Abstract.–Models are formulated for estimating tag-shedding rates from recapture records for eight double-tagging experiments with southern bluefin tuna (*Thunnus maccoyii*) in three Australian fishing areas. These models incorporate either a constant or time-varying rate of tag shedding and allow for the possibility of immediate tag shedding. Likelihood ratio tests are used to select the most parsimonious model for each data set. The probability of a tag being shed after 4 years at liberty (the length of the most recent experiments) varied from around 0.2 for the 1983 and 1984 experiments to 0.5–0.7 for the experiments carried out in the 1960s and 1970s. Although a single, best-fitting model was selected in all but one experiment and despite the large total numbers of recoveries, precise estimates of long-term shedding rates could not be obtained because there were relatively few long-term data. This has significant implications for analyses of tag-return data that give heavy weighting to long-term recaptures.

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Tag Shedding by Southern Bluefin Tuna *Thunnus maccoyii*

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Southern bluefin tuna *Thunnus maccoyii* were tagged throughout the 1960s in three areas of major Australian commercial fishing activity: 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). During the 1970s, tagging took place mainly off WA. The aim of these experiments was to provide information on movements, growth, and mortality of the southern bluefin. In 1983 and 1984, new experiments were initiated off WA and SA in order to answer more specific questions relating to fishery interactions, yield-per-recruit, and schooling behavior, as well as to update information obtained from the previous experiments (Majkowski and Murphy 1983). Apart from the period prior to 1963, almost all fish were double tagged.

Quantitative analyses of tagging data that require an estimate of the total number of recaptures of tagged fish (e.g., fishery interactions, yield-per-recruit, and mortality) need to take account of tag loss due to shedding. As reviewed by Wetherall (1982), this problem can be approached in two ways. If estimation of mortality rates is the main objective of the analysis, one can attempt to model the entire process of removal of tags from the population directly by incorporating into the model parameters that account for all sources of removal, i.e., natural mortality, fishing mortality, permanent emigration, nonreporting of recaptured tags, and tag shedding. Alternatively, tag-shedding rates may be estimated independently from a double-tagging experiment and the recovery data adjusted accordingly before proceeding with further analyses (other losses, e.g., non-reporting, may also require independent estimation). A disadvantage of the former approach is that, even if simple functions are chosen to describe mortality, emigration, and tag shedding, the model will inevitably be parameter-laden, and therefore difficult to estimate. In any case, such models will not necessarily lend themselves to analyses of interactions and yields-per-recruit, where the mortality and emigration processes are embedded in the recapture statistics and do not necessarily require explicit resolution (Majkowski et al. 1984).

The aim of this paper is to estimate tag-shedding rates for a number of southern bluefin tuna double-tagging experiments, with a view to using these estimates as the basis for correcting for tag shedding in other analyses. Hynd (1969) made a preliminary estimate of the tag-shedding rate, assumed constant, based on recoveries up to 1968 only. Subsequently, Kirkwood (1981) developed generalized tag-shedding models and analyzed recoveries of southern bluefin tuna that were double tagged during the period 1962–76 but excluded all tagging that was contracted to fishermen. In both cases, these analyses used tag-recovery data that were grouped by time of recovery. A reevaluation of southern bluefin tuna tag shedding is now appropriate because, (1) for a number of present

Table 1
Double-tagging experiments of southern bluefin tuna in the New South Wales (NSW), South Australia (SA), and Western Australia (WA) areas.

Experiment number	Area	Years	Carried out by	Fishing method	Tagging method	Number released	Number[1] recovered with 2 tags	Number[1] recovered with 1 tag
1	NSW	1963–70	CSIRO	Pole	Board[2]	2770	253	153
2	NSW	1963–70	Fishermen under contract to CSIRO	Troll	Board	9513	3199	862
3	SA	1964–69	CSIRO	Pole	Board	7328	929	300
4	SA	1977	CSIRO	Pole	Board	908	164	54
5	WA	1963–67	CSIRO	Pole	Board	12826	264	264
6	WA	1970–78	WA Dep. Fisheries	Pole	Board	5692	236	120
7	WA	1983	CSIRO	Pole	Cradle[3]	6907	1853	472
8	SA	1984	CSIRO	Pole	Cradle	3211	1117	176

[1]Excludes recoveries for which an accurate recapture date was not available.
[2]Fish placed on a measuring board for tagging.
[3]Fish placed in a specially designed cradle for tagging.

applications, it is necessary that the data be analyzed as a series of separate release sets rather than as a pooled data set, and corresponding shedding-rate estimates are thus required; (2) there are now reliable recovery data for 10,416 double-tagged southern bluefin available for analysis (compared with the 1511 recoveries considered by Kirkwood 1981); and (3) models are now available that utilize exact periods at liberty rather than data aggregated by time period. Provided accurate recapture times are available (as is the case here), these new models are preferable because of their greater ability to deal with low recovery numbers towards the end of an experiment.

Tagging data and tagging methods

The tagging data used in this analysis consist of all records received by 31 March 1987 of southern bluefin that were originally double-tagged and that had accurate recapture dates. Recovery dates were considered accurate if at least the month of recapture was known with certainty. In total, there were 10,416 recoveries that met this criterion. Of these, there were 671 recoveries for which the month of recapture was known but the exact day was uncertain; however in almost all of these cases, the uncertainty was estimated to be no more than ±5 days.

The data were grouped into eight double-tagging experiments: (1) NSW releases 1963–70 (CSIRO*); (2) NSW releases 1963–70 (fishermen contracted by CSIRO); (3) SA releases 1964–69 (CSIRO); (4) SA releases 1977 (CSIRO); (5) WA releases 1963–67 (CSIRO); (6) WA releases 1970–78 (WA Dep. Fish.); (7) WA 1983 (CSIRO); and (8) SA 1984 (CSIRO). This classification of the data was made to ensure that, within experiments, the geographical area, fish size, tagging and fishing methods, and tagging personnel were as similar as possible.

Except for experiment 2, the primary method used to catch fish for tagging was commercial bait and pole; in experiment 2, trolling was used. In all experiments, fork lengths of the fish selected for tagging were measured before tagging. For the first six experiments, this was done by placing the fish on a measuring board. In experiments 7 and 8, the fish were placed in a specially designed vinyl cradle supported by a metal frame and their fork lengths measured using graduations marked on the cradle. While the fish were restrained on the measuring board or in the cradle, two numbered tuna tags of a standard type (Williams 1982) were inserted forward into the musculature at an angle of about 45°, 1–5 cm below either side of the posterior insertion of the second dorsal fin. Ideally, the tag barb anchored behind the second dorsal fin ray extensions or the neural spines, and in experiments 7 and 8 greater effort was made to achieve this than in earlier experiments.

A summary of the fishing method, tagging method, and the numbers of tuna released and recovered is given for each experiment in Table 1. For ease of presentation, the numbers of recoveries in each experiment are grouped by period at liberty in Table 2; as noted above, exact times at liberty for each recovery were used in the subsequent analyses.

*Tagged by staff of the Commonwealth Scientific and Industrial Research Organization (CSIRO).

Table 2

Numbers of double-tagged southern bluefin tuna, for which accurate recapture dates are known, that were reported to have retained both tags (D) or only one tag (S) on recapture, listed by period at liberty.

Period at liberty (yr)	Experiment number 1		2		3		4		5		6		7		8	
	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
0–1	175	61	2638	467	831	158	128	23	166	84	205	73	1428	314	644	64
1–2	70	61	517	329	51	76	30	15	72	108	23	31	306	102	381	75
2–3	6	21	37	52	15	19	3	11	18	27	2	7	101	40	82	35
3–4	1	1	4	5	11	9	2	4	—	8	3	4	18	16	10	2
4–5	1	1	1	1	10	11	—	—	3	15	1	2				
5–6	—	—	—	1	2	10	—	—	3	9	—	2				
6–7	—	2	1	2	2	7	—	—	1	4	2	1				
7–8	—	2	—	1	2	1	—	—	—	—	—	—				
8–9	—	1	—	1	2	6	1	1	—	4	—	—				
9–10	—	1	—	1	2	—	—	—	—	1	—	—				
10–11	—	—	1	1	—	1	—	—	—	—						
11–12	—	—	—	—	1	1			—	1	—	—				
12–13	—	—	—	—	—	—			—	—	—	—				
13–14	—	—	—	—	—	—			—	2	—	—				
14–15	—	2	—	—	—	—			—	—	—	—				
15–16	—	—	—	—	—	—			—	1	—	—				
16–17	—	—	—	1	—	1			—	—	—	—				
17–18	—	—	—	—	—	—			1	—						

Tag-shedding models

Various models have been proposed to describe the process of tag loss (Beverton and Holt 1957 and reviews by Ricker 1975; Wetherall 1982). Tag losses can be classified as type I losses, which effectively reduce the number of tags released (immediate tag shedding, immediate tagging mortality, and non-reporting), and type II losses which occur steadily over time (natural mortality, fishing mortality, permanent emigration, and long-term tag shedding). Considering the shedding process only, the simplest model is that proposed by Beverton and Holt (1957) for type II shedding, where the instantaneous rate of shedding (L) is constant over time. In this model, if for a fish originally single-tagged, $Q(t)$ is the probability of the tag being retained at time t after release, then

$$Q(t) = e^{-Lt} \quad (1)$$

If immediate tag shedding occurs, with a probability $1-\rho$ of this occurring, then

$$Q(t) = \rho\, e^{-Lt} \quad (2)$$

In some cases, it may be inappropriate to assume a constant shedding rate. Some tags may deteriorate over time, causing their shedding rate to increase (Baglin et al. 1980). Alternatively, some tags may become more securely fixed over time, e.g., through the gradual laying down of tissue around the tag, causing the shedding rate to decrease (Kirkwood 1981). More generally, Kirkwood (1981) has noted that if individual tags have a different propensity for shedding, then the apparent average shedding rate will decrease with time at liberty, as the tags with the higher shedding rate are lost first. Kirkwood modeled this process by allowing the shedding rate to be a gamma-distributed random variable, rather than a constant; however, his model did not allow for an increasing shedding rate. An alternative approach was adopted by Wetherall (1982), who assumed that the probability of a tag being shed was time-dependent. He proposed a flexible function that allowed either an increasing or decreasing shedding rate.

In this paper, we adopt a time-dependent shedding-rate model that allows the probability of an individual tag being shed to decrease over time in an identical fashion to the average shedding rate of the Kirkwood (1981) model. In this case, we now assume that the rate of shedding at time t after release follows the functional form

$$L(t) = \frac{b\lambda}{b + \lambda t}.$$

It then follows that

$$Q(t) = e^{-\int_0^t L(u)\,du} = \left[\frac{b}{b+\lambda t}\right]^b. \qquad (3)$$

Note that as $b \to \infty$, $\left[\frac{b}{b+\lambda t}\right]^b \to e^{-\lambda t}$ and $L \to \lambda$. That is, the variable-rate model reverts to the constant-rate model. If a proportion 1-ρ of tags are shed immediately, then

$$Q(t) = \rho\left[\frac{b}{b+\lambda t}\right]^b. \qquad (4)$$

Parameter estimation

Because only tag returns with accurate recapture dates are considered, an extension of the maximum likelihood estimation procedure used by Kirkwood and Walker (1984) can be used. Suppose fish are double tagged and all tags not immediately shed have identical shedding probabilities that are independent of their companion tags' status (already shed or still retained). Then, if $p_2(t)$, $p_1(t)$, and $p_0(t)$ are the probabilities of a fish retaining two, one, and zero tags, respectively, at time $t\,(0<t<\infty)$ after release,

$$p_2(t) = Q(t)^2,$$

$$p_1(t) = 2Q(t)\,[1-Q(t)]$$

and

$$p_0(t) = [1-Q(t)]^2.$$

A fish that has shed both tags will not normally be distinguishable from a fish that was never tagged. Consequently, the tag-recapture data consist of recoveries of fish retaining one or more tags. Conditional on retention of at least one tag, the probability of a recaptured fish retaining two tags at time t is

$$\frac{p_2(t)}{1-p_0(t)}$$

and that of a recaptured fish retaining one tag is

$$\frac{p_1(t)}{1-p_0(t)}$$

Following an initial release of double-tagged fish at time $t=0$, suppose m fish bearing two tags were recaptured at times $t_{2i}(i=1,\ldots,m)$, and n bearing one tag were recaptured at times $t_{1j}(j=1,\ldots,n)$. Then, the log-likelihood L of the data, conditional on the recapture times $\{t_{2i}\}$ and $\{t_{1j}\}$, is

$$L = \sum_{i=1}^{m} \ln\left[\frac{p_2(t_{2i})}{1-p_0(t_{2i})}\right] + \sum_{j=1}^{n} \ln\left[\frac{p_1(t_{1j})}{1-p_0(t_{1j})}\right].$$

Estimates of the model parameters incorporated in $p_2(t)$, $p_1(t)$, and $p_0(t)$, and their asymptotic variances, can then be obtained by maximizing L using standard methods (e.g., Bard 1974).

Model selection

For each of the experiments, we attempted to select the most parsimonious model. Accordingly, we first fitted model (4), which incorporates immediate tag shedding and (with $b<\infty$) a time-varying shedding rate. Then likelihood-ratio tests (Kendall and Stuart 1961) were carried out to test the null hypotheses that (1) $\rho=1$ (no immediate tag shedding), (2) $b=\infty$ (constant shedding rate), and (3) both $\rho=1$ and $b=\infty$. Unfortunately, since these hypotheses are not fully nested, some ambiguity can still remain. The choice is clear-cut if none of the three hypotheses is rejected, or if all but one are rejected. However, it is possible that while hypothesis (3) is rejected, neither (1) nor (2) is rejected. In that case, there is no reliable basis to distinguish between models (2) and (3).

Particularly when performing non-linear estimations such as these, it is essential to examine the fit of the estimated model to the observed data. Unfortunately, since we are maximizing a likelihood conditional on the observed recapture times, there is no exact way of doing this. As an approximation, however, we can examine the fit of the estimated models to recovery data grouped by time intervals. From the data in Table 2, it is a simple matter (e.g., based on equation 9 in Wetherall 1982) to calculate, for each k, estimates of the proportions of tags shed (P_k) by time t_k, the midpoint of the k-th time interval since release, as well as exact 95% confidence intervals for these proportions based on the binomial distribution. If it is assumed that all tags shed during the k-th time interval were shed at time t_k, then the fitted model and "observed" proportions can be displayed on the same graph. For the grouped data in Table 2, time intervals of one year were used for the first five periods after release. The relatively few longer-term recoveries were grouped into periods at liberty of 5–10 years and 10–20 years.

Table 3
Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using ungrouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm$SE	$\beta \pm$SE	$\rho \pm$SE
1	2	0.29±0.05	∞	0.93±0.02
	3	1.00±0.33	0.26±0.10	1.0
2	2	0.17±0.01	∞	0.976±0.006
3	3	0.78±0.12	0.26±0.05	1.0
4	2	0.17±0.04	∞	0.96±0.01
5	3	1.04±0.28	0.36±0.11	1.0
6	2	0.19±0.05	∞	0.90±0.02
7	3	5.08±2.02	0.031±0.004	1.0
8	2	0.049±0.008	∞	0.970±0.007

Results

Maximum likelihood estimates of the tag-shedding parameters and of their standard errors are given in Table 3. Curves, based on these parameter estimates, that describe the time-dependent probability of tag shedding, together with estimates of the proportion of tags lost (with 95% confidence intervals) based on grouped data, are shown in Figure 1.

In experiment 1, it proved impossible to distinguish either statistically or visually between a constant-rate model with immediate tag shedding (model 2) and a decreasing-rate model with no immediate tag shedding (model 3). Although the plots of $[1 - Q(t)]$ against t (Fig. 1a) are strikingly different for longer recapture times, apparently both can be accommodated by the grouped recovery data because the number of long-term recoveries is small, resulting in wide confidence intervals for proportions shed.

In all other experiments, it was possible to select a single most appropriate model on statistical grounds. However, wide confidence intervals for the estimates of proportions of tags shed were still evident in most experiments for the longer-term recovery periods. In experiment 2 and the medium-term experiments (4 and 6), a constant-rate model with some immediate tag shedding was selected (Fig. 1b, d, f). In the other long-term experiments (3 and 5), model (3) provided the best fit, and the shedding rate showed a marked tendency to decrease with time (Fig. 1c, e).

The most striking difference among the experiments was the very low shedding rates observed in experiments 7 and 8 (Fig. 1g, h) compared with the other experiments. After 4 years, the probability of shedding, as predicted by the fitted models, was approximately 0.2 for experiments 7 and 8, whereas it was 0.5–0.7 for the earlier experiments.

Discussion

The tag-shedding rates estimated for experiments 1–6 are of a similar order to those obtained for southern bluefin tuna by Kirkwood (1981), who used a restricted subset of the data pooled across these experiments. Constant rates of tag shedding have been estimated by Hynd (1969) for southern bluefin tuna (0.26/yr), by Bayliff and Mobrand (1972) for yellowfin tuna (0.278/yr), and by Lenarz et al. (1973) and Baglin et al. (1980) for Atlantic bluefin tuna (0.210/yr and 0.205/yr, respectively). The essentially constant rates estimated in this paper for experiments 2, 4, and 6 are generally slightly lower then these, but still comparable. However, the shedding rates estimated for experiments 7 and 8 are very much lower than for any previously reported tuna double-tagging experiment with substantial numbers of recoveries. The low estimates of shedding rates obtained by Laurs et al. (1976) for north Pacific albacore and Lewis (1981) for south Pacific skipjack were based on very small numbers of tag recoveries.

As mentioned earlier, most previous estimates of tag-shedding rates have been calculated using recovery data grouped by period at liberty. For this method to be effective, the number of observations in each grouping interval must be above a certain minimum. Where the data are sparse, the grouping intervals must cover longer periods. This can result in loss of information, as is seen, for instance, in Table 1 for the longer periods at liberty. Worse, as Kirkwood and Walker (1984) found for a double-tagging data set with very few recoveries, the grouped data estimates may be highly dependent on the grouping intervals used. Here, building on Kirkwood and Walker (1984), we have adopted an estimation procedure that uses exact periods at liberty, which—at least in principle—gets around this problem. However, this is not achieved without a price:

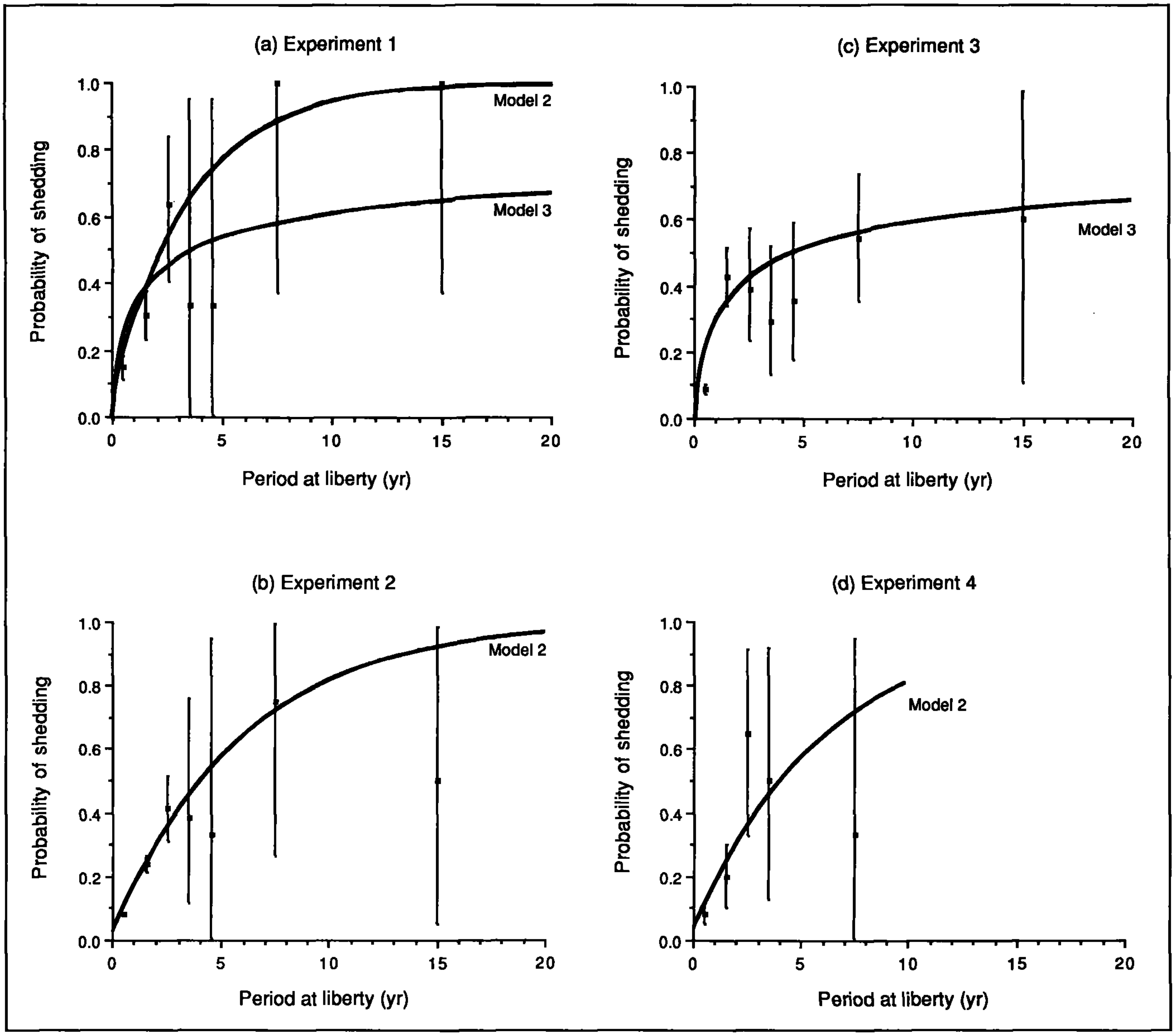

Figure 1

Comparisons of the probabilities of tag shedding by southern bluefin tuna as predicted by the best fitting models, with the proportions of tags shed as calculated from grouped data. Bars represent 95% confidence intervals on the proportions.

having to condition on the observed times at liberty, the calculated standard errors of the estimated parameters are almost certainly biased downwards. As the numbers of recaptures increase and the grouping intervals shorten, estimates based on grouped and ungrouped data should converge. However, the rate of convergence may be slower than might be expected. Table 4 gives parameter estimates that were calculated by applying the Kirkwood (1981) method to the grouped data in Table 2. Comparison of estimates using ungrouped data (Table 3) and grouped data (Table 4) reveals substantial differences, not only in terms of the parameter estimates themselves (e.g., experiments 3 and 5) but even in the model selected (e.g., experiments 6 and 7), despite the relatively large numbers of recaptures.

No formal statistical analysis is needed to conclude that the shedding rates in experiments 7 and 8 are significantly lower that those in experiments 1–6. We believe that the most likely explanation for these reduced shedding rates lies in differences in tags and tagging methods. Some of the tags used in the early experiments were reported to have inadequately attached streamers (Hynd et al. 1967). If so, this would

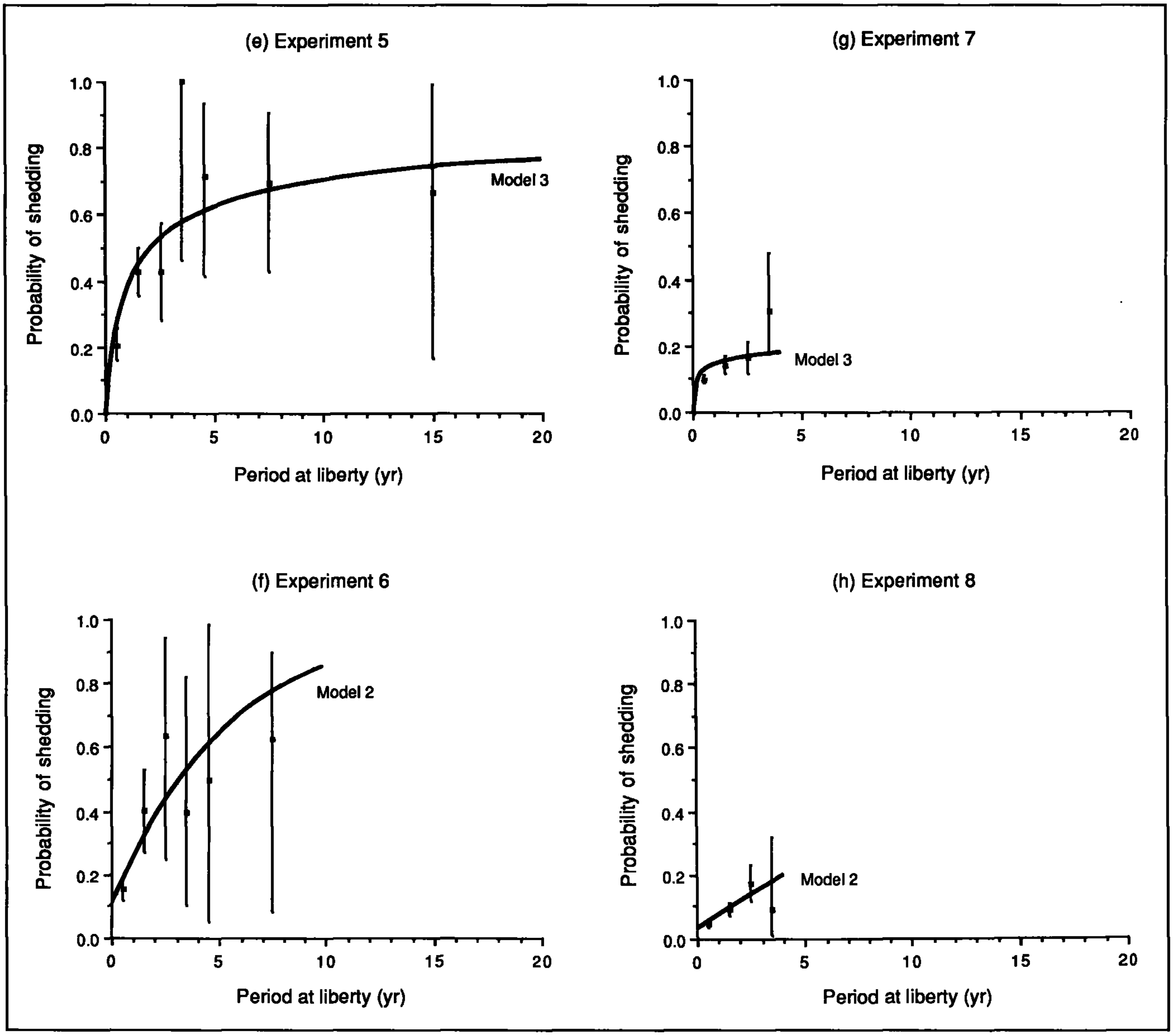

Figure 1 (continued)

Table 4

Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using grouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm$SE	$\beta \pm$SE	$\rho \pm$SE
1	2	0.26±0.05	∞	0.98±0.05
2	1	0.18±0.01	∞	1.0
3	3	0.27±0.07	0.55±0.37	1.0
4	1	0.20±0.04	∞	0.96±0.01
5	3	0.56±0.14	0.66±0.32	1.0
6	3	0.43±0.09	0.53±0.27	1.0
7	2	0.053±0.010	∞	0.93±0.01
8	2	0.055±0.011	∞	0.98±0.01

result in a higher rate of shedding. Tags used in the latest experiments do not appear to have suffered from such defects. In experiments 7 and 8, the use of a specially designed tagging cradle may have resulted in more effective and less traumatic tagging than in earlier experiments, where fish were tagged on a measuring board. Also in experiments 7 and 8, a deliberate effort was made to anchor the tags behind the second dorsal fin ray extensions. Tags successfully attached in this way should have a very small probability of shedding. Unfortunately, little quantitative information is available on the efficacy of the technique of tag attachment adopted for experiments 1–6, but it is known that greater care was taken in tag attachment in the later experiments. If the proportion of ideally attached tags in experiments 1–6 differed markedly from those for experiments 7 and 8, then commensurate differences in shedding-rate estimates would result.

While the lower tag shedding rates in experiments 7 and 8 are obvious on first inspection, the situation is less clear for the earlier experiments. In general terms, the precision of estimates of shedding rates, particularly long-term rates, will increase with the size of the database. On these grounds, pooling of the data for experiments 1–6 would appear to be an attractive option. However, it would be appropriate to do so only if the assumptions underlying the analysis of the pooled data remained valid. Critical among these assumptions is that all tags have identical and independent shedding probabilities. The primary reason for classifying the tag releases in the 1960s and 1970s as six separate experiments was a suspicion that these probabilities may well have been heterogeneous. As mentioned earlier, with this classification we were attempting to minimize within-experiment differences in geographical area, fish size, capture and tagging methods, and tagging personnel. While in principle further subdivision is possible, for example by tagging vessel in order to take account of different tagging teams, we felt this may leave too few data in each subset to obtain reliable estimates of shedding rates. Also, no assertion is made that the classification chosen is an optimal one; indeed it is by no means obvious that suitable criteria for optimality could be defined. A statistical way of examining whether or not it is appropriate to pool data for experiments 1–6 is to carry out a likelihood ratio test of the hypotheses that the tag shedding parameters for each experiment are equal. This hypothesis proved to be resoundingly rejected ($P<0.001$). It appears that pooling is not a viable option for these experiments.

One of the subsequent analyses that we had envisaged for recovery data adjusted for tag shedding involved application of the method of Hearn et al. (1987) to obtain estimates of natural and fishing mortality rates. This method, which is essentially a cohort analysis of the tagging data, gives particular weight to long-term recaptures and therefore requires accurate estimates of long-term shedding rates. Despite the large numbers of recoveries in the experiments described in this paper, precise estimation of long-term shedding rates has not been possible. This is best exemplified in the results of experiment 1, where no single best fitting model was obtained, and for which the point estimates of long-term shedding rates differ markedly. Even where a single best-fitting model was available, considerable uncertainty still remained about the long-term shedding rates. It therefore seems essential to take account of this uncertainty in any subsequent analyses using methods such as that of Hearn et al. (1987). This is the subject of further research.

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