A TWO-FISHERY TAG ATTRITION MODEL FOR THE ANALYSIS OF MORTALITY, RECRUITMENT AND FISHERY INTERACTION

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PREFACE

The Skipjack Survey and Assessment Programme, which commenced in August 1977 and concluded in September 1981, was an externally funded part of the work programme of the South Pacific Commission. The governments of Australia, France, Japan, New Zealand, United Kingdom and the United States of America provided funding for the Programme, which worked in the waters of all of the countries and territories within the area of the South Pacific Commission and in New Zealand and Australia.

The Skipjack Programme has been succeeded by the Tuna and Billfish Assessment 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 work described here is part of investigations begun by the Skipjack Programme to evaluate interactions between skipjack fisheries using tag release and recapture data. Whatever measure of success achieved depends to a large extent on previous work (Kleiber, Argue & Kearney 1983; Kleiber, Argue, Sibert & Hammond 1984). All members of the Tuna and Billfish Assessment Programme provided useful advice and criticism. In particular, we would like to thank A.W. Argue for helping to keep practical ends in view and David Fournier for suggesting more reasonable mathematical interpretations.

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.S. Farman, D. Fournier, R.D. Gillett, L.S. Hammond, J.R Sibert, W.A. Smith and M.J. Williams; Research Assistant, Veronica van Kouwen; and Programme Secretary, Carol Moulin.

Tuna Programme
South Pacific Commission

ABSTRACT

This article briefly reviews simple models of tag attrition used for analysis of tag and recapture experiments as applied to single fisheries for skipjack tuna. The problems of separating attrition into components due to natural mortality and migration are discussed. A model of tag attrition in two fisheries is presented which explicitly includes migration terms. These terms enable the separation of mortality from emigration and the calculation of interaction between fisheries. The model is fitted to an example data set derived from tagging of skipjack tuna in the Papua New Guinea and Solomon Islands pole-and-line fisheries. It is concluded that models of tag attrition and exchange can be used to obtain reasonable estimates of population parameters. For the example data set, it would appear that migration is a minor component of attrition and that the fisheries in the two countries affect one another to a very limited extent.

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1.0 INTRODUCTION

Analysis of tag return data is often used to assess populations of skipjack tuna (Katsuwonus pelamis), e.g. Joseph & Calkins (1969). Between 1977 and 1981, the Skipjack Survey and Assessment Programme of the South Pacific Commission tagged and released over 140,000 skipjack throughout the central and western Pacific Ocean (Kearney 1983). Models of population dynamics were used to analyse the rate of return of tags yielding estimates of various parameters of the skipjack populations and fisheries in the study area. (Kleiber, Argue & Kearney 1983). The parameter estimates were used further to calculate a statistic which expresses the potential for interaction between various pairs of fisheries (Kleiber, Argue, Sibert & Hammond 1984). The derivation, use and evaluation of these models can be found in Kleiber et al. (1983) and Kleiber, Sibert & Farman (ms.).

The models used by Kleiber et al. (1983) as well as those of Joseph & Calkins (1969) lack terms explicitly describing movement of fish between fisheries. Furthermore, as discussed by Joseph & Calkins (1969), emigration of fish out of the population is confounded with other components of attrition such as natural mortality, and immigration of fish into the population is confounded with other components of accretion such as recruitment. In fact, most models of tag attrition, almost by definition, lack terms describing accretion of fish to the population. The purpose of this paper is to present a model which explicitly includes the exchange of fish between two fisheries. The explicit inclusion of exchange between fisheries enables the components of attrition and accretion due to mortality, emigration, and immigration to be separated. In order to present a context for the development of the fishery exchange model, previously used models are briefly reviewed. The model is then fitted to an example data set.

2.0 METHODS

2.1 Single-Fishery Model

In differential equation form, the previously used single-fishery model is

$$\frac{dP}{dt} = -(M+F)P + R \tag{1}$$

where P is the biomass of fish (tonnes), F is the attrition due to fishing (per month), M is natural mortality (per month), R is recruitment (tonnes per month), and t is time (months). Recruitment is assumed to be independent of population size, occurs continuously, and implicitly includes immigration, growth into the size classes vulnerable to the fishery, and reproduction. Attrition $(M+F)$, the total losses from the population, also includes a diversity of processes. Fishing mortality is explicitly included as the parameter F. Natural mortality (M), however, subsumes all causes of attrition not attributable to fishing such as emigration, growth out of the size classes vulnerable to the fishery, death from "natural" causes, plus all other processes which remove fish from the population. This simple model describes a population which is fundamentally stable. It will closely approach a steady state from arbitrary initial conditions with

$$\langle P \rangle = \frac{R}{(M+F)} \tag{2}$$

after a period of time, typically less than 12 months with parameters applicable to skipjack.

For a population of fish described by Equation 1, the appropriate model for the number of tags at large is given by

$$\frac{dN}{dt} = -(M+F)N \qquad \text{At } t=0,\ N = \alpha \cdot N^* \tag{3}$$

where N is the number of tags at liberty, α is the proportion of tags surviving initial losses immediately after tagging, N^* is the number of tags released, and the other parameters are as above. The equation merely states that, after initial losses, the processes controlling the number of tags at liberty are identical to those regulating the population as a whole without recruitment. Equation 3 is the starting point in the derivation of the Joseph & Calkins (1969) model I of tag attrition, and may be found in many other discussions of tag attrition.

The rate of return of tags from the fishery can be expressed as

$$\frac{dr}{dt} = \beta F N \tag{4}$$

where r is the number of tags returned, β is the proportion of tags caught by the fishery which are actually returned with useful information, and the other variables are defined as above. The solutions of Equations 3 and 4 are the basis for the tag attrition model described in Kleiber et al. (1983).

2.2 Two-Fishery Model

2.2.1 Formulation: stock dynamics

The two-fishery model consists of a pair of simultaneous differential equations analogous to Equation 1

$$\frac{dP_1}{dt} = -(M_1+F_1+T_{12})P_1 + T_{21}P_2 + R_1 \tag{5}$$

$$\frac{dP_2}{dt} = -(M_2+F_2+T_{21})P_2 + T_{12}P_1 + R_2$$

where P_1 and P_2 are biomass of fish in populations 1 and 2, F_1 and F_2 are instantaneous fishing mortality rates for populations 1 and 2, M_1 and M_2 are instantaneous natural mortality rates for populations 1 and 2, T_{12} is the instantaneous transfer rate from population 1 to population 2, T_{21} is the instantaneous transfer rate from population 2 to population 1, and R_1 and R_2 are recruitments to populations 1 and 2. The difference between this model and the previous one (Equation 1) is that the parameters T_{12} and T_{21} have been added. The terms $-T_{12}P_1$ and $T_{21}P_2$ in Equations 5 represent components of attrition and accretion for population 1. Similarly, the terms $-T_{21}P_2$ and $T_{12}P_1$ in Equations 5 represent components of attrition accretion for population 2. These terms couple the two fisheries, and partition both accretion and attrition into components due to migration to and from the other population. If the migration parameters, T_{12} and T_{21}, in Equations 5 are equal, then the model becomes diffusion-like with movement between populations proportional to differences in population size.

This system of equations is also unconditionally stable because it inevitably tends to equilibrium. The equilibrium values of P_1 and P_2, found by setting the derivatives in Equations 5 equal to zero, are

$$\langle P_1 \rangle = \frac{T_{21}R_2 + A_2R_1}{A_1A_2 - T_{12}T_{21}} \qquad (6)$$

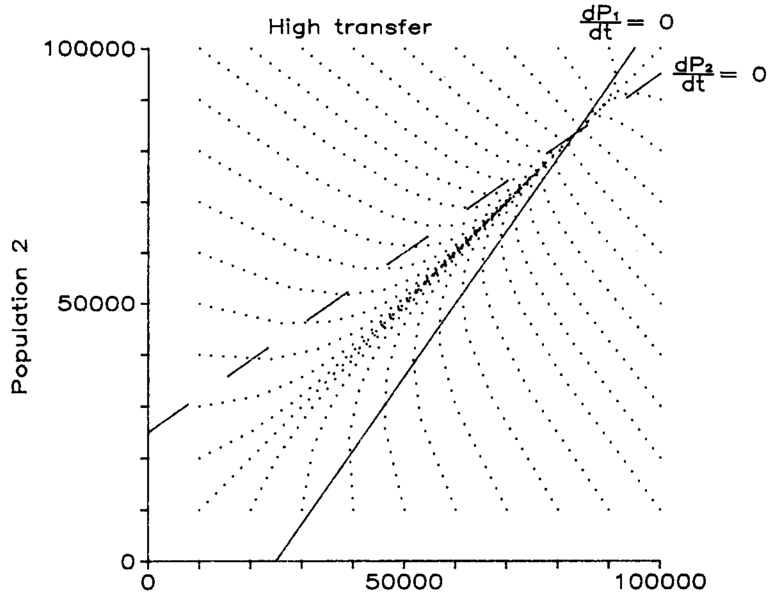
$$\langle P_2 \rangle = \frac{T_{12}R_1 + A_1R_2}{A_1A_2 - T_{12}T_{21}}$$

where $A_1 = M_1 + F_1 + T_{12}$ and $A_2 = M_2 + F_2 + T_{21}$. The behaviour of the model can be explored by plotting the values of P_2 as a function of the values of P_1. Figure 1 demonstrates the relationship between P_1 and P_2 at two levels of mortality and transfer. In both cases, the total attrition rate, fishing mortality, and recruitment are the same, but in the upper figure, T_{12} and T_{21} are both high and M_1 and M_2 are both low (high transfer), while in the lower figure, T_{12} and T_{21} are both low and M_1 and M_2 are both high (low transfer). The two diagonal straight lines are values of P_1 and P_2 found by setting Equations 5 equal to zero. The point where they cross satisfies Equations 6, and is the global steady state when both populations are in equilibrium. The curved dotted lines in Figure 1 are trajectories followed by the two populations when displaced from equilibrium. Each dotted line is 12 months long. Note that they invariably tend to the global equilibrium. All of this means that, if the system is displaced from global equilibrium it will either return to the previous equilibrium point if the parameters are unchanged or it will reach a new equilibrium if the parameters are different. With reasonable numerical parameter values the system moves very close to equilibrium within 12 months.

Figure 2 shows the global equilibria for several values of R_1 and constant R_2 at the two previously used levels of mortality and transfer. As in the single-fishery model, the equilibrium population levels depend heavily on recruitment (Equations 2 and 6). If recruitment is low, equilibrium population size will be low also.

The slopes of the equilibrium lines in Figures 1 and 2 reflect the effects of the transfer terms. At low transfer, the equilibrium lines are nearly parallel to the axes indicating that there is little effect of one population on the other. At high transfer, the lines are more oblique indicating that there are larger interactions between the two populations.

FIGURE 1. BEHAVIOUR OF ONE POPULATION AS A FUNCTION OF THE OTHER IN THE TWO-POPULATION MODEL, EQUATIONS 5. The solid diagonal line represents the values of P_1 and P_2 which cause Equations 5 (dP_1/dt) to be zero. The dashed diagonal line represents the values of P_1 and P_2 which cause Equations 5 (dP_2/dt) to be zero. The dotted lines are the trajectories followed by the two populations when the system is displaced from its global equilibrium. The upper figure represents the case when transfer between populations is high ($T_{12}=T_{21}=0.28$) and mortality is low ($M_1=M_2=0.02$). The lower figure represents the case when transfer between populations is low ($T_{12}=T_{21}=0.02$) and mortality is high ($M_1=M_2=0.28$). In both the upper and lower figures total attrition, fishing mortality, and accretion are the same ($A_1=A_2=0.4$, $F_1=F_2=0.1$, and $R_1=R_2=10000$).



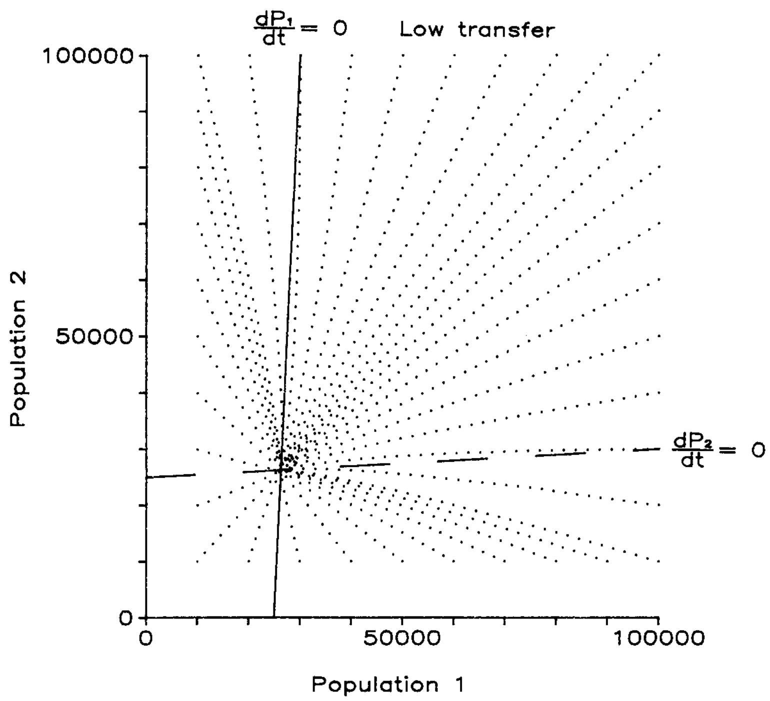
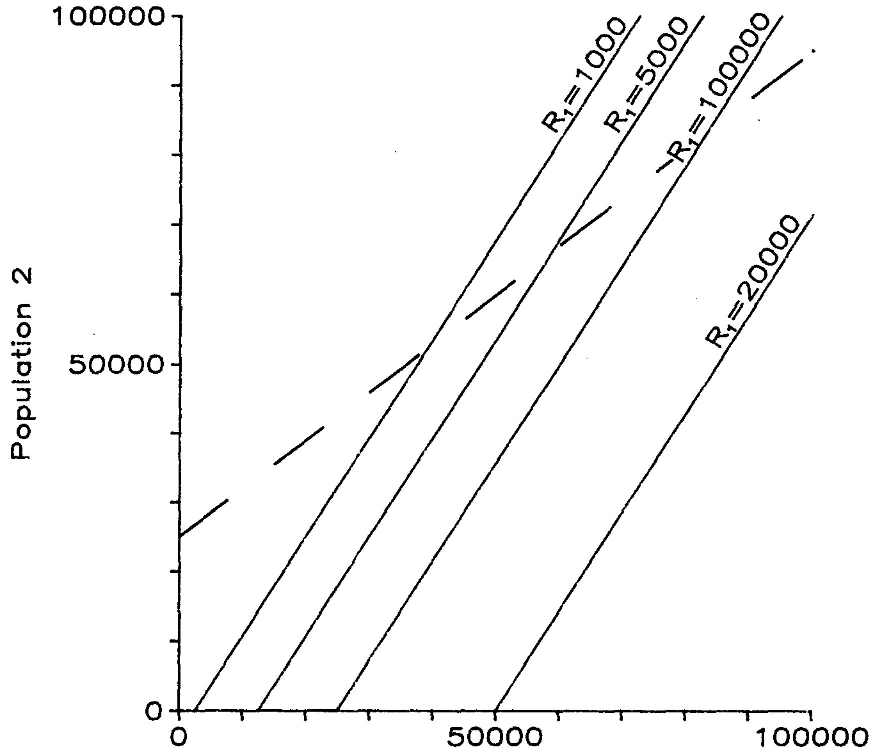
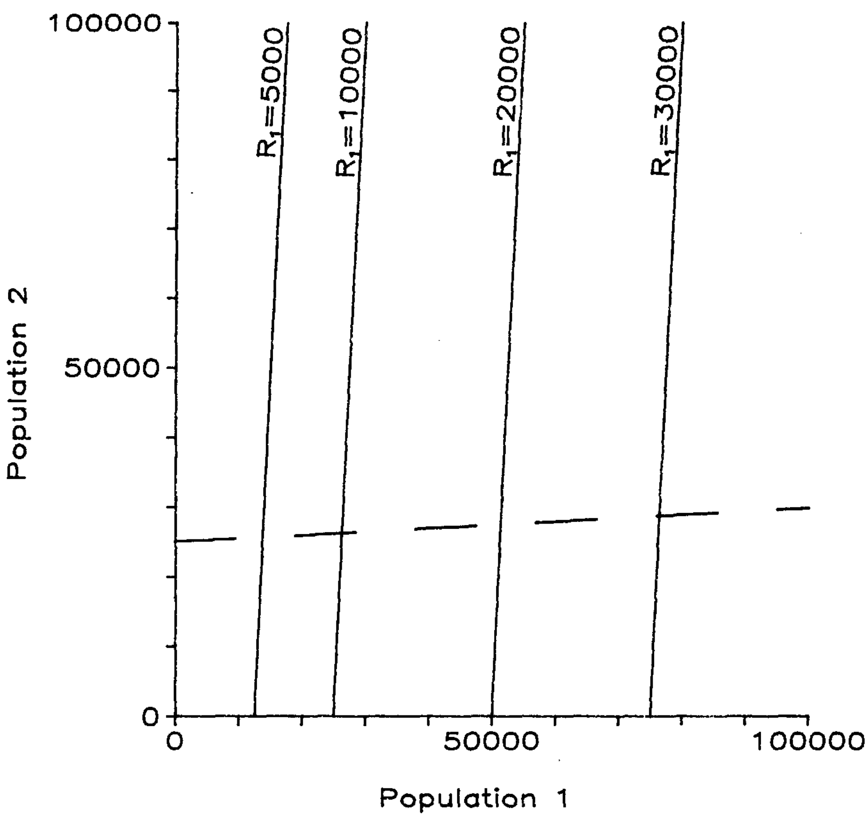


FIGURE 2. BEHAVIOUR OF ONE POPULATION AS A FUNCTION OF THE OTHER IN THE TWO-POPULATION MODEL, EQUATIONS 5, FOR SEVERAL VALUES OF R_1. Attrition and R_2 parameters for the upper and lower figures are the same as in Figure 1. The solid diagonal lines represent the values of P_1 and P_2 which cause Equations 5 (dP_1/dt) to be zero for the values of R_1 shown. The dashed diagonal line represents the values of P_1 and P_2 which cause Equations 5 (dP_2/dt) to be zero.





Letting $\langle C_1\rangle=F_1\langle P_1\rangle$ and $\langle C_2\rangle=F_2\langle P_2\rangle$, the catches (or yields) at equilibrium, it is possible to write Equations 6 in terms of $\langle C_1\rangle$ and $\langle C_2\rangle$.

$$\langle C_1\rangle = F_1\frac{T_{21}R_2+A_2R_1}{A_1A_2-T_{12}T_{21}} \tag{7}$$

$$\langle C_2\rangle = F_2\frac{T_{12}R_1+A_1R_2}{A_1A_2-T_{12}T_{21}}$$

These equations express the catch in one fishery at equilibrium as a function of conditions in both fisheries. The effects on one fishery of a change in the other can be expressed by calculating the partial derivatives of equilibrium catch in the recipient fishery with respect to parameters of the donor fishery, namely fishing mortality.

$$\frac{\partial\langle C_1\rangle}{\partial F_2} = -\frac{F_1T_{21}(T_{12}R_1 + A_1R_2)}{(A_1A_2 - T_{21}T_{12})^2} \tag{8}$$

$$\frac{\partial\langle C_2\rangle}{\partial F_1} = -\frac{F_2T_{12}(T_{21}R_2 + A_2R_1)}{(A_1A_2 - T_{21}T_{12})^2}$$

Noting that $dF_2/dC_2=1/P_2$ and that $dF_1/dC_1=1/P_1$,

$$\frac{\partial\langle C_1\rangle}{\partial C_2} = -\frac{F_1T_{21}}{A_1A_2 - T_{21}T_{12}} \tag{9}$$

$$\frac{\partial\langle C_2\rangle}{\partial C_1} = -\frac{F_2T_{12}}{A_1A_2 - T_{21}T_{12}}$$

These derivatives express the effect of a change in catch in the donor fishery on the equilibrium catch in the recipient fishery and can be used as unitless measures of interaction between fisheries.

2.2.2 Formulation: tag dynamics

Four separate groups of tag returns are appropriate to this model: N_{11} are the tags released into fishery 1 and at large in fishery 1, N_{12} are the tags released into fishery 1 and at large in fishery 2, N_{21} are the tags released into fishery 2 and at large in fishery 1, and N_{22} are the tags released into fishery 2 and at large in fishery 2. In the same manner that Equation 3 was derived from Equation 1, the number of tags at liberty in each group can be derived from Equations 5 and expressed as two pairs of simultaneous differential equations, shown with their initial conditions.

$$\frac{dN_{11}}{dt} = -(M_1+F_1+T_{12})N_{11} + T_{21}N_{12} \qquad \text{At } t=0,\ N_{11} = \alpha_1\cdot N_1^* \tag{10}$$

$$\frac{dN_{12}}{dt} = -(M_2+F_2+T_{21})N_{12} + T_{12}N_{11} \qquad \text{At } t=0,\ N_{12} = 0$$

$$\frac{dN_{21}}{dt} = -(M_1+F_1+T_{12})N_{21} + T_{21}N_{22} \qquad \text{At } t=0,\ N_{21} = 0$$

$$\frac{dN_{22}}{dt} = -(M_2+F_2+T_{21})N_{22} + T_{12}N_{21} \qquad \text{At } t=0,\ N_{22} = \alpha_2\cdot N_2^*$$

In analogy with Equation 4, there are also four equations for the instantaneous rate of tag return.

$$\frac{dr_{11}}{dt} = \beta_1 F_1 N_{11} \tag{11}$$

$$\frac{dr_{12}}{dt} = \beta_2 F_2 N_{12}$$

$$\frac{dr_{21}}{dt} = \beta_1 F_1 N_{21}$$

$$\frac{dr_{22}}{dt} = \beta_2 F_2 N_{22}$$

The Equations 11 can be used to describe the rate of returns of tags released in each fishery and recaptured in each fishery. The simultaneous solutions of Equations 10 and 11 form the basis for a two-fishery tag attrition model.

The solutions to Equations 10, obtained by applying a decoupling transformation (Arrowsmith & Place 1982) and integrating between time t and time $t+\Delta t$ are

$$N_{11(t)} = \frac{1}{1+ab}\left\{a\left[bN_{11(t-\Delta t)} + N_{12(t-\Delta t)}\right]e^{-u\Delta t} + \left[N_{11(t-\Delta t)} - aN_{12(t-\Delta t)}\right]e^{-v\Delta t}\right\} \tag{12}$$

$$N_{12(t)} = \frac{1}{1+ab}\left\{\left[bN_{11(t-\Delta t)} + N_{12(t-\Delta t)}\right]e^{-u\Delta t} - b\left[N_{11(t-\Delta t)} - aN_{12(t-\Delta t)}\right]e^{-v\Delta t}\right\}$$

$$N_{21(t)} = \frac{1}{1+ab}\left\{a\left[N_{22(t-\Delta t)} + bN_{21(t-\Delta t)}\right]e^{-u\Delta t} + \left[N_{21(t-\Delta t)} - aN_{22(t-\Delta t)}\right]e^{-v\Delta t}\right\}$$

$$N_{22(t)} = \frac{1}{1+ab}\left\{\left[N_{22(t-\Delta t)} + bN_{21(t-\Delta t)}\right]e^{-u\Delta t} - b\left[N_{21(t-\Delta t)} - aN_{22(t-\Delta t)}\right]e^{-v\Delta t}\right\}$$

where a and b, the coefficients of the decoupling transformation, are roots of the following two quadratic equations

$$T_{12}a^2 - (A_2 - A_1)a - T_{21} = 0 \tag{13}$$

$$T_{21}b^2 - (A_2 - A_1)b - T_{12} = 0$$

and

$$v = \frac{A_1 + bT_{21} + abA_2 + aT_{12}}{1 + ab} \tag{14}$$

$$u = \frac{A_2 - aT_{12} + abA_1 + bT_{21}}{1 + ab}$$

The solutions (12) can be substituted into Equations 11 and the resulting equations can be solved by integrating between time t and time $t+\Delta t$ to yield the total number of returns between time t and time $t+\Delta t$.

$$r_{11(t)} = \frac{\beta_1 F_1}{1+ab}\left\{a\left[\frac{bN_{11(t-\Delta t)} + N_{12(t-\Delta t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{11(t-\Delta t)} - aN_{12(t-\Delta t)}}{v}\right](1-e^{-v\Delta t})\right\} \quad (15)$$

$$r_{12(t)} = \frac{\beta_2 F_2}{1+ab}\left\{\left[\frac{bN_{11(t-\Delta t)} + N_{12(t-\Delta t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{11(t-\Delta t)} - aN_{12(t-\Delta t)}}{v}\right](1-e^{-v\Delta t})\right\}$$

$$r_{21(t)} = \frac{\beta_1 F_1}{1+ab}\left\{a\left[\frac{N_{22(t-\Delta t)} + bN_{21(t-\Delta t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{21(t-\Delta t)} - aN_{22(t-\Delta t)}}{v}\right](1-e^{-v\Delta t})\right\}$$

$$r_{22(t)} = \frac{\beta_2 F_2}{1+ab}\left\{\left[\frac{N_{22(t-\Delta t)} + bN_{21(t-\Delta t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{21(t-\Delta t)} - aN_{22(t-\Delta t)}}{v}\right](1-e^{-v\Delta t})\right\}$$

When Δt is 1 month, these equations give the expected number of tags returned per month. Equations 15 thus form a complete model of tag returns in two fisheries that can be applied to real data.

2.2.3 Parameter estimation

There are 10 parameters to be estimated for the model in Equations 15: M_1, F_1, T_{12}, M_2, F_2, T_{21}, α_1, α_2, β_1, β_2. It is reasonable to assume that the effects of tagging on survival do not differ appreciably from fishery to fishery so that $\alpha_1 = \alpha_2$ and the number of parameters is reduced from 10 to 9. It is also assumed that all parameters except F_1 and F_2 are constant over time. Kleiber, Sibert & Farman (ms.) found the single-fishery model (Equations 3 and 4) to be relatively insensitive to violation of this assumption. F_1 and F_2 are of course dependent on the status of the fishery at any particular time, and can be reparameterised as functions of either the observed catch or effort. Thus,

$$F_1 = Q_1 E_{1k} = \frac{C_{1k}}{\overline{P_1}} \qquad k = 1,2,\ \dots\ ,n \qquad (16)$$

$$F_2 = Q_2 E_{2k} = \frac{C_{2k}}{\overline{P_2}} \qquad k = 1,2,\ \dots\ ,n$$

where Q_1 and Q_2 are the catchability for fishery 1 and 2, $\overline{P_1}$ and $\overline{P_2}$ are the average population sizes in fishery 1 and 2, n is the number of months considered, C_{1k} the observed catch in fishery 1 during month k, C_{2k} the observed catch in fishery 2 during month k, E_{1k} the observed effort in fishery 1 during month k, and E_{2k} the observed effort in fishery 2 during month k. The total number of parameters remains nine and either Q_1 and Q_2 or $\overline{P_1}$ and $\overline{P_2}$ can be estimated depending on whether effort or catch data are used. In the case of catch data, Equations 16 are approximations. An exact representation would require solution of Equations 5 and their substitution into Equations 16. If the population is near equilibrium, Equations 16 are sufficiently accurate however, and $\overline{P_1}$ and $\overline{P_2}$ can be used to estimate $\langle\overline{P_1}\rangle$ and $\langle\overline{P_2}\rangle$.

Parameters were estimated by the numerical least squares reduction using the function minimisation algorithm of Nelder & Mead (1965). Following Kleiber et al. (1983) a square root transformation was employed. Since this model is in reality four models sharing a common set of parameters, there are four sums of squared differences between observed and expected to be considered:

$$s_{ij}^2 = \sum_{k=1}^{n} \left(\sqrt{r_{ijk}} - \sqrt{\hat{r}_{ijk}}\right)^2 \quad i,j=1,2;\ k=1,2,\ \ldots\ ,n \tag{17}$$

where the circumflex ($\hat{}$) over r indicates the expected number of returns per month calculated by Equations 19. Returns of tags from within the fishery of release (r_{11} and r_{22}) in general greatly exceed returns from outside the fishery of release (r_{12} and r_{21}), and the residual sums of squares associated with these returns will be much higher than the others. A sum of squares minimisation procedure will tend to minimise the larger sums and ignore the smaller, thereby producing biased parameter estimates. A more reasonable approach is to minimise some weighted average sum of squares. Brownlee (1965) gives a convenient formula for calculating an unbiased mean from several samples with different variances. The variance of tag returns per month for each set of tag returns is

$$v_{ij}^2 = \sum_{k=1}^{n} \left(\sqrt{r_{ijk}} - \overline{\sqrt{r_{ij}}}\right)^2 \quad i,j=1,2;\ k=1,2,\ \ldots\ ,n \tag{18}$$

A useful set of weights can be calculated from these variances by

$$w_{ij} = \left[v_{ij}^2 \left(\frac{1}{v_{11}^2} + \frac{1}{v_{12}^2} + \frac{1}{v_{21}^2} + \frac{1}{v_{22}^2} \right) \right]^{-1} \tag{19}$$

and the mean observed (weighted) sum of squares becomes

$$V = w_{11}v_{11}^2 + w_{12}v_{12}^2 + w_{21}v_{21}^2 + w_{22}v_{22}^2 \tag{20}$$

and the mean residual (weighted) sum of squares is

$$S = w_{11}s_{11}^2 + w_{12}s_{12}^2 + w_{21}s_{21}^2 + w_{22}s_{22}^2 \tag{21}$$

This weighting scheme will subsequently be referred to as "variance"; the alternative is "uniform" in which all of the w's equal 0.25. An intermediate weighting scheme can be devised by substituting standard deviations for the v's in Equation 19; this form of weighting is referred to as "standard deviation". The solution to the parameter estimation problem is therefore the set of parameters which minimises the weighted sum of squares, 21.

Goodness of fit was calculated as the proportion of the observed variance (V) which is made up or "explained" by the model. This measure or G statistic is calculated simply by

$$G = 1 - \frac{S}{V} \cdot \frac{n}{n-m} \tag{22}$$

where m is the number of parameters estimated.

One of the strengths of the Nelder-Mead algorithm is the relative ease with which additional information may be included. In this case, there is prior information about the range of the correct values of certain parameters. For instance, Kleiber et al. (1983) publish ranges for the correct values of β, values of α must lie between 0 and 1, and the components of attrition are never less than zero. This information is used by applying a penalty to the residual sum of squares (21) when the parameter estimates move beyond a specified range. When such conditions are imposed, the fits are labelled "constrained", as opposed to "unconstrained". (See Schnute & Fournier 1980 for an example of the use of penalties in non-linear parameter estimation.) Also, selected parameters can be fixed at arbitrary constants and the algorithm allowed to find a minimum residual sum of squares by varying the unfixed parameters.

The joint confidence region surrounding the estimates of a pair of parameters provides useful information about the model and the parameter estimates. The size of the region indicates the accuracy of the estimate. Narrow regions indicate that the parameters are well determined by the data. The shape of the regions are indicative of the distribution of the errors. Regions with circular or elliptical shapes indicate that the errors are approximately normal. The orientations of the region indicate the relationship between the parameters. Elliptical or otherwise elongated regions with oblique orientations indicate that the two parameters may be correlated. Overlapping regions indiate that differences between the two pairs of parameter estimates are not significant.

Approximate 95 per cent confidence regions were calculated by the method outlined by Draper & Smith (1980) for non-linear regressions. (Note that it is the confidence level that is approximate; the regions are exact, and the levels are exact if the errors are normal.) In cases where the fits involved constrained parameters, these constraints were relaxed for the purpose of calculating confidence regions.

2.2.4 Data sources

The model requires two sets of tag return data from each of two releases and catch or effort data from both of the fisheries. There are few such sets of data available in Tuna Programme files. The most promising sets are those which derive from the May/June 1979 tagging in Papua New Guinea (visit PNG2) and the June 1980 tagging in Solomon Islands (visit SOL2). There were considerable numbers of returns from both releases in the other country and catch and effort statistics are available from both of the local pole-and-line fisheries for the entire period during which tags were recovered (May 1979 through December 1981). Two criteria were used by Kleiber et al. (1983) to exclude data from the analysis. First, certain releases were excluded to ensure that all releases were in a discrete area and that all fish were of the size generally caught by the commercial fishery. Second, returns from the first one or two months at liberty were excluded to ensure that tagged fish were more uniformly distributed in the population. These data sets have the advantage that both were previously analysed by Kleiber et al. (1983) so that comparisons can be made. All tagging data were derived from Kleiber et al. (1983) and where supplementary catch and effort data were not available from that source they were obtained from Argue & Kearney (1982) and Tuna Programme (1984). The raw data sets are presented in Table 1.

TABLE 1. DATA SET USED TO TEST TWO-FISHERY MODEL WITH RELEASE AND RECAPTURE EXCLUSIONS DESCRIBED IN KLEIBER ET AL. (1983). First line is documentation of data set. Second line gives date and number of tags released for visits PNG2 (N_{11}^{*}) and SOL2 (N_{22}^{*}) respectively. Third line gives average catch and effort for the Papua New Guinea and Solomon Islands pole-and-line fishery during the period tags were returned (May 1979 through December 1980). The remaining lines give the year and month (first field), PNG2 tags returned in PNG (r_{11}, second field), PNG2 tags returned in SOL (r_{12}, third field), SOL2 tags returned in PNG (r_{21}, fourth field), SOL2 tags returned in SOL (r_{22}, fifth field), catch and effort in PNG (C_1, E_1, fields 6 and 7), and catch and effort in SOL (C_2, E_2, fields 8 and 9). Negative tag returns indicate excluded returns.

PNG2 (PNGPOL) SOL2 (SOLPOL); Kleiber exclusions

7905	6013		8006	2012				
					2293	778	2320	552
7905	-20	0	0	0	379	114	1788	483
7906	-392	0	0	0	2153	598	2955	528
7907	208	0	0	0	2972	1035	3195	561
7908	100	1	0	0	2492	913	2150	566
7909	58	0	0	0	1840	899	2279	600
7910	27	2	0	0	654	614	3330	617
7911	6	0	0	0	811	706	2944	589
7912	3	0	0	0	286	212	2340	616
8001	0	2	0	0	0	0	1614	557
8002	0	0	0	0	0	0	64	38
8003	1	0	0	0	609	440	0	0
8004	5	0	0	0	1956	802	210	88
8005	1	1	0	0	2243	985	1029	386
8006	2	0	0	9	2860	1005	1061	530
8007	3	2	0	28	2878	1068	2250	558
8008	7	1	2	25	5514	1100	2778	554
8009	5	1	0	9	3982	988	2770	574
8010	0	0	1	8	3697	850	3244	566
8011	0	1	0	20	3055	831	3313	566
8012	0	3	0	16	1800	553	2774	594
8101	0	1	1	18	222	99	1531	463
8102	0	0	0	0	0	0	0	0
8103	0	0	2	0	1814	447	0	0
8104	0	0	0	5	4675	918	1210	258
8105	0	0	0	5	3085	977	1881	560
8106	0	0	1	11	3340	962	2934	614
8107	1	0	1	4	3421	1077	2796	628
8108	1	0	0	6	2100	964	3474	640
8109	0	0	0	2	1660	805	2631	639
8110	0	0	0	0	1435	626	2087	630
8111	0	0	0	0	426	185	2131	632
8112	0	0	0	1	77	42	1231	415

3.0 RESULTS

3.1 Observed and Predicted Tag Return Rates

Several fits were made to the data using different weighting schemes and requiring different parameters to be constrained. These fits yielded several sets of parameter estimates and predicted numbers of tag returns all of which had a similar correspondence with the observations. Fits 7 and 8 (Table 2) can be used as representative fits to inputs of catch and

TABLE 2. FITS COMPARING EFFECTS OF DIFFERENT WEIGHTS. U indicates uniform weighting, S indicates standard deviation weighting, and V indicates variance weighting. α fixed at 0.9; β_1 fixed at 0.76; b2 fixed at 0.6. Fit 1 is the result from Kleiber et al. (1983) with the input of catch data; fit 2 is the result from Kleiber et al. (1983) with the input of effort data. Also shown are fits in which data from only one of the two fisheries are considered.

Input	Catch						Effort					
Fit	1	3	5	7	9	11	2	4	6	8	10	12
Fishery	B	B	B	B	1	2	B	B	B	B	1	2
Weights	U	U	S	V	U	U	U	U	S	V	U	U
w_{11}	1	.25	.063	.011	.5		1	.25	.063	.011	.5	
w_{12}		.25	.361	.364	.5			.25	.361	.364	.5	
w_{21}		.25	.458	.586		.5		.25	.458	.586		.5
w_{22}	1	.25	.118	.039		.5	1	.25	.118	.039		.5
s_{11}		8.517	8.557	8.612	6.367	283.088		10.314	11.825	11.941	5.230	470.463
s_{12}		1.535	1.292	1.037	.823	2.562		1.621	1.081	.813	.572	14.239
s_{21}		.810	.757	.742	9.325	.354		1.260	.672	.667	10.193	.291
s_{22}		9.866	10.388	11.883	30.020	9.698		11.086	11.441	12.896	34.768	10.689
F_{min}		5.182	2.573	1.366	3.595	5.026		6.070	2.787	1.316	2.901	5.490
G_{11}	.950	.968	.968	.968	.976	(.000)	.950	.962	.956	.956	.981	(.000)
G_{12}		.826	.854	.882	.907	(.710)		.816	.877	.908	.935	(.000)
G_{21}		.705	.724	.730	(.000)	.871		.541	.755	.757	(.000)	.894
G_{22}	.630	.763	.751	.715	(.280)	.767	.650	.734	.726	.691	(.166)	.744
Overall	.790	.917	.916	.908	.980	.948	.800	.904	.902	.895	.984	.944
M_1		.290	.286	.279	.316	.136	.410	.379	.365	.354	.409	.124
M_2		.078	.066	.048	.000	.094	.140	.059	.055	.039	.000	.083
T_{12}		.020	.018	.017	.039	.039		.034	.024	.022	.059	.000
T_{21}		.008	.007	.006	.018	.002		.013	.008	.007	.022	.003
F_1	.058	.095	.093	.092	.115	4.458	.061	.124	.112	.108	.157	.270
F_2	.025	.020	.018	.015	.005	.021	.027	.018	.017	.015	.005	.020
A_1	.380	.405	.397	.388	.469	4.633	.470	.536	.500	.484	.626	.395
A_2	.150	.105	.091	.069	.024	.117	.160	.089	.080	.061	.027	.106
$\langle P_1 \rangle$	35000	24000	25000	25000	20000	5100						
$\langle P_2 \rangle$	89000	120000	130000	150000	430000	110000						
Q_1							.90E-04	.16E-03	.14E-03	.14E-03	.20E-03	.35E-03
Q_2							.56E-04	.32E-04	.31E-04	.27E-04	.90E-05	.37E-04

effort data respectively. Figures 3 and 4 show the observed and predicted number of tags returned per month for each of the four sets of tag returns for these two fits. The model appears to predict the observations reasonably well as indicated by the G statistics and the residual sums of squares. Plots from fits with different weighting schemes and constraints are similar in appearance.

3.2 Weighting

The effect of various weighting procedures is shown in Table 2. Values of α and β have been fixed to the previously used values. In fits 3 and 4 (Table 2), the four model components are given equal weights (i.e. all weights equal 0.25). The overall fit to the data is reasonable and somewhat better than that obtained by Kleiber et al. (1983). However, the fits to the individual model components are uneven. Fits to the fisheries of release are very good (G=0.96 in the best case), but fits to the other fishery are not so good (G=0.54 in the worst case). Standard deviation and variance weighting (fits 5, 6, 7, and 8) yield slightly lower overall G statistics, although still higher than Kleiber et al. (1983). In these cases, the fits to the individual model components are more even. Fits to the fishery of release are slightly worse, but fits to the other fishery are better. The effect of variance weighting, that is, of removing bias introduced by the fishery of release sum of squares, is to decrease both natural mortality and transfer estimates. Estimates of fishing mortality remain relatively unaffected; thus, overall attrition estimates are decreased. Unless indicated otherwise, variance weighting was used for all fits.

By giving 0 weight to certain model components, these components are excluded from the residual sum of squares (Equation 21), i.e. they are "ignored" by the fitting procedure. In this manner, the returns to one fishery are used to predict the returns to the other. Fits 9 and 10 use only Papua New Guinea data in the analysis and fits 11 and 12 use only Solomon Islands data in the analysis. The overall and component G statistics, measuring goodness of fit to the input data only, are in all cases high. Surprisingly, the fits to the excluded model components, bracketed figures in Table 2, are in one case quite close.

3.3 Estimation of α and β

The fits described to this point have been made with α fixed at 0.9 and with β_1 and β_2 fixed at 0.76 and 0.60 respectively. The effects of allowing progressively more liberty in the choice of α and β are shown in Table 3. In all cases, the residual mean square is decreased slightly, but there is little or no improvement in the G statistic. Results are somewhat dependent on whether catch or effort data are used, but there is a general tendency for α to be high (greater than 0.9), β_1 to be low (less than 0.2), and β_2 to be high (greater than 0.8). There is also a tendency for the product $\alpha \times \beta_1$ to be low (<0.15) and the product $\alpha \times \beta_2$ to be high (>0.8).

3.4 Interaction

Estimates of interaction derivatives (Equations 9) are presented in Table 4. For fixed α and β, these estimates fall between -0.001 and -0.003 indicative of a low level of (negative) interaction. An increase in catch of 1000 tonnes in one fishery would cause a decrease of between 1 and 3 tonnes in the steady state catch of the other. For free α and β, the estimates are very much higher.

FIGURE 3. OBSERVED AND PREDICTED NUMBER OF TAG RETURNS PER MONTH USING INPUT OF CATCH DATA (FIT 7). The upper figure represents tags relesed in Papua New Guinea in 1979 and recaptured in Papua New Guinea (stars) and Solomon Islands (triangles). The lower figure represents tags released in Solomon Islands in 1980 and recaptured in Solomon Islands (stars) and Papua New Guinea (triangles). Solid lines are the model predictions. Note the "square root" scale of the ordinate.

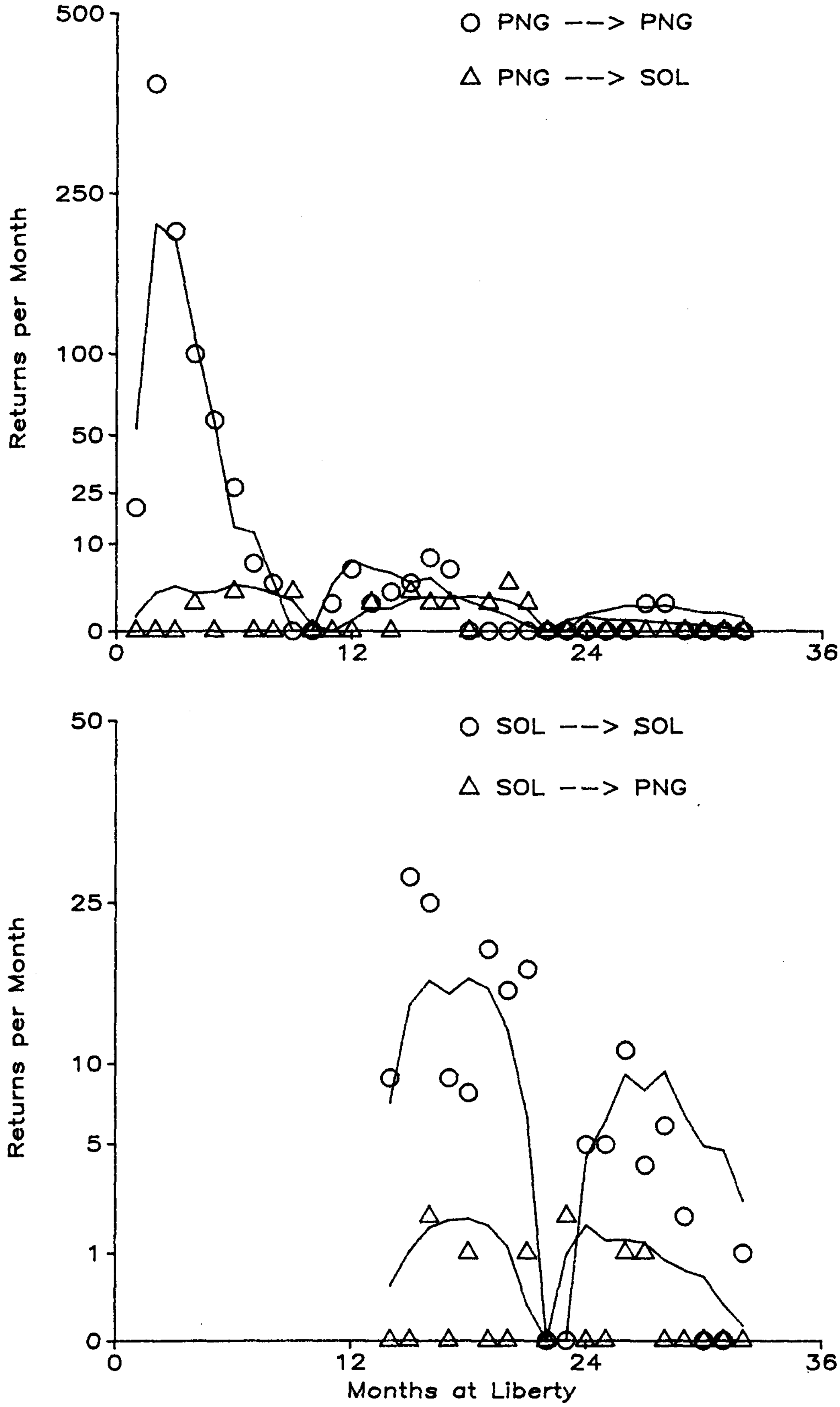


FIGURE 4. OBSERVED AND PREDICTED NUMBER OF TAG RETURNS PER MONTH USING INPUT OF EFFORT DATA (FIT 8). Otherwise this figure is similar to Figure 3.

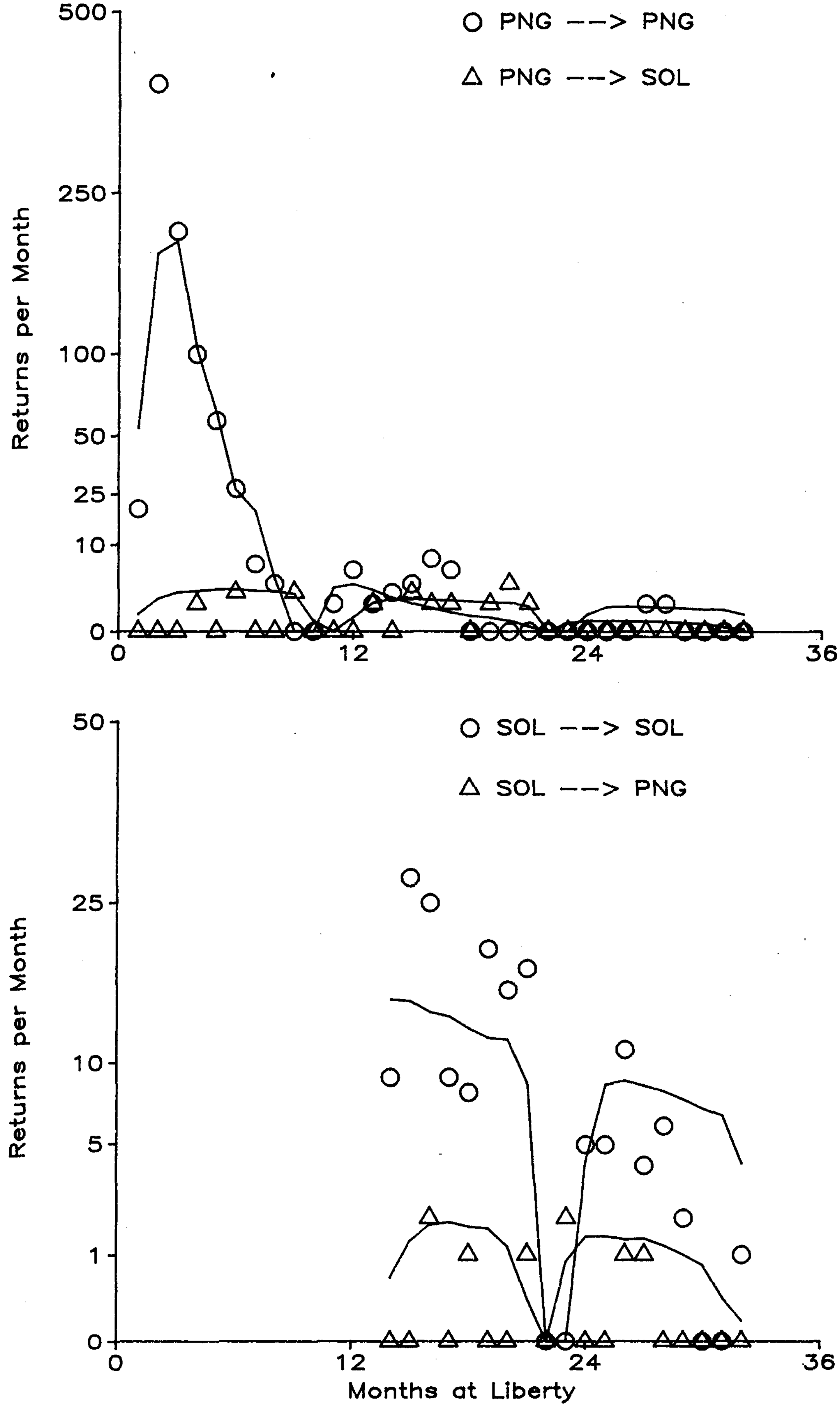


TABLE 3. FITS DEMONSTRATING STEPWISE RELAXATION OF CONSTRAINTS ON α AND β. Data from both fisheries are used and weighting by variance. Asterisks (*) indicate parameters fixed at constant indicated. Curly brackets {} around estimates of β_1 and β_2 indicate that β_1 is constrained to the interval 0.62-0.90 and β_2 is constrained to the interval 0.43-0.77.

Input	Catch						Effort					
Fit	7	13	15	17	19	21	8	14	16	18	20	22
s_{11}	8.612	15.867	15.595	15.280	15.296	8.809	11.947	12.457	12.026	11.992	11.981	11.837
s_{12}	1.037	1.179	1.170	1.161	1.160	1.054	.813	.926	.865	.856	.856	.819
s_{21}	.742	.296	.280	.262	.262	.700	.667	.272	.244	.213	.214	.631
s_{22}	11.883	12.739	12.752	12.779	12.794	11.965	12.896	13.498	13.879	13.676	13.676	12.939
F_{min}	1.366	1.269	1.254	1.238	1.238	1.353	1.316	1.155	1.126	1.096	1.097	1.297
G_{11}	.968	.938	.934	.935	.938	.964	.956	.952	.949	.949	.951	.952
G_{12}	.882	.861	.850	.851	.858	.871	.908	.891	.889	.890	.895	.899
G_{21}	.730	.883	.867	.876	.887	.698	.757	.892	.884	.899	.908	.728
G_{22}	.715	.669	.603	.602	.638	.661	.691	.649	.567	.574	.613	.633
Overall	.908	.878	.860	.861	.871	.893	.895	.885	.865	.866	.877	.879
α	.900*	.239	.290	1.000	.900*	.900*	.900*	.222	.245	.945	.900*	.900*
β_1	.760*	.760*	{.620}	.181	.201	{.620}	.760*	.760*	{.620}	.155	.163	{.620}
β_2	.600*	.600*	{.765}	.888	.983	{.769}	.600*	.600*	{.770}	1.000	.987	{.688}
$\alpha\beta_1$	.684*	.182*	.180	.181	.181*	.558*	.684*	.169*	.152	.147	.147*	.558*
$\alpha\beta_2$	.540*	.144*	.222	.888	.884*	.692*	.540*	.133*	.188	.945	.888*	.619*
M_1	.279	.094	.097	.102	.102	.270	.354	.103	.085	.081	.082	.336
M_2	.048	.004	.021	.043	.043	.050	.039	.000	.009	.036	.036	.040
T_{12}	.017	.009	.008	.008	.008	.017	.022	.008	.007	.006	.006	.021
T_{21}	.006	.007	.007	.007	.007	.006	.007	.008	.008	.008	.008	.007
F_1	.092	.499	.487	.470	.471	.116	.108	.470	.476	.467	.466	.134
F_2	.015	.054	.035	.009	.009	.012	.015	.058	.041	.008	.009	.013
A_1	.388	.602	.592	.581	.582	.403	.484	.581	.568	.555	.554	.490
A_2	.069	.066	.063	.059	.059	.068	.061	.066	.058	.052	.052	.060
$\langle P_1 \rangle$	24000	4600	4700	4900	4900	20000						
$\langle P_2 \rangle$	140000	43000	66000	270000	270000	200000						
Q_1							.14E-03	.60E-03	.61E-03	.60E-03	.60E-03	.17E-03
Q_2							.27E-04	.11E-03	.73E-04	.15E-04	.16E-04	.24E-04

TABLE 4. FITS COMPARING VARIOUS PARAMETERS USED IN STOCK ASSESSMENT AND FISHERY INTERACTION. Weighting is by variance. Fit 1 is the result from Kleiber et al. (1983), with the input of catch data; fit 2 is the result from Kleiber et al. (1983), with the input of effort data.

Input	Catch			Effort		
Fit	1	7	17	2	8	18
s_{11}		8.612	15.280		11.941	11.992
s_{12}		1.037	1.161		.813	.856
s_{21}		.742	.262		.667	.213
s_{22}		11.883	12.779		12.896	13.676
F_{min}		1.366	1.238		1.316	1.096
G_{11}	.950	.968	.935	.950	.956	.949
G_{12}		.882	.851		.908	.890
G_{21}		.730	.876		.757	.899
G_{22}	.630	.715	.602	.650	.691	.574
Overall	.790	.908	.861	.800	.895	.866
α	.900*	.900*	1.000	.900*	.900*	.945
β_1	.756*	.760*	.181	.756*	.760*	.155
β_2	.600*	.600*	.888	.600*	.600*	1.000
$\alpha\beta_1$	.680*	.684*	.181	.680*	.684*	.147
$\alpha\beta_2$	.540*	.540*	.888	.540*	.540*	.945
M_1		.279	.102	.410	.354	.081
M_2		.048	.043	.140	.039	.036
T_{12}		.017	.008		.022	.006
T_{21}		.006	.007		.007	.008
F_1	.058	.092	.470	.061	.108	.467
F_2	.025	.015	.009	.027	.015	.008
A_1	.380	.388	.581	.470	.484	.555
A_2	.150	.069	.059	.160	.061	.052
$\langle P_1 \rangle$	35000	25000	4900			
$\langle P_2 \rangle$	89000	150000	270000			
Q_1				.90E-04	1.4E-04	6.0E-04
Q_2				.56E-04	.27E-04	.15E-04
Import 1		895	1930		1070	2330
Import 2		436	41		459	32
Throughput 1	13000	9710	2830		10200	2720
Throughput 2	13000	10400	15700		9470	15000
Import/Throughput 1	.035	.0092	.682		.104	.854
Import/Throughput 2	.040	.0042	.0003		.0048	.0002
Harvest ratio 1	.15	.236	.810	.13	.224	.842
Harvest ratio 2	.16	.222	.148	.17	.245	.154
$\partial\langle C_1\rangle/\partial C_2$		-.0020	-.10		-.0025	-.13
$\partial\langle C_2\rangle/\partial C_1$		-.0010	-.0002		-.0011	-.0002

3.5 Confidence Regions

In a nine parameter model, there are 36 pairs of joint confidence regions, but only a few of these were examined. Figures 5 and 6 present joint confidence regions of α and β for both fixed (solid lines) and unfixed (dotted lines) fits with catch and effort input respectively. There is evidence of an inverse relationship between α and β and higher values of both parameters are preferred. Catch- and effort-based fits yield indistinguishable estimates. For the fixed cases, confidence regions around β_1 and β_2 overlap. When parameters are free, estimates of α and β_2 fall reasonably close to their a priori values, and are indistinguishable from those of the fixed case, but the estimate of β_1 is very low. This relationship can be seen more clearly in Figure 7 which shows the joint confidence region around β_1 and β_2 at optimum Q.

FIGURE 5. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR α AND β FROM CATCH-BASED FITS. Point estimates are indicated by the crosses. The number adjacent to each point estimate indicates whether the region refers to β_1 or β_2. The solid regions are from fit 7 with fixed α and β; the dotted regions are from fit 8 with free α and β.

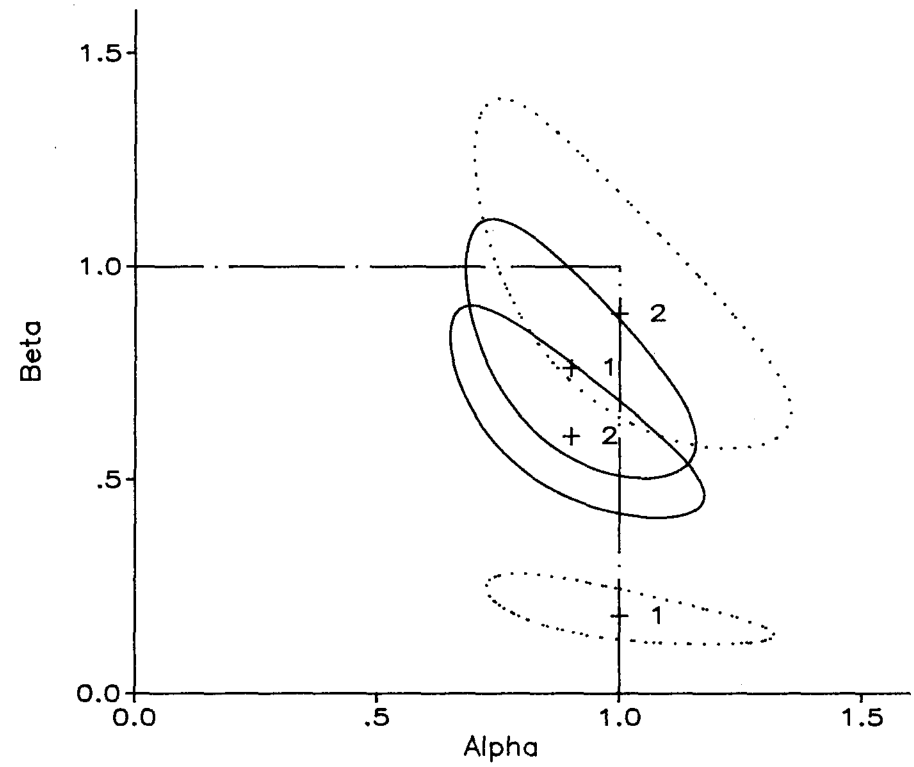


FIGURE 6. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR α AND β FROM EFFORT-BASED FITS. Otherwise this figure is similar to Figure 5.

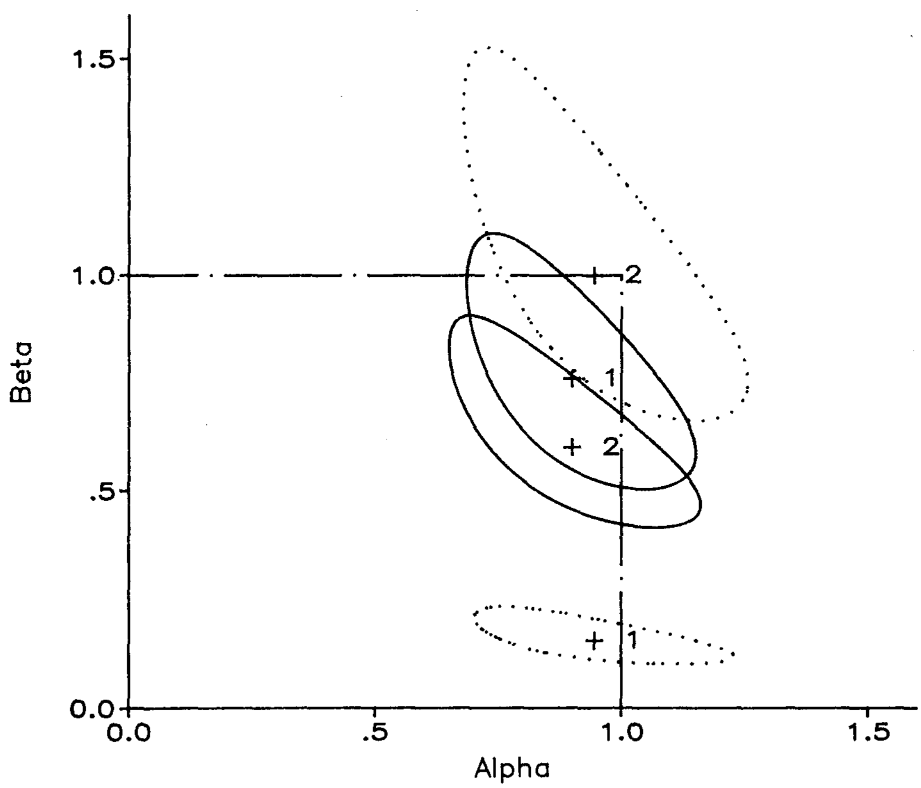


FIGURE 7. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR β_1 AND β_2 FROM BOTH CATCH- AND EFFORT-BASED FITS. Point estimates are indicated by the crosses. The letter adjacent to each point estimates indicates whether estimates are based on catch (C) or effort (E). The solid regions are from fits 7 and 8 with fixed α and β; the dotted regions are from fits 17 and 18 with free α and β. The diagonal dashed line is the line $\beta_1=\beta_2$.

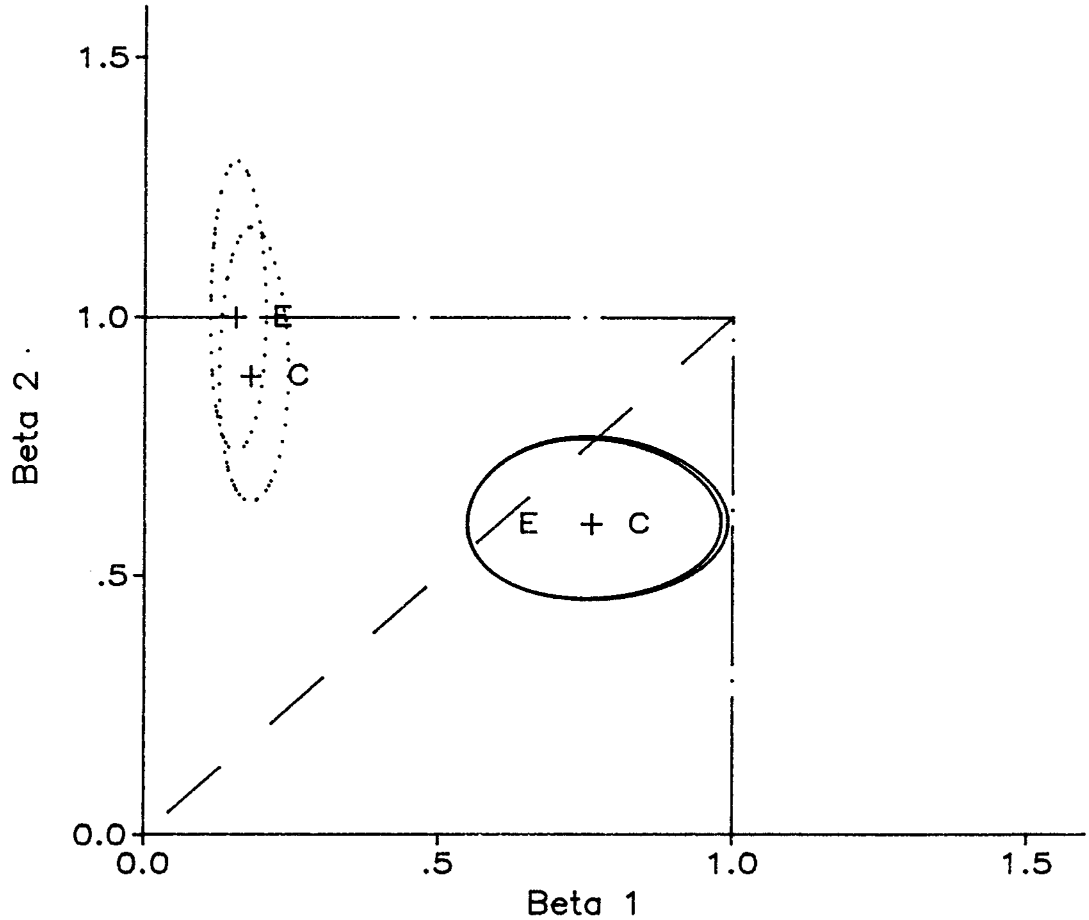


Figure 8 illustrates the joint confidence region for α and ⟨P⟩. ⟨P_1⟩ is more precisely defined by the data than is α, and there is a suggestion of dependency between α and ⟨P_2⟩. Figure 9 illustrates the joint confidence region for β and ⟨P⟩ for catch-based fits. For the fixed case and for the unconstrained Solomon Islands case, these regions appear to be parabolic and open in the direction of high estimates of both parameters. For the unconstrained Papua New Guinea fit, low estimates of both β_1 and ⟨P_1⟩ appear to be well determined. Figure 10 illustrates the joint confidence region for β and Q for effort-based fits. These figures appear to be open in the direction of high β for fixed fits and for the unfixed fit in the case of Papua New Guinea. In the unfixed fit for Papua New Guinea, β is well described, but there is some uncertainty in Q.

FIGURE 8. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR α AND POPULATION ESTIMATES. Point estimates are indicated by the crosses. The number 1 adjacent to the point estimates indicates Papua New Guinea population estimates and the number 2 indicates Solomon Islands population estimates. The solid regions are from fit 7 with fixed α and β; the dotted regions are from fit 17 with free α and β.

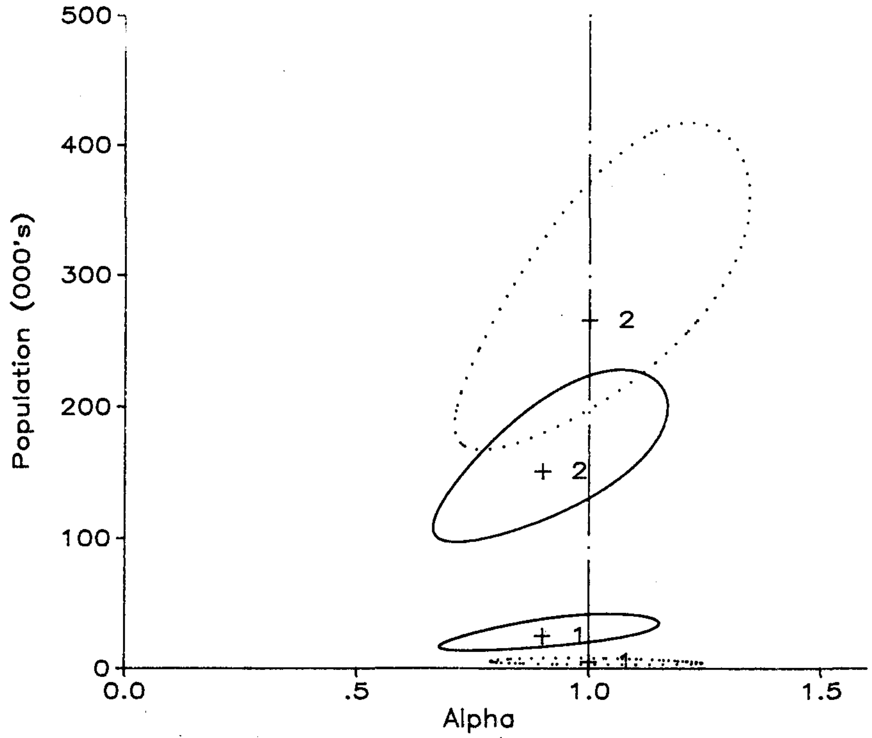


FIGURE 9. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR β AND POPULATION ESTIMATES. Otherwise this figure is similar to Figure 8.

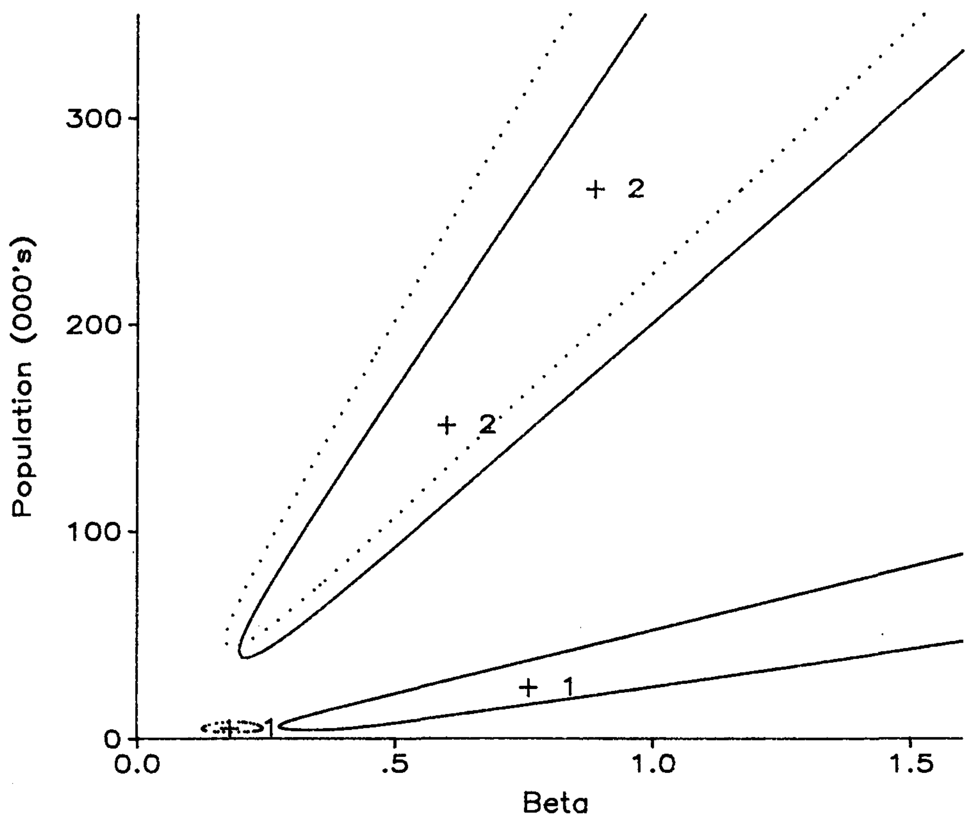


FIGURE 10. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR β AND CATCHABILITY ESTIMATES. Point estimates are indicated by the crosses. The number 1 adjacent to the point estimates indicates Papua New Guinea catchability estimates and the number 2 indicates Solomon Islands catchability estimates. The solid regions are from fit 8 with fixed α and β; the dotted regions are from fit 18 with free α and β.

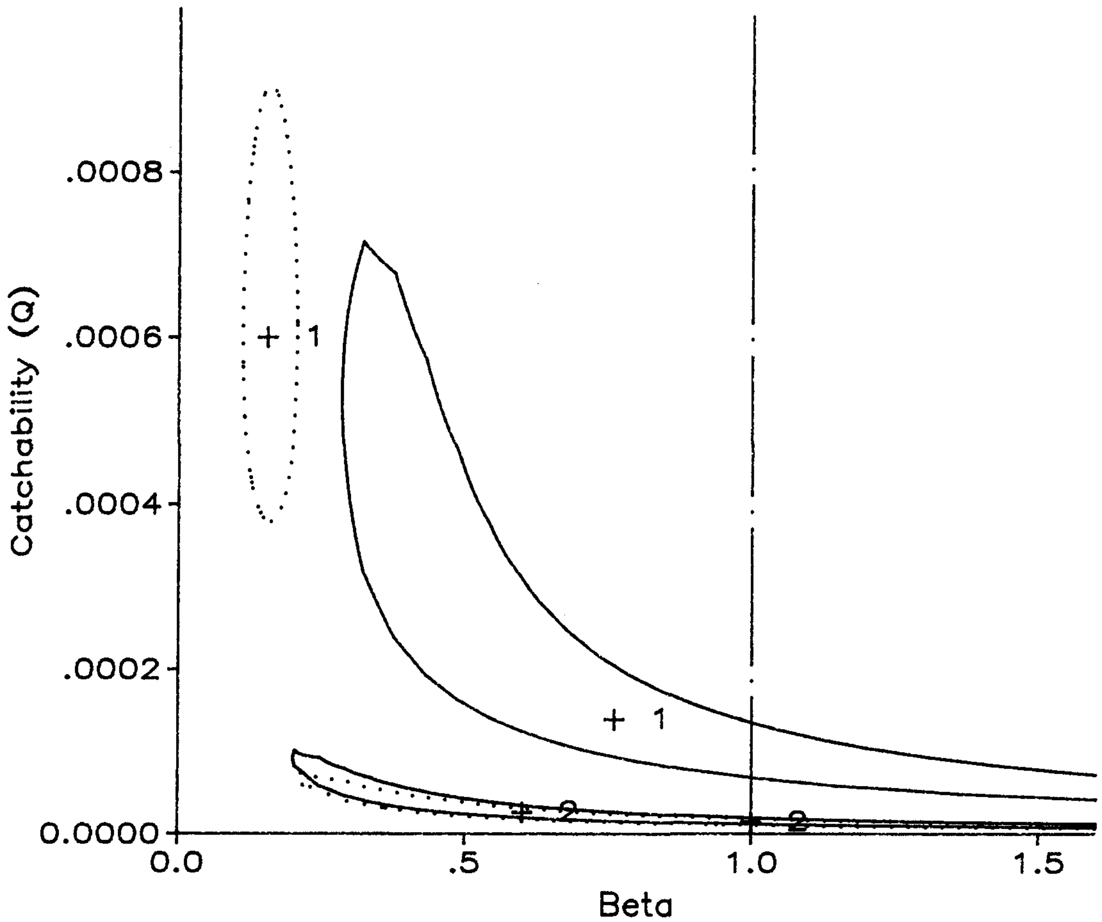


Figure 11 illustrates the joint confidence region around T_{12} and T_{21} for both catch and effort inputs and for both fixed (solid) and unfixed (dotted) α and β. Input of catch and effort produces statistically indistinguishable estimates. Relaxation of constraints of α and β decreases the estimated values of T_{12} so that T_{12} is indistinguishable from T_{21}. Figure 12 illustrates the joint confidence region around transfer and natural mortality estimates based on catch. For fixed α and β the parameter estimates for Papua New Guinea and Solomon Islands are distinct. Allowing α and β to vary caused estimates of transfer and mortality for each country to become indistinguishable between countries. There is a suggestion of dependency between transfer and mortality estimates.

Joint confidence regions around population estimates are shown in Figure 13. There is no suggestion of dependency between estimates, but those with fixed α and β are distinct from unconstrained estimates.

FIGURE 11. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR TRANSFER BETWEEN FISHERIES. Point estimates are indicated by the crosses. The letters adjacent to the point estimates indicate whether estimates are based on catch (C) or effort (E). The solid regions are from fits 7 and 8 with fixed α and β; the dotted regions are from fits 17 and 18 with free α and β. The dashed diagonal line is the line $T_{12}=T_{21}$.

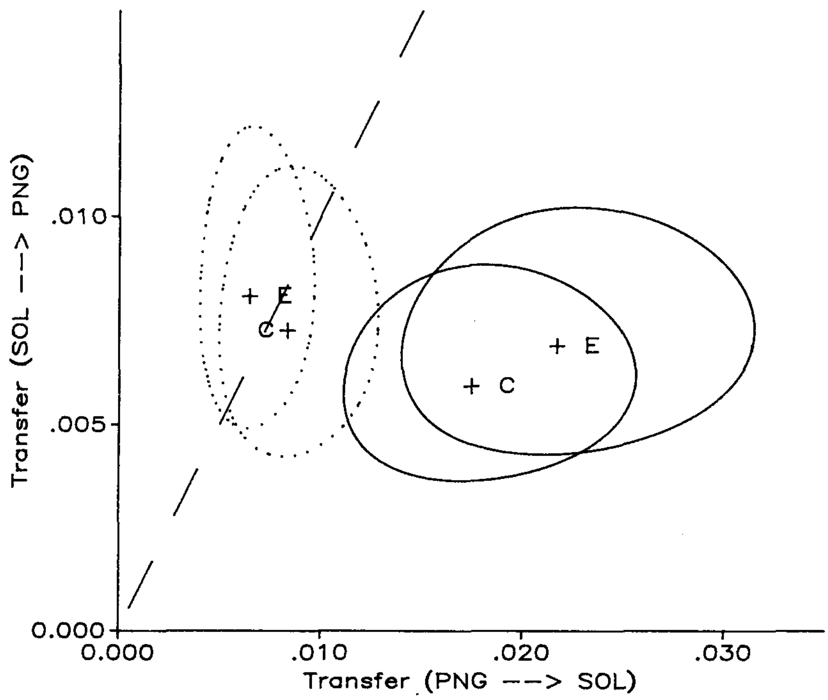


FIGURE 12. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR NATURAL MORTALITY AND TRANSFER BASED ON CATCH. Point estimates are indicated by the crosses. The solid regions are from fit 7 with fixed α and β; the dotted regions are from fit 17 with free α and β.

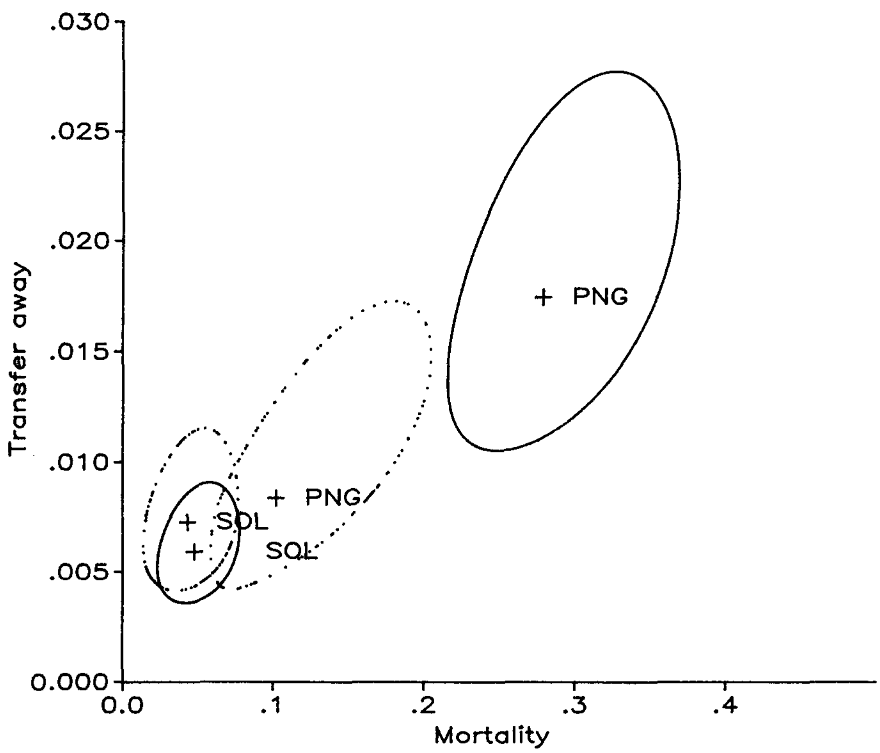
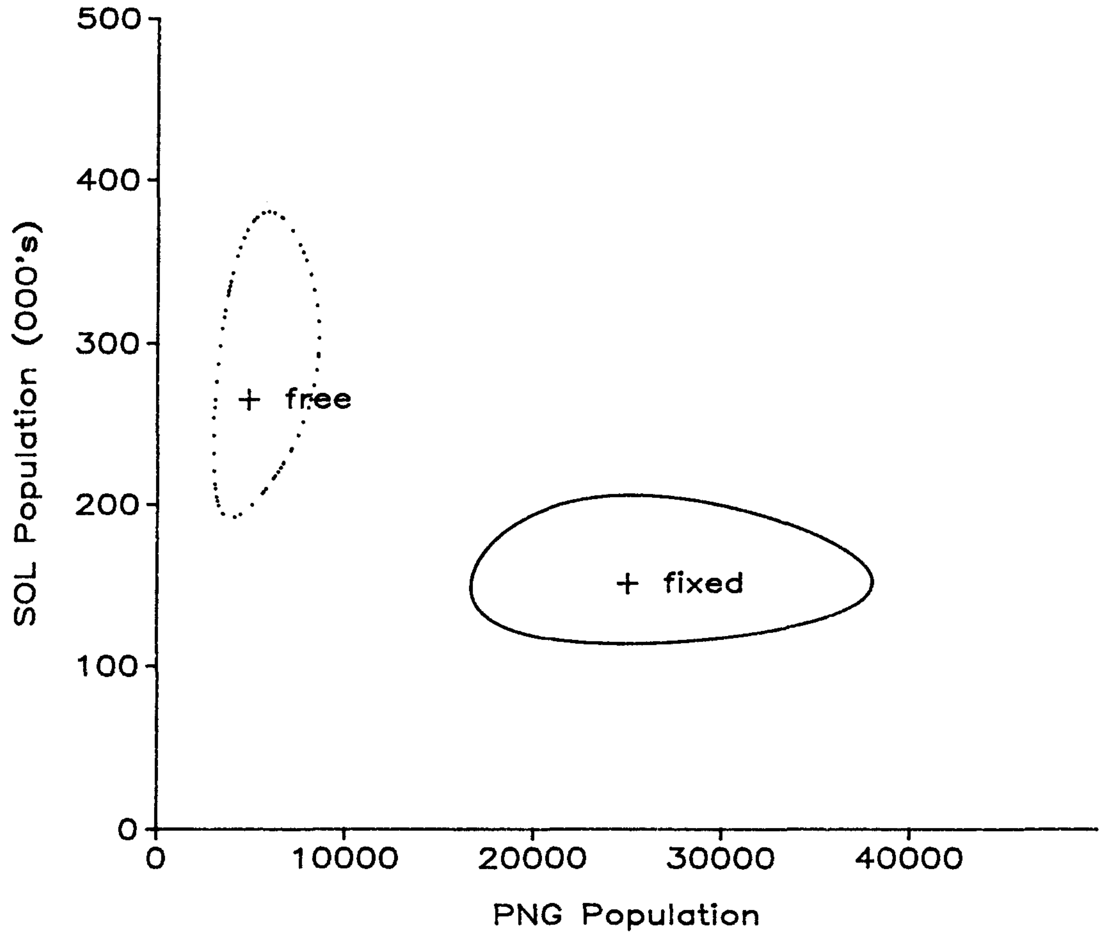


FIGURE 13. NINETY-FIVE PER CENT JOINT CONFIDENCE REGIONS FOR POPULATION ESTIMATES. Point estimates are indicated by the crosses. The solid region is from fit 7 with fixed α and β; the dotted regions are from fit 17 with free α and β.



4.0 DISCUSSION AND CONCLUSIONS

The two-fishery model provides a good, and reasonably parsimonious, representation of the monthly rate of return of four categories of tags from releases in two fisheries. In absolute terms, approximately 90 per cent of the total variance in monthly return rates is "explained" by the model. Nine parameters, all of which are estimable, are required. In contrast, the previously used model represented the monthly rate of return of one category of tag from releases in a single fishery, "explained" 63 to 95 per cent of the variance, and used four parameters, of which two were confounded.

Uncertainty about the values of α and β restricts the accuracy of parameter estimates derived from all tagging experiments, and has been the subject of much work in the analysis of the data sets used in the present analysis (Skipjack Programme 1981). Researchers often release fish with two tags (see Wetherall 1982 for a review), and infiltrate tagged fish into the holds of fishing boats in an attempt to provide independent estimates of these two parameters. As noted by Paulik (1963), α and β are separable in a multiple release tagging experiment. In the two-fishery model, a special case of the multiple release situation, α and β are in principle not confounded, and it provides the first independent estimates (with confidence limits) of these parameters for skipjack. Estimates of α and β_2 seem reliable, not dependent on other parameters, and are generally close to the values previously estimated by the Programme. The estimate of β_1 also seems reliable, but is much less than the lower limit published by Kleiber et al. (1983) of 0.6. It should be noted, however, that by using a modified form of their model, Kleiber et al. (1983) were able to estimate the product $\alpha \times \beta$. These estimates were quite low for both the Solomon Islands and Papua New Guinea data sets, approximately 0.2, and consistent with the low value of β_2 estimated by the two-fishery model. Clearly more effort will be needed both to ensure that β is high and to obtain independent estimates of this parameter in future tagging experiments.

The odd and open nature of the joint confidence regions involving β and $\langle P \rangle$ or Q is difficult to interpret. Draper & Smith (1980) point out that these shapes are often the rule in problems of non-linear parameter estimation. (For further examples from skipjack data see Sibert, Kearney & Lawson 1983). Kendall & Stuart (1979) also allude to the problem and suggest that it is caused, not by ill-defined parameters but by the inappropriate choice of the statistical model used in calculating confidence regions. Unfortunately, the statistical literature offers no general solution of practical use to the problem.

The parameters estimated by the new model tend to be generally similar to those published by Kleiber et al. (1983) when α and β are fixed. For instance, catch-based attrition estimates for Papua New Guinea and Solomon Islands are 0.39 and 0.07 respectively, in comparison with the published values of 0.38 and 0.15. However, when α and β are free, parameter estimates are quite different, reflecting the low estimate of β_2. Derived statistics naturally behave similarly.

The most important feature of the new model is the explicit partitioning of both attrition and accretion into components due to emigration and immigration. The results for the two countries studied indicate that migration is a small component of attrition and that most tagged skipjack die within the country of release. This feature also facilitates the calculation of a fishery interaction parameter based on the transfer parameters, T_{12} and T_{21}. For the example data, these interaction parameters are very low, of the order of -0.1 per cent. Thus low migration relative to mortality produces the situation where catch in one country has little effect on catch in the other. The low interaction estimates produced by the two-fishery model are consistent with previous Tuna Programme results, and are attributable, in a large part, to the relatively long distance between the two fisheries.

There are few data sets in the Tuna Programme files for which this model is appropriate, so the model would appear to have limited application. (The author would be pleased to have the opportunity to test the model on suitable data from interested readers.) However, the results indicate that it is possible to apply the model to the returns from a single release recovered in two fisheries. This option has not been extensively tested, but the results in Table 2 indicate that it would probably be successful. A more promising application may be as an aid in planning future tagging experiments designed specifically to elucidate interaction between two fisheries.

Several extensions of the two-fishery model are possible. First, the structure of the model as presented in Equations 5, 10 and 11 is easily generalised to an arbitrary number of fisheries. Although the system of linear differential equations may be soluble, the problems of estimating the rather large number of parameters would be formidable. Second, the results of the test presented here indicate that the transfer coefficients are equal, i.e. $T_{12}=T_{21}$, suggesting that a diffusion model could be used. In both of the above cases, however, it may be difficult to find data sets to which the model can be applied. Third, a method of examining the correlation between parameter estimates could be developed in several ways, either from the Nelder-Mead algorithm or by numerical approximation of the required partial derivatives. This information would be very useful in evaluating the relationships between the parameters.

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