherland submitted). It can be presumed that this emigration takes place at the ends of the fishing seasons in the three areas under consideration (K. Williams pers. comm.). If this is not the case and the period required for good mixing within each area is long, the unknown emigration and mortality could cause an uncertainty in the estimates (these two factors affect the number of tagged fish present within each area at the beginning of the period for which good mixing was achieved). Determination of the degree of emigration during the fishing season seems to be extremely difficult. If this emigration took place continuously throughout the fishing season, it could be assumed on the basis of results derived by Murphy and Sutherland (submitted) that the fish fraction of about $e^{0.06}$ would emigrate per month from each area. The influence of this rate of emigration upon the estimates can be judged when the period required for good mixing within each area is known.

Other assumptions associated with the method for estimating the abundance on the basis of the proposed tagging program seem to be satisfied for the same reasons as those presented in the Method of Analysis. Assumption (ii) could be checked within the new tagging program by comparing the ratio of the number of recovered tags to the catch for different (for example, one month) periods within the chosen period τ. If the sub-population is not joined by new fish during the period τ, this ratio should be constant.

Since the fishing seasons off the coasts of WA, SA, and NSW are at different periods (Majkowski *et al.* 1981) and there is exchange of fish among these areas (Murphy 1977; Shingu 1978), this exchange should be accounted for when the estimate of the entire subpopulation exploited by the Australian fishery is made. The degree of fish exchange among the areas could be assessed on the basis of the number of fish recovered in an area different to that of release.

Such an approach would eliminate the necessity of good mixing of tagged fish in the entire area of the Australian fishery. Also, the uncertainty around assumption (b) would be significantly reduced since the time interval between the tagging operation and a redefined period τ would be generally much smaller than that in the present analysis. The second factor which would possibly decrease this uncertainty was mentioned early in the paper. The results of the tagging program designed in such a way should be analysed during the initial 1-3 years of tagging and then, the program should be reviewed from the viewpoint of its suitability for achieving the objective of the studies.

Finally, it is desirable that the tagging program should be restarted in order to update the information on the rates of total, natural, and fishing mortalities for the subpopulation exploited by the Australian fishery and for the older age groups of southern bluefin tuna (8-16 years) fished mainly by the Japanese longliners. This information is required for management purposes of the southern bluefin tuna population. The tagging program designed in such a way as proposed in this paper would also suit the other purposes mentioned above.

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Table 1. Results (rounded) of tagging data analysis for fish released at age 1 to 2 years.

Notation: T_o - the number of fish released with attached tags (the ratio given in the brackets provides the fractions of fish released off the coasts of NSW, SA, and WA, respectively),

R - the number (after accounting for tag shedding) of fish with attached tags recaptured by Australian fishermen in the calendar year following the calendar year during which the fish were tagged (the ratio given in the brackets provides the fractions of fish recovered off the coasts of NSW, SA, and WA, respectively),

C - the Australian catch (in thousands of fish) from the cohort under consideration derived in the calendar year following the year of tagging (the ratio given in the brackets provides the fractions of fish caught off the coasts of NSW, SA, and WA, respectively),

u - the calculated yearly exploitation rate of the cohort under consideration (only for the subpopulation exploited by the Australian fishery) during the calendar year following the calendar year of tagging (the successive estimates were derived under assumptions (a), (b), and (c), respectively),

N - the calculated number (in millions) of fish (only the subpopulation exploited by the Australian fishery) from the cohort under consideration at the beginning of the calendar year following the calendar year of tagging (the successive estimates were derived under assumptions (a), (b), and (c), respectively; the number in the brackets provides with the coefficient of variation for N),

N_c - the abundance corresponding to that denoted by N for the global population estimated on the basis of cohort analysis. (Murphy and Sutherland submitted)

Cohort	1962	1965	1966	1974	1977
T_o	353(0.71 : 0.28 : 0.01)	325(0.72 : 0.00 : 0.28)	858(1.00 : 0.00 : 0.00)	586(1.00 : 0.00 : 0.00)	1058(0.92 : 0.00 : 0.8)
R	12(0.00 : 0.00 : 1.00)	18(0.07 : 0.00 : 0.93)	36(0.00 : 0.09 : 0.91)	28(0.91 : 0.00 : 0.09)	21(0.39 : 0.19 : 0.48)
C	229.7(0.00 : 0.00 : 1.00)	265.1(0.00 : 0.03 : 0.97)	790.5(0.00 : 0.01 : 0.99)	389.2(0.04 : 0.91 : 0.05)	220.5(0.00 : 0.99 : 0.01)
u	0.034 ; 0.045 ; 0.069	0.055 ; 0.074 ; 0.113	0.042 ; 0.061 ; 0.084	0.048 ; 0.076 ; 0.097	0.019 ; 0.024 ; 0.40
N	6.71 ; 5.16(0.29) ; 3.32	4.77 ; 3.56(0.24) ; 2.35	11.52 ; 7.97(0.17); 5.73	8.05 ; 5.09(0.19) ; 4.03	11.21 ; 8.93(0.22) ; 5.57
N_c	5.45	4.64	4.74	5.68	*

* Not provided by Murphy and Sutherland (submitted)

Table 2. Results (rounded) of tagging data analysis for fish released at age 2 to 3 years (for notation see Table 1)

Cohort	1961	1962	1963	1964
T_o	5874(0.87 : 0.01 : 0.12)	5103(0.82 : 0.01 : 0.17)	1659(0.98 : 0.00 : 0.02)	810(0.50 : 0.00 : 0.50)
R	103(0.00 : 0.72 : 0.28)	169(0.00 : 0.10 : 0.90)	46(0.00 : 0.35 : 0.65)	16(0.00 : 0.34 : 0.66)
C	221.1(0.00 : 0.82 : 0.18)	166.1(0.00 : 0.40 : 0.60)	217.2(0.00 : 0.66 : 0.32)	123.2(0.00 : 0.75 : 0.25)
u	0.018 ; 0.025 ; 0.032	0.034 ; 0.047 ; 0.067	0.028 ; 0.040 ; 0.057	0.020 ; 0.024 ; 0.039
N	12.29 ; 8.72(0.10) ; 6.19	4.88 ; 3.55(0.08); 2.46	7.73 ; 5.32(0.15) ; 3.83	6.21 ; 5.03(0.25) ; 3.14
N_c	4.65	4.46	3.79	3.65
Cohort	**1965**	**1966**	**1971**	**1973**
T_o	4173(0.99 : 0.01 : 0.00)	371(0.00 : 1.00 : 0.00)	621(1.00 : 0.00 : 0.00)	259(1.00 : 0.00 : 0.00)
R	88(0.00 : 0.81 : 0.19)	17(0.00 : 0.71 : 0.29)	10(0.00 : 1.00 : 0.00)	13(0.18 : 0.82 : 0.00)
C	292.1(0.00 : 0.61 : 0.39)	258.4(0.00 : 0.70 : 0.30)	216.8(0.01 : 0.82 : 0.17)	264.5(0.02 : 0.96 : 0.02)
u	0.021 ; 0.031 ; 0.043	0.056 ; 0.074 ; 0.094	0.012 ; 0.019 ; 0.022	0.018 ; 0.033 ; 0.034
N	13.61 ; 9.35(0.10) ; 6.81	4.63 ; 3.47(0.24) ; 2.75	26.50 ; 16.70(0.32) ; 14.47	12.19 ; 6.52(0.28) ; 6.36
N_c	3.79	3.89	4.27	11.91*

* This estimate is regarded by Murphy and Sutherland (submitted) as unreliable.

Table 3. Results (rounded) of tagging data analysis for fish released at age 3 to 4 years (for notations see Table 1)

Cohort	1961	1962	1963
T_o	2195(0.00 : 0.98 : 0.02)	576(0.00 : 0.59 : 0.41)	497(0.00 : 0.62 : 0.38)
R	70(0.00 : 0.96 : 0.04)	12(0.00 : 0.81 : 0.19)	20(0.00 : 1.00 : 0.00)
C	189.2(0.00 : 0.86 : 0.14)	266.7(0.00 : 0.91 : 0.09)	133.1(0.00 : 0.92 : 0.08)
u	0.032 ; 0.054 ; 0.064	0.022 ; 0.031 ; 0.043	0.042 ; 0.060 ; 0.083
N	5.88 ; 3.48(0.12) ; 2.91	11.95 ; 8.63(0.29) ; 6.14	3.17 ; 2.12(0.22) ; 1.59
N_c	3.74	3.45	3.09

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