

Abstract.— Two models were fit to data from four experiments in which tagged southern bluefin tuna *Thunnus maccoyii* were released in Australian coastal waters and recaptured in the Australian surface fisheries and the Japanese longline fishery. The principal objective of the analysis was to estimate the instantaneous rate of natural mortality (M). Movement rates and catchability coefficients were also estimated using the second model. The first model (HSH) was fit to exact recapture times assuming, *inter alia*, that the tagged population was extinct at the time of the last tag return. The second model (SE) was fit to grouped data classified by two release fisheries and three recapture fisheries, explicitly incorporating movement between the geographically separated release fisheries and permanent emigration from the release fisheries into the Japanese longline fishery. Using the HSH model, estimates of M ranged from 0.20 to 0.42/year for the different experiments if full reporting of recaptured tags was assumed. The estimates decreased slightly as assumed reporting rate was decreased. The SE model yielded estimates of M ranging from 0.20 to 0.23/year with M constrained to be equal in each of the recapture fisheries. Unconstrained- M estimates were obtained which suggested higher levels of natural mortality in the release fisheries; however, these estimates were considered unreliable because of their large standard errors and high degree of confounding with other parameters of the model. Simulation trials indicated that input parameters used to generate simulated tag-return data sets could be accurately retrieved using the SE model. However, the HSH model produced positively biased estimates of M because of the low level of apparent fishing mortality in the Japanese longline fishery.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Natural Mortality and Movement Rates from Tagging Experiments

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The rate at which members of a fish population die from causes other than fishing, the so-called instantaneous rate of natural mortality (M), has a large bearing on the population and fishery dynamics of an exploited species. Natural death is rarely directly observable in fish populations, making M notoriously difficult to estimate, and much attention has been given over the years to devising experimental and statistical techniques to do so. The experimental technique most frequently used is tagging and recapture, the object of which, as stated by Beverton and Holt (1957), is "... to set up and examine the properties of an 'experimental' population of marked fish in which certain parameters that would be difficult or impossible to estimate in the 'natural' population can be determined with some accuracy".

A variety of statistical techniques has been developed to estimate M and other parameters from tagging experiments. One of the simplest is that of Gulland (1955), who derived maximum likelihood estimators for M and the fishing mortality rate (F) (both assumed constant over time) for a completed tagging experiment (i.e., one in which no tagged fish remain alive at the time of the last tag recapture). Hearn et al. (1987) generalized the Gulland (1955) method by allowing F to vary with time. Other models based on log-linear regression (Sandland 1982) or maximum likelihood estimation (Seber 1973, Wether-

all 1982) normally require M and F to be constant; however, some of the more sophisticated methods allow F to vary with time as a function of fishing effort or catch (e.g., Lucas 1975, Kleiber et al. 1987). As an extension of these single-fishery models, Sibert (1984) developed a two-fishery model in which estimates of M , F , and the rates of movement between the fisheries could be obtained.

The southern bluefin tuna *Thunnus maccoyii* for many years has been the subject of an important fishery in southern Australian waters, where juveniles form surface schools and are captured principally by pole-and-line and purse-seine gears. In addition, a large fleet of Japanese longliners has targeted the adults in the higher, southern latitudes of the Indian, Southern, Pacific, and Atlantic Oceans since 1952.

Tagging experiments conducted by the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) have demonstrated that these fisheries exploit a common stock (Hampton 1989), and that there is considerable movement of juvenile fish between fishing grounds off the south coast of western Australia (WA), in the Great Australian Bight off south Australia (SA), and off the south coast of New South Wales (NSW). Throughout the juvenile phase, southern bluefin move away from the Australian coast and subsequently become recruited to the Japanese longline fishery (Fig. 1).

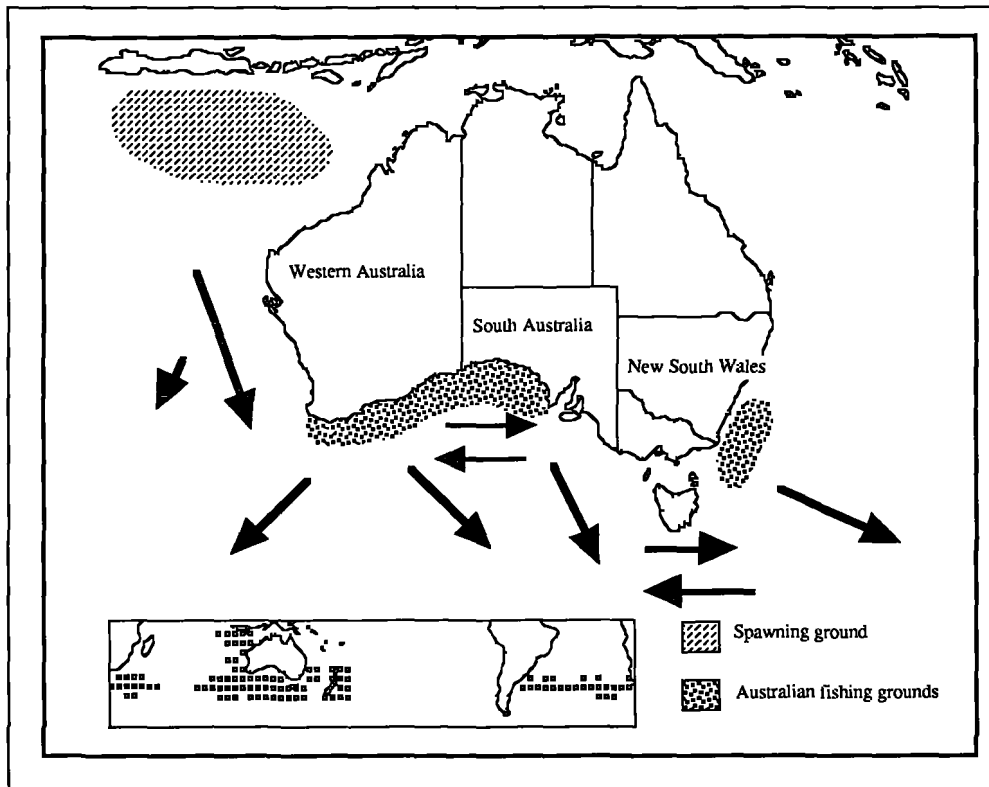


Figure 1

Geographical distribution of the Australian and Japanese (inset) southern bluefin tuna fisheries. Arrows indicate movement of fish in and away from Australian coastal waters. Black squares on the inset map indicate areas of higher Japanese catch.

During the 1980s, scientists became concerned that the fishery was being overexploited, and recent stock assessments have indicated the possibility that a decline in recruitment to the surface fishery could have occurred (Caton et al. 1990). These stock assessments have been based almost exclusively on cohort analysis (Gulland 1965) and other age-structured models, all of which require an estimate of M .

Despite its importance in stock assessment, the natural mortality rate of southern bluefin tuna has never been investigated in detail. Hayashi et al. (1969) considered a value of 0.2/year to be appropriate, based on a somewhat *ad hoc* comparison with growth parameter estimates. This value of M has been preferred in most stock assessments, although a range of values has also been used at various times (e.g., Hampton et al. 1984, Hampton and Majkowski 1986). More recently, the application of the Hearn et al. (1987) method to southern bluefin tagging data suggested that M could be somewhat higher than the "traditional" value of 0.2/year, possibly in excess of 0.4/year. However, the authors acknowledged that this was probably an overestimate because of likely non-compliance with various assumptions.

In this paper, selected southern bluefin tuna tagging experiments are analysed for the purpose of deriving estimates of M consistent with the tagging data. The

Hearn et al. (1987) model (referred to as the HSH model) and an extension of the Sibert (1984) model (referred to as the SE model), which also provides estimates of movement rates between geographically separated fisheries and catchability coefficients, are applied. These models are tested using a simulation model that reflects characteristics of the southern bluefin population and fisheries.

Tagging data

Between 1959 and 1984, the CSIRO supervised the tagging of more than 60,000 southern bluefin tuna, mostly aged 2–4 years, of which approximately 12,000 have been recaptured and the tags returned. From these data, four tagging experiments from which no further returns are expected were defined (Table 1). Although other groupings of the tagging data are possible, the experiments were defined in this way so that they represent reasonably homogeneous groups in terms of release area, size of tagged fish, time period of release, fishing method, and tagging personnel involved. All fish were double-tagged using methods described by Williams (1982). All returns from these experiments were included in the analyses, with best estimates of recapture times (normally the midpoint of the fishing

Table 1

Southern bluefin tuna double-tagging experiments off Australia. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Experiment no.	Area	Years	Carried out by	Fishing method	No. released	No. recovered
1	NSW	1963-70	CSIRO	Pole-and-line	2770	433
2	NSW	1963-70	Fishermen under contract to CSIRO	Troll	9513	4205
3	SA	1964-69	CSIRO	Pole-and-line	7328	1276
4	WA	1963-67	CSIRO	Pole-and-line	12826	563

season) used for those returns where an exact recapture time was not available. The numbers of such returns were relatively few (experiment 1: 27, experiment 2: 114, experiment 3: 47, experiment 4: 35).

Methods of analysis

General assumptions of tagging experiments

Before describing the analytical methods used in this study, some discussion of general assumptions required for the estimation of mortality rates from tag-return data is warranted. These assumptions relate mostly to accounting for all forms of tag loss. In particular, tag losses due to tag shedding, tagging-induced mortality (e.g., through infection, or increasing the probability of predation or capture), and non-reporting of recovered tags must be absent or accounted for. This is frequently achieved by carrying out separate experiments to estimate parameters of models that describe these processes, e.g., double-tagging experiments to estimate tag-shedding rates, holding-tank experiments to test for tagging-induced mortality, and tag-seeding experiments to estimate the proportion of recovered tags that are returned to the tagging authority. The approach taken in this paper was to account for tag shedding using estimates derived by Hampton and Kirkwood (1990), assume tagging-induced mortality to be absent on the basis of various field observations, and repeat the parameter estimations over a range of plausible tag-reporting rates.

In addition to assumptions regarding tag loss, for analyses that include parameters or data relating to the recapture fishery, it is necessary to assume that the tagged and untagged populations are equally vulnerable to capture from the moment of release. Compliance with these and other assumptions for the present application are discussed in a later section.

The HSH model

In addition to the assumptions regarding tag loss, it is assumed here that all recapture times are accurate-

ly known, M is constant, the experiment is completed (i.e., no tagged fish remain alive at the time of the last tag recapture), and all tagged fish remain vulnerable to the fishery through a possibly variable but ultimately non-zero level of fishing mortality. Cessation of fishing would violate the assumption of completion, while permanent emigration of tagged fish away from the fishery would violate the assumption of complete vulnerability.

Let N_0 fish be released and n recaptures recorded at times $t_1 < t_2 < \dots < t_n$ after release. If the above assumptions are satisfied, the natural mortality rate estimator, \hat{M} , is obtained by solving the equation, derived by Hearn et al. (1987),

$$N_0 - \sum_{i=1}^n e^{Mt_i} = 0, \quad (1)$$

using a numerical method such as the Newton-Raphson (Courant 1937).

Tag shedding is accounted for by introducing for each return a correction factor, w_i , which is the probability of a tagged fish retaining at least one tag at time t_i . For double-tagging experiments,

$$w_i = Q(t_i) [2 - Q(t_i)], \quad (2)$$

where $Q(t_i)$ is the probability of a tag being retained at time t_i after release. Tag-shedding models have been fit to double-tagging data for each of the experiments (Hampton and Kirkwood 1990), the results of which are given in Table 2.

The tag-shedding correction is incorporated into Equation (1) as follows:

$$N_0 - \sum_{i=1}^n \frac{e^{Mt_i}}{w_i} = 0. \quad (3)$$

Similarly, the non-reporting of recaptured tagged fish can be allowed for if the fraction, R , of recaptured tagged fish actually reported to the tagging authority is known or assumed. Equation (3) then becomes

Table 2

Tag-shedding models and parameter estimates (from Hampton and Kirkwood 1990) used in the estimation of natural mortality rate and related parameters of southern bluefin tuna.

Experiment	Tag-shedding model	Parameter estimates		
		λ	b	ρ
1	$Q(t) = \rho e^{-\lambda t}$	0.29		0.93
1	$Q(t) = \left[\frac{b}{b+\lambda t} \right]^b$	1.00	0.26	
2	$Q(t) = \rho e^{-\lambda t}$	0.17		0.98
3	$Q(t) = \left[\frac{b}{b+\lambda t} \right]^b$	0.78	0.26	
4	$Q(t) = \left[\frac{b}{b+\lambda t} \right]^b$	1.04	0.36	

$$N_0 R - \sum_{i=1}^n \frac{e^{Mt_i}}{w_i} = 0.$$

If there is a long-term mortality associated with bearing tags, this will be incorporated into \hat{M} and be indistinguishable from it. An initial mortality due to tagging simply reduces the effective number of releases; if known, it can be included in the model in an identical fashion to R .

As discussed in Hearn et al. (1987), an estimate of the standard error of \hat{M} is not available by conventional means because the estimate is conditional on the distribution of the data t_i . There is also no guarantee that the estimator is unbiased. A statistical tool that is commonly used in applied statistics both to reduce the bias of an estimator and to provide an approximate standard error is the jackknife (Cox and Hinkley 1974). This technique is not described in detail here; suffice to say that it is based on N_0 separate estimates of M that are obtained by removing, in turn, each tagged fish (whether recaptured or not) from the data. The mean of these estimates is the jackknife estimate of M , and their standard error is the jackknife estimate of the standard error of \hat{M} .

The SE model: An extension of the Sibert model

This model, unlike the HSH model, is fit to data grouped into time intervals, rather than individual, exact recapture times. In common with traditional

single-release tag-attribution models (as described in detail, for example, in Seber 1973 and Wetherall 1982) that have been used extensively in the analysis of mark-recapture data, the SE model is based on classical population dynamics theory, as embodied in the Baranov catch equation (Baranov 1918).

The SE model extends the work of Sibert (1984), who developed a method of analyzing a tagging experiment in which tagged fish are released (not necessarily simultaneously) into two geographically separate fisheries that interact through the movement of fish. Sibert accomplished this basically by adding a spatial dimension and incorporating movement rates into the Baranov catch equation. Tag returns and catch or effort from the two fisheries, by time interval, form the observations to which the model is fit, yielding estimates of movement rates between the two fisheries, and estimates of M , catchability coefficient (when effort is used), and average population size (when catch is used) for each fishery. Recently, Hilborn (1990) developed a model similar to Sibert's in terms of estimation of movement rates; however, natural mortality rate is not specified in the population dynamics and therefore cannot be estimated using the Hilborn model.

To facilitate analyses of southern bluefin tagging experiments, Sibert's two-fishery model is extended in this paper to incorporate a third recapture fishery (the Japanese longline fishery). It is now assumed that there is movement of tagged fish from fisheries 1 and 2 (the release fisheries) into fishery 3. Movement between fisheries 1 and 2 can take place in both directions, but movement into fishery 3 is assumed to be permanent, i.e., there is no possibility of movement back to either fishery 1 or 2 once a fish has moved to fishery 3. This restriction of the model is adopted to avoid the necessity of estimating two additional movement parameters about which little information is available in the absence of releases into fishery 3 (large-scale tagging in the longline fishery is not feasible for southern bluefin tuna). However, this assumption is consistent with the known migratory behavior and the age composition of catches of southern bluefin from the Australian and Japanese fisheries (Hampton 1989).

In addition to the normal assumptions regarding tag loss, equal vulnerability of tagged and untagged fish must be assumed since catch and/or effort statistics are required for the analysis. It is also assumed, for simplicity, that M is constant over time within recapture fisheries.

Model derivation Following release, the tagged fish fall into six categories: the numbers released into fishery 1 that are at large in fishery 1 (N_{11}), fishery 2 (N_{12}), and fishery 3 (N_{13}), and the numbers released into fishery 2 that are at large in fishery 1 (N_{21}),

fishery 2 (N_{22}), and fishery 3 (N_{23}). The way in which these quantities change over time can be represented by six simultaneous differential equations

(assuming, for the moment, that tag losses due to tag shedding, tag-induced mortality, and non-reporting are absent):

$$\begin{aligned} \frac{dN_{11}}{dt} &= -(M_1 + F_1 + T_{12})N_{11} + T_{21}N_{12} && (\text{at } t = 0, N_{11} = N_{01}) \\ \frac{dN_{12}}{dt} &= -(M_2 + F_2 + T_{21})N_{12} + T_{12}N_{11} && (\text{at } t = 0, N_{12} = 0), \\ \frac{dN_{13}}{dt} &= -(M_3 + F_3)N_{13} + T_{13}N_{11} + T_{23}N_{12} && (\text{at } t = 0, N_{13} = 0), \\ \frac{dN_{21}}{dt} &= -(M_1 + F_1 + T_{12})N_{21} + T_{21}N_{22} && (\text{at } t = 0, N_{21} = 0), \\ \frac{dN_{22}}{dt} &= -(M_2 + F_2 + T_{21})N_{22} + T_{12}N_{21} && (\text{at } t = 0, N_{22} = N_{02}), \\ \frac{dN_{23}}{dt} &= -(M_3 + F_3)N_{23} + T_{23}N_{22} + T_{13}N_{21} && (\text{at } t = 0, N_{23} = 0), \end{aligned} \quad (4)$$

where N_{01} and N_{02} are the number of releases into the two fisheries, M_1 , M_2 , and M_3 are the rates of natural mortality operating in the three fisheries, F_1 , F_2 , and F_3 are the rates of fishing mortality specific to the three fisheries (assumed, for the moment, to be constant over time), and T_{12} , T_{13} , T_{21} , and T_{23} are movement rates (the first subscript denoting the donor fishery and the second subscript denoting the recipient fishery).

Tag returns from the three fisheries can be classified in a similar fashion to numbers at large, i.e., r_{11} , r_{12} , and r_{13} are the numbers of returns of fish released in fishery 1 that are recaptured in fisheries 1, 2, and 3, respectively, and r_{21} , r_{22} , and r_{23} are the numbers of returns of fish released in fishery 2 that are recaptured in fisheries 1, 2, and 3, respectively. The estimated rates of return in these categories can be written as:

$$\begin{aligned} \frac{df_{11}}{dt} &= F_1 N_{11}, \\ \frac{df_{12}}{dt} &= F_2 N_{12}, \end{aligned}$$

$$\frac{df_{13}}{dt} = F_3 N_{13},$$

$$\frac{df_{21}}{dt} = F_1 N_{21},$$

$$\frac{df_{22}}{dt} = F_2 N_{22},$$

and

$$\frac{df_{23}}{dt} = F_3 N_{23}. \quad (5)$$

Equations (4) and (5) are solved by integrating between times t and $t + \Delta t$. For ease of notation, define $A_1 = M_1 + F_1 + T_{12} + T_{13}$, $A_2 = M_2 + F_2 + T_{21} + T_{23}$, and $A_3 = M_3 + F_3$. Integrating Equations (4) is accomplished by applying a decoupling transformation (see Sibert 1984 for details) and results in the following set of delay-difference equations,

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

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

$$N_{13(t+\Delta t)} = N_{13(t)} e^{-A_3\Delta t} + \frac{T_{13}}{A_1 - A_3} N_{11(t)} [e^{-A_3\Delta t} - e^{-A_1\Delta t}] + \frac{T_{23}}{A_2 - A_3} N_{12(t)} [e^{-A_3\Delta t} - e^{-A_2\Delta t}],$$

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

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

and

$$N_{23(t+\Delta t)} = N_{23(t)} e^{-A_3\Delta t} + \frac{T_{23}}{A_2 - A_3} N_{22(t)} [e^{-A_3\Delta t} - e^{-A_2\Delta t}] + \frac{T_{13}}{A_1 - A_3} N_{21(t)} [e^{-A_3\Delta t} - e^{-A_1\Delta t}], \quad (6)$$

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

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

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

and

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

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

Substituting Equations (6) into Equations (5) and integrating, the estimated numbers of tagged fish of each category recaptured between times t and $t+\Delta t$ are obtained:

$$\hat{r}_{11(t)} = \frac{R_1 F_1}{1+ab} \left\{ a \left[\frac{bN_{11(t)} + N_{12(t)}}{u} \right] (1 - e^{-u\Delta t}) + \left[\frac{N_{11(t)} - aN_{12(t)}}{v} \right] (1 - e^{-v\Delta t}) \right\},$$

$$\hat{r}_{12(t)} = \frac{R_2 F_2}{1+ab} \left\{ \left[\frac{bN_{11(t)} + N_{12(t)}}{u} \right] (1 - e^{-u\Delta t}) - b \left[\frac{N_{11(t)} - aN_{12(t)}}{v} \right] (1 - e^{-v\Delta t}) \right\},$$

$$\hat{r}_{13(t)} = R_3 F_3 \left\{ \left[\frac{T_{13}}{A_1 - A_3} N_{11(t)} + N_{13(t)} \right] \frac{(1 - e^{-A_3\Delta t})}{A_3} - \frac{T_{13}}{A_1 - A_3} N_{11(t)} \frac{(1 - e^{-A_1\Delta t})}{A_1} \right\},$$

$$\hat{r}_{21(t)} = \frac{R_1 F_1}{1+ab} \left\{ a \left[\frac{N_{22(t)} + bN_{21(t)}}{u} \right] (1 - e^{-u\Delta t}) + \left[\frac{N_{21(t)} - aN_{22(t)}}{v} \right] (1 - e^{-v\Delta t}) \right\},$$

$$\hat{f}_{22}(t) = \frac{R_2 F_2}{1+ab} \left\{ \left[\frac{N_{22}(t)+bN_{21}(t)}{u} \right] (1-e^{-u\Delta t}) - b \left[\frac{N_{21}(t)-aN_{22}(t)}{v} \right] (1-e^{-v\Delta t}) \right\},$$

and

$$\hat{f}_{23}(t) = R_3 F_3 \left\{ \left[\frac{T_{23}}{A_2 - A_3} N_{22}(t) + N_{23}(t) \right] \frac{(1-e^{-A_3\Delta t})}{A_3} - \frac{T_{23}}{A_2 - A_3} N_{22}(t) \frac{(1-e^{-A_2\Delta t})}{A_2} \right\}. \quad (7)$$

Equations (6) and (7) describe the dynamics of tagged fish as a function of the parameters M_1 , M_2 , M_3 , F_1 , F_2 , F_3 , T_{12} , T_{13} , T_{21} , and T_{23} . Fishery-specific reporting rates, R_1 , R_2 , and R_3 , have been introduced and are assumed known. The tag-shedding correction factor, w_t , (Eq. 2) can be introduced in a similar fashion to R (i.e., as a multiplier of F). Note that w_t now refers to the probability of retaining at least one tag at the midpoint of period $t + \Delta t$ and may differ according to fishery of release.

In practice, it is likely that the F s will vary with time. If catch or effort data are available by time period (indexed by i), F_1 , F_2 , and F_3 can be reparameterized as

$$\begin{aligned} F_{1i} &= q_1 f_{1i} \sim \frac{C_{1i}}{P_1}, \\ F_{2i} &= q_2 f_{2i} \sim \frac{C_{2i}}{P_2}, \\ F_{3i} &= q_3 f_{3i} \sim \frac{C_{3i}}{P_3}, \end{aligned} \quad (8)$$

where q_1 , q_2 , and q_3 are catchability coefficients for the three fisheries, f_{1i} , f_{2i} , and f_{3i} are the fishing efforts in the three fisheries in time period i , P_1 , P_2 , and P_3 are mean population sizes available to the three fisheries over the course of the tagging experiment, and C_{1i} , C_{2i} , and C_{3i} are catches in the three fisheries during period i (expressed in the same units

as P). Variable F can now be accommodated without the addition of extra parameters to the model. This, as noted above, involves the assumption that the tagged and untagged fish are equally vulnerable from the moment of release. The choice of which parameterization to use will ultimately depend on the data available and how one views the relationship between catch, effort, catchability, and population size. In fisheries for surface schooling tunas, effective effort is extremely difficult to quantify, and no such estimates are available for the southern bluefin fisheries. For this reason, I have preferred the parameterization using catch in this paper, although for ease of presentation of simulation results, this has been done by assuming the catch to be an index of effective effort and estimates of q , rather than P , obtained. (By so doing, P is in fact the reciprocal of q .) Note that Equations (8) are approximations in the case of catch data, and require that the populations be close to equilibrium for unbiased estimates to be obtained.

Sibert (1984) used a least-squares technique to obtain estimates of the various parameters for the two-fishery model, and employed a square-root transformation as a weighting scheme for observations within the four tag-recovery categories. Several methods of weighting the four individual sums of squares were also tested. Difficulties can arise in choosing the most appropriate weighting scheme, both for observations within and between return categories. These problems can be avoided by using a maximum-likelihood technique based on multinomial probabilities (Seber 1973). Here, a likelihood function can be constructed for each fishery of tag release, e.g., for releases into fishery 1,

$$f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) = \frac{N_{01}! (1 - Pr_1)^{N_{01} - n_1} \prod_{i=1}^k \{p_{11(i)}^{r_{11(i)}} p_{12(i)}^{r_{12(i)}} p_{13(i)}^{r_{13(i)}}\}}{\left\{ \prod_{i=1}^k r_{11(i)}! r_{12(i)}! r_{13(i)}! \right\} (N_{01} - n_1)!},$$

where n_1 is the total number of returns from fishery 1 releases, up to and including period k , $p_{11(i)}$ is the probability of recovery in fishery 1 during period i ($p_{11(i)} = \frac{\hat{f}_{11(i)}}{N_{01}}$), $p_{12(i)}$ is the probability of recovery in fishery 2 during

period i ($p_{12(i)} = \frac{\hat{r}_{12(i)}}{N_{01}}$), $p_{13(i)}$ is the probability of recovery in fishery 3 during period i ($p_{13(i)} = \frac{\hat{r}_{13(i)}}{N_{01}}$), and

$$Pr_1 = \sum_{i=1}^k p_{11(i)} + p_{12(i)} + p_{13(i)}$$

An equivalent function, $f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})$ can be written for releases into fishery 2. Estimates of parameters may then be found by minimizing

$$L = -\log_e [f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) \cdot f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})]$$

with an estimate of the variance-covariance matrix found using the inverse-Hessian method (Bard 1974).

Simulation trials using the model described below showed that unbiased results are obtained using the maximum-likelihood technique, whereas unbiased results could not be guaranteed with the least-squares approach. In the applications of the SE method presented here, the maximum-likelihood estimation technique is used.

Simulation model

In order to examine the behavior of the HSH and SE estimates, a simulation model was developed. The simulation model determines the fate of each tagged fish released into the two fisheries in a probabilistic fashion. For the moment, consider only releases into fishery 1. During the first time period after release, a tagged fish will either:

- (i) be recaptured in fishery 1;
- (ii) die from natural causes in fishery 1;
- (iii) survive in fishery 1 to the end of the first period and then be subject to all possibilities in the next time period;
- (iv) migrate to fishery 2 at time $x < 1$;
- (v) migrate to fishery 3 at time $x < 1$;
- (vi) given (iv), be recaptured in fishery 2 at time y ($x < y < 1$);
- (vii) given (iv), die from natural causes in fishery 2 at time y ($x < y < 1$);
- (viii) given (iv), survive in fishery 2 until the end of time period 1 and then be subject to possibilities (vi) through (x) in the next time period;
- (ix) given (iv), migrate back to fishery 1 at time y ($x < y < 1$) and then be subject to all possibilities for the remainder of time period 1;
- (x) given (iv), migrate to fishery 3 at time y ($x < y < 1$) and then be subject to possibilities (xi) through (xiii) in fishery 3 for the remainder of time period 1;

- (xi) given (v), be recaptured in fishery 3 at time y ($x < y < 1$);
- (xii) given (v), die from natural causes in fishery 3 at time y ($x < y < 1$);
- (xiii) given (v), survive in fishery 3 until the end of time period 1 and then be subject to possibilities (xi) through (xiii) in the next time period.

The probabilities of each of these events occurring are (omitting, for convenience, the time subscript):

$$P(i) = [1 - e^{-A_1}] \frac{F_1}{A_1},$$

$$P(ii) = [1 - e^{-A_1}] \frac{M_1}{A_1},$$

$$P(iii) = e^{-A_1},$$

$$P(iv) = [1 - e^{-A_1}] \frac{T_{12}}{A_1},$$

$$P(v) = [1 - e^{-A_1}] \frac{T_{13}}{A_1},$$

$$P(vi) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{F_2}{A_2},$$

$$P(vii) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{M_2}{A_2},$$

$$P(viii) = P(iv) \cdot e^{-A_2(1-x)},$$

$$P(ix) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{T_{21}}{A_2},$$

$$P(x) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{T_{23}}{A_2},$$

$$P(xi) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{F_3}{A_3},$$

$$P(xii) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{M_3}{A_3},$$

and

$$P(xiii) = P(v) \cdot e^{-A_3(1-x)}.$$

F_1 , F_2 , and F_3 may be allowed to vary by specifying a constant q or P and dependent f or C (as per Equations 8). An identical process deals with releases into fishery 2.

To determine which of the possible outcomes (i) to (v) first befalls a tagged fish, a pseudorandom number, α , uniformly distributed on $[0, 1]$ is generated using a computer subroutine (e.g., subroutine URAND given in Forsythe et al. 1977:245). If $\alpha < P(i)$, outcome (i) is chosen; if $P(i) < \alpha < [P(i) + P(ii)]$, outcome (ii) is chosen; if $[P(i) + P(ii)] < \alpha < [P(i) + P(ii) + P(iii)]$, outcome (iii) is chosen; and so on. Additional pseudorandom numbers are generated and further tests relating to outcomes (vi) to (xiii) applied as necessary until the fish is deemed to have been recaptured, died naturally, or survived to the end of the experiment. When the fates of all tagged fish released into both fisheries are determined in this way, the six tag-return vectors, r_{11} , r_{12} , r_{13} , r_{21} , r_{22} , and r_{23} are established. The SE model can then be fit to these data and the estimated parameter values compared with the "real" values input to the

simulation model. The HSH model can be similarly tested, with exact recapture times within the determined period of capture simulated by randomly sampling from a truncated exponential distribution (truncated at one year in this case) as shown in Hearn et al. (1987).

Results

HSH model

The jackknife estimates of M and their standard errors obtained by fitting the HSH model to data from experiments 1-4 are given in Table 3. If full reporting of tags is assumed, the estimates of M range from just less than 0.2/year to just more than 0.4/year; the estimates decrease slightly as reporting rate decreases.

It is clear that the tag-shedding model used to weight the returns has a large bearing on the estimate of M obtained. For experiment 2, the best fitting tag-shedding model (constant shedding rate) predicts a very low probability of tag retention after long periods at liberty (Hampton and Kirkwood 1990). Therefore, those returns from the Japanese fishery at liberty for longer than, say, 6 years will receive large weight in the analysis using the HSH method; this is one of the main reasons for the relatively low estimate of M (0.2275/year for a reporting rate of 1.0). In contrast, a decreasing tag-shedding rate model provided the best fit to the double-tagging data from experiments 3 and 4. Here, there is little change in the probability of tag retention after about 3 or 4 years at liberty (Hampton and Kirkwood 1990). All returns after this time will, then, receive similar weight from the tag-shedding model; accordingly, relatively high estimates of M are obtained for experiments 3 and 4 (0.4165/year and

0.4163/year, respectively, for a reporting rate of 1.0). The most direct test of the effect of the different tag-shedding models is the application of both constant and decreasing shedding-rate models to the analysis of experiment 1 (these tag-shedding models provided equally good fits to experiment 1 double-tagging data, and could not be distinguished on the statistical criterion used by Hampton and Kirkwood 1990). Here, the estimate of M obtained when the constant shedding-rate model was used

Table 3

Estimates of the rate of natural mortality (M) and their standard errors (SE) for different reporting rates (R) obtained from fitting the HSH model to data from experiments 1-4 (see Table 1 for descriptions). Separate estimates are given for two tag-shedding models derived for experiment 1. All estimates are in units per year.

R	Experiment 1				Experiment 2		Experiment 3		Experiment 4	
	Constant shedding rate		Decreasing shedding rate		Constant shedding rate	SE	Decreasing shedding rate	SE	Decreasing shedding rate	
	M	SE	M	SE					M	SE
1.0	0.1987	0.0681	0.4038	0.0634	0.2275	0.1740	0.4165	0.0860	0.4163	0.0646
0.9	0.1896	0.0674	0.3941	0.0625	0.2239	0.1604	0.4091	0.0815	0.4098	0.0633
0.8	0.1792	0.0665	0.3827	0.0613	0.2194	0.1420	0.4002	0.0763	0.4023	0.0619
0.7	0.1669	0.0654	0.3693	0.0599	0.2122	0.1158	0.3891	0.0702	0.3937	0.0601
0.6	0.1519	0.0640	0.3527	0.0580	0.1965	0.0733	0.3748	0.0628	0.3835	0.0581
0.5	0.1330	0.0620	0.3312	0.0553	0.1148	0.0205	0.3549	0.0538	0.3710	0.0556

(0.1987/year for a reporting rate of 1.0) is less than half the estimate obtained when the decreasing shedding-rate model was used (0.4038/year for a reporting rate of 1.0).

SE model

The SE model was fit to the tag-return data from experiments 2 and 3 (analysis A) and experiments 2 and 4 (analysis B). These data, along with the catch data used to parameterize F_s , are shown in Tables 4 and 5, respectively. For analysis A, returns from the NSW fishery (fishery 1) were defined by recapture positions east of 145°E. SA fishery (fishery 2) returns were defined by recapture positions west of 145°E. No returns from these experiments were recorded in WA (defined for these purposes as west of 125°E) as commercial tuna fishing in WA did not begin until 1969. For analysis B, there is a slight complicating factor in that southern bluefin were tagged in WA before substantial commercial fishing began in 1969; the majority of the few returns recorded in WA from experiment 4 were from the tagging vessel. However, because the tagged fish were released in the WA area, fishery 2 for analysis B is defined as the SA and WA areas combined. For both analyses, fishery 3 is the Japanese long-line fishery with no geographical restrictions.

As mentioned earlier, the use of catch data to parameterize F involves an assumption that the population is in equilibrium for the duration of the tag-recovery period. This is not an unreasonable assumption for the juvenile population available to the surface

Table 4

Numbers of tag returns from experiment 2 and experiment 3 by period at liberty and related catch statistics used in analysis A of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963-70 for NSW and 1964-71 for SA. The Japanese (fishery 3) catch used is the 1964-85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia.

Time at liberty (yr)	Experiment 2 releases (NSW)			Experiment 3 releases (SA)			Catches ($\times 10^3$)		
	Returns from			Returns from			NSW	SA	Japan
	NSW	SA	Japan	NSW	SA	Japan			
0-1	3144	55	4	159	842	14	3.445	3.968	45.216
1-2	854	24	12	37	77	24	3.748	3.825	45.216
2-3	64	8	17	7	3	28	4.232	4.089	45.216
3-4	5	0	4	0	0	23	4.177	4.213	45.216
4-5	0	0	2	0	0	23	4.569	4.395	45.216
5-6	2	0	0	0	0	12	4.418	4.896	45.216
6-7	0	0	3	0	0	9	3.815	5.588	45.216
7-8	0	0	2	0	0	3	3.681	5.815	45.216
8-9	0	0	1	0	0	8	3.772	6.005	45.216
9-10	0	0	1	0	0	3	3.594	6.315	45.216
10-11	0	0	2	0	0	1	3.256	6.695	45.216
11-12	0	0	0	0	0	2	3.438	7.415	45.216
12-13	0	0	0	0	0	0	2.984	8.539	45.216
13-14	0	0	0	0	0	0	2.788	8.974	45.216
14-15	0	0	0	0	0	0	2.764	9.284	45.216
15-16	0	0	0	0	0	0	2.163	10.178	45.216
16-17	0	0	1	0	0	1	1.626	10.856	45.216

Table 5

Numbers of tag returns from experiment 2 and experiment 4 by period at liberty and related catch statistics used in analysis B of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963-70 for NSW and 1964-71 for SA. The Japanese (fishery 3) catch used is the 1964-85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Time at liberty (yr)	Experiment 2 releases (NSW)			Experiment 4 releases (WA)			Catches ($\times 10^3$)		
	Returns from			Returns from			NSW	SA/WA	Japan
	NSW	SA/WA	Japan	NSW	SA/WA	Japan			
0-1	3144	55	4	37	220	6	3.445	4.094	45.216
1-2	854	24	12	109	75	3	3.748	4.026	45.216
2-3	64	8	17	12	11	28	4.232	4.385	45.216
3-4	5	0	4	0	1	10	4.177	4.547	45.216
4-5	0	0	2	0	0	21	4.569	4.763	45.216
5-6	2	0	0	1	0	14	4.418	5.407	45.216
6-7	0	0	3	0	0	5	3.815	6.148	45.216
7-8	0	0	2	0	0	0	3.681	6.443	45.216
8-9	0	0	1	0	0	4	3.772	6.775	45.216
9-10	0	0	1	0	0	1	3.594	7.299	45.216
10-11	0	0	2	0	0	0	3.256	7.879	45.216
11-12	0	0	0	0	0	1	3.438	8.914	45.216
12-13	0	0	0	0	0	0	2.984	10.481	45.216
13-14	0	0	0	0	0	2	2.788	11.768	45.216
14-15	0	0	0	0	0	0	2.764	12.283	45.216
15-16	0	0	0	0	0	1	2.163	13.334	45.216
16-17	0	0	1	0	0	0	1.626	13.925	45.216
17-18	0	0	0	0	0	1	1.175	13.353	45.216

Table 6

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

Parameter	Reporting rate					
	1.0		0.9		0.8	
	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.7135	0.4354	0.6336	0.5673 E-1	0.5295	0.1105
M_2	0.1490 E + 1	0.2555 E + 1	0.1449 E + 1	0.3114	0.1391 E + 1	0.6542
M_3	0.2044	0.1264	0.2019	0.2636 E - 1	0.1975	0.4307 E - 1
q_1	0.2046	0.4249 E - 2	0.2267	0.4705 E - 2	0.2544	0.5276 E - 2
q_2	0.8595 E - 1	0.4330 E - 2	0.9512 E - 1	0.4806 E - 2	0.1072	0.5397 E - 2
q_3	0.6147 E - 3	0.2762 E - 2	0.6912 E - 3	0.4003 E - 3	0.7526 E - 3	0.8415 E - 3
T_{12}	0.1176	0.1330 E - 1	0.1182	0.1347 E - 1	0.1169	0.1322 E - 1
T_{13}	0.9667 E - 1	0.4348	0.9452 E - 1	0.5432 E - 1	0.9758 E - 1	0.1092
T_{21}	0.1750	0.1435 E - 1	0.1751	0.1437 E - 1	0.1750	0.1437 E - 1
T_{23}	0.5691	0.2553 E + 1	0.5637	0.3283	0.5784	0.6462
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.3582	0.9196 E - 1	0.2232	0.1346	0.8865 E - 2	0.9048 E - 1
M_2	0.1090 E + 1	0.5488	0.1213 E + 1	0.7968	0.1239 E + 1	0.5315
M_3	0.2057	0.2837 E - 1	0.1890	0.6001 E - 1	0.1660	0.7660 E - 1
q_1	0.2900	0.6015 E - 2	0.3367	0.6969 E - 2	0.4014	0.8306 E - 2
q_2	0.1224	0.6177 E - 2	0.1431	0.7218 E - 2	0.1715	0.8655 E - 2
q_3	0.6118 E - 3	0.3980 E - 3	0.9476 E - 3	0.1225 E - 2	0.1476 E - 2	0.1649 E - 2
T_{12}	0.1172	0.1326 E - 1	0.1155	0.1312 E - 1	0.1151	0.1301 E - 1
T_{13}	0.1382	0.9035 E - 1	0.1026	0.1339	0.7884 E - 1	0.8817 E - 1
T_{21}	0.1754	0.1440 E - 1	0.1760	0.1441 E - 1	0.1764	0.1443 E - 1
T_{23}	0.8203	0.5449	0.6121	0.7933	0.4735	0.5314

fisheries as long as recruitment was reasonably constant during this period. The stability of the surface catches during the 1960s and early 1970s and cohort analysis (Hampton 1989) would suggest that this was the case. Although the adult population declined during several periods since exploitation began, Japanese catch was fairly constant during these tagging experiments, and parental biomass also appeared to be relatively stable. Therefore, the use of catch data to parameterize F should not cause major difficulties in this case.

In these experiments, tagged southern bluefin were released over a period of years; therefore, returns within a specific time-at-liberty category cannot be related to a catch in any one year. In these cases, the catch (or effort) data used are normally averaged over time, assuming a constant F within each fishery (e.g., Kleiber et al. 1987). This was the approach taken for the Japanese fishery, where catch was in fact quite constant over most of the return period (mid-1960s to early 1980s). For the Australian surface fisheries, an 8-year moving average (equivalent to the total release period for experiments 2, 3, and 4) was used so that the gradual decline of the NSW fishery and gradual in-

crease in the SA and WA fisheries (Hampton 1989) could be represented.

Analysis A The first fit to the data allowed M to vary among the three fisheries. The resulting estimates of the three natural mortality parameters, three catchability parameters and four movement parameters and their standard errors, for reporting rates between 1.0 and 0.5, are presented in Table 6. There is no *a priori* reason why reporting rate should be the same for the three fisheries. In the absence of any information on the actual reporting rates, they have been assumed here, for simplicity, to be the same for the three fisheries.

For a reporting rate of 1.0, the estimates of M for the three fisheries are 0.71/year, 1.5/year, and 0.20/year, respectively. M_2 and M_3 decrease slightly as reporting rate decreases; however, M_1 decreases substantially with decreasing reporting rate. This is because the tag recapture rate in NSW is very high even if a reporting rate of 1.0 is assumed; therefore, even relatively small reductions in reporting rate from 1.0 require substantial compensatory changes in M_1 .

Catchability in the NSW fishery is very high and suggests a fishing mortality rate of approximately 0.8/year, reflecting the high recapture rate there (33% of experiment 2 releases recaptured within 1 year and 42% recaptured within 2 years). Catchability is substantially lower in the SA and Japanese fisheries, suggesting rates of fishing mortality of approximately 0.35/year and 0.03/year, respectively. The catchability coefficients increase steadily with decreasing reporting rates, approximately doubling with a reduction in assumed reporting rate from 1.0 to 0.5. Rates of movement are slightly higher in the SA→NSW direction (0.17/year) than in the NSW→SA direction (0.12/year). Apparent movement into the Japanese fishery is substantially higher from the SA fishery (0.57/year) than from the NSW fishery (0.10/year). The movement parameters are relatively unaffected by changing the assumed reporting rate within the range 1.0–0.5.

Table 7

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 6) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.99	1.00								
M_3	-0.98	-0.99	1.00							
q_1	0.01	-0.01	-0.01	1.00						
q_2	0.03	0.04	-0.03	-0.04	1.00					
q_3	0.99	0.99	-0.98	-0.01	0.02	1.00				
T_{12}	-0.06	-0.04	0.04	-0.09	-0.15	-0.04	1.00			
T_{21}	0.00	0.01	-0.01	-0.10	0.37	0.00	0.04	1.00		
T_{13}	-0.99	-0.99	0.98	0.01	-0.02	-0.99	-0.04	-0.00	1.00	
T_{23}	-0.99	-0.99	0.98	0.01	-0.02	-0.99	-0.04	0.00	0.99	1.00

The standard errors of the parameters are large, particularly for M_1 , M_2 , T_{13} , and T_{23} . The correlation matrix for the parameters (Table 7) indicates several cases of extreme confounding of estimates. The Ms are very highly correlated with one another and individually with q_3 , T_{13} , and T_{23} . The latter three parameters are also very highly correlated with one another. These high correlations and standard errors suggest that the model is overdetermined (too many parameters).

Table 8

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

Parameter	Reporting rate					
	1.0		0.9		0.8	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.2299	0.2326 E-1	0.2288	0.2285 E-1	0.2278	0.2224 E-1
q_1	0.2042	0.4244 E-2	0.2263	0.4697 E-2	0.2543	0.5278 E-2
q_2	0.8616 E-1	0.4341 E-1	0.9560 E-1	0.4820 E-2	0.1075	0.5416 E-2
q_3	0.1614 E-3	0.1981 E-4	0.1912 E-3	0.2349 E-4	0.2363 E-3	0.2917 E-4
T_{12}	0.1230	0.1393 E-1	0.1215	0.1372 E-1	0.1204	0.1355 E-1
T_{13}	0.5705	0.3142 E-1	0.4906	0.3050 E-1	0.3922	0.2923 E-1
T_{21}	0.1749	0.1433 E-1	0.1748	0.1434 E-1	0.1748	0.1432 E-1
T_{23}	0.1848 E+1	0.9067 E-1	0.1805 E+1	0.8919 E-1	0.1756 E+1	0.8755 E-1
Parameter	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
	M	0.2184	0.2061 E-1	0.1871	0.1717 E-1	0.1188
q_1	0.2898	0.6007 E-2	0.3345	0.6881 E-2	0.3842	0.7657 E-2
q_2	0.1226	0.6181 E-2	0.1440	0.7239 E-2	0.1757	0.8793 E-2
q_3	0.2961 E-3	0.3617 E-4	0.3572 E-3	0.4162 E-4	0.3685 E-3	0.4209 E-4
T_{12}	0.1163	0.1295 E-1	0.1065	0.1164 E-1	0.8711 E-1	0.1536 E-1
T_{13}	0.2795	0.2638 E-1	0.1662	0.2031 E-1	0.8650 E-1	0.1259 E-1
T_{21}	0.1758	0.1440 E-1	0.1787	0.1458 E-1	0.1895	0.1536 E-1
T_{23}	0.1691 E+1	0.8503 E-1	0.1625 E+1	0.8109 E-1	0.1548 E+1	0.7539 E-1

Table 9

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 8) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q ₁	q ₂	q ₃	T ₁₂	T ₂₁	T ₁₃	T ₂₃
M	1.00							
q ₁	-0.02	1.00						
q ₂	-0.04	-0.04	1.00					
q ₃	0.81	-0.03	-0.06	1.00				
T ₁₂	0.01	0.09	-0.16	0.05	1.00			
T ₂₁	-0.02	-0.10	0.37	-0.02	-0.04	1.00		
T ₁₃	-0.76	0.24	0.07	-0.65	-0.31	-0.05	1.00	
T ₂₃	-0.30	-0.03	0.68	-0.26	0.06	0.39	0.17	1.00

Consequently, in the second fit to the data, M was assumed to be equal for the three fisheries (constrained M), thus reducing the number of parameters from ten to eight. A likelihood ratio test (Kendall and Stuart 1979) was conducted with the constrained-M fit defined as the null hypothesis and the unconstrained-M fit as the alternative hypothesis (assuming $R = 1.0$). The test indicated that the unconstrained-M fit was significantly better than the constrained-M fit ($P < 0.01$). However, the constrained-M fit resulted in much smaller standard errors for the critical parameters (Table 8); q₃ has a coefficient of variation (CV) of 15%, with all other parameters having CVs of less than 10%. The correlation among the parameters is also much more acceptable (Table 9), although M is still correlated to a degree with q₃ and T₁₃, as are the q_s with their respective incoming and outgoing movement parameters.

There are substantial changes in some of the parameter estimates obtained from the constrained-M fit. The overall estimate of M is 0.23/year, which is similar to the estimate of M₃ obtained from the unconstrained-M fit, but is much smaller than the M₁ and M₂ estimates. There is little change in q₁, q₂, T₁₂, or T₂₁; however, T₁₃ and T₂₃ are much larger in the constrained-M fit. These higher values compensate for the reduced M₁ and M₂ estimates (now assumed equal to M₃) in order to maintain the observed high rate of attrition of tagged fish in the NSW and SA fisheries. With the higher movement rates into the Japanese fishery, q₃ is smaller in the constrained-M fit so that

the observed rate of return of tags from that fishery is still well described by the model. The estimate of M is insensitive to reductions in reporting rate to about 0.7, while the other parameter estimates behave similarly to those of the unconstrained-M fit.

Plots of observed numbers of returns and the numbers expected on the basis of the constrained-M fit for each of the release-recapture categories do not reveal any glaring deficiencies in the model (Fig. 2). Plotting expected numbers of returns using the unconstrained-M fit produced an essentially identical result.

Analysis B The results of the unconstrained-M fits to the results of experiments 2 and 4 are given in Table 10. The estimate of M₁ is substantially smaller (0.28/year) than that obtained from analysis A. To maintain the observed rate of attrition of tagged fish in the NSW

Table 10

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 5). All mortality and movement parameters are in units per year. Estimates were not available for reporting rates less than 0.8 because of a boundary condition on the M₁ estimate.

Parameter	Reporting rate					
	1.0		0.9		0.8	
	Estimate	SE	Estimate	SE	Estimate	SE
M ₁	0.2810	0.2446	0.1612	0.5384	0.3555 E-1	0.6471 E-1
M ₂	0.1158 E+1	0.3541	0.1207 E+1	0.7392	0.1170 E+1	0.8124 E-1
M ₃	0.1909	0.5157 E-1	0.2064	0.9149 E-1	0.2043	0.2620 E-1
q ₁	0.2032	0.4287 E-2	0.2253	0.4768 E-2	0.2526	0.5369 E-2
q ₂	0.9334 E-2	0.6819 E-3	0.1020 E-1	0.7734 E-3	0.1146 E-1	0.8439 E-3
q ₃	0.4623 E-3	0.9814 E-3	0.4932 E-3	0.2231 E-2	0.4590 E-3	0.1241 E-3
T ₁₂	0.5384	0.6562 E-1	0.5652	0.6965 E-1	0.5655	0.7271 E-1
T ₁₃	0.1094	0.2329	0.1211	0.5424	0.1447	0.3296 E-1
T ₂₁	0.4508 E-1	0.4324 E-2	0.4364 E-1	0.4265 E-2	0.4354 E-1	0.4232 E-2
T ₂₃	0.1636	0.3466	0.1614	0.7162	0.1913	0.4084 E-1

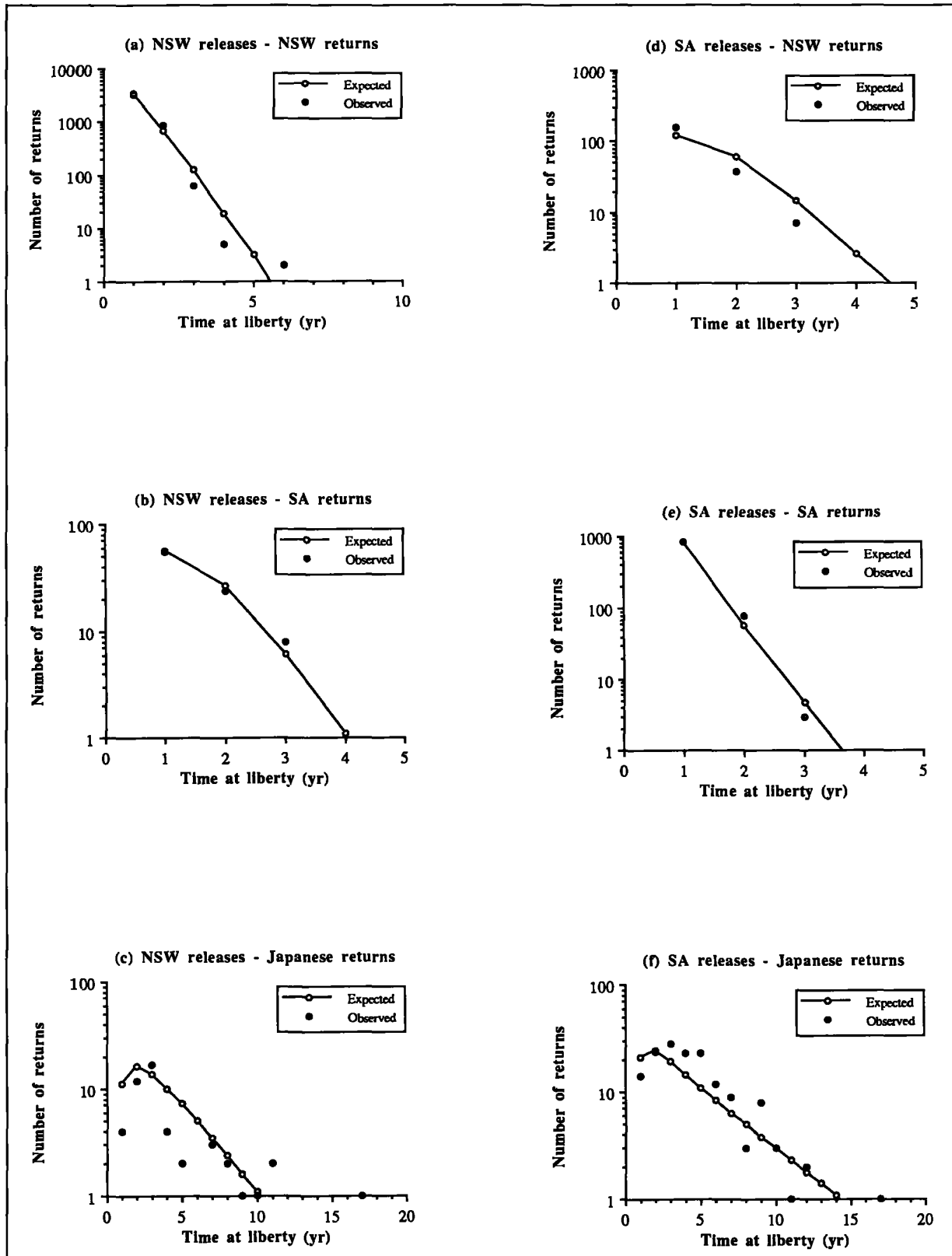


Figure 2

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis A. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 11

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 10) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.94	1.00								
M_3	-0.85	-0.87	1.00							
q_1	-0.01	-0.02	0.01	1.00						
q_2	0.10	0.14	-0.07	-0.07	1.00					
q_3	0.97	0.98	-0.86	-0.01	0.03	1.00				
T_{12}	-0.31	-0.05	0.07	0.13	-0.29	-0.07	1.00			
T_{21}	0.00	0.01	-0.03	-0.08	0.35	-0.00	0.03	1.00		
T_{13}	-0.97	-0.98	0.87	0.01	-0.03	-0.99	0.06	-0.00	1.00	
T_{23}	-0.96	-0.98	0.88	0.01	-0.02	-0.99	0.07	0.01	0.99	1.00

fishery, a compensatory increase in T_{12} is observed. The estimate of M_2 is again relatively high (1.16/year) while the estimate of M_3 compares closely with that obtained from the unconstrained-M fit in analysis A. Recall that releases into fishery 2 (SA/WA) for analysis B were made some distance away from the commercial fishery operating at the time. This could explain the much lower estimate of q_2 , and as a result, fishing mortality (~ 0.04 /year). Similarly, the smaller estimates of movement from WA/SA into the NSW and Japanese fisheries is likely to be due to the fish being released further away from those fisheries.

The standard errors of the estimates that were obtained for the unconstrained-M fit are somewhat less than the equivalent values for analysis A, but are nonetheless far too high for the estimates to be considered reliable. The correlation matrix (Table 11) reveals a similar pattern of correlation among the parameters as was observed for analysis A.

It was not possible to obtain estimates of standard errors for reporting rates less than 0.8 because of a boundary condition with respect to the M_1 estimate, which approached zero for low reporting rates (the Hessian matrix could not be inverted because it was not positive definite). This also indicates that the parameter estimates obtained from this data set for reporting rates less than 0.8 are not the maximum likelihood estimates and therefore cannot be considered reliable.

A constrained-M fit resulted in much smaller standard errors, changes in parameter estimates consistent with analysis A (Table 12) and much lower correlation among parameters (Table 13). A likelihood ratio test (assuming $R=1.0$) again indicated that the unconstrained-M fit is significantly better than the constrained-M fit ($P<0.01$). However acceptance of the more complex model cannot be justified in view of the large standard errors and correlations among the

parameter estimates. Plots of observed and expected numbers of returns (Fig. 3) indicate a good fit of the constrained-M model to the data.

Simulation results

Simulated data sets were analysed in order to test the performance of the HSH and SE models. The simulations were designed to produce data sets identical in their characteristics to experiment 2 and 3 (analysis A), with the exception that tag shedding and non-reporting were not considered. Two sets of simulations were performed: type 1 simulations used the results of the analysis A unconstrained-M fit as input parameters; type 2 simulations used the results of the analysis A constrained-M fit as input parameters. Thirty data sets were produced for each simulation. Type 1 simulated data were analysed by the SE model using both unconstrained-M and constrained-M fits. Type 2 simulated data were analysed using the SE model constrained-M fits and the HSH model in order to provide a basic comparison between the two models.

Parameter estimate means and their standard deviations for type 1 simulations are given in Table 14 for the unconstrained-M fits and Table 15 for the constrained-M fits. These results indicate that (i) the unconstrained-M fit provides unbiased estimates of all parameters, and (ii) the constrained-M fit to simulated data behaves in an identical fashion to similar fits to real data in terms of the changes in the estimates of q_3 , T_{13} , and T_{23} . Moreover, the accurate recovery of parameters input to the simulation model demonstrates the soundness of the SE method as applied to southern bluefin tuna tagging data.

Table 16 provides a direct comparison of parameter estimates obtained by fitting the HSH and SE models to type 2 simulated data. The results indicate that the HSH model considerably overestimates M . The mean estimates from simulated experiments 2 and 3 and the mean estimate based on pooled data are almost identical (0.42–0.43/year) and are nearly double the value of M input to the simulation model. The SE model, on the other hand, is able to accurately retrieve the parameters input to the simulation model. This result casts considerable doubt on the estimates of M for southern bluefin tuna obtained using the HSH model.

The reason for the biased estimates of M obtained using the HSH model appears to lie in the very low

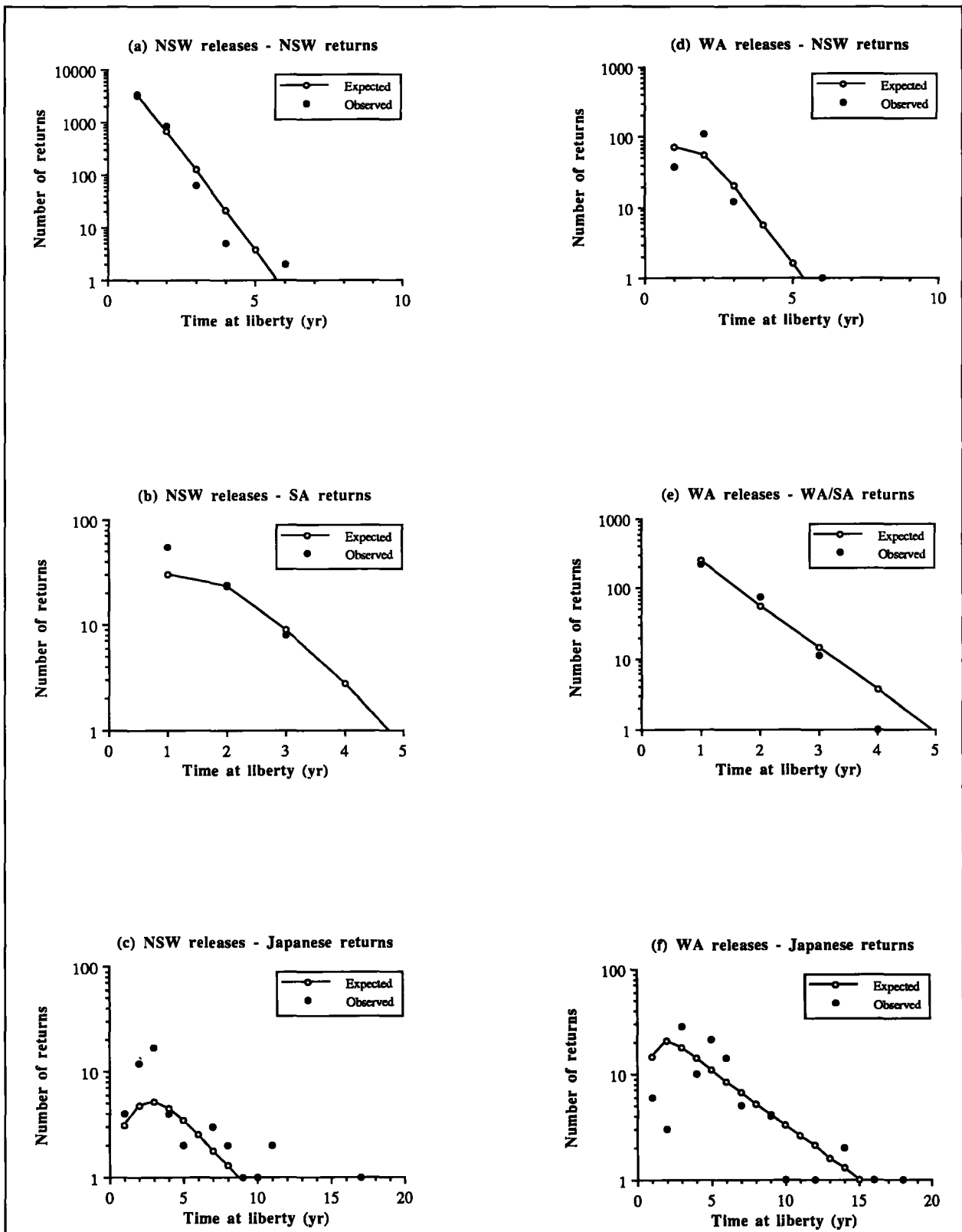


Figure 3

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis B. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 12

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 4). All mortality and movement parameters are in units per year.

Parameter	Reporting rate					
	1.0		0.9		0.8	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.1997	0.2409 E-1	0.1902	0.2312 E-1	0.1775	0.2184 E-1
q ₁	0.2034	0.4277 E-2	0.2253	0.4728 E-2	0.2524	0.5292 E-1
q ₂	0.9575 E-2	0.6858 E-3	0.1076 E-1	0.7666 E-3	0.1221 E-1	0.8666 E-3
q ₃	0.8078 E-4	0.1169 E-4	0.8863 E-4	0.1270 E-4	0.9765 E-4	0.1379 E-4
T ₁₂	0.4123	0.4112 E-1	0.3837	0.3748 E-1	0.3475	0.3313 E-1
T ₁₃	0.3163	0.4327 E-1	0.2748	0.3907 E-1	0.2249	0.3385 E-1
T ₂₁	0.4429 E-1	0.4230 E-2	0.4470 E-1	0.4258 E-2	0.4489 E-1	0.4262 E-2
T ₂₃	0.1082 E+1	0.7458 E-1	0.1087 E+1	0.7400 E-1	0.1083 E+1	0.7267 E-1
Parameter	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
	M	0.1575	0.2000 E-1	0.1215	0.1753 E-1	0.6137 E-1
q ₁	0.2857	0.5968 E-2	0.3272	0.6776 E-2	0.3746	0.7561 E-2
q ₂	0.1422 E-1	0.1004 E-2	0.1701 E-1	0.1195 E-2	0.2106 E-1	0.1471 E-2
q ₃	0.1055 E-3	0.1460 E-4	0.1073 E-3	0.1461 E-4	0.9352 E-4	0.1292 E-4
T ₁₂	0.2994	0.2796 E-1	0.2389	0.2214 E-1	0.1694	0.1618 E-1
T ₁₃	0.1713	0.2755 E-1	0.1175	0.2036 E-1	0.7254 E-1	0.1342 E-1
T ₂₁	0.4534 E-1	0.4288 E-2	0.4643 E-1	0.4376 E-2	0.4936 E-1	0.4620 E-2
T ₂₃	0.1091 E+1	0.7116 E-1	0.1109 E+1	0.6899 E-1	0.1151 E+1	0.6650 E-1

apparent fishing mortality inflicted upon the tagged population by the Japanese fishery. Recall that one of the assumptions of the HSH method is that fishing mortality is maintained on the tagged population until completion of the experiment. However, as F approaches zero for older age classes, overestimates of M result from this model. To confirm this, the type 2 simulations were rerun, with the only change being an increased input value of q_3 such that F for the Japanese fishery was increased to 0.2/year (the value derived

from real data and previously used in the simulations involving the HSH method was 0.007/year). Under these conditions, the HSH model provided mean estimates of M of 0.24/year for the analysis of experiment 2, experiment 3, and the two experiments pooled. This agrees well with the value for M of 0.23/year input to the simulation model.

Discussion

This paper represents the first specific attempt to estimate the southern bluefin tuna natural mortality rate from tagging data. The simulation results confirm that the method of Hearn et al. (1987) will overestimate M substantially when the apparent fishing mortality inflicted on the tagged population in the latter part of the experiment is very low. Also, the sensitivity of the M estimates to the tag-shedding model adopted makes interpretation of the results difficult, particularly as it was demonstrated by Hampton and Kirkwood (1990) that long-term shedding rates are very uncertain.

Table 13

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 12) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q ₁	q ₂	q ₃	T ₁₂	T ₂₁	T ₁₃	T ₂₃
M	1.00							
q ₁	0.02	1.00						
q ₂	-0.07	-0.06	1.00					
q ₃	0.81	0.02	-0.11	1.00				
T ₁₂	-0.11	0.15	-0.21	-0.01	1.00			
T ₂₁	-0.06	-0.09	0.36	-0.08	0.02	1.00		
T ₁₃	-0.44	0.06	0.20	-0.43	-0.75	-0.05	1.00	
T ₂₃	-0.45	-0.07	0.62	-0.41	0.07	0.48	0.16	1.00

Table 14

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (unconstrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were $N_{01} = 9513$ and $N_{02} = 7328$.

Parameter	"Real" value	Mean	SD
M_1	0.71	0.69	0.016
M_2	1.49	1.55	0.087
M_3	0.20	0.20	0.018
q_1	0.20	0.21	0.0047
q_2	0.086	0.086	0.0040
q_3	0.00061	0.00067	0.000085
T_{12}	0.012	0.12	0.0099
T_{21}	0.017	0.18	0.014
T_{13}	0.097	0.11	0.011
T_{23}	0.57	0.53	0.067

Table 15

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were $N_{01} = 9513$ and $N_{02} = 7328$.

Parameter	"Real" value	Mean	SE
M_1	0.71		
M_2	1.49	0.23	0.016
M_3	0.20		
q_1	0.20	0.20	0.0044
q_2	0.086	0.087	0.0037
q_3	0.00061	0.00017	0.000018
T_{12}	0.012	0.12	0.015
T_{21}	0.017	0.17	0.014
T_{13}	0.097	0.51	0.029
T_{23}	0.57	1.86	0.088

The development of a population dynamics model for tagged southern bluefin that incorporates movement between the NSW and SA/WA fisheries and offshore movement into the Japanese longline fishery, as well as natural mortality and fishery-specific catchability, appears to overcome these difficulties. Although the unconstrained-M version of the model could not provide useful parameter estimates because of high parameter correlation, accurate estimates were obtained by assuming that the natural mortality rate was the same in all fisheries, thus reducing the number of parameters to be estimated by two. For a large highly-mobile apex predator, this may not be an unreasonable assumption.

Table 16

A comparison of mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the HSH and SE models (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were $N_{01} = 9513$ and $N_{02} = 7328$.

Parameter	"Real" value	Mean	SD
HSH model			
M (experiment 2)	0.23	0.42	0.023
M (experiment 3)	0.23	0.43	0.031
M (pooled data)	0.23	0.43	0.015
SE model			
M	0.23	0.23	0.016
q_1	0.20	0.20	0.0045
q_2	0.086	0.085	0.0043
q_3	0.00016	0.00016	0.000017
T_{12}	0.12	0.12	0.014
T_{21}	0.17	0.17	0.015
T_{13}	0.57	0.58	0.027
T_{23}	1.85	1.80	0.066

However, this simplification of the model was not achieved without a small, though significant, loss in likelihood of the data.

The substantial differences in some of the parameter estimates produced by the unconstrained-M and constrained-M versions of the model simply mean that the observed data could have been produced in a number of alternative and similarly likely ways. It is unlikely that M could vary amongst the three fisheries as much as was suggested by the unconstrained-M estimates in analysis A. It is noteworthy, however, that the estimate of M_3 was similar for both analyses and also compared well with the constrained-M estimates.

Compliance with model assumptions is usually difficult to assess, and this case is no exception. Tag-shedding was incorporated into both models used; therefore, in theory, the tag-shedding assumption was satisfied. In practice, the estimated shedding rates are very uncertain, particularly for the older recaptures. It would be desirable in the future to develop a method whereby uncertainties in tag-shedding rates were reflected in the standard errors of the estimated mortality and movement parameters. This might be achieved by the simultaneous estimation of shedding, mortality, and movement rates from double-tagging data.

There are no data available on which the calculation of reporting rates could be based; all estimations were therefore carried out for a range of reporting rates. Fortunately, the M estimates were largely insensitive to assumed reporting rates greater than about 0.7 in the case of the constrained-M estimates. It is worth

noting that the high recovery rate of tags released in NSW would suggest a high reporting rate in that fishery at least.

The few data available suggest that mortality associated with tagging southern bluefin tuna is slight. Animals have been reported to survive in good condition for 80 hours in a live bait tank after having been tagged (Robins 1963). Furthermore, Hynd and Lucas (1974) considered that the behavior of the fish immediately following tagging was consistent with slight or no tagging mortality. Personal observations in the field also support this hypothesis. If tagging mortality occurred and was immediate or nearly so, its effect on the parameter estimates would be slight and identical to that of non-reporting. If there was significant, continuous tag-induced mortality (which is unlikely), M would tend to be overestimated by both methods used in this paper.

The assumption of constant M has not been tested in this paper, but the possibility that a model with age-dependent M might provide a better fit to the tagging data should not be ruled out. Generalization of the SE model in this regard would be possible and may yield useful results, although similar estimation problems to those of the unconstrained- M fits might occur.

The final assumption concerns equal vulnerability of the tagged and untagged populations and is possibly the most difficult with which to comply. Strict compliance would require that either the fishing effort is distributed randomly with respect to both the tagged and untagged populations, or that the tagged population is distributed randomly with respect to the untagged population. The first possibility is seldom seen in practice because fishermen tend to direct their effort in areas of high fish concentration. If these areas happen to coincide with the areas of tag release (as is often the case), the number of recaptures during the first period after release may be larger than expected. This would result in overestimates of M and other components of tag attrition using the SE method. Similarly, the second possibility is not usually feasible, as it would require tagged fish to be released over a wide area within a short space of time. However, for highly mobile tunas such as southern bluefin, mixing is likely to be rapid, thus lessening the problem to a large extent. In the case of the NSW fishery, many tagged fish were released prior to the fishing season, which would tend to enhance mixing. Division of the Australian fishery into two components also helps compliance with this assumption. From this point of view, even further stratification would have been desirable; however, this would greatly complicate the algebra and probably result in statistical problems with parameter estimation.

The fishing mortality inflicted on tagged southern bluefin by the Japanese fishery would appear to be

slight ($<0.06/\text{year}$ for assumed reporting rates >0.5) compared with values of 0.15–0.40/year obtained from cohort analysis (Hampton 1989). This discrepancy could result because southern bluefin migrating through Australian coastal waters are subsequently somewhat less available to the longline fishery than the population in general. Such differential availability to surface and longline fisheries has been noted for other tuna stocks, e.g., populations of yellowfin tuna in the Pacific (Lenarz and Zweifel 1979, Suzuki 1988) and Atlantic Oceans (Fonteneau 1986, Suzuki 1988). While not necessarily affecting the estimates of M , caution should be exercised in the interpretation of estimates of fishing mortality derived from these tagging experiments.

The results of estimations using the SE method were consistent in suggesting a value of M , in the Japanese fishery at least, of approximately 0.2/year. There was little information in the data regarding M in the Australian surface fisheries; however, a value similar to the above is not an unreasonable, if tentative, conclusion. Analysis of more recent tagging experiments may, in due course, help to resolve this question.

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