

Abstract.—Estimates of tag-shedding and tag-reporting rates are required for an estimation of fishing and natural mortality rates from tagging data. For this purpose, double-tagging and tag-seeding experiments were undertaken by the South Pacific Commission, in conjunction with a large-scale tuna tagging program, in the western tropical Pacific Ocean during 1989–1992. Estimates of tag-shedding rates indicated that 89% (95% confidence interval of 82%–94%) of tagged tuna still retained their tags after two years at liberty. Differences in shedding rates among skipjack, yellowfin, and bigeye tuna, and differences in shedding rates among taggers were found not to be statistically significant. Tag seeding carried out on board purse seiners by observers resulted in 342 returns of the 532 tags seeded, for a return rate of 64% (60%–68%). The return rate of seeded tags varied significantly by unloading location (most tags were recovered during unloading), but not by species. The highest return rates of seeded tags occurred from American Samoa, Philippines, and Solomon Islands, whereas Korea and Thailand had the lowest return rates. The overall average reporting rate, weighted by the estimated numbers of tags recovered at each location, was 0.59. A bootstrap procedure was used to estimate a 95% confidence interval of 0.49–0.67. These results implied that, of the 146,581 tags released during the large-scale tagging program, 31,166 (27,208–37,264) were recaptured, of which 18,266 were returned to the South Pacific Commission.

Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean

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Tag release-recapture experiments are commonly used to estimate parameters, such as growth, mortality, and population size, of exploited fish stocks (Beverton and Holt, 1957; Seber, 1973). One method used to estimate mortality rates is to fit a tag-attribution model to a time series of tag-return data (Seber, 1973; Kleiber et al., 1987). In its simplest form, the tag attrition model can be expressed as

$$\hat{\phi}_j = (1 - \alpha)T \exp \left[-(F + M + \lambda)(j - 1) \right] \frac{F}{F + M + \lambda} [1 - \exp(-F - M - \lambda)], \quad (1)$$

where $\hat{\phi}_j$ is the predicted number of tag returns in time period j , α represents all type-1 tag losses, T is the number of tag releases, F is the instantaneous rate of fishing mortality (assumed constant), M is the instantaneous rate of natural mortality (assumed constant), and λ represents all continuous type-2 tag losses. Type-1 tag losses include immediate tag shedding, immediate tagging-induced mortality, and failure to report recovered tags. Type-2 tag losses include continuous tag shedding, continuous mortality directly attributable to the tag, and emigration of tagged fish away from the area of the fishery. For unbiased estimates of F and M to be obtained,

it is clear from Equation 1 that these tag losses must be estimated and included in the tag-attribution model.

In general, type-1 and type-2 loss rates cannot be estimated directly from tag-return data, although estimation of type-1 losses may be possible under circumstances where fishing intensity is highly variable (Beverton and Holt, 1957). More commonly, loss rates are estimated from independent experiments carried out in conjunction with a tagging program. Tag-shedding rates may be estimated from double-tagging (two tags per fish) experiments (Wetherall, 1982) or from direct observation of tagged fish held in captivity. Tag-reporting rates may be estimated from tag-seeding experiments (Youngs, 1974; Green et al., 1983; Campbell et al., 1992), from sequential observations of recoveries at different stages of catch handling and processing (Hilborn, 1988), and by comparing tag return rates from the fishery with those from a control group (such as vessels carrying fisheries observers) assumed a priori to report all tag recoveries (Paulik, 1961; Seber, 1973). Type-1 and type-2 tagging mortality rates may, for some species, be estimated from observations of tagged and untagged fish held in captivity.

The South Pacific Commission (SPC) recently conducted a large-

scale tuna tagging program, the Regional Tuna Tagging Project (RTTP), in the western tropical Pacific. From 1989 to 1992, 146,581 tagged skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*, were released throughout the western tropical Pacific from the Philippines and eastern Indonesia to approximately 170°W. This area is fished by purse-seine, pole-and-line, longline, handline, and troll vessels, which have collectively harvested more than one million metric tons of tuna per year since 1989 (Lawson, 1994). As of 31 May 1995, 18,266 tagged fish had been recaptured and the tags and accompanying recapture information returned to SPC. Tagged tuna were recaptured by all of the fishing methods of the western Pacific fishery. Most tag returns (76%) originated from purse seiners, consistent with the proportion of total catch attributed to that gear (67% for 1990–1993). Few additional tag recoveries are expected.

One of the major objectives of the tagging program was to estimate the rates of fishing-induced and natural mortality by using models similar to Equation 1, so that the impacts of the fishery on the stocks could be assessed. It was therefore necessary to obtain estimates of type-1 and type-2 tag losses. In this paper, I focus on the estimation of tag-shedding rates and tag-reporting rates. Tag-shedding rates were estimated from double-tagging experiments carried out in conjunction with the tag-release program. Differences in shedding rates among species and differences among individual taggers were evaluated. Tag-reporting rates were estimated from tag-seeding experiments in which tuna caught by purse seiners were surreptitiously tagged by fisheries observers prior to the fish being placed in the fish wells. Differences in the rates of reporting seeded tags by species, time, and port of unloading were investigated. An estimate of the overall reporting rate of recovered RTTP tags and its variability, which takes into account the variability in tag reporting among unloading ports, was obtained.

Materials and methods

Double-tagging experiments

Field operations Tagging was carried out on a pole-and-line vessel from which tuna were captured with standard commercial gear. Only uninjured fish that were cleanly hooked in the jaw were selected for tagging. Fish with excessive mouth damage, eye damage, or gill damage were not tagged. Selected fish were placed in a vinyl tagging cradle and their fork lengths measured to the nearest centimeter. For

single-tagged fish, a Hallprint™ 13 cm dart tag was inserted by using a sharpened stainless steel applicator, into the musculature at an angle of about 45°, 1–2 cm below the posterior insertion of the second dorsal fin. Smaller (10-cm) tags were used for tuna less than 35 cm FL. Ideally, the tag barb was anchored behind the pterygiophores of the second dorsal fin.

Throughout the three-year tag release program, a small sample (approximately 3%) of the tagged tuna were double tagged. Double tagging occurred on particular days chosen in advance by the cruise leader and on such days, most fish were double tagged. The objectives were for each principle tagger to double tag at least 400 tuna, and for the double-tag releases to be as representative as possible of the species and size composition of the single-tag releases. These objectives were largely accomplished (Fig. 1).

The technique for double tagging was identical to that of single tagging, with the exception that a second tag was inserted on the opposite side of the fish, 1–2 cm anterior to the first tag to avoid damaging it with the applicator. For single and double tagging, fish were generally out of the water for less than ten seconds.

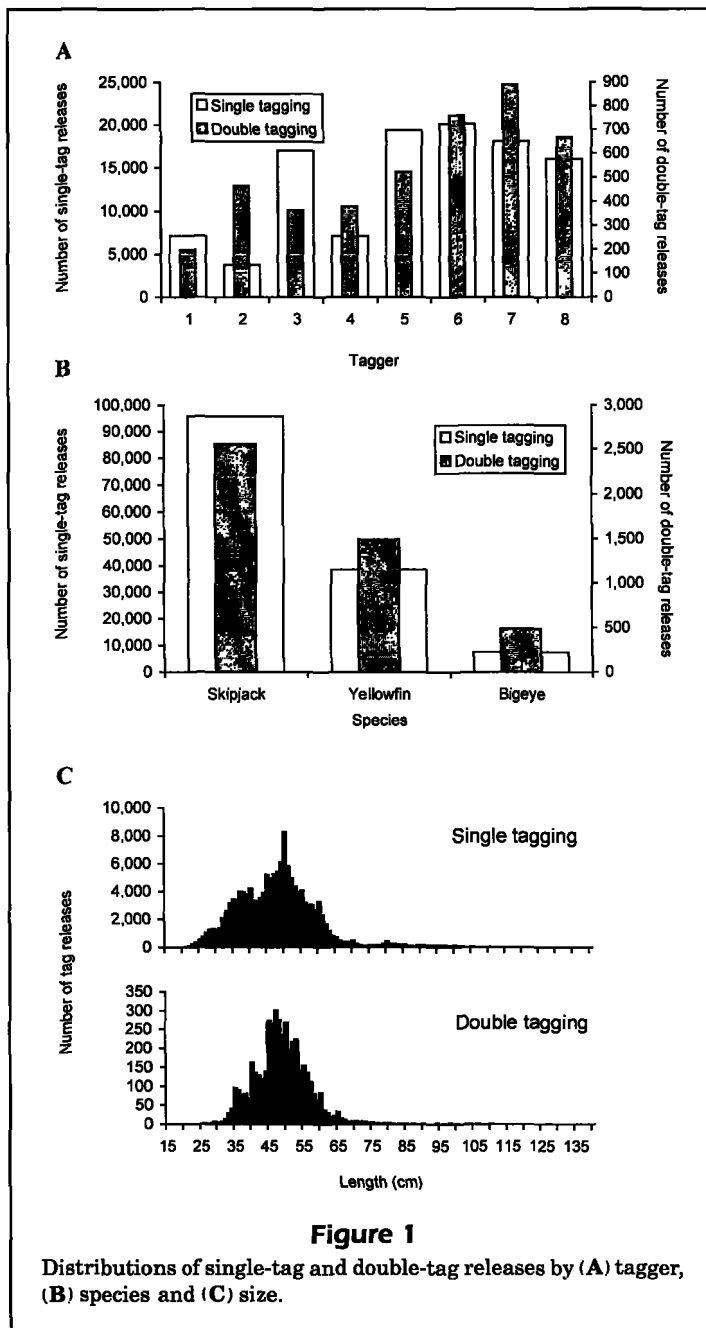
Data analysis Observations of the numbers of tags retained by double-tagged tuna at recapture can be used to estimate tag-shedding rates. I used a simple tag-shedding model (Beverton and Holt, 1957; Hampton and Kirkwood, 1990), which defines the probability, $Q(t)$, of a tag being retained at time t after release as

$$Q(t) = (1 - \rho)\exp(-Lt), \quad (2)$$

where ρ is the immediate type-1 shedding rate and L is the continuous type-2 shedding rate. These parameters can be estimated from a double-tagging experiment under the assumption that all tags not immediately shed have identical shedding probabilities that are independent of the status of the companion tag. Given this assumption, the probabilities of two, one, and no tags being retained at time t after release are, respectively,

$$\begin{aligned} P_2(t) &= Q(t)^2, \\ P_1(t) &= 2Q(t)[1 - Q(t)] \\ P_0(t) &= [1 - Q(t)]^2. \end{aligned} \quad (3)$$

Consider a double-tagging experiment resulting in m recaptures of fish bearing two tags at times t_{2i} ($i = 1, \dots, m$) and in n recaptures bearing one tag at times t_{1j} ($j = 1, \dots, n$). The negative log likelihood of the data (t_2, t_1) given the model parameters ρ and L is



$$\Omega(t_2, t_1 | \rho, L) = -\sum_{i=1}^m \ln \left[\frac{P_2(t_{2i})}{1 - P_0(t_{2i})} \right] - \sum_{j=1}^n \ln \left[\frac{P_1(t_{1j})}{1 - P_0(t_{1j})} \right], \quad (4)$$

where the terms in square brackets represent the probabilities of two tags and one tag being observed for each recapture, given that at least one tag is observed. Maximum-likelihood estimates of ρ and L can

therefore be obtained by minimizing Ω with respect to the parameters.

The model was fit to pooled recapture data, to data classified by species, and to data classified by tagger. As an approximate indication of the overall losses due to tag shedding for each data set, the proportion of tags retained after two years (99% of RTTP tag returns were recaptured within two years of release), Q_{2yr} , was calculated from Equation 2 by using the estimated parameters. Approximate 95% confidence intervals for Q_{2yr} were obtained by the percentile method (Efron, 1982) applied to distributions of Q_{2yr} generated from 1,000 parametric bootstrap (or Monte Carlo) replicates of each data set. The replicates were constructed by using the observed distributions of times at liberty, and the numbers of tags observed for each pseudo-return were determined randomly with the conditional probabilities of a recaptured tuna bearing two tags or one tag, i.e. $\frac{P_2(t)}{1 - P_0(t)}$ and $\frac{P_1(t)}{1 - P_0(t)}$, respectively, given the estimated parameters.

The statistical significance of improvements in fit of models that included species-specific and tagger-specific shedding parameters was determined by using likelihood-ratio tests (Kendall and Stuart, 1961).

Tag-seeding experiments

Rationale Tag seeding was carried out by observers placed on board purse-seine vessels as part of regional and national observer programs. The purse-seine fleet was targeted for tag-seeding experiments for several reasons. First, purse seiners account for most of the tuna catch in the western Pacific (and also recovered most tags); the estimation of reporting rates for this gear type in particular was therefore of critical importance. Second, the large, modern purse seiners typical of the western Pacific fleet handle large quantities of tuna very rapidly, with little opportunity for onboard inspection of individual fish for tags. As a result, tagged tuna recaptured by purse seiners were mostly detected during unloading (when individual fish are handled) or during the initial stages of processing in canneries. The efficacy of tag detection during these periods was unknown prior to the commencement of the tagging experiment; it was feared that delayed detection of tags might result in significant losses which, if ignored, would compromise the objectives of the tagging experiment. Third, the very fact that most tagged tuna recaptured by purse seiners

would be detected during or after unloading of the catch in port offered the opportunity for tagged tuna to be planted in the catches before these detection processes began. Furthermore, the layout of purse-seine vessels and the method of onboard handling of the catch facilitated the opportunity for planting tagged tuna surreptitiously, out of sight of the vessel's crew. Such tag-seeding operations would be more difficult on other types of vessels, e.g. pole-and-liners and longliners, operating in the fishery.

Field operations Selected observers on purse seiners were asked to plant up to five tagged tuna in the catch during a voyage. The number of tagged tuna was limited to five so as not to attract undue attention during unloading; it was not unusual during the RTTP for five (and sometimes more) tagged tuna to be recovered from a single unloading. The exact timing of tagging individual fish depended on the circumstances encountered during a cruise, particularly the frequency of successful sets. Therefore, the period over which the five tags were seeded ranged from a few days to several weeks.

Fish were tagged discretely, usually on the well deck (one level below the work deck where the fish are landed), as they passed down the chute just prior to entering the well. The tags and manner of attachment were identical to those used in the tagging program proper. Tag numbers, dates, species, sizes, and well numbers were recorded and the information sent to SPC at the completion of the voyage. Upon recovery, seeded tags were processed in the same fashion as genuine tag recoveries. Tag finders were paid the standard reward for seeded tags and were not informed that the tags were part of a seeding experiment.

Estimation of return rates of seeded tags Return rates of seeded tags were calculated for the overall data set, for the three species (skipjack, yellowfin, and bigeye tuna) and for the seven unloading locations represented in the data (American Samoa, Japan, Korea, Philippines, Puerto Rico, Solomon Islands, and Thailand). For one unloading location (American Samoa), there were sufficient returns to estimate reporting rates by time period (year). Differences in seeded tag-return rates among species, unloading locations, and time periods were assessed by using chi-square tests (Sokal and Rohlf, 1981).

Return rates were estimated by assuming that the number of returns, r , in a given category was a binomial variate. Given the number of tags seeded, N , the estimated return rate is given by $\hat{p} = r/N$. Under these conditions, 95% confidence limits for return rates were also obtained. Lower and upper confidence limits, p_A and p_B , for p were determined by solving the equations

$$\sum_{i=r}^N \binom{N}{i} p_A^i (1-p_A)^{N-i} = \alpha \text{ and}$$

$$\sum_{i=0}^r \binom{N}{i} p_B^i (1-p_B)^{N-i} = \alpha,$$

where $1-2\alpha$ is the confidence level (0.95 in this instance). Solutions for p_A and p_B can be easily obtained using an optimization program, such as the Microsoft Excel Solver.

Estimation of overall reporting rate for the RTTP An unbiased estimate of the overall return rate of recovered tags (i.e. the total number of tags returned divided by the total number of tags recaptured) is required for the estimation of fishing and natural mortality rates from the RTTP data. The return rates of seeded tags can be considered as sample means of the overall (population) mean reporting rate. It transpired that seeded tag-return rates varied greatly by unloading location, requiring that the data be stratified by unloading location in the estimation procedure. The parametric bootstrap (or Monte Carlo) approach was used to obtain approximate 95% confidence intervals for the overall reporting rate and its components (with the percentile method), taking account of the different probability distributions of reporting rate by unloading location. One thousand simulations (or bootstrap replicates) were run. In each, the weighted average reporting rate across locations is given by

$$p' = \sum_j R_j / \sum_j \frac{R_j}{p'_j},$$

where R_j is the number of tags returned from location j and p'_j is the bootstrap (or pseudo) reporting rate for location j .

For each replicate, the p'_j were randomly sampled from probability distributions. For recoveries in locations covered by tag-seeding experiments, beta distributions $B(x_j, y_j, a_j, b)$ were used to represent the probability distributions of the true reporting rates. These continuous distributions are related to the binomial distributions defined by the tag-seeding data by $x_j = r_j$ and $y_j = N_j - r_j + 1$ (Mendenhall and Scheaffer, 1973). The limits of the distributions, a and b , would normally be 0 and 1, respectively. In this case, we assumed $b=1$ and set the lower limit of reporting rate for location j , a_j , to the local tag-return rate (i.e. number of local returns divided by the number of local releases), so as to avoid the possibility of estimated recoveries out-numbering releases for any replicate. For two locations, Solomon Islands and Philippines,

there were local tag releases that resulted in most of the tag returns from those locations. These local tag-return rates (0.126 and 0.223, respectively) were used as the lower bounds for the reporting rate distributions for Solomon Islands and Philippines. For the other locations, it was not possible to identify sets of local releases to calculate local tag-return rates because the release locations of the local returns were widely distributed throughout the tag release area, not just in the vicinity of the unloading ports. In these cases, I made the minimal assumption that the "local" releases comprised all tag releases except those returned from other locations. Thus, the shapes of the reporting-rate probability distributions are determined by the tag-seeding data and by this notional minimum possible return rate. Note that the means and medians of such distributions could be quite different from the tag-seeding sample means \hat{p}_j . In general, the differences will be greatest where \hat{p}_j is close to 0 or 1 and n is small.

For returns from locations where no tag-seeding data were available or for tag returns that could not reasonably be pooled with purse-seine returns because the recovery processes were different (14% of all returns), values of p_j' were sampled from uniform distributions $U(0.5, 1.0)$. While somewhat arbitrary, this procedure is meant only to reflect some knowledge of the minimum possible reporting rate from these locations. In fact, this assumption prob-

ably understates the likelihood of tags being reported; almost all of these tags were recovered in Indonesia and in Pacific Island countries, where widespread publicity and the attractiveness of cash rewards are likely to have resulted in high reporting rates.

Results

Tag shedding

In all, 4,541 tuna (2,557 skipjack, 1,493 yellowfin, and 491 bigeye) were double-tagged during the RTTP. Return rates of double-tagged tuna were comparable to those of single-tagged tuna.

Returns from 525 double-tagged tuna were available for analysis. Fitting the model specified in Equation 2 to the pooled data provided estimates of ρ and L that, according to the model, would result in 89% (95% confidence interval of 82%–94%) of the original tags being retained after two years at large (Table 1). Both $\hat{\rho}$ and \hat{L} were significantly different from zero ($P < 0.001$).

Fitting the model to the three species separately, although yielding somewhat different tag-retention rates (Table 1), did not result in an overall statistically significant improvement in fit ($P = 0.334$, Table 2). Similarly, there were differences in tag-shedding estimates for the different taggers (Table 1), but over-

Table 1

Double-tagging results (m is the number of returns bearing two tags and n is the number of returns bearing one tag), tag-shedding parameter estimates, the estimated proportion of tags retained after two years at liberty (Q_{2yr}), and likelihood function values (Ω) for fits of the tag-shedding model to the various data sets.

Data set	$m+n$	m	n	Tag-shedding parameters			95% confidence interval for Q_{2yr}	Ω
				ρ	L (/mo.)	Q_{2yr}		
Pooled data	525	457	68	0.05861	0.002312	0.89	0.82–0.94	201.498
Skipjack tuna	241	211	30	0.03485	0.007179	0.81	0.68–0.93	87.637
Yellowfin tuna	204	176	28	0.06574	0.001532	0.90	0.81–0.95	81.434
Bigeye tuna	80	70	10	0.06667	0.000000	0.93	0.74–0.97	30.142
Total	525	457	68					199.213
Tagger 1	42	40	2	0.01111	0.002788	0.92	0.76–1.00	7.909
2	45	36	9	0.07348	0.009636	0.74	0.42–0.93	22.023
3	45	39	6	0.07143	0.003400	0.86	0.76–0.94	17.670
4	53	47	6	0.06000	0.000000	0.94	0.68–0.98	18.718
5	106	94	12	0.03604	0.004257	0.87	0.73–0.96	36.533
6	68	57	11	0.08800	0.000000	0.91	0.70–0.95	30.096
7	81	67	14	0.00000	0.018460	0.64	0.50–0.85	34.184
8	60	53	7	0.03566	0.007403	0.81	0.55–0.97	21.110
Other taggers	25	24	1	0.00000	0.003059	0.93	0.78–1.00	3.600
Total	525	457	68					191.843

all, classification of the model by tagger did not result in a significant improvement in fit ($P=0.253$, Table 2). It is therefore appropriate to use the parameter estimates for the pooled model in models such as that defined by Equation 1.

Tag reporting

Return rates of seeded tags by species, unloading location, and time period Tag seeding was carried out on 111 observer cruises between May 1990 and September 1994. During these cruises, 532 tuna were tagged and placed in fish wells. Of these, 342 (64%) were later recovered during unloading or processing of catches in canneries. The species breakdown of seeded tag releases and returns is given in Table 3. The numbers of returns by species did not differ significantly from those expected from the return rate pooled across species ($P=0.648$). On this basis, reporting of tags can be assumed to be independent of species.

Most tag-seeding cruises (77) were undertaken on United States purse seiners because this fleet had the highest observer coverage during the period of the experiment. Tag-seeding cruises were also undertaken on purse seiners from Japan (18), Taiwan (8), Korea (4), Federated States of Micronesia (3), and

Solomon Islands (1). It was expected that the tag-reporting rate would vary by fleet, not because of variable cooperation by fishing vessel crews, but because different fleets tend to unload their catches in different ports. As tag detection took place during unloading of catches and at later stages of processing, it was suspected that variation in the effectiveness of tag detection and reporting at unloading ports would result in large differences in tag-reporting rates. The individual tag-seeding cruises were therefore classified by unloading location. In several instances, a vessel's catch was transhipped to two or more ports. In these cases, the seeded tags were classified individually according to the destination of fish in the wells into which the seeded tags had been placed.

The numbers of seeded tag releases and returns, by unloading location, are given in Table 4. The return rates vary considerably among unloading locations; for example, the 95% confidence intervals on the return rates for the two unloading locations with the largest numbers of seeded tags, American Samoa and Thailand, do not overlap and are in fact widely separated. Not surprisingly, the observed numbers of returns by unloading location differed significantly from those expected from the return rate pooled across unloading locations ($P<0.001$).

For American Samoa, there were sufficient seeded tags to test the hypothesis of constant return rate of seeded tags over time. The return rate was low in 1990 but was consistently high for 1991 through 1994 (Table 5). The differences in return rates among years were statistically significant ($P=0.005$), but this was due entirely to the lower than expected (on the basis of the return rate pooled across years) number of seeded tags returned in 1990. The differences among years 1991 through 1994 were not statistically significant ($P=0.706$). Other locations (Japan and Thailand) also had highly variable reporting rates across years, but the numbers of seeded tags for these locations were too few to support a statistical treatment of the data.

Table 2

Statistical tests of the pooled tag-shedding model versus species-specific and tagger-specific tag-shedding models.

Model	No. of parameters	Ω	χ^2	df	P
Pooled	2	201.498	4.570	4	0.334
Species-specific	6	199.213			
Pooled	2	201.498	19.310	16	0.253
Tagger-specific	18	191.843			

Table 3

Numbers of seeded tag releases and returns, by species. The 95% confidence intervals were calculated assuming a binomial distribution.

Tuna species	Number seeded	Number returned	Return rate	95% confidence interval
Skipjack	333	222	0.667	0.613–0.717
Yellowfin	158	94	0.595	0.514–0.672
Bigeye	35	23	0.657	0.478–0.809
Unknown	6	3	0.500	0.118–0.882
Total	532	342	0.643	0.600–0.684

Table 4

Numbers of seeded-tag releases and returns, by unloading location. The 95% confidence intervals were calculated assuming a binomial distribution.

Unloading location	Number seeded	Number returned	Return rate	95% confidence interval
American Samoa	324	254	0.784	0.735–0.828
Japan	80	39	0.487	0.374–0.602
Korea	16	0	0.000	0.000–0.206
Philippines	5	4	0.800	0.284–0.995
Puerto Rico	16	9	0.562	0.299–0.802
Solomon Islands	5	5	1.000	0.478–1.000
Thailand	86	31	0.360	0.260–0.471
Total	532	342	0.643	0.600–0.684

Table 5

Numbers of seeded tag releases and returns from American Samoa, by year. The 95% confidence intervals were calculated assuming a binomial distribution.

Year	Number seeded	Number returned	Return rate	95% confidence interval
1990	23	3	0.130	0.028–0.336
1991	116	95	0.819	0.737–0.884
1992	50	48	0.960	0.863–0.995
1993	101	83	0.822	0.733–0.891
1994	34	25	0.735	0.556–0.871
Total	324	254	0.784	0.735–0.828

Estimation of overall reporting rate for the RTTP The variation in return rates of seeded tags by unloading location (and possibly over time for some locations) means that the simple, pooled return rate of seeded tags may provide a biased estimate of the overall tag-reporting rate for the RTTP. Therefore, the tag-seeding data were stratified by unloading location, and an overall average reporting rate weighted by the estimated numbers of RTTP tags recovered at those locations was determined. I did not attempt to take into account the possible variation in reporting rates by time because of insufficient information for most locations.

The estimates of the numbers of RTTP tags recovered at various locations and in total are shown in Table 6. Median reporting rates, numbers of tags recovered, and their 95% confidence intervals are based on bootstrap sampling from the reporting-rate probability distributions indicated in Table 6. The relationships between the bootstrap distributions and the sample means \hat{p}_j from tag seeding are shown in Figure 2. For some locations, notably Philippines and Solomon Islands, \hat{p}_j overestimates the median of the probability distribution of p_j . This is due to

the small numbers of seeded tags in these locations and the resulting effect on the shape of the assumed underlying probability distributions.

The estimation of tag recoveries and reporting rates for Korea and Taiwan had to be treated differently because no RTTP tags were returned from Taiwan and only four tags were returned from Korea (which were given to a SPC staff member during a brief visit). Additionally, it was not possible to seed tagged fish into shipments bound for Taiwan. Therefore, there was no basis for estimating tag recoveries and reporting rates in Korea and Taiwan directly from tag-seeding and RTTP tag-return data.

However, other information was available to derive estimates for these locations. During the period of the RTTP, approximately 100,000 t of tuna was processed annually by canneries in Korea, all of which was supplied by Korean purse seiners (Lewis¹).

¹ Lewis, A.D. 1993. Product flows of tuna in the western Pacific, 1991 with likely trends during 1992. Sixth standing committee on tuna and billfish; 16–18 June 1993, Pohnpei, Federated States of Micronesia, South Pacific Commission, Noumea, New Caledonia. Information paper 2, 7 p.

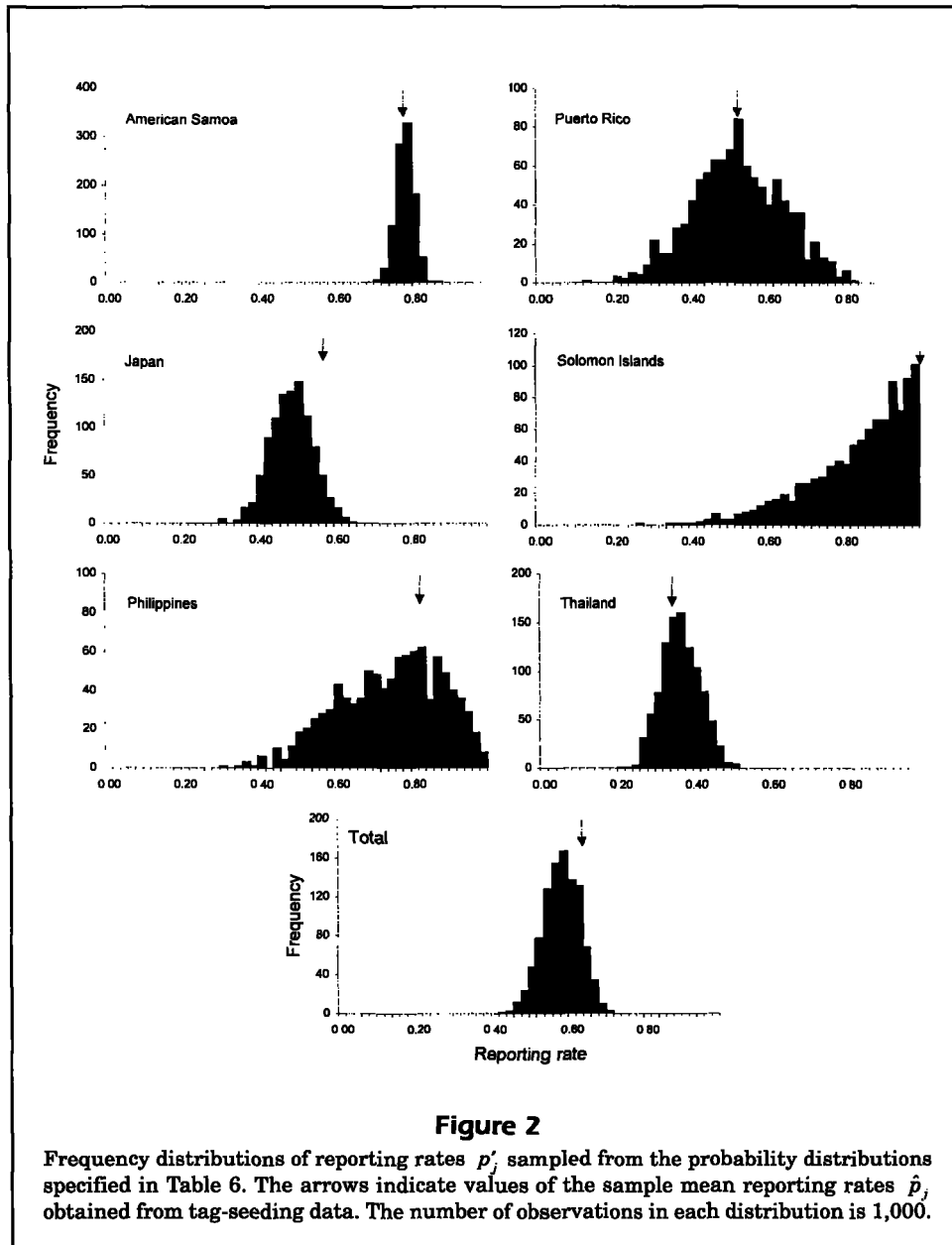


Figure 2

Frequency distributions of reporting rates p_i sampled from the probability distributions specified in Table 6. The arrows indicate values of the sample mean reporting rates \hat{p}_i obtained from tag-seeding data. The number of observations in each distribution is 1,000.

A similar quantity of the Korean purse-seine catch in the western Pacific was delivered to canneries in Thailand. Assuming a similar occurrence of tagged tuna in these components of the Korean catch, the number of tagged tuna in catches delivered to Korea can be approximated by the tag returns from Korean purse seiners unloading in Thailand (658) divided by the estimated reporting rate for Thailand (0.355). On this basis, 1,798 (95% confidence interval of 1,412–2,386) tagged tuna are estimated to have been landed in Korea, of which only four were returned to SPC under the special circumstances described above. Similarly, the disposition of the Taiwanese purse-seine catch (approximately 20,000 t to Taiwan

and 155,000 t to Thailand annually) and tag returns from Taiwanese purse seiners unloading in Thailand (928) implies that 327 (257–434) tagged tuna were present in catches delivered to Taiwan.

Summing across locations, it is estimated that 31,166 (27,208–37,264) RTTP tags were recovered from all fisheries in the western Pacific, resulting in an overall reporting rate of 0.586 (0.490–0.671).

Discussion

The objective of this study was to quantify two sources of tag loss, tag shedding and failure to re-

Table 6

Numbers of tags returned and estimates of numbers of tags recovered from various unloading locations. Median reporting rates, median numbers of tags recovered, and their respective 95% confidence intervals, were determined from 1,000 bootstrap replications based on random sampling from the specified beta (B) or uniform (U) distributions. Parameters for the beta distributions $B(x,y,a,b)$ are $x=r$, $y=N-r+1$, where N is the number of tags seeded, r is the number of seeded tags returned, a is the minimum possible reporting rate (based on the local tag-return rate), and b is the maximum possible reporting rate (1). The estimations for Korea and Taiwan could not be carried out in the usual way because of zero or very small numbers of seeded or RTTP (or both) tag returns. Estimations for these locations are described fully in the text.

Unloading location	Number of tags returned	Probability distribution	Reporting rate		Number of tags recovered	
			Median	95% confidence interval	Median	95% confidence interval
American Samoa	2,070	$B(254,71,0.016,1)$	0.784	0.739–0.826	2,639	2,505–2,802
Japan	1,969	$B(39,42,0.015,1)$	0.492	0.386–0.595	4,000	3,307–5,104
Korea	4		0.002	0.002–0.003	1,798	1,412–2,386
Philippines	6,671	$B(4.2,0.223,1)$	0.764	0.476–0.961	8,727	6,940–14,003
Puerto Rico	297	$B(9,8,0.002,1)$	0.525	0.301–0.753	565	395–988
Solomon Islands	2,226	$B(5,1,0.126,1)$	0.877	0.526–0.994	2,540	2,239–4,232
Taiwan	0		0.000	0.000–0.000	327	257–434
Thailand	2,218	$B(31,56,0.017,1)$	0.366	0.276–0.466	6,061	4,761–8,043
Tagging vessel	243		1.000	1.000–1.000	243	243–243
Other	2,568	$U(0.5,1.0)$	0.746	0.518–0.987	3,442	2,601–4,956
Total recoveries	18,266		0.586	0.490–0.671	31,166	27,208–37,264

port tags, in a large-scale tuna tagging experiment in the western tropical Pacific Ocean.

Tag-shedding rates were estimated by fitting a tag-shedding model to double-tagging data. The application of a double-tagging experiment to the estimation of the rate at which tags are shed from single-tagged fish requires several assumptions that are discussed in detail by Beverton and Holt (1957). In this study, there are four assumptions that warrant discussion. First, it must be assumed that the shedding rates of tags applied in the double-tagging experiment are the same as those for single-tagged fish. This assumption might fail if, for example, less care was taken with double tagging than with single tagging because of the need to return fish to the water within certain time limits. In the RTTP tagging experiment, taggers were instructed to take as much care in implanting each tag in double-tagged tuna as they would for single-tagged tuna. Although it is not possible to test this assumption with the limited amount of double-tagging data, the similarity in return rates of double- and single-tagged tuna (South Pacific Commission²) suggests that there had not

been a gross violation. If the assumption did fail, as described above, the shedding rates as applied to single-tagged tuna would be overestimated.

Second, it is necessary to assume for double-tagged fish that the events potentially resulting in shedding of tags are random and independent with respect to the two tags. If this assumption fails, there will be fewer observations of fish retaining one tag, and consequently shedding rates will be underestimated. This assumption is difficult to test unless it is possible to identify fish that have shed both tags, which of course will not normally be the case under field conditions. The techniques adopted in this experiment (individual tag placement on opposite sides of the fish) were designed to facilitate compliance with this assumption, but the actual extent of compliance remains unknown.

Third, it must be assumed that the first (primary) and second (companion) tags applied to fish in a double-tagging experiment have the same probabilities of shedding. This assumption might fail if, for example, the companion tag is less securely implanted because tagging on the opposite side of the fish is an unfamiliar task. This assumption can be tested by using the frequencies of primary and companion tag retention in fish that were recaptured bearing one tag. In this double-tagging experiment, there were 68 returns that consisted of one tag. Of

² South Pacific Commission. 1994. Oceanic Fisheries Programme work programme review 1993–94 and work plan 1994–95. Seventh standing committee on tuna and billfish; 5–8 August 1994, Koror, Palau, South Pacific Commission, Noumea, New Caledonia. Working paper 5, 66 p.

these, 29 returns were of the primary tag and 39 were of the companion tag. The cumulative binomial probability of 29 or less of either the primary or companion tag being found in a sample size of 68 is 0.275, indicating that there is a reasonable chance of the assumption being satisfied.

Fourth, in the analysis carried out here, it was assumed that tag pairs (from fish recovered with two tags) are reported (or not) as a pair—i.e. either both, or none are reported. Furthermore, it was assumed that the probability of reporting a tag pair was the same as that of reporting a single tag. I will refer to this as the dependent hypothesis. An alternative hypothesis is that the reporting of individual tags forming a pair is completely independent; whether or not one tag of a pair is reported has no effect on the probability that the other will be reported. I will refer to this as the independent hypothesis. Under either hypothesis, we can define the probability, $U(t)$, that a tag is retained at recapture time t and is reported as

$$U(t) = pQ(t | \rho, L) = p(1 - \rho) \exp(-Lt). \quad (2a)$$

However, the probabilities of two, one, and no tags being retained at recapture time t , and, in the case of at least one tag being retained, also reported, are different under the two hypotheses, as follows:

$$\begin{aligned} P_{d2}(t | \rho_d, L_d) &= p^2 Q(t | \rho_d, L_d)^2 \\ P_{d1}(t | \rho_d, L_d) &= 2pQ(t | \rho_d, L_d)[1 - Q(t | \rho_d, L_d)] \\ P_{d0}(t | \rho_d, L_d) &= pQ(t | \rho_d, L_d)^2 - 2pQ(t | \rho_d, L_d) + 1 \end{aligned} \quad (3a)$$

and

$$\begin{aligned} P_{i2}(t | \rho_i, L_i) &= p^2 Q(t | \rho_i, L_i)^2 \\ P_{i1}(t | \rho_i, L_i) &= 2pQ(t | \rho_i, L_i)[1 - pQ(t | \rho_i, L_i)] \\ P_{i0}(t | \rho_i, L_i) &= [1 - pQ(t | \rho_i, L_i)]^2, \end{aligned} \quad (3b)$$

where the d and i subscripts indicate the dependent and independent hypotheses, respectively.

It can be shown that substitution of the right-hand sides of Equations 3a into the log-likelihood Equation 4 produces an identical result to substitution of Equation 3; the p 's cancel out and reporting rate has no influence on the estimates $\hat{\rho}_d$ and \hat{L}_d when the dependent hypothesis is true. This is therefore equivalent to using Equation 2 as the tag-shedding and reporting model, as I have done in this study.

Under the independent hypothesis, substitution of the right-hand sides of Equations 3b into the log-likelihood Equation 4 does not result in a canceling out of p terms, and therefore p must be included in the tag-shedding and reporting model as shown in

Equation 2a. However, p is totally confounded with $1 - \rho_i$, and cannot be estimated from the double-tagging data. If an independent estimate of p is available (for example, from a tag-seeding experiment), Equation 2a can be applied and ρ_i estimated free of the effects of p .

For most double-tagging experiments, it will not be known with any certainty whether the dependent or independent hypothesis is more appropriate. The following procedure may provide some insight in this regard:

- 1 Obtain tag-shedding parameter estimates $\hat{\rho}_d$ and \hat{L}_d , assuming that the dependent hypothesis is true (using Equations 2 and 3).
- 2 If an independent estimate of the reporting rate, \hat{p} , is available, obtain tag-shedding parameter estimates $\hat{\rho}_i$ and \hat{L}_i , assuming that the independent hypothesis is true (using Equations 2a and 3b). Small values of \hat{p} (less than $1 - \hat{\rho}_d$) will usually result in $\hat{\rho}_i$ entering an unreasonable (negative) domain. Alternatively, if \hat{p} is constrained to be nonnegative, \hat{L}_i will differ from \hat{L}_d and the fit to the data will degrade (i.e. $\Omega_i > \Omega_d$). In either case, this indicates inconsistency between the reporting rate estimate \hat{p} and the independent hypothesis. In the present study, the estimated reporting rate (0.586) was much smaller than $1 - \hat{\rho}_d$ (0.941, see Table 1). If \hat{p} is applicable to the double-tagged tuna, this implies that the independent hypothesis is inappropriate for these data.

In reality, it is likely that the actual situation with respect to the reporting of tag pairs will lie somewhere between completely dependent and completely independent reporting. It is possible to generalize the tag-shedding model with respect to these hypotheses by defining a coefficient of independence, c , such that

$$U(t) = \frac{p(1 - \rho) \exp(-Lt)}{c(1 - p) + p}$$

Setting $c=0$ is equivalent to the dependent hypothesis, $c=1$ is equivalent to the independent hypothesis, while $0 < c < 1$ implies partial independence. For the RTTP double-tagging data and $\hat{p} = 0.586$, $c < 0.088$ allows an unconstrained \hat{p} to remain nonnegative. This range of possible values of c implies that the dependent hypothesis is likely to be appropriate for these data.

The tag-shedding model fitted to the double-tagging data assumes that the rate of tag shedding is constant over time. Kirkwood (1981) and Hampton and Kirkwood (1990) found that, in some cases, a model that allowed the probability of shedding to

decrease over time provided a better fit to double-tagging data for southern bluefin tuna, *Thunnus maccoyii*, than the model used in this study. They reasoned that tags might become more securely fixed over time, and thus less likely to be shed, as the fish grows and tissue is built up around the tag shaft. I fitted the three-parameter variable-rate shedding model (model 4 in Hampton and Kirkwood [1990]) to the pooled data set and to the three species-specific data sets and found that the improvement in fit over the constant shedding-rate model was negligible in each case and did not warrant the addition of the extra parameter. There is thus little evidence of a decline in shedding rates over time in these data. This may in part be due to the relatively short periods at liberty (maximum of 2 years) of the double-tagged tuna in this study compared with those for the southern bluefin tuna (up to 18 yr) analyzed by Hampton and Kirkwood (1990).

Given compliance with the assumptions of the experiment and the appropriateness of the model, it can be concluded that losses of tags through shedding are relatively modest (about 11% after two years) for the RTTP. This shedding rate is comparable to those reported by Hampton and Kirkwood (1990) for the more recent southern bluefin tuna double-tagging experiments (16% and 12% after two years for experiments 7 and 8, respectively), where comparable tags and techniques to those used in this experiment were used. Other tuna tagging experiments have reported substantially higher tag losses after two years, e.g. 30%–50% for the early southern bluefin tuna experiments (Hampton and Kirkwood, 1990), 43% for eastern Pacific yellowfin tuna (Bayliff and Mobrand, 1972), and 35% for Atlantic bluefin tuna (Lenarz et al., 1973; Baglin et al., 1980). It is possible that the higher shedding rates observed in some of these experiments were due to inferior tags, in which the streamers were prone to detach from the tag head. The streamers of tags used in this experiment and the recent southern bluefin tuna experiments were heat fused to the tag heads, making detachment impossible under normal conditions.

The analysis of tag-seeding and associated data indicated that, despite extensive publicity and attractive rewards for tag finders, failure to report tags was a significant source of tag loss in the RTTP. Given the diverse nature of the fishery, its spatial extent, and the methods of processing large quantities of fish caught by purse seiners in particular, this is hardly surprising. The estimated overall reporting rate in fact compares more than favorably with those for some tagging experiments carried out on more local scales (e.g. Campbell et al., 1992 for coastal shrimp in the Gulf of Mexico). My estimates of reporting rates

based on tag-seeding data may, if anything, err on the pessimistic side. It is suspected that one cause of failure to report purse-seine-caught tagged tuna may be the detachment of tags (through abrasion) from fish while they are held in the vessels' wells. If this occurs, detached tags would likely be flushed out of the wells into the sea, after which detection would be highly improbable. It is possible that tags placed in dead tuna by observers were more prone to detachment in the well than tags placed in live tuna that had been at liberty for some time. The tag head and the portion of the tag shaft imbedded in the musculature of live tuna were frequently observed to be encased in a fibrous capsule, which would tend to fix the tags more securely than tags placed in dead tuna. "Shedding" of seeded tags could conceivably result in losses of seeded tags of the same order as, or greater than, the immediate tag-shedding rates estimated from the double-tagging experiment on live tuna (about 6%). It may be possible to estimate the extent of this problem by conducting a double-tagging experiment for seeded tags.

The main purpose of estimating tag-shedding and reporting rates is to allow these processes to be incorporated into analyses of the tagging data for the purpose of estimating mortality rates. Typically, this would involve substitution of the point estimates of the parameters into equations such as Equation 1; mortality rates that are free of the effects of these tag losses could then be estimated from the tagging data (e.g. Kleiber et al., 1987). However, where the ultimate objective of the analysis (mortality rate estimation) is stock assessment related, it is important to have not only estimates of the mean rates but also estimates of their precision that are unconditional on estimates of nuisance parameters such as tag-shedding and reporting rates.

In this study, estimates of precision (expressed as 95% confidence intervals) of tag-shedding and reporting rates were obtained by using the percentile method applied to the bootstrap distributions of the parameter estimates. For the tag-shedding analysis, I confined this to estimates of precision of Q_{2yr} , although confidence intervals for the model parameters could be similarly derived. The advantage of the bootstrap approach as applied to the analysis of tag reporting is that it allowed the precision of the overall reporting rate to be easily determined given some knowledge, or reasonable assumptions, regarding the reporting-rate probability distributions for differing components (in this case, based on unloading location) of the data set. The approach also provided a convenient means of integrating uncertainties in tag-shedding and reporting rates (via the individual bootstrap values) into a similarly structured bootstrap

procedure for the estimation of mortality rates from the overall RTTP tagging data. The precision of the mortality rates estimated with such a procedure will then incorporate uncertainties in the estimates of tag-shedding and reporting rates and not be conditional on point estimates of these parameters.

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