ASSESSMENT OF SKIPJACK (*Katsuwonus pelamis*) RESOURCES IN THE CENTRAL AND WESTERN PACIFIC BY ESTIMATING STANDING STOCK AND COMPONENTS OF POPULATION TURNOVER FROM TAGGING DATA

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PREFACE

The Skipjack Survey and Assessment Programme was an externally funded part of the work programme of the South Pacific Commission. Governments which provided funding for the Programme were Australia, France, Japan, New Zealand, United Kingdom and the United States of America.

The Skipjack Programme has been succeeded by the Tuna and Billfish Programme which is receiving funding from Australia, France, New Zealand and the United States of America. The Tuna Programme is designed to improve understanding of the status of the stocks of commercially important tuna and billfish species in the region. Publication of final results from the Skipjack Programme is continuing under the Tuna Programme.

The staff of the Programme at the time of preparation of this report comprised the Programme Co-ordinator, R.E. Kearney; Research Scientists, A.W. Argue, C.P. Ellway, R. Farman, R.D. Gillett, P. Kleiber, J. Sibert, W.A. Smith and M.J. Williams; Research Assistants, Susan Van Lopik and Veronica van Kouwen; and Programme Secretary, Carol Moulin.

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Tuna Programme
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ABSTRACT

Surface fisheries for skipjack in the central and western Pacific have intensified in recent years. The South Pacific Commission's Skipjack Survey and Assessment Programme released more than 140,000 tagged skipjack between October 1977 and August 1980 over a large portion of the central and western Pacific to assess the dynamics of the skipjack resource exploited by these fisheries. Tag returns now exceed 6,000. Tag release and return data and catch and effort statistics, for countries and territories in the Skipjack Programme study area, were used to assess the status of both the total resource and the resource within individual countries and territories. A tag attrition model was developed. Non-return of tags and loss of tags due to tag shedding and to mortality caused by tagging were accounted for in the model. Alternative forms of the model based on either catch or effort statistics were used to provide estimates and confidence intervals for standing stock, attrition (including losses due to natural mortality, fishing mortality and emigration), fishing mortality, catchability, throughput (standing stock multiplied by attrition) and harvest ratio (fishing mortality divided by attrition) for the study area as a whole and for individual countries and territories.

The estimate of total standing stock was three million tonnes, with 95 per cent confidence limits of 2.5 to 3.7 million tonnes. The overall attrition rate was 0.17 per month [0.15 - 0.20], which under the assumption of steady state conditions would represent the rate of renewal of the skipjack resource. Total annual throughput was estimated to be 6.2 million tonnes [5.5 to 7.1 million tonnes]. The overall harvest ratio was 0.04. Harvest ratios for the six countries and territories for which detailed catch and effort statistics were available ranged from 0.02 to 0.46; only one exceeded 0.17. Low harvest ratios over a large portion of the central and western Pacific study area during the period tags were at large imply a potential for greatly increased skipjack catches in many areas and for the region as a whole.

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1.0 INTRODUCTION

Annual skipjack (*Katsuwonus pelamis*) catches from the area of the South Pacific Commission increased rapidly from less than 5,000 tonnes in the early 1960s to approximately 220,000 tonnes in the period of this tagging experiment. With increased catches came concern by many countries in the region that interactions among surface fisheries might be sizeable, and that increased yields might not be sustainable. The Skipjack Survey and Assessment Programme was undertaken by the Commission to assess the status of the skipjack resource and its ability to support this increased fishing pressure. Tagging was adopted as the principal stock assessment technique (Anon 1975). Between October 1977 and August 1980 the Skipjack Programme tagged and released approximately 140,000 skipjack (Figure 1) throughout and beyond the area of the South Pacific Commission (Figure A, inside front cover). To April 1983 over 6,000 of these tagged fish have been recaptured and reported to the Commission; the tag return rate is now less than one per month.

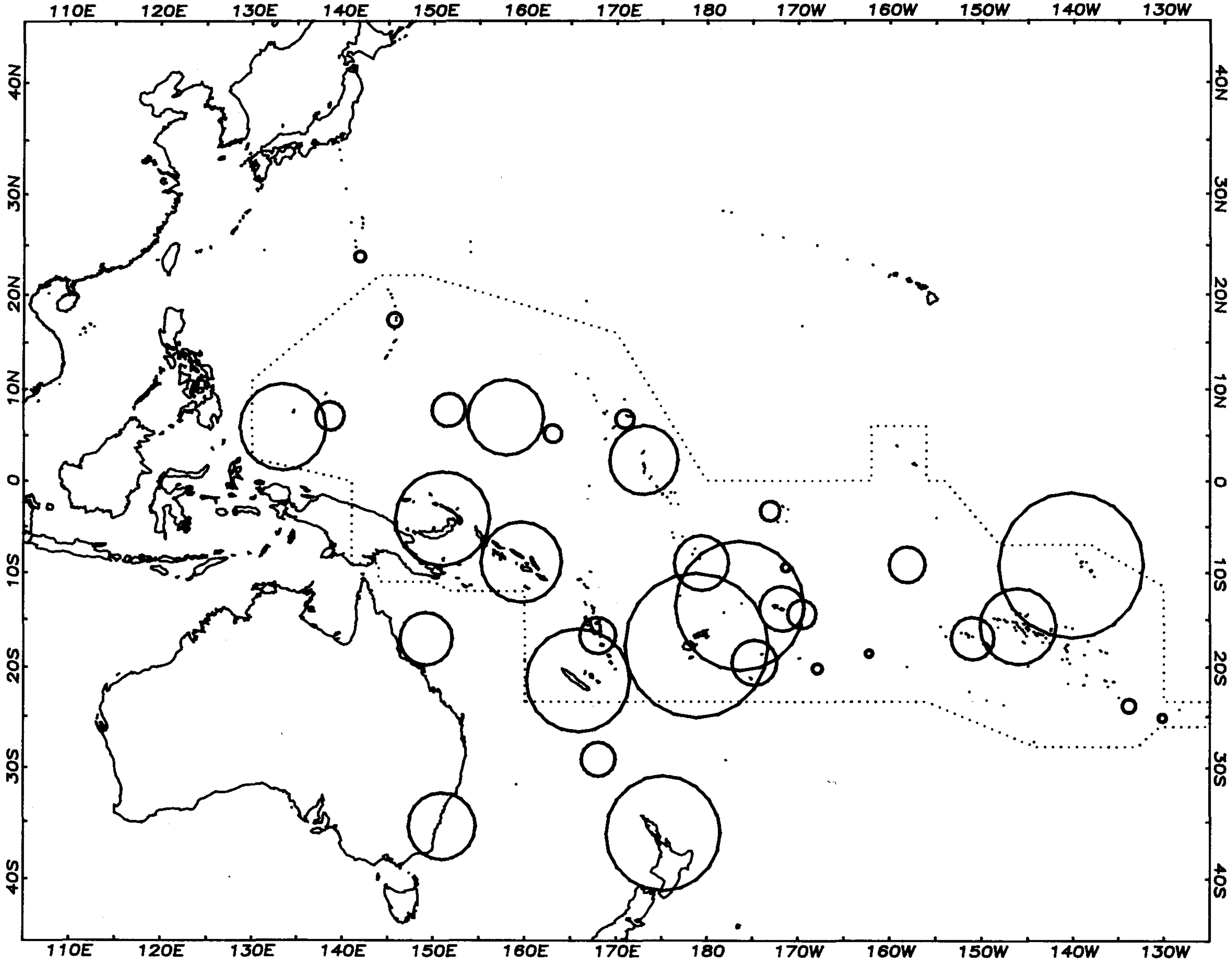
This paper presents an analysis of tag release and recovery data for the purposes of assessing the standing stock of skipjack, rate of renewal (turnover rate) of the skipjack resource and current levels of fishing pressure on the skipjack resource in the region as a whole, and in the waters of individual countries and territories for which detailed catch and effort data were available. This represents the first such application of tagging data for quantitative assessment of the skipjack resource in the central and western Pacific. Joseph and Calkins (1969) have used tagging data and fishing effort in two analytical models to investigate the rate of renewal and impact of fishing for northern and southern components of the eastern Pacific skipjack resource. In our paper an analytical model is developed which, using tagging data and catch and effort statistics, gives estimates and confidence limits for the following parameters used in defining the status of a population that is supporting a fishery:

1) Standing stock - the quantity of skipjack which are in a size range vulnerable to the fishing gear and are within the neighbourhood in which the fishery operates (or close enough to that neighbourhood that there is a reasonable chance that they will enter the neighbourhood in their lifetime).

2) Attrition - the proportional rate at which the standing stock diminishes with time due to natural mortality, fishing mortality, emigration and other factors. If the standing stock is at steady state, then the attrition rate is an estimate of the turnover or rate of renewal of the stock.

3) Fishing mortality - the proportional rate at which the standing stock is harvested per unit time.

FIGURE 1. DISTRIBUTION OF TAG RELEASES (circles) AND BOUNDARIES OF THE SOUTH PACIFIC COMMISSION REGION (dotted line). The circles are centred on each country, territory and subdivision thereof in which tags were released. The areas of the circles are proportional to the number of tagged skipjack released in each country and territory.



4) Throughput - the product of attrition and standing stock; a measure of the flux of biomass through the stock. It is the sum of death, emigration and growth out of the vulnerable size class. Under steady state conditions, it is also the sum of in situ productivity and immigration of vulnerable sized individuals. The throughput is perhaps a better measure of the resource than the standing stock because it has the same units as the catch rate (biomass per unit time), and it can therefore be more directly compared to the catch rate.

5) Harvest ratio - defined as the ratio of catch rate to throughput (equivalent to the ratio of fishing mortality to attrition). If fishing mortality is small relative to the population turnover, i.e. the harvest ratio is low, it is likely that fishing is having little impact on the population and total yield could be increased by increasing fishing pressure. The level to which total yield could be increased on a sustained basis would depend on the population size and the relationship between population size and recruitment.

2.0 TAGGING AND TAG RECOVERY METHODS

Tagging was carried out over a period of three years in three ten-month cruises each using one chartered Japanese pole-and-line vessel. Over the three years, all countries and territories of the South Pacific Commission were visited at least once. The itinerary of the tagging vessel was influenced by a desire to cover the whole study area, which includes the area of the South Pacific Commission and some adjacent waters where skipjack were known to be abundant (Kearney 1982). The number of tags released in each area was not uniform as the tagging success depended on the fishing conditions, which were quite variable in space and time. Figure 1 shows the geographic distribution of skipjack tag releases.

Skipjack were captured by pole-and-line fishing. The fish were poled onto tagging cradles where they were measured and tagged with a plastic dart tag according to the technique described by Kearney and Gillett (1982). Fishermen on local and foreign-based fleets and workers at processing facilities were the primary sources of returned tags. Locally based fisheries within the study area were the pole-and-line operations in Papua New Guinea, Solomon Islands, Fiji and Palau, the alia fishery in Western Samoa, the bonitier fishery in the Society Islands of French Polynesia and the purse-seine fishery in New Zealand. Information on local fisheries is contained in the final reports to the individual countries by the Skipjack Programme (e.g. Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983). Foreign fleets taking significant quantities of skipjack at the time most tags were at large were the long-range, Japanese pole-and-line fleet, and steadily increasing Japanese and United States purse-seine fleets.

Rewards were given and lotteries conducted in order to encourage return of tags (Kearney 1982b). It was possible to check efficiency of part of the tag return system with a tag-plant experiment in which 131 fish from the holds of purse-seiners were tagged and replaced in the holds by New Zealand Ministry of Agriculture and Fisheries personnel during the 1980/1981 New Zealand fishing season.

In order to investigate tag shedding and mortality due to tagging, a double tagging experiment was carried out in the waters of Fiji in 1980, during which 5,399 double tagged skipjack were released, interspersed with 5,626 single tagged fish (Skipjack Programme 1981).

Data processing procedures used for recording, verifying and accessing the tagging results are described by Kleiber and Maynard (1982).

3.0 ANALYTICAL METHODS

The assessment of the population parameters of concern was carried out by analysing tag attrition curves which are plots of the tag return rate (number of tags returned per unit time) against time at large. The number of tags returned per unit time is expected to decrease with time since the tag density in the fished population should decline due to a variety of factors (e.g. mortality, emigration, tag shedding). The analyses described in this report were performed by use of a model in which tag return rates are predicted as a function of time from release and in which variations in fishing pressure are taken into account. The model has two basic forms, one requiring input of catch data and one requiring input of effort data.

3.1 Derivation of the Analytical Model

Immediately following tagging, loss of tagged fish is expected before any tagged fish have a chance of being recaptured. This loss would result from short-term mortality due to the trauma of having been handled and tagged, and from immediate tag shedding. Immediate mortality and shedding have been defined as type 1 losses by Bayliff and Mobrand (1972). These losses reduce the effective number of tagged fish at large at time zero. Thus if N_o fish are tagged and if α is the proportion of tagged fish which survive the type 1 losses (i.e. 1 minus the product of type 1 mortality and type 1 tag shedding), then the effective number of tagged fish at the start is αN_o.

Following type 1 losses, a number of other factors reduce the population of tagged fish. Factors that affect all fish, with or without tags, include natural mortality, emigration, fishing mortality, and growth out of vulnerability to the fishery. In addition, the population of tagged fish can undergo what is called type 2 or long-term loss by tag shedding and extra mortality due to carrying a tag. All post-type 1 attrition factors are assumed to operate such that the tagged population decreases exponentially. Therefore if A is the instantaneous total attrition rate (units of inverse time) embodying all attrition factors, then the number of tagged fish at large as a function of time will be

$$N = \alpha N_o e^{-At} \qquad (1)$$

where t is the time from release. If F is the instantaneous fishing mortality (units of inverse time), then the number of tag recaptures per unit time will be FN.

Defining r to be the cumulative number of useable tag returns, the rate at which useable tags are returned is given by

$$\frac{dr}{dt} = \beta F N = \alpha\beta N_o F\, e^{-At} \tag{2}$$

where β is the proportion of recaptured tags which are actually returned with useable recapture information. (Not all tag returns could be used in the analysis since some had unknown or imprecisely known times of recapture.) It is assumed that β and A are approximately constant in time, and F is allowed to vary with time.[1]

Integrating Equation 2 to get the accumulated tag returns in the i-th time unit following tagging gives

$$r_i = \alpha\beta N_o F_i \int_{i-1}^{i} e^{-At} dt = \frac{\alpha\beta N_o F_i}{A} e^{-iA}\left(e^{A}-1\right) \tag{3}$$

where F_i is an average fishing mortality during time unit i. The above result can also be derived by applying the standard catch equation (Baranov 1918) to the successive time units. F_i can be approximated by

$$F_i \cong \frac{C_i}{P} \cong Q E_i \tag{4}$$

where C_i = catch in biomass units in time unit i

P = standing stock in biomass units (assumed constant in time)

Q = catchability coefficient, or fraction of the standing stock harvested by one unit of fishing effort, and measured in inverse units of fishing effort (assumed constant in time)

E_i = units of fishing effort in time unit i.

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1 An internal inconsistency arises here since the varying F is a component of what is assumed to be a constant A. However, for the case where catch data are used, the model is more tractable if A is held constant (see Section 3.4). The inconsistency is minimal if F is small relative to A (see Section 3.6).

The model can have two forms depending on which term in Equation 4 is substituted for F_i in Equation 3:

$$r_i = \frac{\alpha\beta N_o C_i}{P A_c} e^{-iA_c}\left(e^{A_c}-1\right) \tag{5}$$

$$r_i = \frac{\alpha\beta N_o Q E_i}{A_e} e^{-iA_e}\left(e^{A_e}-1\right) \tag{6}$$

where the attrition parameter has a subscript, c , in the catch based form and a subscript, e , in the effort based form. Note that these are in reality two-parameter models since $\alpha\beta N_o$ cannot be separated from P and Q. To estimate P or Q by fitting the model to the tag return data, a value for the quantity $\alpha\beta N_o$ must be used. In general, N_o is precisely known, but the values of α and β must be estimated.

Except for P, the standing stock, the parameters in Equations 5 and 6 do not correspond directly to the parameters of interest that are listed in the introduction. The total attrition rate, A, contains a component due to type 2 tag shedding and tag mortality. Defining this component to be ψ (units of inverse time), we have

$$Z_c = A_c - \psi \quad ; \quad Z_e = A_e - \psi \tag{7}$$

where Z_c and Z_e are the catch based and effort based attrition rates respectively for a cohort of untagged fish. The throughput (biomass per unit time) is then given by

$$T = Z_c P \tag{8}$$

The fishing mortality is not treated as a constant in the model, but a measure of the average fishing mortality can be obtained. If we have an average catch rate, $\overline{C}$, or an average effort rate, $\overline{E}$, then the average fishing mortality is given by

$$F_c = \frac{\overline{C}}{P} \quad ; \quad F_e = Q\overline{E} \tag{9}$$

The harvest ratio (unitless) is then given by

$$H_c = \frac{F_c}{Z_c} = \frac{\overline{C}}{T} \quad ; \quad H_e = \frac{F_e}{Z_e} \tag{10}$$

Estimates for the parameters defined by Equations 7 through 10 can be calculated using Equations 7 through 10, parameter estimates from the forms of the model in Equations 5 and 6, and values for $\overline{C}$, $\overline{E}$, and ψ. In practice, it was more convenient when dealing with some of the parameters, particularly when obtaining confidence limits (see Section 3.3), to use Equations 7 through 10 to derive new forms of the model containing the desired parameters and to get estimates directly by fitting the reparameterised forms. The form of the model or the equation used to estimate each parameter value is detailed in Table 1 along with a list of the necessary input data.

3.2 Fitting the Model

Parameters were estimated by fitting the forms of the model given in Table 1 to the tag return results, with input of catch or effort data and input of estimates of $\alpha\beta N_0$ and ψ. Since all forms of the model are non-linear, an iterative regression procedure was used to fit each model by finding the pair of parameter values which gave the best match of the tag return values predicted by the model and the observed tag return values. The best match is obtained when the parameters in the model are adjusted so that the sum of squares of differences between observed and predicted values is minimised. The specific fitting procedure was adapted from the generalised Marquardt algorithm (Conway, Glass and Wilcox 1970). The procedure was modified so that more than one set of tag release and recovery data could be used in a single analysis, in order to get a single set of parameter values best explaining the results from all data sets. This was done because in some cases tags were released over two consecutive time periods (months or 10-day periods). Without this feature, it would have been necessary to treat these results separately or to assume a common time of release.

A square root transformation of both observed and predicted tag return values was used. The square roots of the predicted values were matched to the square roots of the observed values, so that the minimum sum of squares was the sum of squares of differences between the square roots of the observed and predicted values. On the one hand, if the fitting is done without transformation, the difference between one and two tag returns in a given time period would have the same weight in the analysis as the difference between 100 and 101 returns, even though the proportional differences are very different in the two cases. On the other hand, if a logarithmic transformation is used, then the difference between 1 and 2 returns would have the same weight as the difference between 100 and 200 returns, even though it is likely that the statistical uncertainties are proportionally much greater for the case of a few returns than for the case of a few hundred returns. The square root transformation is a compromise between the above two extremes. Furthermore, given that the ratio of tagged to untagged fish is small, it is reasonable to expect that sampling for tagged fish approximates a rare event or Poisson sampling process. Under the assumption that the number of returns in a month is in fact a Poisson variate, the use of the square root transformation is equivalent to weighting each point by the reciprocal of its standard deviation.

TABLE 1. FORMS OF THE MODEL USED FOR DIRECTLY ESTIMATED POPULATION PARAMETERS, EQUATIONS USED FOR CALCULATED POPULATION PARAMETERS, AND LIST OF NECESSARY INPUT DATA

Parameter		Form of Model
attrition standing stock	Z_c P	$r_i = \frac{\alpha\beta N_o C_i}{P(Z_c+\psi)} e^{-i(Z_c+\psi)}\left(e^{Z_c+\psi}-1\right)$
attrition catchability	Z_e Q	$r_i = \frac{\alpha\beta N_o Q E_i}{Z_e+\psi} e^{-i(Z_e+\psi)}\left(e^{Z_e+\psi}-1\right)$
attrition throughput	Z_c T	$r_i = \frac{\alpha\beta N_o Z_c C_i}{T(Z_c+\psi)} e^{-i(Z_c+\psi)}\left(e^{Z_c+\psi}-1\right)$
attrition harvest ratio	Z_e H_e	$r_i = \frac{\alpha\beta N_o H_e Z_e E_i}{\bar{E}(Z_e+\psi)} e^{-i(Z_e+\psi)}\left(e^{Z_e+\psi}-1\right)$

Parameter		Equation
fishing mortality	F_c	$F_c = \frac{\bar{C}}{P}$
fishing mortality	F_e	$F_e = Q\bar{E}$
harvest ratio	H_c	$H_c = \frac{\bar{C}}{T}$

Input Data

r_i = tag returns by time period

C_i = catch by time period

E_i = effort by time period

$\bar{C}$ = average catch per time period

$\bar{E}$ = average effort per time period

α = type 1 tag retention and survivorship

β = proportion of recaptured tags reported with useful information

N_o = number of tags released

ψ = type 2 tag slippage and tag mortality

3.3 Confidence Limits

To indicate the precision of the parameter estimates, 95 per cent confidence intervals were derived in the following manner. The residual sum of squares as a function of the two parameter values forms a three dimensional bowl-shaped surface whose lowest point, S_{min}, defines the best fitting parameter values. The boundary of the joint confidence region of the two parameter estimates corresponds to a contour line on the sum-of-squares surface at which the residual sum of squares is equal to a critical value defined by

$$S_{crit} = S_{min}\left[1 + \frac{2}{n-2} F_{.05(2,n-2)}\right] \tag{11}$$

where $F_{.05(2,n-2)}$ is the critical value of the F-distribution at probability level $.05$ and 2 and $n-2$ degrees of freedom, and where n is the number of data points used in the analysis (Conway, Glass and Wilcox 1970). A numerical searching algorithm was devised to trace the S_{crit} contour on the sum-of-squares surface. An example of a sum-of-squares surface and a joint 95 per cent confidence region is shown in Figure 2. Confidence intervals for the individual parameters were obtained from the extremes of the 95 per cent confidence region.

As shown in Table 1, some parameter values were not estimated directly from the model, but were calculated from other directly estimated parameter values. In all such cases, the calculation made use of only one of the directly estimated parameters. Confidence limits for the calculated parameter were obtained by using the confidence limits of the directly estimated parameter in the same calculation. For example,

$$F_e = Q\overline{E}$$

1st confidence limit of F_e = (1st confidence limit of Q)$\overline{E}$

2nd confidence limit of F_e = (2nd confidence limit of Q)$\overline{E}$

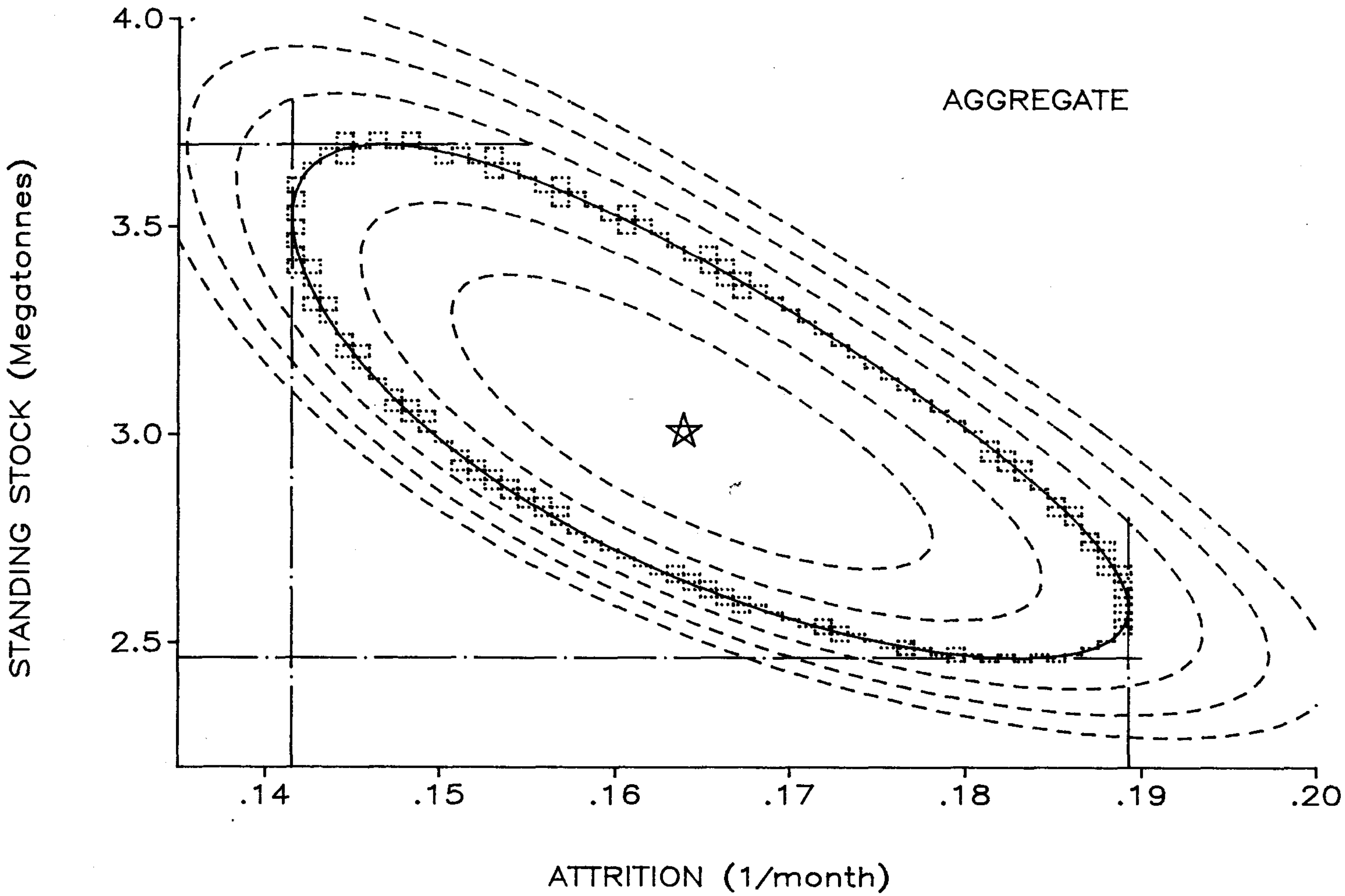
Note that except for the actual observed tag return data, uncertainties in values of input data are ignored in both methods of calculating confidence intervals (the input data are listed in Table 1).

3.4 Effort Form of Model with Varying Attrition

The forms of the model derived so far allow the fishing mortality to vary with time, but contain the paradoxical assumption that the attrition rate is constant. In the catch forms of the model, this inconsistency is difficult to correct because to be entirely consistent, the standing stock would also have to be allowed to vary. The model would therefore need to have some form of recruitment built into it with an attendant list of further assumptions. However, in the effort forms of the model, it is logically consistent to allow a varying attrition rate and still assume a constant catchability. The model takes the following form:

$$r_i = \frac{\alpha\beta N_o Q E_i}{M + Q E_i + \psi}\left(\prod_{j=1}^{i} e^{-i(M + Q E_j + \psi)}\right)\left(e^{(M + Q E_i + \psi)} - 1\right) \tag{12}$$

FIGURE 2. **EXAMPLE OF A CONFIDENCE REGION, DEFINED BY THE SUM-OF-SQUARES SURFACE, SHOWN AS A FUNCTION OF STANDING STOCK AND ATTRITION.** The dashed lines are contour lines on the sum-of-squares surface. The star is plotted at the lowest point on the surface and corresponds to the best fitting pair of parameter values. The solid line is the contour line for the critical sum-of-squares value given by Equation 11. This line encloses the 95 per cent confidence region, and the projections of the extremes of this curve onto the parameter axes define the 95 per cent confidence regions for these parameters. The dotted line shows the path taken by the numerical searching algorithm in tracing the critical sum-of-squares contour line.



where a constant, M , includes all forms of attrition except fishing and type 2 mortality, and the total attrition, $M+QE_i+\psi$, varies with varying effort, E_i . With a constant effort, this equation reverts to the form of the model in Equation 6 which has two estimated parameters. However, if effort varies, Equation 12 has three parameters, M , Q , and $\alpha\beta$ (since N_0 is known and ψ was estimated independently). Therefore, in theory at least, this equation could be used to estimate $\alpha\beta$.

Equation 12 was fitted to subsets of the tag return data for which corresponding effort data were available. The method for fitting this form of the model was similar to that described in Section 3.2, except that a different routine was used for searching for the minimum sum of squares. The method used was the simplex algorithm of Nelder and Mead (1965), which was more convenient for dealing with Equation 12, and which allowed convenient selection of individual parameters in the equation either to remain fixed, or to be adjusted by the fitting procedure.

For obtaining confidence limits when all three parameters were fitted, it was necessary to trace a critical sum-of-squares shell in three-dimensions in a manner analogous to that described in Section 3.3, but with the critical sum-of-squares defined by

$$S_{crit} = S_{min}\left[1+\frac{3}{n-3}F_{.05(3,n-3)}\right] \quad (13)$$

3.5 Determining Values for β

Estimating β is complicated by the fact that tagged fish can be found in a variety of ways, e.g. during fishing while on board a variety of types of fishing vessels, during unloading, and during processing in a cannery. The probability of finding and returning tags differs among the various modes of discovery, therefore each discovery mode has its own β value. An expression for an overall β for more than one discovery mode can be derived as follows:

Let p_j = the number of useable returns from discovery mode j

q_j = the number of unuseable returns from discovery mode j

ζ_j = proportion returned of tags discovered in mode j.

The β factor is the ratio of the number of useable returns to the total number of recaptures and is given by

$$\beta = \frac{\sum p_j}{\sum \frac{p_j+q_j}{\zeta_j}} \quad (14)$$

3.6 Assumptions of the Model

A series of assumptions were made in deriving the various forms of the analytical model. Simulations were carried out to investigate the consequences to parameter estimates of violating some of these assumptions. The results of these simulations, which are as yet unpublished, are summarised in this section. Further details are given in Section 5.3.3.

3.6.1 Distribution of tag releases

One assumption is that all tags are released at time zero rather than throughout the first time interval. This is correct for the aggregate data set used in this report (see Section 4.1.1), but is not true for the other data sets. The simulation results showed that the analytical model is insensitive to this problem as long as tag returns are available for more than a few time intervals.

3.6.2 Steady state

A principal assumption in the model is that there is little variation during the tagging experiment in the values of the parameters appearing in the form of the model being used. To use the catch forms of the model, the population and the attrition rate should be constant; to use the effort forms of the model, the catchability and the attrition rate should be constant. A subsidiary assumption, for all forms except Equation 12, is that if the fishing mortality varies, it does so within a range of values that is small relative to the total attrition rate. Various non-steady-state situations were examined by varying the standing stock, the recruitment, the natural mortality, the fishing effort, and the catchability. The model appears to be robust to large variations from steady state if the variations are cyclical in nature. That is, the analytical model yielded parameter estimates which were close to the average values of the variables in the simulation. If there are large one-way trends, the model appears to be less robust, and the standing stock and catchability estimates tend to reflect the starting values more than the averages. For the most part, the parameter estimate was closer to the average of the corresponding variable in the simulation than it was to extreme values of the variable.

A result detrimental to fishery management would occur if the harvest ratio was so underestimated that the fishery appeared capable of sustaining increased fishing pressure when in fact it could not. In the simulation exercise, the scenarios under which this could happen involved a drastic downward trend in the population, particularly when this was in response to an immediate decrease in recruitment or an immediate increase in mortality. An immediate order of magnitude decrease in recruitment or increase in mortality caused underestimation of the harvest ratio by less than a factor of four, and gradual order of magnitude changes over two years caused underestimation of the harvest ratio by less than a factor of two. An immediate decrease in recruitment or increase in mortality by a factor of two caused underestimation of the harvest ratio by less than a factor of 1.4. Thus, large departures from steady state cause smaller underestimates of the harvest ratio.

3.6.3 Territory covered by tagging experiment

An implicit assumption in the derivation of the model is that the stock, of which P is a measure, is a clearly defined entity. However, in a situation where the area of operation of a fishery is surrounded by unfished areas, and where the fish occupying the fished and unfished areas can exchange by virtue of diffusive or diffusive-like behaviour, then the effective boundary of the stock which the tagged fish represent is not so clearly defined. The territory occupied by a cohort of tagged fish can be expected to expand with time. However, the number of tagged fish simultaneously diminishes due to attrition, which thereby limits the duration of the experiment. The effective size of the territory covered by the tagging experiment would thus represent a trade-off between migratory expansion and attrition. This effect is the subject of ongoing simulation modelling. Results thus far suggest that the standing stock estimate corresponds to the population occupying an area larger than the actual fished area, and the degree to which the area occupied by the stock exceeds the fished area depends on the degree of diffusive behaviour. For a fished zone of the approximate size of that covered by the Solomon Islands or Papua New Guinea local fisheries, and with a diffusion rate high enough to explain the observed movement of tags from Solomon Islands to Papua New Guinea, simulation showed that the estimated stock corresponded to the population occupying an area approximately 10 per cent larger than the fished zone. Thus, the operational measure of standing stock obtained in this instance corresponds with the definition of standing stock given in the introduction. That is, the stock includes those fish that are outside the fished area but are close enough that there is a reasonable chance that they will enter the fished area in their lifetime.

3.6.4 Other assumptions

There are other assumptions involved in using the analytical model that have not been investigated by simulation. For example, it is assumed in this and most other analyses of tag results, that the tagged fish have the same probability of being caught as untagged fish. That is, the tagged fish should be randomly distributed in the population, and they should be neither more nor less vulnerable to fishing gear than untagged fish. It is also assumed that β is constant in time. If such is not the case, in particular if β declines with time, then some part of the observed decrease in tag return rate would be due to the decline in β, and the attrition values obtained by the model would be overestimates.

4.0 DATA USED IN ANALYSES

4.1 Tag Returns, Catch, and Effort

Table 2 gives the tag return results and other input data used in the analytical model. The aggregate data set is shown as well as subsets of the tag return data corresponding to cohorts of tagged skipjack released in particular countries in particular months (10-day periods in the case of New Zealand). The countries included are those for which catch and/or effort information was available for some or all of the fleets operating within the waters of the country. The catch data, and effort data if available, are included in Table 2.

TABLE 2. TAG RETURN AND OTHER DATA USED TO ESTIMATE POPULATION PARAMETERS. Aggregate and individual country data sets are included. Section 4.1 fully explains symbols and data sources used in this table.

Aggregate data

Average Catch = 19000
$\alpha\beta$ = 0.60

	t	r	C_i
a	1	2820	19000
	2	506	19000
	3	379	19000
	4	261	19000
	5	198	19000
	6	120	19000
	7	115	19000
	8	93	19000
	9	94	19000
	10	114	19000
	11	142	19000
	12	106	19000
	13	72	19000
	14	62	19000
	15	75	19000
	16	42	19000
	17	17	19000
	18	24	19000
	19	16	19000
	20	23	19000
	21	13	19000
	22	8	19000
	23	10	19000
	24	11	19000
	25	3	19000
	26	6	19000
	27	8	19000
	28	7	19000
	29	2	19000
	30	0	19000
	31	1	19000
	32	1	19000
	33	1	19000
	34	1	19000
	35	0	19000
	36	1	19000
	37	0	19000
	38	0	19000
	39	0	19000
	40	0	19000
	41	0	19000

Papua New Guinea

$\bar{C}$ = 2000
$\bar{E}$ = 670
$\alpha\beta$ = 0.68
N_o = 6009

	t	r	C_i	E_i
a	7905	20	379	114
a	7906	391	2153	598
	7907	208	2972	1035
	7908	100	2492	913
	7909	58	1840	899
	7910	27	654	614
	7911	5	811	706
	7912	3	286	212
	8003	1	609	440
	8004	5	1956	802
	8005	1	2243	985
	8006	2	2860	1005
	8007	3	2878	1068
	8008	7	5514	1100
	8009	5	3982	988
	8010	0	3697	850
	8011	0	3055	831
	8012	0	1800	553
	8101	0	222	99
	8103	0	1814	447
	8104	0	4675	918
	8105	0	3085	977
	8106	0	3340	962
	8107	1	3421	1077
	8108	1	2100	964
	8109	0	1660	805
	8110	0	1435	626
	8111	0	426	185
	8112	0	77	42

Solomon Islands (1977)

$\bar{C}$ = 1200
$\bar{E}$ = 340
$\alpha\beta$ = 0.64
N_o = 1709

t	r	C_i	E_i
7711	17	754	317
7712	10	365	397
7801	0	15	73
7803	0	15	34
7804	3	941	460
7805	5	888	465
7806	1	1526	515
7807	5	1973	551
7808	3	1587	512
7809	4	2304	517
7810	7	2317	497
7811	5	2915	514
7812	5	2723	518
7901	1	1106	223
7904	2	1438	305
7905	0	1788	485

Solomon Islands (1980)

$\bar{C}$ = 2200
$\bar{E}$ = 490
$\alpha\beta$ = 0.54
N_o = 2012

t	r	C_i	E_i
8006	9	354	179
8007	28	2550	558
8008	25	2778	554
8009	9	2770	574
8010	8	3244	566
8011	20	3313	566
8012	16	2774	594
8101	18	1531	463
8104	5	1210	258
8105	5	1881	560
8106	11	2934	614
8107	4	2796	628
8108	6	3474	640
8109	2	2631	639
8110	0	2087	630
8111	0	2131	632
8112	1	1231	415
8112	1	1231	415

Fiji

$\bar{C}$ = 350
$\bar{E}$ = 120
$\alpha\beta$ = 0.80
N_o = 11646

	t	r	C_i	E_i
a	8004	594	185	76
a	8005	183	65	86
	8006	6	76	42
	8007	11	116	33
	8008	19	90	49
	8009	2	99	20
	8010	2	79	21
	8011	2	106	45
	8012	11	229	41
	8101	27	737	198
	8102	42	862	161
	8103	35	953	193
	8104	8	605	150
	8105	12	536	138
	8106	10	418	132
	8107	5	387	140
	8108	1	76	23
	8110	3	77	33
	8111	1	143	82
	8112	2	298	147
	8201	0	600	224
	8202	1	686	226
	8203	1	696	241
	8204	0	485	231
	8205	0	589	275
	8206	0	285	168
	8207	0	118	81
	8208	0	42	31

Gilbert Group, Kiribati

$\bar{C}$ = 20
$\alpha\beta$ = 0.82
N_o = 4403

t	r	C_i
7807	26	22.6
7808	159	49.5
7809	82	63.5
7810	78	76.3
7902	0	0.8
7903	0	3.8
7904	1	9.4
7905	0	8.3
7906	0	26.8
7907	0	8.8
7908	0	12.1
7909	0	6.8

Society Islands, French Polynesia

$\bar{C}$ = 100
$\alpha\beta$ = 0.82
N_o = 823

	t	r	C_i
a	7812	0	60
	7901	1	56
	7902	4	64
	7903	4	91
	7904	1	110
	7905	3	170
	7906	2	130
	7907	0	94
	7908	0	89
	7909	0	48
	7910	0	62
	7911	0	100

N_o = 896

	t	r	C_i
a	7901	0	7
	7902	2	64
	7903	1	91
	7904	0	110
	7905	0	170
	7906	0	130
	7907	0	94
	7908	0	89
	7909	0	48
	7910	0	62
	7911	0	100
	7912	1	54
	8001	0	190
	8002	0	130
	8003	0	83
	8004	0	82
	8005	0	160
	8006	0	97
	8007	1	78
	8008	0	32
	8009	0	55
	8010	0	150
	8011	0	130
	8012	0	180

New Zealand

$\bar{C}$ = 2300
$\bar{E}$ = 150
$\alpha\beta$ = 0.37
N_o = 2678

t	r	C_i	E_i
790221	2	336	37
790301	223	2396	120
790311	7	148	18
790321	30	215	24
790401	1	3	1
791121	0	25	7
791201	0	15	7
791221	0	35	6
800101	5	1319	94
800111	0	2100	87
800121	1	1186	86
800201	3	1986	135
800211	1	142	18
800221	0	219	33

N_o = 6298

t	r	C_i	E_i
790301	280	1917	96
790311	8	148	18
790321	48	215	24
790401	0	3	1
791121	0	25	7
791201	0	15	7
791221	0	35	6
800101	5	1319	94
800111	3	2100	87
800121	6	1186	86
800201	6	1986	135
800211	1	142	18
800221	0	219	33
800301	1	1191	76
800311	0	493	36
800321	1	113	19
800501	0	18	5
800521	0	49	5
800601	2	35	9
800611	0	12	2

For each data set in Table 2, the t column gives the time tags were at liberty for the aggregate data, or the time period during which tags were recaptured for the individual country data sets. For the aggregate data set, the time is the months-at-large category, and for individual countries the date is the calendar year and month of tag recapture, except for New Zealand where the starting date of the 10-day period is given. The r column gives the number of useable recaptures in the given month or 10-day period. Recaptures by the tagging vessel were excluded from all data sets because the fishing effort of this vessel was, for the most part, identical to the places and times of tag release. Returns with unknown dates of recapture were also excluded. If an imperfectly known recapture date could be ascertained to fall within a range of dates such that the extent of the range was less than half the time from release to the midpoint of the recapture range, then the return was accepted and the recapture date taken to be the midpoint of the range. Otherwise the return was rejected. For some individual countries, the returns were additionally filtered (see Section 4.1.2).

The C_i column in Table 2 gives the tonnes of skipjack caught in the time period, and the E_i column, if present, gives the effort in boat days, or purse-seine sets in the case of New Zealand. Catch and effort for the first time period in each country data set were pro-rated to adjust for timing of tag releases during the initial period. Average monthly catch, $\overline{C}$, and effort, $\overline{E}$, were used for some of the population parameters derived from the basic model parameters. These are given at the head of each data set. The averages were calculated over the period of time included in the data set. Months with zero catch and effort were included in the average. Catch and effort in individual months could be considerably different from the average, particularly for the highly seasonal New Zealand fishery. Catch and effort were averaged for December through March in New Zealand.

In several cases, the first one or two time periods in a data set were disregarded in the analysis. In Table 2 the rows corresponding to these time periods are preceded by an "a". The early returns in any tagging experiment can easily be "out of line" because of inadequate mixing of tagged fish in the untagged population. In the present analysis, early returns were disregarded if there was good reason to assume a problem with mixing in the first time period(s), and if doing so significantly improved the ability of the model to fit the data.

4.1.1 Aggregate data set

To apply the analytical model to the aggregate data, a constant monthly catch rate had to be assumed because the actual catch rates in effect for the different months-at-large categories were not known. The actual catch rates were not known because a) the catch data for the whole study area were not available, and b) the returns appearing in any one months-at-large category were not all recovered in a single calendar month. The assumed value of 19,000 tonnes per month (223,000 tonnes per year) includes catch from the study area by the Japanese long-range, pole-and-line fleet; catch by the four principal, joint venture fisheries in the region (Papua New Guinea, Solomon Islands, Fiji, and Palau); catch by the purse-seine fleet operating in New Zealand, and estimates of catch from the study area for Japanese and United States long-range, purse-seine fleets.

4.1.2 Individual country data sets

The data set for Papua New Guinea in Table 2 corresponds to tag releases in two consecutive calendar months, May and June 1979. Since the 2,718 releases in May were all within five days of the end of the month, they were combined with the 3,291 June releases to make one data set. The returns include only those from the local pole-and-line fleet operating in Papua New Guinea. Furthermore, the data include only releases, recaptures and catch statistics from the eastern Bismarck Sea, which is the principal fishing area of the local fleet. Fishery statistics were obtained from the Papua New Guinea Department of Primary Industry. More details on the selection of tag returns and on the local pole-and-line fishery are given by Ellway and Kearney (MS).

The two data sets for Solomon Islands derive from batches of tags released in November 1977 and June 1980. The data include releases, recaptures, and catch statistics from the local Solomon Islands pole-and-line fleet operating only in The Slot and nearby waters. Tag releases and returns from one school of predominantly small fish were excluded in order to match more accurately the size distribution of tagged fish with the size distribution in the catch of the local fleet. Fishery statistics were provided by the Solomon Islands Ministry of Natural Resources. More details on the selection of tag returns and on the local pole-and-line fishery are given by Argue and Kearney (1982).

The New Zealand data sets correspond to tags released in New Zealand in two consecutive 10-day periods between late February and mid-March 1979. The data include releases, recaptures and catch statistics from purse-seiners operating in New Zealand waters. Fishery statistics were obtained from the Fisheries Research Division, New Zealand Ministry of Agriculture and Fisheries and from Habib et al. (1980a, 1980b). As the statistics were organised by 10-day period, the tag return data were also broken into 10-day periods. More details on the selection of tag returns and on the purse-seine fishery in New Zealand are given by Argue and Kearney (1983).

The Fiji data set includes tags released only in April 1980, and tag recaptures and catch statistics from the local pole-and-line fleet operating in Fiji. Fishery statistics were obtained from Anon (1982). More details on the selection of tag returns and on the local pole-and-line fishery in Fiji are given by Kearney (1982a). Two additional tag recaptures have been included in the present analysis, along with fishery statistics which have recently become available for 1982. These data were provided by Fisheries Division, Fiji Ministry of Agriculture and Fisheries.

The Kiribati data set is restricted to tag releases in the Gilbert Group, primarily in the vicinity of Butaritari, and recoveries in the same area by two pole-and-line survey vessels operated consecutively by the Japanese International Co-operation Agency in 1978, and the United Nations in 1979. Catch data were supplied by the Ministry of Natural Resources, Kiribati. More details on the selection of tag returns and on the survey fishery are given by Kleiber and Kearney (1983).

The two data sets for the Society Islands in French Polynesia include only returns from bonitiers, the local trolling boats that use pearl-shell lures. Catch data were taken from Marcille et al. (1979) and Chabanne and Marcille (1980). More details on the selection of tag returns and on the bonitier fishery are given by Gillett and Kearney (1983).

4.2 Number of Tag Releases, N_0

The number of skipjack releases corresponding to each data set is given in Table 2 at the head of each data set. N_0 was in fact not known with complete precision. This was because approximately seven per cent of all fish tagged were of species other than skipjack (over 99% yellowfin), and occasional failures in the shipboard data recording system meant that for some of the releases (approximately 0.5%) the species was not recorded. To estimate the number of skipjack released, the releases for which species was not recorded were apportioned, for each school, into skipjack and yellowfin according to the ratio of known skipjack to known yellowfin encountered in the particular school (released or retained on board). The estimated number of skipjack among the releases with unrecorded species was then added to the number of recorded skipjack releases to estimate the total skipjack releases. The estimate of N_0 for the aggregate data set is 140,433 skipjack tag releases. Of these 139,960 were recorded as skipjack, and the 740 unknown species were apportioned into 473 skipjack and 267 yellowfin. Thus the total number of skipjack released was certainly between 139,960 (no unknowns assumed to be skipjack) and 140,700 (all unknowns assumed to be skipjack).

4.3 Type 1 Survival and Tag Retention, α, and Return Rate of Tags, β

Considerable effort was expended to maintain high standards in the tagging procedure (Kearney and Gillett 1982) in order to maximise α, and in the tag return system (Kearney 1982b) to try to maximise β. To analyse the results, however, it was necessary to estimate values for $\alpha\beta$.

4.3.1 Attempt to estimate $\alpha\beta$ with the three-parameter model

The three parameter form of the analytical model given in Equation 12 could theoretically be used to estimate the value of $\alpha\beta$. To try to do this, Equation 12 was fitted to the five data sets containing effort in Table 2. N_0 was set to the values given in Table 2, and the parameters M, Q, and $\alpha\beta$ were adjusted by the fitting procedure. In three cases the process converged to impossible values (negative M or $\alpha\beta$ greater than 1.0), and in two cases possible values resulted. Investigation of the three-dimensional confidence regions for the latter two cases (Figures 3 and 4) revealed that $\alpha\beta$ was very ill-defined by the analysis. The 95 per cent confidence range [approximately 0.05--1.0] covers most of the possible range of the parameter [0--1.0]. It is also evident from the upper plots in Figures 3 and 4 that if the value of $\alpha\beta$ can be constrained by independent evidence (i.e. an experiment or experiments designed to measure this factor), then the confidence in the other parameters is improved. The tag plant and double tagging experiments provided such independent evidence for some of the components of α and β.

4.3.2 Estimation of β

Of the tags planted on purse-seiners in New Zealand, 25 per cent were returned. All returns were from shore-based processing facilities, principally in Pago Pago where most of the seine catch was unloaded. This experiment was carried out more than one year after most of the recoveries from the regular tagging programme were obtained from shore

FIGURE 3. CONFIDENCE REGIONS FOR ESTIMATES OF THE THREE PARAMETERS OF THE VARIABLE ATTRITION MODEL USING THE PAPUA NEW GUINEA DATA SET. In the upper plot, slices through the confidence region at various levels of $\alpha\beta$ are shown. The $\alpha\beta$ axis extends downward from the plane of the page. In the lower plot the figure is rotated forward about the M axis so that the Q axis rises upward from the plane of the page. Slices at various levels of Q are shown. In the upper plot, the crosses give the best fitting Q and M values with $\alpha\beta$ fixed at each level, and in the lower plot the crosses give the best fitting $\alpha\beta$ and M values with Q fixed at each level. The star in each plot gives the best fitting point for the three parameter fit.

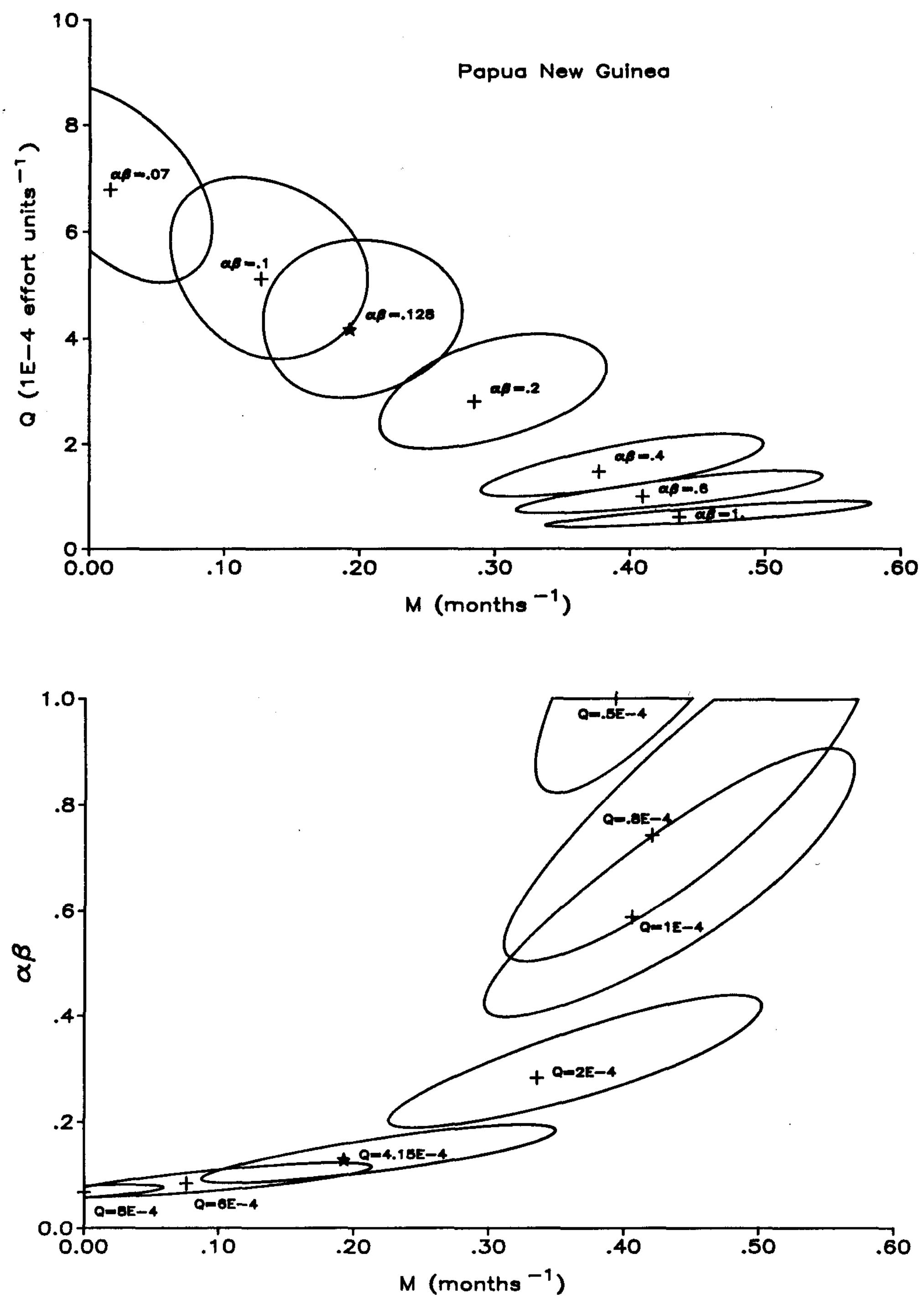
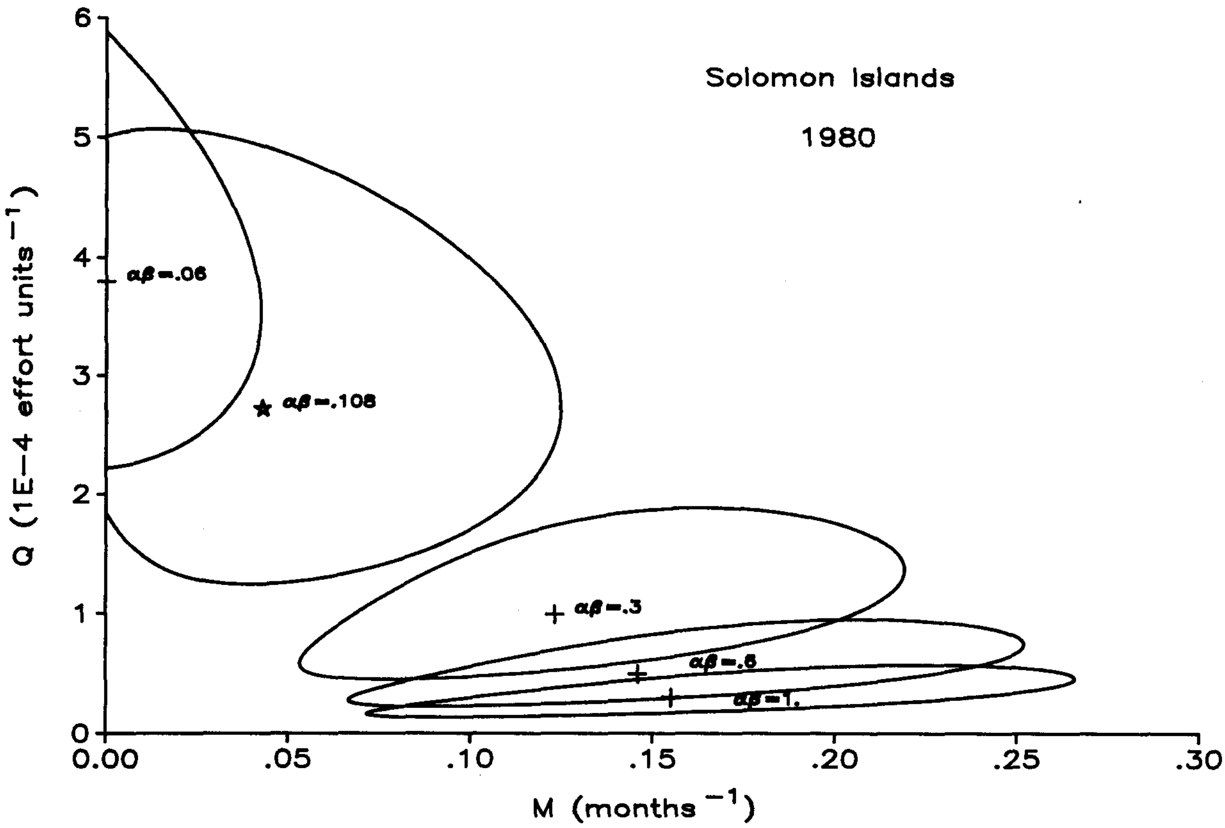
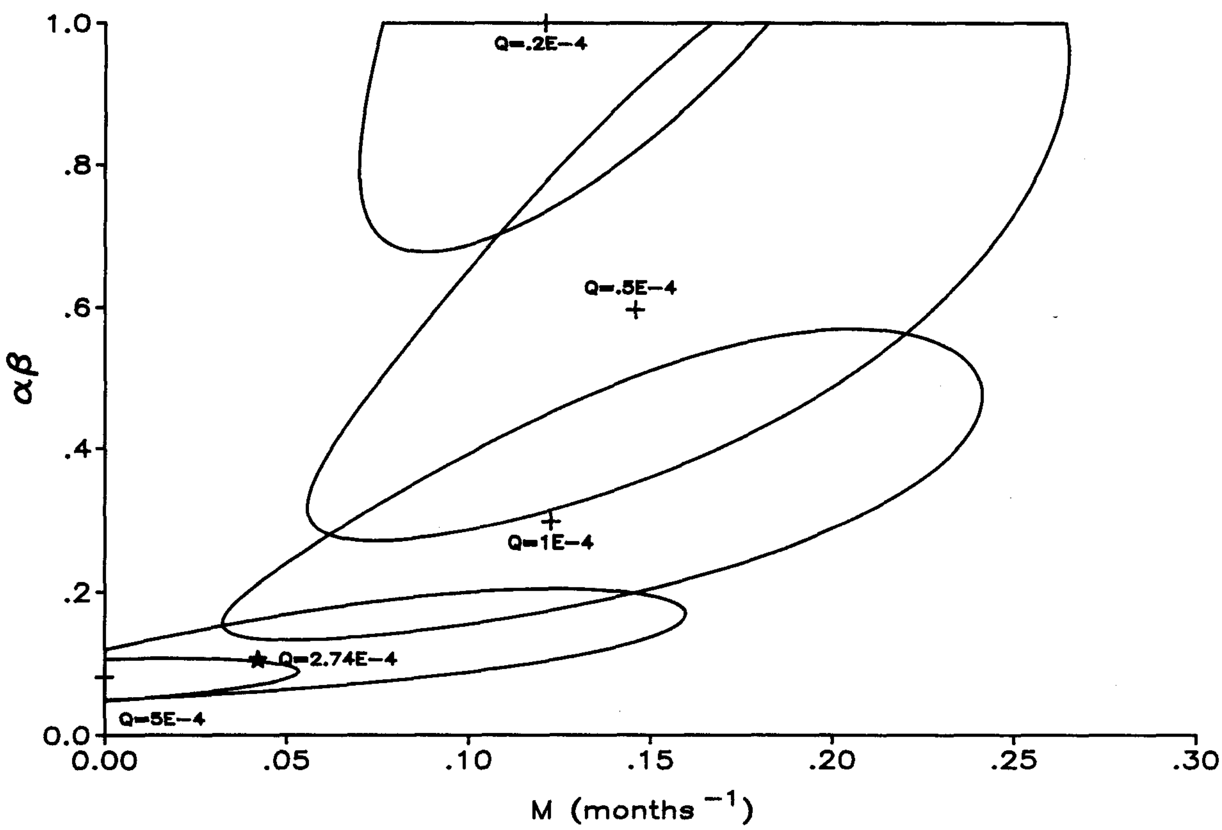


FIGURE 4. CONFIDENCE REGIONS FOR ESTIMATES OF THE THREE PARAMETERS OF THE VARIABLE ATTRITION MODEL USING THE 1980 SOLOMON ISLANDS DATA SET. In other respects, this figure is similar to Figure 3.





facilities. Thus, it is possible that the low returns of planted tags reflect a more recent problem in the tag recovery system, or one that was specific to seine caught fish from New Zealand that were processed in Pago Pago. Unfortunately, tag plant experiments were not done on pole-and-line caught fish or on fish destined for other processing facilities. It is also possible that tags placed in dead fish are more easily lost from the fish than are tags placed in live fish. Taking the tag plant results at face value, the value of ζ_s, the combined ability of shore-based processing personnel to find tags and their propensity to return them, could have been as low as 0.25 for shore facilities at the time of the tag plant experiment. However, the ζ_s value might very well have been higher for Pago Pago and other processing facilities during the time that tagged fish from Skipjack Programme releases were passing through these facilities. Worst and best case values of 0.25 and 1.0 were assumed for ζ_s.

A range of values for ζ_f, the propensity of pole-and-line fishermen to return tags, can be obtained from the double tagging results in Fiji. From analysis of the double tagging data using the approach of Bayliff and Mobrand (1972), an estimate of 0.997 with a 95 per cent confidence range of [0.82--1.0] was obtained for the quantity, $\rho\zeta_f$, where ρ is the short-term (type 1) tag retention (1 minus rate of tag shedding) (Tuna Programme, unpublished analyses). This range applies to ρ and ζ_f individually, because both quantities can only be in the range [0--1.0].

Assuming two modes of discovery, 1) by fishermen aboard their fishing vessels and 2) by personnel of processing facilities, and assuming the ranges given above for the corresponding ζ factors, worst and best case values of β were calculated by Equation 14 and are given in Table 3.

4.3.3 Estimation of α

α depends on type 1 mortality and type 1 tag shedding. As shown above, the type 1 tag shedding, $1-\rho$, must be low. Type 1 tagging mortality is more difficult to determine. However, high tag return rates (>50%) have been observed in the eastern Pacific (W.H. Bayliff, personal communication) from tagging using similar but perhaps less exacting methods than those used by the Skipjack Programme. This strongly suggests that the combination of type 1 tagging mortality and tag shedding was low. In the absence of further quantitative information, a figure of 10 per cent has been assumed here for the type 1 losses, that is, a value of 0.9 for α.

4.3.4 Assumed values of $\alpha\beta$

The values of $\alpha\beta$ used as input to the analytical model are given at the head of each data set in Table 2. These were derived from an assumed value of 0.9 for α and a β value midway between the worst and best case values given in Table 3 (see Section 4.3.2). The resulting $\alpha\beta$ values used in the present analysis are different in some cases from the values assumed in previous reports of specific country results (Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983). This is because in the face of large uncertainty, the choice is somewhat arbitrary and subject to the rationale of individual authors.

TABLE 3. CALCULATION OF β. Worst and best case values of β are calculated from Equation 14 using worst and best case assumptions about ζ.

	Where Found	Tag Returns: Useable	Tag Returns: Reject	ζ: Worse Case	ζ: Best Case	β: Worse Case	β: Best Case
Aggregate	fishermen	4641	125	0.82	1.0	0.47	0.87
	shore	711	706	0.25	1.0		
Papua New Guinea	fishermen	838	7	0.82	1.0	0.62	0.90
	shore	0	82	0.25	1.0		
Solomon Islands 1977	fishermen	65	1	0.82	1.0	0.55	0.88
	shore	3	8	0.25	1.0		
Solomon Islands 1980	fishermen	167	6	0.82	1.0	0.43	0.77
	shore	0	45	0.25	1.0		
New Zealand	fishermen	231	12	0.82	1.0	0.19	0.64
	shore	403	352	0.25	1.0		
Fiji	fishermen	977	23	0.82	1.0	0.80	0.98
	shore	1	0	0.25	1.0		
Gilbert Group	fishermen	346	0	0.82	1.0	0.82	1.0
Society Islands	fishermen	20	0	0.82	1.0	0.82	1.0

4.4 Type 2 Tag Loss, ψ

A common value of ψ, the type 2 tag loss factor, was assumed for all data sets. Type 2 shedding was estimated from the double tagging experiment (Skipjack Programme 1981). Type 2 mortality is not so readily estimated. The proportion returned of the double tagged skipjack was not significantly less than that of single tagged skipjack released at the same time, except for fish less than or equal to 45 cm (Skipjack Programme 1981). Therefore, if type 2 tag mortality was of significance, it must not have been increased by the presence of a second tag, except possibly in small fish. The difference noted for small fish could have been a type 1 or a type 2 effect, but as shown in the Appendix, there is no detectable difference in attrition rate between fish less than 45 cm and fish from 45 to 55 cm. This suggests that the reduction in returns for the small double tagged fish was predominantly a type 1 phenomenon. In any case, these small fish accounted for less than 15 per cent of the returns considered in this report. For the purposes of this analysis, type 2 mortality is assumed to be zero, and the value of ψ is taken to be 0.0073 per month, the estimate of type 2 tag shedding.

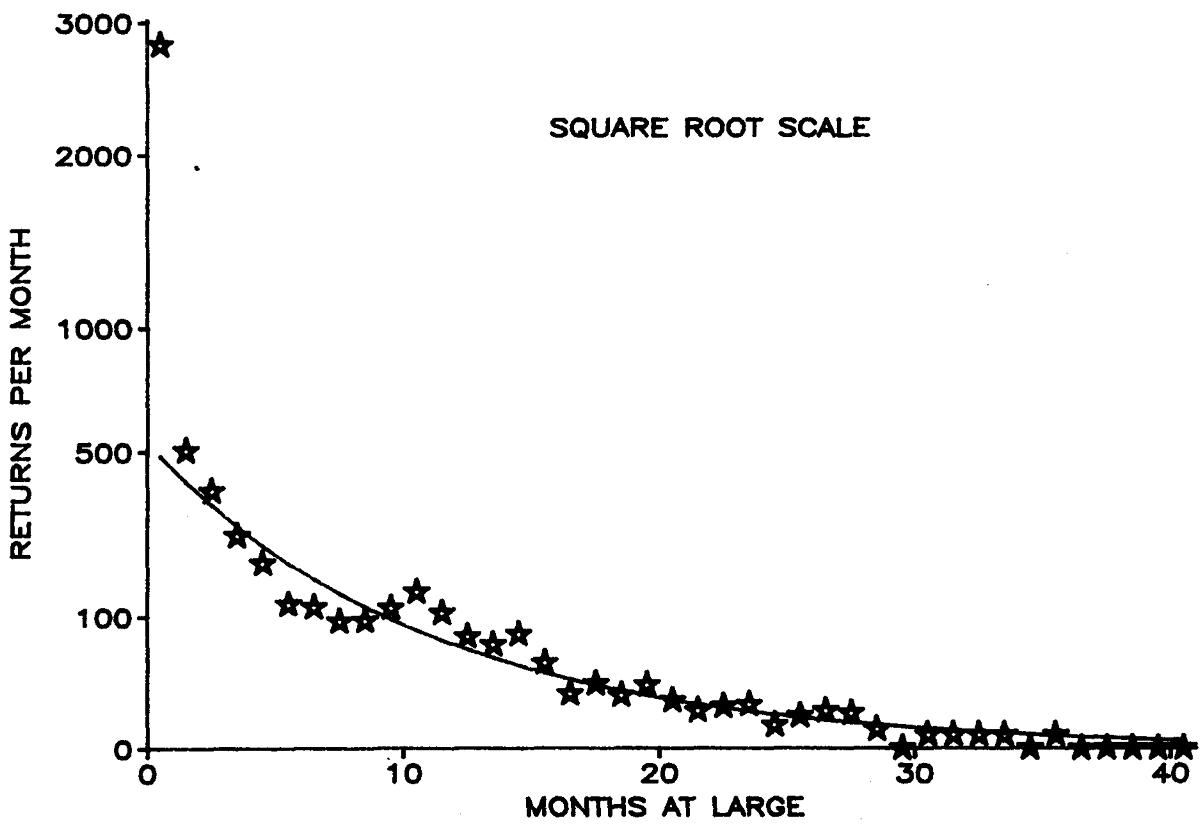
5.0 RESULTS AND DISCUSSION

5.1 Tag Attrition Curves

Figure 5 shows two graphs of tag returns against time-at-large for the aggregate data set in Table 2. The solid lines represent predicted values from the best fit of the analytical model. The upper graph is plotted with a square root scale for the Y-axis because the square root transformation was used in fitting the model. Thus, the fitting procedure minimised differences between the points and the line as they appear in the upper graph. A semi-logarithmic plot of the same results is given in the lower graph, but the points corresponding to zero returns in a given month cannot, of course, be included. The returns per month in Figure 5 decrease with time, as expected, and follow an approximately straight line on the semi-logarithmic plot. The solid line estimated from the fitting procedure is straight in the semi-logarithmic plot because of the assumed constant catch rate. The bump in the observed data at approximately one year could be the result of seasonality in the fisheries. Most fisheries in the region have a period of higher fishing effort each year lasting from a little over a month (New Zealand) to several months (Papua New Guinea). Since tags tended to be released during these periods in any particular area, it is to be expected that a surge of tag returns would coincide with increased fishing, approximately one year following tagging.

Figure 6 shows an example of a tag attrition plot for an individual country data set in Table 2. In this case the X-axis represents calendar months, as is the case for other individual country data sets. The scatter is greater than in Figure 5 because of increased statistical variability due to fewer data, and because of variable fishing activity during the period of the experiment. Where detailed information on catch and/or effort was available, these data were used in the analytical model to correct for the vagaries of fishing intensity. The solid line in Figure 6 is not smooth because it reflects variation in catch, as well as the steady decline due to all the components of attrition.

FIGURE 5. AGGREGATE TAG ATTRITION CURVES. Stars are the observed aggregate tag return rates given in Table 2. The solid lines give the expected values based on the best fit of the form of the analytical model that uses catch data. The Y-axis of the upper figure is a square root scale, and in the lower figure it is a logarithmic scale.



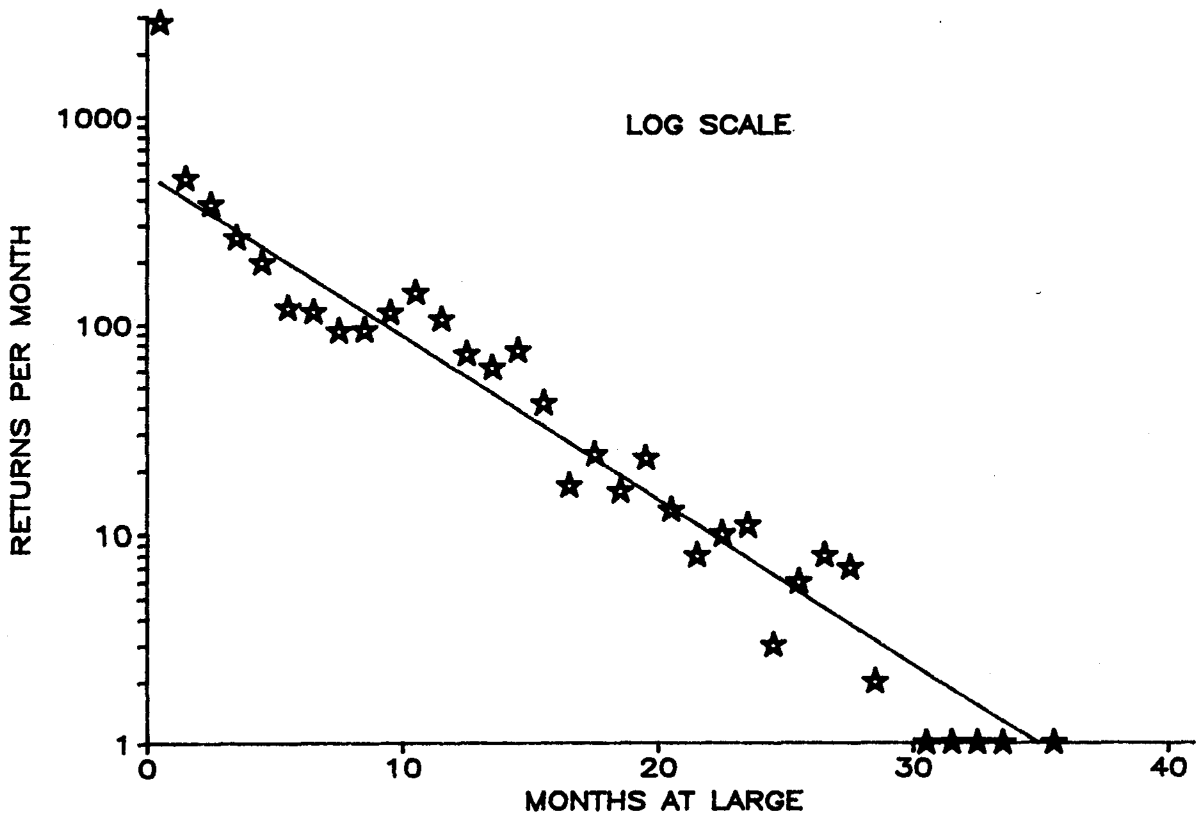
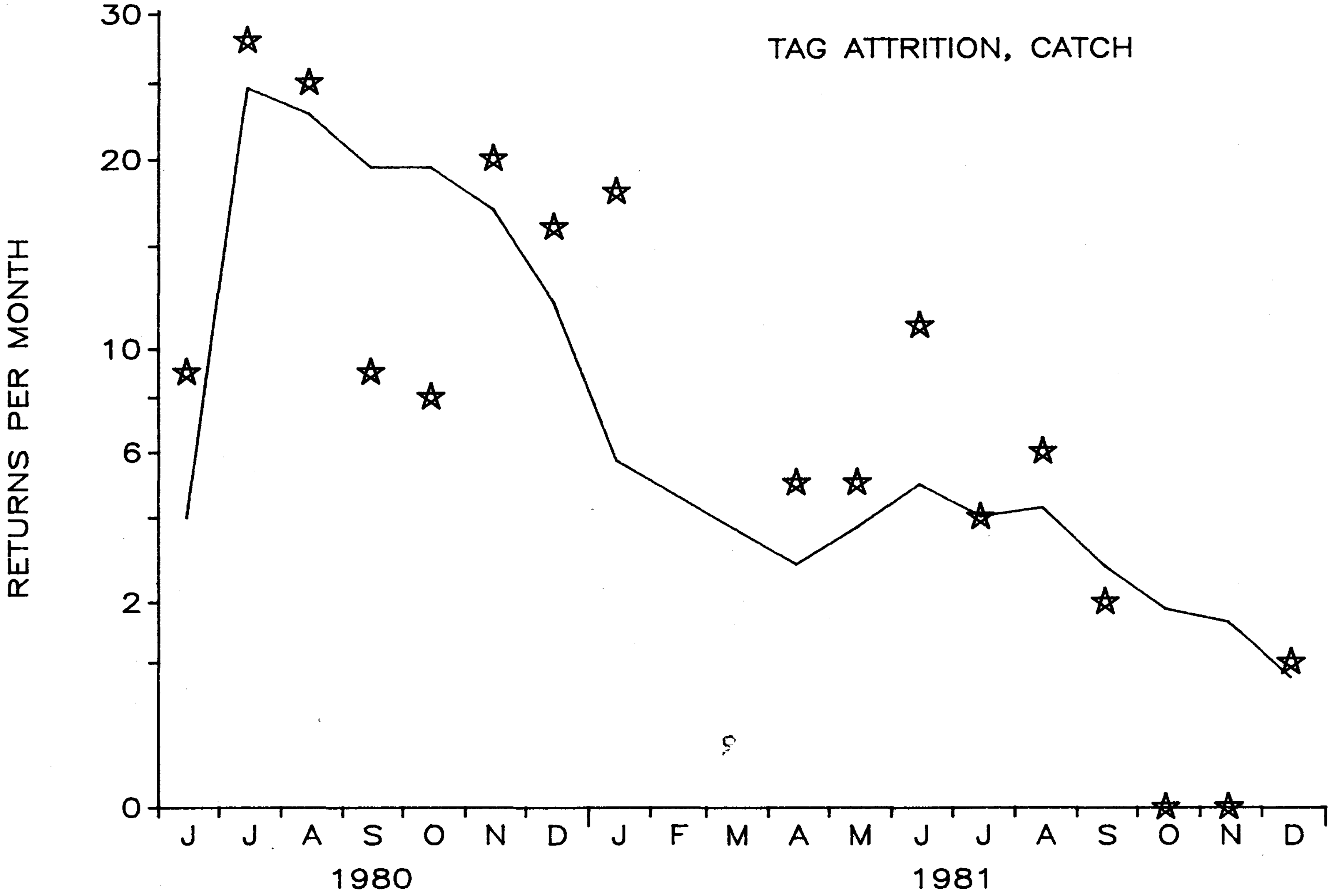


FIGURE 6. EXAMPLE TAG ATTRITION CURVE FOR AN INDIVIDUAL COUNTRY (Solomon Islands, June 1980).



5.2 Parameter Estimates from the Analytical Model

Parameter estimates obtained from the forms of the model in Table 1 are given in Table 4, along with their 95 per cent confidence ranges. The columns in Table 4 correspond to the data sets given in Table 2, except that data sets from releases in consecutive months (10-day periods for New Zealand) were combined in one fitting. The two Solomon Island data sets were treated separately since the times of release differ by two years and seven months, so the conditions in the fishery could not be assumed to be similar for the two data sets.

The first two rows in Table 4 are the average catch and effort values given for the input data sets in Table 2. The row labelled G_c gives an index of how well the catch forms of the model fit the data, and G_e, the fit of the effort forms (effort data were not available for all areas). The value given in each case is the proportion of the total variance in the observed data that is removed by fitting the model. That is,

$$\left.\begin{matrix} G_c \\ G_e \end{matrix}\right\} = 1 - \frac{S_{min}/(n-2)}{\text{total variance}} \qquad (15)$$

where the total variance is the variance of square roots of the observed return rates in the input data set about the mean of the square roots.

Table 5 gives the parameter estimates obtained by fitting the variable attrition form of the model (Equation 12) to the data sets for which effort data were available. For the results given in Table 5, the parameter $\alpha\beta N_o$ was fixed in the fitting process to the values calculated from $\alpha\beta$ and N_o given in Table 2 (i.e. the same values used to obtain the results in Table 4). The quantities in row G are analogous to G_c and G_e defined above (Equation 15). The M and Q rows in Table 5 give, respectively, the estimates of attrition exclusive of fishing mortality, and catchability. For comparing the estimates of M with the results in Table 4, the values of Z_e minus F_e from Table 4 are given in the last row of Table 5.

The results obtained with Equation 12 (Table 5) are close in most cases to the corresponding results (Table 4) from the fixed attrition forms of the model. The proportion of variance removed by the model is not reduced by using Equation 12 (G_e in Table 4 and G in Table 5). The catchability estimates are likewise much the same in the two tables. The last two rows in Table 5 match well except for the New Zealand results. In this case the discrepancy between the variable attrition and fixed attrition forms of the model may be due to the large degree of seasonality in the New Zealand fishery, the resulting large variation in attrition being more easily accounted for by the variable attrition form than the fixed attrition forms of the model.

5.3 Discussion of the Estimates

The results given in Section 5.2 form the basis of Skipjack Programme reports to individual countries. Detailed discussion of the implications of these results to individual countries is deferred to these country reports.

TABLE 4. RESULTS FROM THE FORMS OF THE ANALYTICAL MODEL GIVEN IN TABLE 1 USING DATA GIVEN IN TABLE 2. The upper figure in each cell is the best parameter estimate, and if given, the lower two figures are the 95 per cent confidence limits. Some numbers have exponential multiplers of the form, for example, 19E3. This has the meaning, 19×10^3. The confidence limits carry the same multipliers as the estimates they refer to, but the multipliers are not shown. The symbols that label each row are defined below. Effort data was not available for all data sets, therefore there are blank cells in the effort row as well as in rows of quantities that depend on the effort value. Bracketed abbreviations under column headings refer to the computer files that contain tagging data and catch statistics.

	Aggregate data (AGGPLO)	Papua New Guinea (P79C)	Solomon Islands 1977 (SOF3)	Solomon Islands 1980 (SOF1)	Fiji (FIJPLO)	Gilbert Group (KIRPLO)	Society Islands (SOCPLO)	New Zealand (ZC1.2)
$\bar{C}$	19E3	2000	1200	2200	350	20	100	2300
$\bar{E}$		670	340	490	120			150
G_c	0.95	0.96	0.69	0.63	0.80	0.91	0.36	0.91
G_e		0.95	0.52	0.68	0.68			0.85
P	3.0E6 2.5 - 3.7	35E3 27 - 45	49E3 25 - 124	89E3 48 - 185	39E3 20 - 79	1.0E3 0.5 - 2.1	9.7E3 1.8 - 67.1	13E3 10 - 17
Q		0.90E-4 0.60 - 1.44	0.27E-4 0.08 - 0.65	0.56E-4 0.29 - 0.96	0.81E-4 0.36 - 1.64			0.0012 0.0008 - 0.0017
Z_c	0.17 0.15 - 0.20	0.38 0.32 - 0.46	0.23 0.13 - 0.34	0.15 0.07 - 0.26	0.19 0.13 - 0.26	0.37 0.16 - 0.69	0.59 0.20 - 1.30	0.38 0.30 - 0.52
Z_e		0.47 0.35 - 0.65	0.14 0.01 - 0.29	0.16 0.09 - 0.26	0.19 0.12 - 0.26			0.39 0.29 - 0.62
F_c	0.63E-2 0.51 - 0.77	0.058 0.045 - 0.075	0.024 0.010 - 0.049	0.025 0.012 - 0.046	0.0091 0.0044 - 0.0174	0.019 0.009 - 0.038	0.010 0.001 - 0.055	0.17 0.13 - 0.22
F_e		0.061 0.040 - 0.097	0.0092 0.0027 - 0.0223	0.027 0.014 - 0.047	0.0097 0.0043 - 0.0197			0.18 0.12 - 0.25
T	0.52E6 0.46 - 0.59	13E3 11 - 16	11E3 7 - 19	13E3 9 - 22	7.3E3 4.8 - 11.4	0.38E3 0.24 - 0.64	5.7E3 2.1 - 20.1	5.0E3 3.8 - 7.0
H_c	0.037 0.032 - 0.042	0.15 0.13 - 0.18	0.11 0.06 - 0.17	0.16 0.10 - 0.25	0.048 0.031 - 0.072	0.052 0.031 - 0.083	0.017 0.005 - 0.048	0.46 0.33 - 0.60
H_e		0.13 0.10 - 0.16	0.067 0.034 - 0.270	0.17 0.11 - 0.24	0.056 0.030 - 0.084			0.46 0.29 - 0.65

Symbol definitions:

$\bar{C}$ = average catch during tagging experiment (tonnes/month)
$\bar{E}$ = average effort during tagging experiment (effort units/month)
G_c = per cent of variance explained by model with input of catch data
G_e = per cent of variance explained by model with input of effort data
P = standing stock (tonnes)
Q = catchability (effort units^{-1}, sets in New Zealand, vessel days elsewhere)
Z_c = attrition (months^{-1}) with input of catch data
Z_e = attrition (months^{-1}) with input of effort data
F_c = fishing mortality (months^{-1}) with input of catch data
F_e = fishing mortality (months^{-1}) with input of effort data
T = throughput (tonnes/month)
H_c = harvest ratio (dimensionless) with input of catch data
H_e = harvest ratio (dimensionless) with input of effort data

TABLE 5. RESULTS FROM EFFORT MODEL WITH VARYING ATTRITION. The format of the entries in each cell is the same as in Table 4. For comparing **M** with results from the fixed attrition model, values of attrition minus fishing mortality ($Z_e - F_e$) from Table 4 are included in the last row of this table.

	Papua New Guinea	Solomon Islands 1977	Solomon Islands 1980	Fiji	New Zealand
G	0.95	0.51	0.68	0.68	0.85
Q	0.88E-4 0.60-1.3	0.26E-4 0.08-0.64	0.55E-4 0.39-0.96	0.79E-4 0.35-1.56	0.13E-2 0.09-0.18
M	0.41 0.31-0.55	0.13 <0.01-0.27	0.14 0.07-0.22	0.18 0.12-0.24	0.35 0.25-0.58
$Z_e - F_e$	0.41	0.13	0.13	0.18	0.21

5.3.1 Reliability of the parameter estimates

It should be emphasised that the confidence limits reported in Tables 4 and 5 do not reflect uncertainty in the values of $\alpha\beta N_o$ and ψ, and therefore the confidence ranges in the tables are minimum estimates.

Accounting for uncertainty in ψ (the type 2 shedding rate) would directly affect the confidence ranges of attrition, and as a result the estimates of throughput and harvest ratio to a similar extent. The 95 per cent confidence range of ψ is [0.0031--0.0116] months^{-1}. However, given the magnitude of ψ (0.0073 months^{-1}) relative to the attrition rate (0.17 months^{-1} in the aggregate case), consideration of the variance of ψ is unlikely to expand the confidence ranges of any of the above parameters by more than 10 per cent.

Accounting for the uncertainty in the value of $\alpha\beta N_o$ would affect the confidence ranges of all parameters except the attrition, Z_c and Z_e. The uncertainty in N_o is small. As shown above for the aggregate case (Section 4.2), it must be between 139,960 and 140,700, a 0.5 per cent range. The uncertainties in α and β are much higher. The range between the best and worst case estimates of β can be large (Table 3), and the assumed value of α is a guess based on little quantitative information. Experiments are underway to get more precise quantitative information on α and β, but in the meantime, it should be emphasised that the confidence ranges given in Tables 4 and 5 would be larger if uncertainties in α and β had been included. Figures 3 and 4 give an idea of how much the confidence regions of **M** and **Q** could expand if the uncertainty in $\alpha\beta$ were taken into account. However, it is important to note from Figures 3 and 4 that the effect of uncertainty in $\alpha\beta$ is dependent on whether $\alpha\beta$ is in the upper or lower part of its possible range of [0--1.0]. Thus the confidence range of M is considerably reduced if $\alpha\beta$ is known to be greater than 0.4, but more precise definition of $\alpha\beta$ within the range [0.4--1.0] would not narrow the confidence range of M much further.

It must be stressed that the parameter values for individual countries, and overall, were estimated for relatively short time periods. Steady state is not an unrealistic assumption for the one-to- three-year duration of the tagging experiments, but need not hold true over longer periods if fisheries and recruitment change. Significant changes have occurred in the last few years to several fisheries in the region; and there is evidence of periodic major environmental changes to tropical central and western Pacific waters (Wyrtki 1975; Donguy and Henin 1978) that presumably could affect recruitment.

5.3.2 Standing stock and throughput

The aggregate estimate of skipjack standing stock is three million tonnes and its 95 per cent confidence range is 2.5 to 3.7 million tonnes (Table 4). The aggregate estimate of throughput is 520,000 tonnes/month and its confidence range is 460,000 to 590,000 tonnes/month. The estimate of annual throughput is 6.2 million tonnes (5.5 to 7.1 million tonnes). The precise boundaries of the area to which the aggregate estimates correspond are not well defined (see Section 3.6.3). The effective area presumably includes more than the areas within the region where tagging took place, but whether it covers the whole study area roughly defined by the boundaries of the South Pacific Commission plus the waters of northern New Zealand and eastern Australia (Figure 1) is a subject for further simulation analysis.

The standing stock in different areas, under conditions of uniform stock density, would be proportional to the size of the area. Therefore differences among individual country results would reflect the size of the areas covered by the different tagging experiments, which by design, roughly covered the area of the locally based fisheries. Such is evident in Table 4 in the comparison of P for the Gilbert Group with P for the other individual countries. The Gilbert Group estimate is smaller than all others, and the "fishery" was a single vessel survey concentrated near a single atoll, a much smaller area than the other individual country fisheries. The aggregate estimate of P is much larger than the sum of estimates for individual countries and territories in Table 4 because these are only a portion of all the countries and territories included in the aggregate. Between these extremes, comparisons among individual countries are difficult to interpret, firstly because of the large overlapping confidence intervals, and secondly because the effective area covered by the fisheries during the tagging experiment is difficult to evaluate. As discussed in Section 3.6.3, diffusive movement of the fish can make the effective area somewhat larger than the fished area, even if the latter is constant during the experiment.

Throughput, T, should be only approximately proportional to the size of the fished area since throughput is the product of attrition and standing stock, and attrition has a component due to emigration which is expected, *a priori*, to vary inversely with the size of the fished area.

5.3.3 Attrition

Attrition and its components are not expected to be proportional to the area covered by the experiment. However, attrition is not necessarily independent of area because attrition estimates include a component due to dispersive movement of fish. This component tends to increase in importance with decreasing size of the area under consideration. Therefore the attrition is expected to vary inversely with area, and, for large areas, approach a dispersion-free attrition rate. It is probably for this reason that the aggregate attrition estimate was lower than all but one of the individual country estimates (though only three have non-overlapping confidence intervals).

Under the assumption of steady state, the attrition rate is also the population turnover rate. Simulation modelling (summarised in Section 3.6.2) showed that in a non-steady state situation the attrition estimate would tend to reflect the average attrition over the time of the experiment. Thus if the lack of steady state is attributable to seasonal fluctuations, and tags are returned over a period of at least one year, then the attrition estimate would reflect the yearly average population turnover. Furthermore, simulation showed that in non-equilibrium conditions (i.e. when the sum of inputs is different from the sum of outputs), the estimate of Z_c tends to be closer to the sum of inputs and Z_e closer to the sum of outputs. The implication is that if Z_c is larger than Z_e, then the population is increasing, whereas if Z_c is less than Z_e, then the population is decreasing. The only cases in which there were appreciable differences between Z_c and Z_e were the results from the 1977 Solomon Islands data set ($Z_c > Z_e$) and from the Papua New Guinea data set ($Z_e > Z_c$).[2] It may be fortuitous that the increasing trend in P in Solomon Islands (October 1977 versus June 1980) was consistent with that predicted by the 1977 estimates of Z_c and Z_e, since the confidence intervals for the two estimates of P are large and overlapping.[3] The trend predicted for Papua New Guinea could not be checked because there was no further tagging experiment in the waters of Papua New Guinea.

The aggregate estimate of attrition is 0.17 months^{-1} with a confidence range of [0.15--0.20] months^{-1}. When fishing mortality, F, is subtracted the remaining attrition is 0.16. Joseph and Calkins (1969) report a comparable estimate of skipjack attrition, excluding F, of 0.14 months^{-1} from a tagging experiment in the northern zone of the eastern Pacific fishery. Ssentongo and Larkin (1973) give a method for calculating

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[2] The confidence regions given in Table 4 are not relevant in judging the significance of a difference between estimates of Z_c and Z_e when these parameters are obtained from the same data set. This is because there is likely to be a high positive co-variance between the two estimates, which would tend to minimise the variance of the difference between the estimates.

[3] In this case where the results from two independent data sets are compared, the confidence regions in Table 4 are relevant.

attrition[4] in exploited fish populations given the length of fish at recruitment, the mean length in the catch, and values for the parameters of the von Bertalanffy growth model. For skipjack, assuming a length at recruitment of 38 cm and a mean length in the catch of 50.4 cm (the mean length of skipjack tagged by the Skipjack Programme), and using values of 62.5 cm and 0.17 months^{-1} for L_∞ and K respectively from the von Bertalanffy model (Sibert, Kearney and Lawson MS), the predicted value of attrition is 0.24 months^{-1}, which drops to 0.23 when our estimate of F is subtracted. Pauly (1979) determined a regression equation for predicting attrition of a fish species, excluding F, given its von Bertalanffy parameter values and its mean environmental temperature. The regression equation was based on attrition estimates from a wide variety of fish families (including skipjack amongst several examples of scombrids). A prediction from the equation is therefore what would be expected of fish in general, for a given set of the independent variates, namely L_∞, K, and water temperature. Assuming the values given above for L_∞ and K and a mean water temperature of 25°C, the predicted attrition for skipjack is 0.18 months^{-1}. This estimate is similar to our overall estimate, to that of Joseph and Calkins and to that obtained by the method of Ssentongo and Larkin. The consistency of these estimates increases the confidence in their accuracy.

5.3.4 Catchability

Catchability coefficients, Q, for pole-and-line gear in Table 4 range from 0.000027 per fishing day for November 1977 tagging in Solomon Islands to 0.000090 per fishing day for May-June 1979 tagging in Papua New Guinea; however, all estimates have overlapping confidence intervals and little can be made of the differences amongst countries. Q for purse-seiners in New Zealand, measured per set, is 0.0012 and the 95 per cent confidence range does not overlap with the confidence range for pole-and-line estimates. Purse-seine Q per set can be converted to Q per fishing day, in order to be in the same time units as pole-and-line Q, by using the average of 1.5 sets per fishing day for the 1979/1980 and 1980/1981 fishing seasons in New Zealand (Argue and Kearney 1983). So calculated, Q for purse-seiners, 0.0018, is 28 times higher than the average of the Q values in Table 4 for pole-and-line gear. This probably reflects greater fishing power for purse-seiners and greater skipjack vulnerability in the coastal waters of New Zealand.

5.3.5 Harvest ratio

Estimates of harvest ratios based on catch, H_c, and their confidence limits were, with exception of 1977 Solomon Islands results, very similar to harvest ratios and confidence limits based on effort, H_e (Table 4). For 1977 Solomon Islands results, H_c (0.11) was greater than H_e (0.067), perhaps reflecting a population increase over the duration of these experiments as hypothesised in Section 5.3.3. In general, H_c values were low, 0.017 to 0.17, and had overlapping confidence intervals. The value for New Zealand was relatively high, 0.46, with a confidence interval of [0.33--0.60].

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4 The term usually used is "mortality" or "natural mortality". Joseph and Calkins (1969) state that their estimate includes emigration, and most other reported estimates of mortality in fish probably also include non-mortal loss factors. We have therefore used the word "attrition".

Having defined the harvest ratio and having obtained estimates thereof, it is useful to have a bench mark to show whether a given estimate is high, indicating heavy fishing pressure, or low, indicating the possibility for increased yield. The harvest ratio is analogous to the X-factor of Gulland (1971), who defines X such that

$$Y = X M_V P_V \tag{16}$$

where Y is the potential yield, M_V is the virgin turnover, and P_V is the virgin stock size. On the basis of two arguments, Gulland suggests that the maximum yield from a fishery is obtained with a value of approximately 0.5 for X. One argument is based on the Schaefer model and has been shown by Francis (1974) to be unreliable. The other argument is based on the Beverton-Holt yield per recruit model wherein for a broad range of conditions, the maximum yield per recruit is obtained with a value close to 0.5 for X. It should be noted that the sustainability of yields under this second argument depends on an assumption of constant recruitment, regardless of standing stock level.

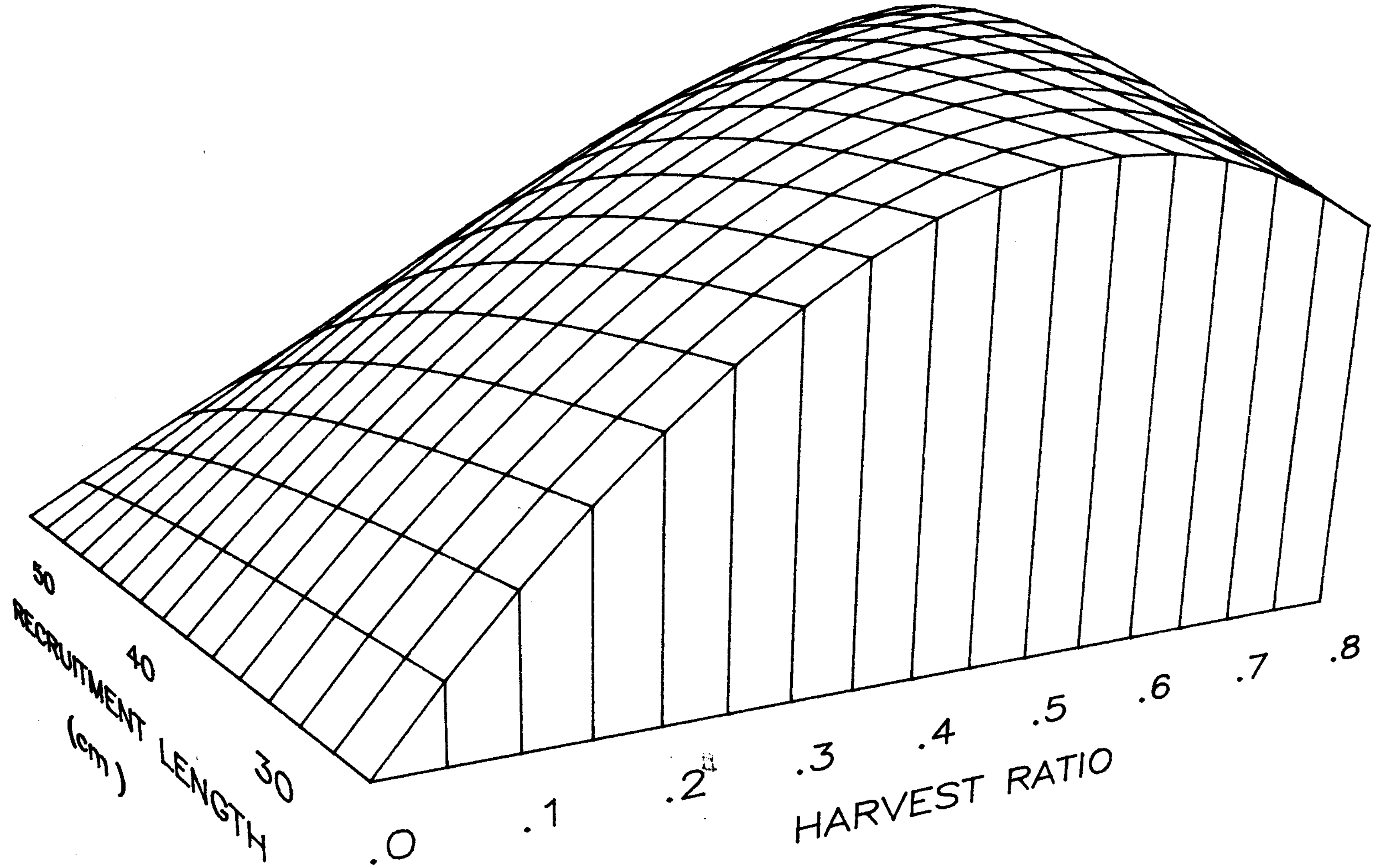
The factors defining an optimal value of X under the Beverton-Holt model are the natural mortality, the size at recruitment to the fishery, and the parameters of the von Bertalanffy growth model. Figure 7 is a plot of the Beverton-Holt yield for various levels of harvest ratio and size at recruitment, and using the assumed values of K and L_∞ from Section 5.3.3 and an assumed natural mortality of 0.16 month^{-1}. Given a size at recruitment between 36 and 40 cm, and constant recruitment, the harvest ratio producing maximum yield is seen to be in the neighbourhood of 0.5 to 0.7.

The harvest ratio estimate, H_C in Table 4, is low (0.04) for the aggregate case, implying that fishing is having little impact on the skipjack resource in the study area as a whole. For individual countries with well-established commercial fisheries, harvest ratios are higher (0.15--0.46), while those countries with small or fledgling fisheries have low harvest ratios (<0.1). Low harvest ratios for a large part of the study area imply that there is a potential for greatly increased skipjack yield, both within individual countries and in the study area as a whole.

6.0 CONCLUSIONS

Analyses in this paper provide evidence that the resource of skipjack in the study area of the Skipjack Programme is large, its rate of turnover is high, and the rate of mortality due to fishing during the study period was only a small fraction, less than 0.05, of the rate of turnover. This implies that skipjack catches over the whole study area could be substantially increased from those of the study period. The tag recapture and attrition model used to obtain aggregate estimates and confidence intervals for standing stock, turnover and fishing mortality was applied to tagging data for countries and territories in the study area with skipjack fisheries for which catch statistics were available. Parameter estimates and confidence intervals so derived suggest that the impact of fishing in the smaller areas is larger than the overall impact of fishing, although in every case there appears to be potential for some increase in catch. These

FIGURE 7. BEVERTON-HOLT YIELD SURFACE. Relative yield is plotted as a function of harvest ratio and length at recruitment. Natural mortality assumed to be 0.16 $month^{-1}$. L_∞ and K of the von Bertalanffy growth model assumed to be 62.5 cm and 0.17 $month^{-1}$ respectively (Sibert, Kearney and Lawson MS).



estimates form the basis for final Skipjack Programme reports in which the status of the skipjack resource within the waters of individual countries and territories is assessed.

The provision of confidence intervals for resource estimates is a principal part of this paper. Confidence intervals presented demonstrate the wide ranges in the probable values of the numerous parameters estimated from the available data. They therefore emphasise the need for care when using these estimates for management purposes. Fisheries in the study area are changing and environmental variability will undoubtedly have its effect. Management practices must take this uncertainty into account, and estimates should continue to be refined as more data become available.

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APPENDIX. EFFECT OF SIZE AT RELEASE ON ATTRITION

In order to test for the effect of size at release on attrition rates, the aggregate tagging data and seven subsets of the data were broken into three categories of size at release, <45 cm, 45-55 cm, and >55 cm. Six subsets consisted of individual country data with enough returns in at least two of the size categories so that the fitting procedure would converge. One additional subset was made up of returns from three countries which in combination gave enough returns for convergence of the fitting procedure. The distribution of total returns in the various size categories is given in Table A. These totals are not necessarily the same as the totals of returns in Table 2 because in Table A, tags were selected with regard to the existence of accurate length measurements at release, but without regard to various other selection criteria involved in assembling the data sets in Table 2.

The aggregate and six of the subsets were put into months-at-large categories in the same way as the aggregate data in Table 2. The New Zealand subset was broken into 10-day periods. The form of the analytical model in Equation 5 was fitted to the data. A constant catch rate was used for individual countries as well as for the aggregate data, under the assumption that the effects of changing catch rate on attrition estimates would be roughly equivalent for the different size classes. For simplicity, the quantities $\alpha\beta$ and ψ were set to one and zero respectively. In any case, these quantities have no effect on the total tag attrition, A_C, the parameter of interest in this case.

The resulting attrition estimates are given in Table B. Because of the way these results were obtained, they should not be used to compare attrition rates between countries, but they can be used to compare size classes within a country or within the aggregate data set. The aggregate and all individual country results show that there are no significant differences between the small and medium size fish. The aggregate data show a significantly higher attrition rate for the large size fish. This result is confounded because the size distribution of tagged skipjack varies between countries (Table A). Comparisons of size classes were carried out for countries or small groupings of countries in which there were sufficient data in more than one size category. None of the differences between size classes was significant. That five of the seven within country comparisons show a higher attrition for the large fish is perhaps indicative of a trend, even though, individually, none of the differences was significant. This observation was tested for significance by a non-parametric paired comparison test, assuming a prior expectation of increased attrition for the larger size (one-tail test). The statistical argument is as follows. Each within-country comparison could go one of two ways, a positive or negative change in attrition with increased fish size. Therefore for seven comparisons the number of possible outcomes is 2^7. There are 29 possible outcomes as extreme as, or more extreme than, that observed, 21 with two negative comparisons, 7 with one negative comparison, and one with no negative comparisons. Thus under the null hypothesis of equal chance of each comparison going either way, the probability of an outcome as extreme as that observed is $29/2^7=0.23$, and the null hypothesis is accepted.

A large proportion of the large size fish were released in Papua New Guinea (Table A), where the attrition rate was particularly high (Table 4). It is thus likely that the higher attrition rate for the large sizes in the aggregate data was due to the combination of these two factors.

TABLE A. DISTRIBUTION OF TAG RETURNS AMONG COUNTRIES FOR THREE CATEGORIES OF SIZE AT RELEASE

	Fork Length			Total Tag Returns
	<45 cm	45-55 cm	>55 cm	
Fiji	139	1380	114	1633
Solomon Islands	157	290	55	502
Papua New Guinea	14	573	311	898
Palau	204	52	51	307
Ponape	1	95	44	140
New Zealand	100	536	8	644
Wallis	3	67	6	76
Tuvalu	1	21	6	28
Gilbert Group	3	354	8	365
Other	12	168	27	207
TOTAL TAG RETURNS	634	3536	630	4800

TABLE B. ESTIMATES OF TAG ATTRITION WITH 95 PER CENT CONFIDENCE INTERVALS FOR THREE CATEGORIES OF SIZE AT RELEASE. Results are given for the aggregate data set and for individual country subsets with enough returns in more than one size category so that the fitting procedure would converge. One country subset, WTG, is a combination of results from Wallis and Futuna, Tuvalu and the Gilbert Group of Kiribati. This was done in order to get one more subgrouping with enough returns in more than one size category.

	Fork Length		
	<45 cm	45 - 55 cm	>55 cm
Aggregate	0.17 [0.15--0.20]	0.17 [0.14--0.20]	0.27 [0.22--0.33]
Fiji	0.18 [0.10--0.32]	0.15 [0.09--0.24]	0.12 [0--0.33]
Solomon Islands	0.17 [0.11--0.26]	0.18 [0.12--0.25]	0.27 [0.17--0.42]
Papua New Guinea		0.34 [0.21--0.58]	0.63 [0.42--0.92]
Palau	0.21 [0.17--0.27]	0.15 [0.08--0.25]	0.37 [0.19--0.69]
Ponape		0.20 [0.13--0.29]	0.22 [0.06--0.48]
New Zealand	1.1 [0.9--10.4]	1.2 [0.9--10.5]	0.12 [0--0.33]
WTG		0.24 [0.14--0.46]	0.30 [0.07--0.69]