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An examination of a tag-shedding assumption, with application to southern bluefin tuna

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The technique of attaching two tags, rather than one tag, to each fish in a tagging experiment is a well-established means of measuring the extent to which tags are shed, by observing the proportion of recaptured tagged fish that have retained only one tag. This commonly requires an assumption that tag-shedding is a random process which is unaffected by the presence of the other tag on the same fish. In theory, this makes possible an estimate of the unobservable number of caught fish that have shed both tags. This paper examines biases that may follow if data are pooled (sometimes unwittingly) from experiments with different tag-shedding rates. It is found that the bias in tag-shedding estimates, due to pooling, can be lowered markedly by reducing either the rate of shedding and/or variability between experiments in the tagging technique. The proportions of fish recovered in different experiments can sometimes be compared to support (or otherwise) the existence of bias. Southern bluefin tuna (*Thunnus maccoyii*) data sub-sets are analysed to illustrate the potential seriousness of tag-shedding bias.

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Introduction

The technique of attaching two tags to a fish to estimate the rate at which tags are shed by observing the proportion of recaptures with one or two tags still attached was originated by Beverton and Holt (1957, pp. 202–208). They took into account the possibility that, while some causes of tag loss would affect each of the two tags independently, others might result in both tags being lost simultaneously; they developed equations for estimating shedding rates according to which of these situations applied. Later authors (e.g. Gulland, 1963; Bayliff and Mobrand, 1972; Kirkwood, 1981; Wetherall, 1982; Kirkwood and Walker, 1984) extended the analytical treatment, introducing in particular more rigorous statistical treatment of the recapture data.

It is now clear, however, that a different kind of problem can arise with the double-tagging technique if recaptures from two or more batches of liberations are pooled. The individual batches may be liable to different shedding rates, because of differences either in the skill of those attaching tags, or in other operating conditions. If the pooled data are then analysed as if they were homogeneous with respect to shedding rates, a bias will be introduced into

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the estimates of the shedding rate, which could be serious. This is true even if the shedding of tags in the individual batches conforms precisely to the assumption that the tags are shed independently of each other.

That pooled data from double-tagging experiments could behave in this way, giving the impression that the assumption of independence is violated, was first noted by Hearn *et al.* (1987). The problem is analysed further in this paper, and the methodology illustrated by application to a large data set derived from double-tagging experiments on southern bluefin tuna carried out by CSIRO in Australia between 1963 and 1984.

Theory

Background

The standard theory of the estimation of tag-shedding rates (e.g. Kirkwood, 1981; Wetherall, 1982; Kirkwood and Walker, 1984) makes the following implicit assumptions:

1. Tags attached to the same fish may be regarded as a random sample from the collection of all tags.

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- 2. The shedding of any tag occurs independently of the shedding of other tags, including the one attached to the same fish.
- 3. Natural mortality, migration, catchability, and reporting of tags by fishermen are independent of the number of tags attached to a fish.

Assumption 1 relates to homogeneity of tags, and still may be satisfied even if the capacity of tags to remain attached to fish is variable, provided (as implicit in Kirkwood, 1981) the tags are randomly mixed at the time of tagging. However, the assumption is violated if all of the tags attached to some fish are of a longer-lasting variety than those attached to other fish. Assumption 2 precludes events that remove all tags at once from some fish, as discussed by Beverton and Holt (1957, p. 203). Assumption 3 ensures that natural mortality, migration, and the number of tagged fish caught and reported in each tag-retention category are in proportion to the number of live tagged fish in that category.

Let N fish be double-tagged, and let there be N(t) of these fish still alive at time t later (the time-at-liberty), with the probability that a tag is retained by a fish being Q(t). Suppose that some tagged fish are caught by fishermen at time t, that n_2 of them have two tags and n_1 have one tag. Fishermen also catch n_0 fish that have shed both tags, but these cannot be identified; therefore n_0 must be estimated.

A binomial distribution of tags in the tag-retention categories implies that n_2/n_1 is an estimate of N(t)Q/ $\{2N(t)(1-Q)\}$, and so an estimator of Q is

$$\hat{\mathbf{Q}} = 2\mathbf{n}_2/(2\mathbf{n}_2 + \mathbf{n}_1),$$
 (1)

which was obtained by Chapman *et al.* (1965, Equation (7)).

To account for fish that have shed both tags it is considered that each tagged fish caught represents W = 1/[Q(2-Q)] fish that were originally tagged. (For a singletagging experiment Wetherall (1982, Equation (8)) used 1/Q to allow for fish that shed their tags.) W is called the weighting factor and its estimator is given by

$$\hat{\mathbf{W}} = 1/(\hat{\mathbf{Q}}(2-\hat{\mathbf{Q}})) = 1 + n_1^2/[4n_2(n_2+n_1)],$$
 (2)

and so an estimator of no is

$$\hat{n}_0 = (n_1 + n_2)(\hat{W} - 1) = n_1^2/4n_2.$$
 (3)

Non-compliance with Assumption 1

Hearn *et al.* (1987) suggested the different tagging proficiencies of the operators attaching tags to southern bluefin tuna may lead to bias in estimating Q from Equation (1), because Assumption 1 would not apply. They claimed that the number of fish to lose both tags would then be Table 1. Proportions of fish that are expected to be caught in each category of number of tags retained from data combined from two sub-populations.

Number of tags	Proportion expected
retained on a fish	to be caught
2 1 0	$ \begin{array}{c} xQ_{A}^{2} + (1-x)Q_{B}^{2} \\ 2xQ_{A}(1-Q_{A}) + 2(1-x)Q_{B}(1-Q_{B}) \\ x(1-Q_{A})^{2} + (1-x)(1-Q_{B})^{2} \end{array} $

underestimated, especially for fish with long periods of freedom.

We will consider the bias in pooling data from two batches of releases, when Assumptions 1–3 are met for each batch; however, Assumption 1 will be violated for the pooled data.

We suppose that two tagging operators are involved: some fish are double-tagged by operator A, and the rest by operator B, who is less skilled in tagging. (For convenience, the corresponding data sub-sets are entitled A and B.) There are other equivalent scenarios; for example, some batches of tags may be more durable than others, or a single operator's tagging technique may improve with experience or vary from day to day (e.g. deteriorate in rough sea conditions). The shedding differences may be attributed to the fish; some days they may struggle more than others and be more difficult to tag, or large fish may be more or less difficult to tag than small ones or shed tags at a slower rate than small fish (as R. O. J. Tilzey, (pers. comm.) shows). Some systematic differences in shedding rates among various data sub-sets may be difficult to observe, or may not be known.

Let operator A attach tags to a fraction x of fish that, at time t, later retain a proportion $Q_A(t)$ of tags. $Q_B(t)$ is similarly defined for the fraction 1-x of fish tagged by operator B. For convenience, we assume that $Q_A(t)$ is greater than $Q_B(t)$. The proportions of fish expected to be caught in each tag-retention category (0, 1, or 2 tags) are listed in Table 1. From these, we calculate the weighting factor

$$W^* = 1/\{xQ_A(2 - Q_A) + (1 - x)Q_B(2 - Q_B)\}.$$
 (4)

On the other hand, if one makes the common assumption that Equation (1) applies, then the proportion Q of tags *apparently retained* is

$$Q = \frac{xQ_{A}^{2} + (1 - x)Q_{B}^{2}}{xQ_{A} + (1 - x)Q_{B}}.$$
(5)

the apparent weighting factor

$$\frac{W}{\{xQ_{A}^{2} + (1-x)Q_{B}\}^{2}} = \frac{\{xQ_{A} + (1-x)Q_{B}\}^{2}}{\{xQ_{A}^{2} + (1-x)Q_{B}^{2}\}\{xQ_{A}(2-Q_{A}) + (1-x)Q_{B}(2-Q_{B})\}}$$
(6)

is obtained by substituting Q into Equation (2).

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Since W* is correct for known Q_A and Q_B , we obtain, from Equations (4) and (6), the relative bias ΔW_r in W,

$$\Delta W_{\rm r} = W/W^* - 1 = \frac{-x(1-x)(Q_{\rm A} - Q_{\rm B})^2}{xQ_{\rm A}^2 + (1-x)Q_{\rm B}^2}.$$
 (7)

The bias is always negative for known Q_A and Q_B , meaning that if Equation (1) is applied the number of fish losing both tags is likely to be underestimated, thus justifying the comment to this effect by Hearn *et al.* (1987).

Two points are evident from Equation (7). First, the bias is highly sensitive to the difference $Q_A - Q_B$ and can be greatly reduced if the difference can be reduced. This could be done, for example, by teaching operator B an improved tagging technique. Secondly, the denominator on the right-hand side of Equation (7) increases if Q_A and Q_B do, which also reduces the bias: thus there are advantages in increasing the skill of both operators.

To illustrate the effectiveness of reducing $Q_A - Q_B$, suppose that $Q_A = 0.9$, $Q_B = 0.3$, and x = 0.25. Then $\Delta W_r = -1/4$. If Q_B increases to 0.6, then $\Delta W_r = -1/28$. So halving the difference between the tag-retention rates reduces the relative bias by a factor of seven. As an example of parallel increases in Q_A and Q_B , suppose that Q_A changes from 0.6 to 0.9 and Q_B from 0.3 to 0.6, with x = 0.25. Then ΔW_r changes from -3/28 to -1/28, reducing the bias by a factor of three.

Sometimes one may wish to estimate the number of recoveries for data sub-sets A and B separately. If Q from Equation (5) is applied to sub-set A, the bias in the estimate of recoveries is positive; if applied to sub-set B, the magnitude of the bias is greater than the magnitude of ΔW_r . In each of the examples given in the previous paragraph the magnitude of the bias associated with sub-set B is more than 50% greater than ΔW_r .

In the above cases, if A or B also conducted singletagging experiments the bias in applying Q from Equation (5) would be at least double ΔW_r . If A (or B) conducted a double-tagging experiment to estimate Q_A (or Q_B), which was then applied to data from a single-tagging experiment conducted by B (or A), the bias could be very large. For such cases, the bias in the above examples would be outside $\pm 30\%$. In one example the estimate of recoveries would be in error by a factor of three.

Sometimes data sub-sets with different rates of tagshedding may have insufficient information to identify them, or the differences may be unsuspected. If knowledge is limited to the time-at-liberty and the number of tags on each recaptured fish, one cannot normally discriminate between pooled and homogeneous data. This is because the latter, with a tag-shedding rate given by Equation (5), would have exactly the same ratio of 1 to 2 tags with time as the pooled data (i.e. $2\{xQ_A(1-Q_A)+(1-x)Q_B(1-Q_B)\}$: $xQ_A^2+(1-x)Q_B^2$ from Table 1). However, there are circumstances in which this equation may be proved to be invalid. These occur when the apparent proportion of tags retained increases over some time interval; this implies that either tags spontaneously reattach themselves to fish (which is nonsense) or that shedding assumptions have been violated.

As an illustration, suppose no tags are ever shed from fish tagged by operator A, while all tags are eventually shed from fish tagged by operator B. Then $Q_A(t) = 1$ for all t and $Q_B(0) = 1$ with $Q_B(t) \rightarrow 0$ as $t \rightarrow \infty$. From Equation (5) the expression for the biased estimator of tag-retention is

$$Q = \frac{x + (1 - x)Q_{B}^{2}}{x + (1 - x)Q_{B}}.$$

This expression is increasing for $Q_B < x^{1/2}/(1+x^{1/2})$, so there is an apparent negative tag-shedding rate over the last part of the experiment.

Cases where the probability of tag-retention apparently increases with time are difficult to detect in practice, because Q_A and Q_B have to be very different, a large number of tags must be recovered, and an appropriate statistical test needs to be developed. Information that would allow identification of data sub-sets which have different proportions of tags shed is generally required to determine whether shedding estimates could be seriously biased.

Statistical tests

We consider cases where two data sub-sets are identified and tag-shedding can be compared by statistical tests. The Kirkwood and Walker (1984) maximum likelihood estimator is used, as it requires knowledge of only the time-atliberty of each recaptured fish and whether one or two tags are still attached. It generalizes Equation (1) to allow the estimation of parameters of time-dependent shedding models.

If a model with k parameters is fitted to two data subsets, and also to the pooled data set, then twice the difference between the maximized log-likelihood from the pooled data and the sum of the maximized log-likelihoods from the separate data sub-sets is compared to a percentile of the chi-squared distribution on k degrees of freedom. If some parameters are constrained to have the same value for both sub-sets, the number of degrees of freedom is reduced by the number of such common parameters.

As a diagnostic tool we put forward the shedding model of Bayliff and Mobrand (1972)

$$Q(t) = \xi \exp\{-Lt\},\tag{8}$$

where t is the time-at-liberty, ξ is the probability that a tag is not shed immediately after tagging, and L is the constant instantaneous rate of shedding afterwards. Estimates ξ_A , L_A , ξ_B , and L_B are obtained for individual data sub-sets, and ξ and L for the pooled data. The chi-squared test with two degrees of freedom is applied. However, if a significant shedding difference is found it does not mean that shedding is always greater in one sub-set than another. Therefore, if the initial test yields statistical significance we test each parameter in Equation (8) separately to determine whether it differs between data sub-sets: the other parameter is forced to have the same value for both sub-sets. Shedding in sub-set A will be less than that in sub-set B if it can be established that either (i) $L_A < L_B$ for ξ estimated jointly (i.e. $\xi_A = \xi_B$) or (ii) $\xi_A > \xi_B$ for L estimated jointly (i.e. $L_A = L_B$).

In practice, we calculate weighting factors parametrically for each observed recapture time. For the pooled data, the weighting factor is equal to $1/{Q(2-Q)}$, where Q is of form (8). To present the results, we sum the weighting factors of all fish recaptured within a few broad time intervals. To each data sub-set we apply the same procedure, using different parameter estimates for each subset. This gives corrected estimates of the number of tagged fish recaptured in each time interval, for which we calculate the bias from the ratio of the pooled estimate to the sum of the unpooled ones.

Where it is shown that the proportion of tags shed is higher for one data sub-set than another, the proportions of fish recovered should also be compared to confirm the conclusions, provided mixing assumptions are met. A high proportion of tags shed should correspond to a low proportion of fish recovered. For valid comparisons between experiments of the proportions of fish recovered, fish of about the same size should be tagged at about the same place and time, and sufficient time be allowed thereafter for thorough mixing to occur (e.g. at the start of the fishing season following tagging).

If N fish are tagged, the proportion recovered after mixing is approximated by

$$n^*/(N - n_c),$$
 (9)

where n_e is the number of fish recaptured during the period of mixing, and n* is the number recaptured thereafter. Sometimes it may be convenient to let n* refer to the number recaptured by a specified fishery component. The statistical significance of differences in the proportions recovered can be evaluated by the conventional chi-squared test with 1 degree of freedom.

Even when allowing for different shedding rates between data sub-sets one must be wary of the results obtained because of possible within-sub-set heterogeneity. The methodology we advocate is intended as a detection tool only and not as a way to solve the problem. We think it quite likely that tagging operators with poor skills will exhibit substantial variation in tagging proficiency with time, which will violate Assumption 1 in the sub-set of fish that they tag.

Application to southern bluefin tuna

Southern bluefin tuna is a highly migratory species which begins spawning at about eight years of age in the only known spawning ground south of Java. After hatching, most fish travel south along the west coast of Australia (Hynd and Lucas, 1974; Murphy, 1977; Harden Jones, 1984) and some reach the south coast of Western Australia by one year of age. They tend to move eastwards along the south coast of Australia, reaching the South Australian and New South Wales fishing grounds by about two years of age, although some juveniles move westwards into the Indian Ocean (Murphy, 1977; Harden Jones, 1984).

A major Australian fishery is based on harvesting juveniles, aged two to six years, in the Australian Fishing Zone south of 30°S. By six years of age most have moved into oceanic waters and are then caught mainly by Japanese long-line vessels in the Eastern Hemisphere between 30° and 50°S. Further details of this species and its fisheries are given in Shingu (1978), Olson (1980), and Hampton and Majkowski (1986).

Estimates of the number of tagged southern bluefin tuna that have subsequently lost all their tags is necessary in many analyses of tag-recapture data (e.g. Hearn et al., 1987; Majkowski et al., 1988). From recaptures to the end of 1968, Hynd (1969) estimated the tag-shedding rate (assumed to be constant) of southern bluefin tuna to be 0.26 yr⁻¹. Kirkwood (1981) developed a model that does not assume the same probability of shedding for each tag, but Assumptions 1 to 3 are implicit. It allows for the possibility that some tags become firmly embedded in southern bluefin tuna after a few years. Kirkwood (1981) analysed data from southern bluefin tuna that were double-tagged between 1962 and 1976. He estimated that about 56% of tags were shed after four years at liberty. Hearn (1986) mentioned that shedding from fish tagged in the 1983-1984 programme was about one-third of that in previous programmes. He suggested that this was evidence of variability in the proficiency of taggers, which would bias estimates of tag-shedding. This is in keeping with the Bayliff (1973) finding for yellowfin tuna of differing shedding rates of tags attached by various operators.

Hampton and Kirkwood (1990) estimated shedding rates for eight experiments, which were classified according to location and time of tagging. They concluded that the probability of a tag being shed after four years at liberty was 0.5-0.7 for experiments in the 1960s and 1970s and about 0.2 for the 1980s.

Between 1959 and 1980, 52 294 juvenile southern bluefin tuna were tagged off southern Western Australia (WA), South Australia (SA), southern New South Wales (NSW), eastern Victoria, and eastern Tasmania, 12 756 were single-tagged, 39 477 were double-tagged, and 61 each had 6 tags attached (Table 2). Of these, 46 525 were supervised by CSIRO, while during the 1970s some 5769 were supervised by the Fisheries Department of Western

					Number recaptured								
							Double						
		Num	ber of fish ta	agged	Sin	gle	A	ust	J	ap	-		
Year	Supervision	Single	Double	Total	Aust	Jap	l tag	2 tags	l tag	2 tags	Total		
1959-1980	CSIRO	12 747	33 778 ¹	46 525	527	40	1554	4932	220	119	7392		
1979-1978	FDWA ²	9	5760	5769	-	-	125	247	8	-	380		
1983–1984	CSIRO	63	10116	10 179	18	-	771	3277	16	27	4109		

Table 2. Numbers of juvenile southern bluefin tuna tagged in Australian waters and associated recaptures. "Aust" refers to the Australian fishery, "Jap" refers to the Japanese fishery, "I tag" refers to fish recaptured with one tag attached and "2 tags" refers to fish recaptured with two tags attached.

¹Of these, 61 each had 6 tags attached of which 3 were recaptured by Japanese, one with 1 tag and two with 2 tags still attached. ²Fisheries Department of Western Australia.

Australia. From 1963 onwards most were double-tagged. Of all fish tagged, both single and double, 7772 were subsequently captured and their tags reported: 7385 by Australian fishermen and 387 by Japanese fishermen. During 1983–1984, CSIRO tagged another 10 179 juvenile southern bluefin tuna off WA and SA. All but 63 were double-tagged, and to July 1990 some 4109 of these have been recaptured: 4066 by Australian fishermen and 43 by Japanese fishermen (Table 2).

Most tagging of southern bluefin tuna was carried out on pole and line fishing boats. Fish for tagging were caught by a feathered lure on a barbless hook joined to a short line attached to a stout pole. However, some fish were caught by trolling with a line and a lure with barbed hook. Each fish was hauled aboard the boat and, if uninjured, was placed on a measuring board (in a vinyl cradle since 1980), where it was measured, tagged, and released to the water; usually within 20–30 sec (Hynd and Lucas, 1974; Kirkwood, 1981; Williams, 1982). The tag numbers, date, geographical location, and the length of each fish released were recorded.

The dart tags used were constructed of a numbered polypropylene tube, 12-15 cm long and 0.3 cm in diameter, glued to a moulded nylon dart head. The dart tag was inserted by an applicator 2.5 cm into each fish about 4.0 cm below the second dorsal fin (Hynd and Lucas, 1974; Kirkwood, 1981; Williams, 1982), with the tag pointing forward at an angle of 45° to the body (Fig. 1). Williams (1982) mentions that the barb should then have been anchored in or around the basal bone elements of the fin rays.

Tagging operators' names were recorded for each trip a boat made to sea, but not for each fish tagged. The tagger of a particular fish can be known only when just one operator was aboard (Mr C. Liron, pers. comm.), which occurred only when tagging was done during commercial fishing, but not from a chartered boat. More than 20 tagging operators were involved in CSIRO programmes during the 1960s, which makes it difficult to compare their skills because often more than one tagging operator was involved or small numbers of fish were recaptured.

Finders of tagged fish were requested to return all tags to CSIRO together with information on the vessel, date and location of recapture, and the length of each fish. Field officers liaised closely with and often collected tags from fishermen and processors. Rewards and release information were sent with letters of acknowledgement to encourage finders to return tags.

The only data analysed here are those pertaining to double-tagged fish with dates of recapture known to be accurate within two weeks. For fish tagged off SA during early 1964, the rates of tag-shedding by fish tagged by two known tagging operators A and B are compared. The only substantive difference found between the tagging operators was that B tagged a higher proportion (52.5%) of fish larger than 80 cm than did A (39.1%).

During a three-month period, each operator tagged fish on about 30 days and in two areas: inshore to the west of Port Lincoln (SA) and to the south on the continental shelf break (200 m depth). The two operators tagged their fish at about the same time in each area, with each tagging about 25% in the inshore area and the remainder at the shelf break. The most fish tagged at one place in one day was 52 by A and 81 by B, which are less than 8% of respective totals. In summary, the release pattern favoured mixing between fish of sub-sets A and B.

The same comparisons are made between fish tagged by the same operators (A and B) after the fish were caught by trolling off NSW during the 1964–1965 fishing season. In addition, the shedding rate of sub-sets A and B combined (A + B) is compared with that of all other fish tagged off NSW during 1964–1965 (including those caught by pole and line), which we denote by sub-set C. The main differences between the tagging operations were: (i) A and B W. S. Hearn et al.

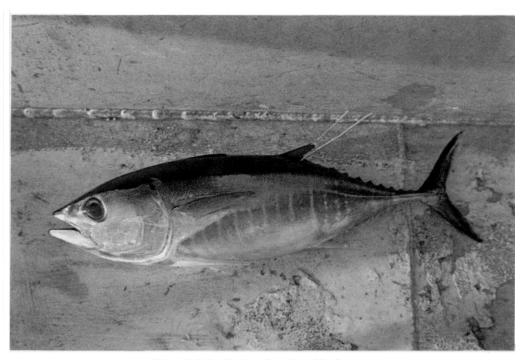


Figure 1. A double-tagged southern bluefin tuna.

tagged fish during late September and October 1964, whereas C continued tagging until early January 1965; and (ii) C tagged a higher proportion (52.0%) of fish larger than 70 cm than did A and B (26.7%).

In the WA tagging programme in early 1983 two operators with limited experience tagged fish together for seven days. The shedding from fish tagged during the first three days (D_1) is compared with that from those tagged in the final four days (D_2). The main difference between the tagging operations was that fish in sub-set D_1 were all tagged east of 122°E, whereas most (86%) of the remaining fish were tagged to the west of that meridian. The sizedistribution of fish tagged also differed: at tagging, about half (49.6%) of sub-set D_1 fish were greater than 60 cm long, while only 13.0% of sub-set D_2 fish were greater than that length.

In all these cases estimates are made of the biases caused by using pooled shedding rates to calculate the numbers of recaptures. After discounting for recaptures during the season of tagging, the proportions recovered are compared between tagging operators and correlated with the respective shedding rates. Season 1 refers to the season of tagging, where we assume the fishing season begins on 1 October each year, which is currently the start of the quota year for Australian southern bluefin tuna fisheries.

Results

Of fish tagged from pole and line boats off SA in early 1964, those tagged by operator A shed tags at a signifi-

cantly different rate from those tagged by operator B (Table 3). By keeping ξ fixed and estimating L_A and L_B jointly, it was shown that fish tagged by A shed tags at a slower rate ($\chi^2 = 6.60$, 1 df, p < 0.025) than those tagged by B (Table 4).

Biases, due to using pooled shedding rates to estimate numbers recovered, are calculated (Table 5) for seasons 2 and 3 combined (2+3) and for later seasons combined (4+). For seasons 2+3 the biases are within $\pm 10\%$, but for seasons 4+ the bias is large (-46.3%) for sub-set B and substantial (-20.8%) for combined sub-sets A+B (i.e. *Total* in Table 5).

After discounting for fish caught during the season of tagging (to allow time for mixing), the recovered proportion of fish tagged by A is more than twice that of those tagged by B (Table 6; $\chi^2 = 28.00$, p < 0.001). This is consistent with the difference in shedding rates found between data sub-sets A and B.

There is no significant difference in the proportions of tags shed by fish tagged by A and B from trolling boats off NSW in the 1964–1965 season (Table 3). This is supported by the discounted recapture rates (Table 6); 32.0% for A and 34.3% for B ($\chi^2 = 0.16$).

Other fish (C) tagged off NSW in 1964–1965 had a significantly different tag-shedding rate from those of subsets A and B (Table 3). By keeping ξ fixed and estimating L_{A+B} and L_C jointly, it was shown that fish tagged by A and B shed tags at a much slower rate ($\chi^2 = 26.06$, 1 df, p < 0.001) than those tagged by C (Table 4). This is consistent with the proportions recovered after discounting

Tagging location	Season	Tagger	ξ	L (yr ⁻¹)	– Log- likelihood	χ^2 (2 df)	р
SA	1964	A	0.648	0.000	50.54	6.62	< 0.05
		В	0.668	0.191	34.22	0.02	< 0.03
		A + B	0.614	0.022	88.07		
NSW 1964–1965	1964-1965	Α	0.961	0.178	57.81	0.30	ns ¹
		В	0.980	0.242	29.22		
		A + B	0.966	0.198	87.18	20.10	
		C	0.812	0.696	37.00	28.10	< 0.001
		A+B+C	0.934	0.282	138.23		
WA	Early 1983	D,	0.783	1.143	14.29	26.00	
	,	\mathbf{D}_{2}^{-1}	0.983	0.057	72.83	36.00	< 0.001
		$D_{1}^{2} + D_{2}$	0.950	0.050	105.12		

Table 3. Estimates of the tag-shedding parameters ξ and L from southern bluefin tuna tagged by different tagging operators at three locations. The negative log-likelihood estimates are listed. The χ^2 and p values relate to comparisons of tag-shedding between adjacent data sets.

¹Not significant.

Table 4. Estimates of two tag-shedding parameters ξ and L from southern bluefin tuna tagged by different tagging operators at three locations. Parameter L is compared between data sets by estimating ξ *jointly* (the joint estimates are in italics). The negative log-likelihood estimates are listed. The χ^2 and p values relate to comparisons of tag-shedding between adjacent data sets.

Tagging location	Season	Tagger	٤	L (yr ⁻¹)	– Log- likelihood	χ^{2} (1 df)	р
SA	1964	A	0.652	0.000	84.77	6.60	< 0.025
		B	0.614	0.180 0.022	88.07	0.00	0.025
		A + B	0.014	0.022	88.07		
NSW 1964–1965	1964-1965	A + B	0.957	0.186 125.20	125.20	26.06	< 0.001
		С		1.019			
		A + B + C	0.934	0.282	138.23		
WA	Early 1983	D_1	0.070	2.265	00.11	22.02	0.001
	•	\mathbf{D}_{2}^{-1}	0.978	0.052	89.11	32.02	< 0.001
		$D_{1}^{2} + D_{2}$	0.950	0.050	105.12		

recaptures during the season of tagging (Table 6), which for combined sub-sets A and B was 32.9% and for C a significantly much lower 7.0% ($\chi^2 = 95.09$, p < 0.001).

For seasons 2+3 the bias (Table 5) in using the pooled shedding rate to estimate the number of recoveries is large (-38.7%) for sub-set C and substantial (-12.9%) for combined sub-sets A+B+C (*Total* in Table 5). For seasons 4+ the bias is likely to be highly uncertain, as only one 4+ fish from sub-set C was recaptured, so this bias is not given in Table 5.

Of fish tagged off WA in early 1983, those belonging to sub-set D_1 shed tags at a significantly different rate than those from sub-set D_2 (Table 3). By keeping ξ fixed and estimating L_{D_1} and L_{D_2} jointly, it was shown that fish from sub-set D_1 shed tags at a faster rate ($\chi^2 = 32.02$, 1 df, p < 0.001) than those from sub-set D_2 (Table 4). This is

consistent with the adjusted proportions recovered (Table 6), which for fish tagged by D_1 was 3.2% and for D_2 a significantly higher 21.5% ($\chi^2 = 39.29$, p < 0.001).

For seasons 2+3 the bias (Table 5) from using the pooled tag-shedding rate is very large (-74.0%) for subset D_1 and substantial (-14.1%) for combined sub-sets D_1+D_2 (*Total* in Table 5). From sub-set D_1 there were no 4+ fish recaptured so the bias cannot be estimated.

Discussion

Southern bluefin tuna

The analyses show considerable differences in the tagshedding rates of various double-tagging experiments on southern bluefin tuna, a finding also obtained by W. S. Hearn et al.

Table 5. Numbers of recaptures of southern bluefin tuna that were double-tagged by tagging operators at three locations. The number recovered in each time interval has been calculated by using tagger-specific shedding-rates to estimate the numbers of fish that have lost both tags. The numbers in parentheses have been calculated from shedding rates estimated from pooled data, and their biases are also listed.

Tagging location	$\mathbf{T}_{\alpha} \mathbf{g}_{\alpha \sigma \sigma} \mathbf{f}_{\alpha}$	Number recovered	Number recovered seasons 2+3	Bias	Number recovered	Bias
season	Tagger(s)	season 1	seasons 2+3	(%)	seasons 4+	(%)
SA	Α	9.1	47.9		30.8	
1964		(9.4)	(50.1)	4.6	(33.9)	10.1
	В	9.1	46.0		37.4	
		(9.4)	(42.9)	-6.7	(20.1)	-46.3
	Total	18.2	93.9		68.2	
		(18.8)	(93.0)	-1.0	(54.0)	-20.8
NSW	A + B	94.5	94.2		_*	
1964-1965		(95.2)	(100.8)	7.0		
	С	30.2	72.7			
		(28.3)	(44.6)	-38.7		
	Total	124.7	166.9			
		(123.5)	(145.4)	-12.9		
WA	D_1	21.8	27.3		_*	
Early 1983	•	(19.1)	(7.1)	-74.0		
•	D_2	122.1	111.8			
	-	(122.5)	(112.4)	0.5		
	Total	143.9	139.1			
		(141.6)	(119.5)	-14.1		

*Estimates of bias cannot be obtained or are unreliable because, for this time interval, the actual number recovered in one sub-set is less than two.

Hampton and Kirkwood (1990). Differences in the skills of tagging operators appears to be a major cause of the observed differences in shedding rates; the inexperience of tagging operators seems to be an important factor.

Near the end of the tagging programme off SA in 1964, operators A and B tagged fish together (these data were not used in these analyses). Off NSW in 1964–1965 the shedding rates of fish they tagged were similar, as were the proportions of recoveries (Tables 3 and 6). Presumably B's improved performance was due to his learning experience with A. In early 1983 two inexperienced taggers considerably improved over a few days of tagging (Table 3). Alternatively, a skilled operator could have mainly tagged in the early period and not in the later, but we have no information on this matter.

The biases due to estimating the number of recoveries by using the pooled shedding rates are considered. For each pair of tagging experiments (Table 5) a serious bias (<-38%) occurs, in one time interval, for the data sub-set with the higher proportion of tags shed. For the estimates of the number of recoveries of the combined sub-sets (i.e. *Total* of Table 5) the bias is substantial (<-12%) for some time interval. (This bias is equivalent to ΔW_r of Equation (7).) If single-tagging experiments had been conducted by these operators it is expected that biases due to using pooled shedding rates would be larger than those of Table 5. Examination of discounted proportions of fish recovered (Table 6) provides confirmation of the results in that low tag-shedding rates correspond to high proportions recovered. However, no statistical analyses were conducted to test for consistency between sub-sets with regard to the different tag-shedding rates and recovery proportions. For the cases compared, all differences in the tagging location, time of tagging, and size distribution of fish tagged were examined, but these aspects had no apparent effect on the proportions recovered.

It might be argued that the different proportions of fish recovered from data sub-sets (A and B) of fish tagged off SA in 1964 (Table 6) could be attributed to differential migration into oceanic waters of various fish schools rather than to differential shedding of tags. However, the release patterns were similar between operators and each of them tagged fish from many schools. Also, of fish tagged by one operator at one place in one day, three fish (of 19 tagged) is the highest number recovered by Japanese longliners. But there were 33 recoveries by long-liners from 693 fish tagged by A and 23 from 1290 tagged by B; thus it appears there is no major clumping in migration patterns.

The analysis yields estimates of tag-shedding rates for some data sub-sets, thus allowing the estimation of the number of southern bluefin tuna that have shed both tags for these sub-sets. This useful bias-reduction technique is essentially the approach of Hampton and Kirkwood

Table 6. Numbers of southern bluefin tuna that were double-tagged by tagging operators at three locations and numbers recaptured during the season of tagging (season 1) and afterwards (seasons 2+). The recovery percentages are discounted for fish recaptured during the season of tagging (Equation (9)). The χ^2 and p values refer to comparisons between discounted recovery percentages of adjacent data sets.

Tagging location and season	Tagger(s)	Number tagged	Number recovered season 1	Number recovered seasons 2+	χ^2 (1 df)	р	Discounted recovery rate (%)
SA	A	693	8	69	28.00	<0.001	10.1
1964	В	1290	8	52	28.00	< 0.001	4.1
NSW	Α	241	69	55	0.14	0.10	32.0
1964-1965	(1)5	0.16	>0.10	34.3			
	A + B	374	94	92	05.00	-0.001	32.9
	С	596	28	40	95.09	< 0.001	7.0
WA	D ₁	240	19	7			3.2
Early 1983	\mathbf{D}_{2}^{-1}	707	122	126	39.29	< 0.001	21.5

(1990). However, there are limitations with this approach, which restricts the use of the southern bluefin tuna tagging data:

- For most fish the tagging operator cannot be identified, so inadvertent pooling may lead to bias. From Equation

 we have seen that the magnitude of bias due to pooled data increases with the degree of heterogeneity and the proportion of tags shed. The level of tagshedding from the 1963–1980 tagging is about three times that from the 1983–1984 tagging (Hampton and Kirkwood, 1990). Therefore, the results obtained from these data sets should be compared with caution.
- 2. The division of the data we analysed into sub-sets to reduce tag-shedding bias could make results pertaining to old fish very uncertain. This is because information is somewhat sparse for times-at-liberty greater than five years with only 90 being at liberty more than that time. This limitation is considered in Hampton and Kirkwood (1990) for southern bluefin tuna.
- 3. In some cases a high proportion of fish may have lost both tags soon after tagging, which does not allow tagshedding to be estimated with any certainty to determine whether it could be a cause of the apparent low proportion of recoveries. During late 1976, for example, 305 fish were double-tagged off WA, but only 1 has been recaptured, so nothing can be deduced about the rate of shedding. The low number recovered could be due to unusual migration by these fish rather than high tag-shedding.

Also, during 1965 and 1966, 61 fish each had 6 tags attached. Only three of these fish were recaptured and their tags reported, two had two tags each and one had one tag. This indicates a serious problem, regardless of whether the other tags from the recaptured fish were shed or merely retained by the finders.

From the evidence presented, it is clear that results from previous analyses of the 1963–1980 tagging data (e.g.

Majkowski, 1982; Hearn *et al.*, 1987; Majkowski *et al.*, 1988; Hampton, 1989; Hampton and Kirkwood, 1990) need re-evaluation. For the 1983–1984 data set, one should consider excluding some data sub-sets from analyses. It would also appear that data from the 12 819 single-tagged southern bluefin tuna are unsuitable for analyses that use estimates of tag-shedding.

The analyses presented have essentially relied upon circumstantial evidence. It would greatly clarify the matter if a double-tagging experiment were conducted with each fish having one tag attached in the ideal manner (Williams, 1982) and the other inserted into the musculature only, as mentioned in Hampton (1986).

Tagging recommendations

In tag-recapture experiments on tunas, fish should be double-tagged, since shedding can vary considerably between experiments and bias in single-tagging experiments could be large. Because biases may be the result of subtle differences in the techniques of different tagging operators, it is important to record the name of the person actually tagging each fish, the side of the fish on which a tag is placed, and tags that are thought to be incorrectly inserted. The tagging operation should be carefully documented, along with any modifications to the tagging technique. Fish should be dissected from time to time to assess the skill of the operator. This may also allow one to rule out high tag-shedding as a possible explanation if an unusually low number of tags is recovered.

These procedures should make it possible to identify the most successful tagging operators, so that their methods may be taught in future training programmes, and also allow data sub-sets with differing tag-shedding rates to be identified and analysed separately. Fish caught a long time after tagging should be classified and analysed for differences in tag-shedding. We have only discussed some aspects of tuna tagging: procedures for tagging tunas and recovering tags are extensively reviewed in Bayliff and Holland (1986).

General comments

Some fishermen may believe that if a fish is captured with two tags the return of one tag is sufficient evidence that a tagged fish has been caught. It should be explained to them why both tags must be returned.

If data sub-sets have high tag-shedding rates it follows that low numbers of tags are likely to be returned. Although it may seem reasonable at first sight to pool these data in order to achieve sufficient numbers for statistical purposes, our analysis indicates that this is highly undesirable, as it will increase heterogeneity, which could lead to a large bias.

Ideally, data sub-sets identified as having high tagshedding rates should be excluded from analysis because biases could be large if there is undetected heterogeneity.

It is clear from the preceding that practical aspects are very important in coping with tag-shedding. When conducting a tag-recapture experiment, the utmost effort should be taken to identify actual and possible causes of tag loss, minimize their effects, and make the tagging procedure as uniform as possible. Mathematical models and adjustments should be the last procedures used to cope with tag-shedding.

We have been concerned only with bias due to noncompliance with Assumption 1 because of evidence that it is critical for southern bluefin tuna. It must be borne in mind that double-tagging experiments on other fish species may not comply with Assumptions 2 and 3.

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