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Covariates of release mortality and tag loss in large-scale tuna tagging experiments

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ABSTRACT

The data from tag-recapture experiments, which are used to help understand animal behaviour and dynamics, and to provide input data for population models such as stock assessments, are affected by mortality associated with tagging and by tag shedding. These processes introduce bias and uncertainty into parameters estimated in population models such as tuna stock assessments. The causes and magnitudes of tag shedding and post-release mortality in tuna tagging experiments are not well understood. We analysed data from tuna tagging experiments in the Western Pacific (330,000 releases) and Indian Oceans (168,000 releases) to investigate factors affecting post-release mortality and tag shedding. Tag return rates were modelled as functions of the tagger identity, tagger experience, tagging assistant, tagging station, treatment of the fish, use of oxytetracycline, tuna species, and size at release. The release event was included in models as a fixed effect, so that differences in recapture rate among release events did not affect other parameter estimates. We found differences in tag return rates among taggers and tagging assistants, with tagger experience, and between tagging stations. Substantially lower return rates were associated with some types of damage to fish and with internally implanted tags, and when oxytetracycline was injected. Return rates varied with tuna size and species. In the Western Pacific yellowfin and bigeye return rates were more affected by some covariates than were skipjack, while differences were not observed in the Indian Ocean, where sample sizes were smaller. Results suggest that tagging mortality may be quite high, and that more care and better recording of fish treatment would increase the reliability of assessment inputs. We provide new effective release numbers that have been adjusted to allow for estimated tagging mortality and tag shedding.

1. Introduction

Tagging experiments are generally used to estimate rates of mortality and movement. However, tagging fish by catch and release inevitably causes some direct mortality and immediate (type 1) tag shedding (Ricker, 1958; Skomal, 2007), so even immediately post-tagging there are fewer tagged fish in the population than the number of fish apparently tagged. Rates of such 'tagging failure' are difficult to distinguish from natural and fishing mortality, which are usually the parameters of interest. Reducing tagging failure increases precision, but it cannot be eliminated. We must therefore estimate the rate at which it occurs, so that models can account for this failure explicitly.

There is also considerable interest in understanding the factors that contribute to tagging failure. There are two components to tagging failure: tag-induced post-release mortality and tag shedding. Tagging failure can also be divided into (a) 'base' levels of mortality and tag shedding, which occur for fish tagged by an expert tagger, and released with well-placed tags and apparently in good condition, and (b) additional effects due to any factors less than ideal. The base level of mortality is unknown, but in tuna tagging a certain amount is unavoidable. Tuna tagging experiments generally use pole-and-line methods, in which the hooked fish is lifted onto the boat by the hook, placed in a tagging cradle, measured, tagged, and released by being dropped over the side. The fish is therefore to some degree stressed, having been removed from the water and from the school, injured by the hook, disoriented, lower on oxygen, and probably more vulnerable to predation. Base levels of tag shedding, however, have been estimated for tuna tagging experiments (Hampton, 1997; Gaertner and Hallier, 2013), and are generally quite low. Gaertner and Hallier (2013) estimated tag shedding shortly after release (type 1) at 0.7% (bigeye and skipjack)

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and 2.3% (yellowfin), and the steady rate of subsequent long term tag shedding (type 2) at 1.7%, 2.9%, and 3.9% per year for bigeye, skipjack, and yellowfin, respectively. If these rates of tag shedding are accurate and/or tagging failure rates are not similarly low, the majority of tagging failure may be due to post-release mortality.

Additional effects on tagging failure include higher rates of post-release mortality of fish kept out of the water longer than usual, or damaged more than normally by the hook or by impact against the vessel during capture and release. If fish condition on release is recorded, we can identify how different types of damage affect survival (e.g. Cooke et al., 2003; Sumpton et al., 2010). Additional tag shedding can occur when a tag is badly placed, and this can also be estimated if tag placement is reported. Inevitably, taggers and tagging assistants vary in the speed with which they prepare and tag the fish, how gently they treat the fish, and in the quality of the tag placement. Proficiency is also likely to increase with experience. Thus, individual taggers and assistants can have different mortality and tag shedding rates, which can be compared by comparing return rates (e.g. Dicken et al., 2009).

Most investigations of post-release mortality have been undertaken by holding fish in captivity for a period after release, which does not account for all the challenges of the wild environment (Raby et al., 2013). The analysis in this paper takes a different approach, by comparing recapture rates among fish released into the wild after different types of treatment. We analyse data from two large-scale tuna tagging experiments in the Western Pacific and the Indian Ocean, which have collectively tagged over 500,000 tuna. In these analyses the tagging event is used as a factor, so estimates of other effects are unaffected by the circumstances shared by all fish at a release event. We estimate rates of tagging failure, and identify some of the primary causes.

Results of these analyses indicate how tagging practices may be changed to reduce tagging failure and increase the number of effective releases. These analyses also provide results that can be used in stock assessments, to adjust these models to account for the variation in the tag return rates that are due to tagging effects rather than natural processes. Accounting for tag shedding and post-release mortality will improve the estimation of fishing mortality rates in these models.

2. Material and methods

Data from the Indian Ocean Regional Tuna Tagging Program (IO-RTTP) were extracted from the IO-RTTP database (Hallier and Million, 2009). IO-RTTP tagging dates ranged from 13 May 2005 to 29 August 2007, and recovery dates from 30 May 2005 to 23 August 2012. The IO-RTTP data contained 168,163 releases and 28,009 recoveries, in 1867 tagging events (Fig. 1). Most tags were released at some distance from the main fishing grounds, and median time between release and recovery was 216 days. Removing tagging events with fewer than 20 tags released left 162,462 releases (96.6%) in 1368 tagging events. Tag reporting rates are estimated from tag seeding to be well over 90% (Hillary et al., 2014). Expected tag shedding after 216 days was 2.4% based on estimates from double tagging (Gaertner and Hallier, 2013).

Data for the Pacific Tuna Tagging Programme (PTTP; Leroy et al., 2013) based on pole-and-line tag releases in the Western Pacific were extracted from the PTTP database (Caillot et al., 2012). PTTP tagging dates ranged from 14 August 2006 to 18 March 2012, and recovery dates from 29 August 2006 to 24 August 2012. The data included 330,128 releases and 53,978 recoveries, from 1492 tagging events. Most tags were released within the main fishing grounds, and median time between release and recovery was 50 days. Tagging events with fewer than 50 tags were removed, leaving 321,198 releases (97.3%) and 52,723 recoveries from 944 tagging events. The removal threshold was applied to accelerate model fitting and reduce computer memory requirements, and was set higher in the PTTP than in the IO-RTTP given the greater number of tags released. The threshold made little difference to parameter estimates or statistical significance. Tag reporting rates are estimated from tag seeding experiments to be approximately 50% (Hoyle, 2011; Hoyle et al., 2011). Expected tag shedding after 50 days was 1.1%, based on estimates from double tagging in the IO-RTTP (Gaertner and Hallier, 2013).

Table 1
Percentage of tags per category for each parameter recorded. The IO-RTTP releases included 162,777 releases while the PTTP included 321,198 releases.

PTTP		IO-RTTP	
Tag type		Tag type	
Conventional 13 cm	70.93	Conventional tag	83.08
Conventional 11 cm	28.86	Double tag	16.73
Archival tag	0.16	Electronic tag	0.17
Sonic tag	0.05	Sonic tag	0.02
Tagging station		Tagging station	
Starboard bow	32.05	Bow	32.68
Port bow	37.00	Front	21.06
Mid	0.47	Mid	40.55
Stern	30.47	Stern	5.71
Condition		Condition	
Good	94.96	Good	97.54
Bleeding	0.46	Bleeding	1.37
Tail damage	0.06	Tail damage	0.03
Shark bite	1.13	Shark bite	0.02
Mouth damage	0.74	Mouth damage	0.38
Eye damage	0.14		
Dropped on deck	2.47	Dropped on deck	0.59
Hit side of boat	0.05	Hit side of boat	0.04
Long time on hook	0.00	Too slow/other	0.01
Quality		Quality	
Good	99.19	Good	98.71
Badly placed	0.73	Badly placed	1.29
Too slow	0.08		
Experience		OTC	
≥2500 fish	78.79	False	96.49
<2500 fish	21.21	True	3.51

Tagging methods differed between the two programmes. Tagging in the IO-RTTP was carried out on two large pole-and-line vessels (Hallier and Million, 2013). The majority of fish (73%) were tagged using the associated school fishing technique, in which a tuna school remains associated with the tuna fishing vessel for long periods. The IO-RTTP tagged most fish off the coast of Tanzania, in an area where purse seine fishing effort is relatively low (Hallier, 2008). Tagging in the Western Pacific was also carried out on a large pole and line vessel, but the vessel had no associated tuna. Tagging occurred in a variety of locations, mostly within the main commercial purse seine fishing ground.

The following parameters were used as covariates in the model. The proportions of fish per category by parameter and tagging programme are recorded in Table 1 and Fig. 2.

2.1. Tagging event

A session of continuous tagging on one day at one location.

2.2. Tagger

The identity of the person applying the tag. A categorical variable with the base level defined as the person releasing the most tags during each program.

2.3. Tagger experience

The number of tags of all types applied by the tagger before the start of each tagging event. For taggers with no tagging experience

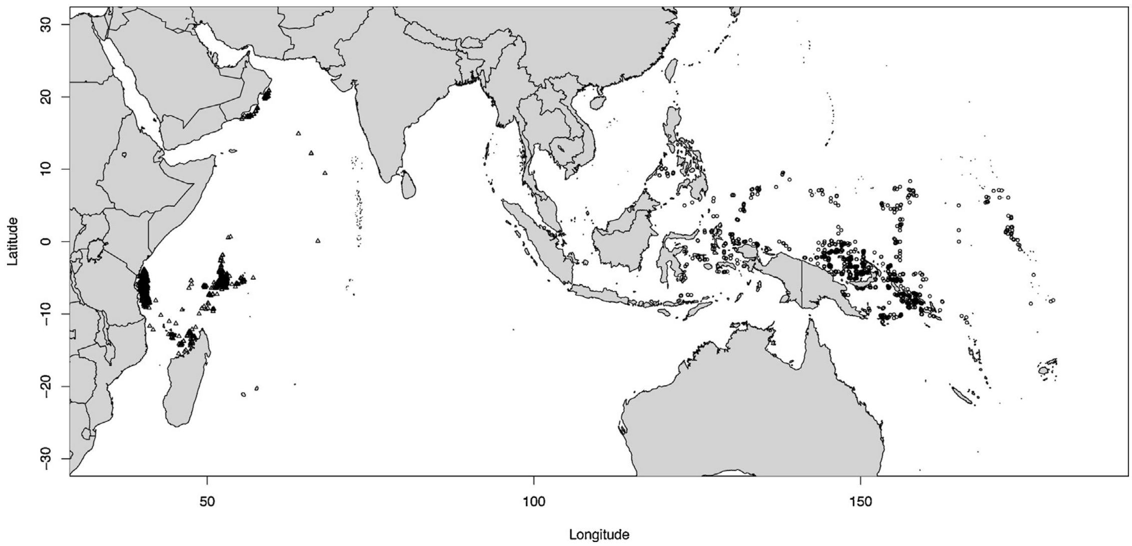

Fig. 1. Map of tag release locations for the IO-RTTP (triangles) and the PTTP (circles).

this started at zero. All experience levels above the maximum level *exp_lim* were set to *exp_lim*. Experienced taggers who had participated in earlier tagging programs started at *exp_lim*. We fitted the model with a range of *exp_lim* levels and compared the fits using the Akaike Information Criterion (AIC; Akaike, 1973).

2.4. Tag type

In the PTTP, tags were classed as conventional, archival, or sonic, with conventional tags further classified by length (11 or 13 cm). In the IO-RTTP, tags were classified as conventional single tags, double (two) tags, or electronic (i.e. either archival or pop-off) tags.

2.5. Tagging assistant

In the PTTP, the identity of the tagging assistant was recorded. The assistant ensures a smooth supply of fish for the tagger, maintains the cleanliness and condition of the tagging cradle, and screens the quality of fish before they reach the tagger. It should be noted that catchers also have a role but were rarely identified in the data, and the assistant's role can vary among tagging stations.

2.6. Double tag

In the IO-RTTP approximately 17% of fish were released with two conventional tags, and return of a double-tagged fish was recorded if the first tag was returned, but not (for the purposes of the analysis) if only the second tag was returned. This factor was not included in the PTTP analysis, because double tagging occurred in only a small proportion of releases, and information was available from previous experiments (Hampton, 1997).

2.7. Fish condition on release

In the PTTP, fish condition was classified into the following categories: good, bleeding, eye damage, mouth damage, tail damage, dropped on deck, hit side of boat, shark bite (fresh bites by cookiecutter shark, *Isistius brasiliensis*), and unknown. In the IO-RTTP, condition was classified as: good, bleeding, tail damage, mouth damage, dropped on deck, hit side of boat, shark bite, too slow/other, and unknown. For both tagging programs, an alternative condition index was used to classify condition as good, damaged (including bleeding, eye, mouth or tail damage), impact (including dropped on deck or hit side of boat), or shark bite.

2.8. Tagging quality

In the PTTP, tagging quality was classified as good, badly placed, too slow, tag rejected, tag lost, or unknown. In the IO-RTTP the categories were good, badly placed, and unknown.

2.9. OTC

The IO-RTTP dataset included 5709 fish injected with oxytetracycline (OTC), and these fish were marked with a white conventional tag. OTC was not used in the Western Pacific component of the PTTP.

2.10. Tagging station

Tagging stations may be expected to have different return rates. In the PTTP, these were defined as stern, midships, port bow, and starboard bow. Stations at the stern were closer to the water, and fish were generally caught at a slower rate which might be expected to result in quicker tag time per fish and lower mortality. On the other hand, the catchers and tagging assistants at the stern were generally less experienced. The port and starboard bow stations were modelled separately for several reasons. The port bow station tagged the most fish because chumming occurred there, and as a result was allocated the most skilled taggers, assistants, and catchers. The position of this station was optimised for catchers to place fish on the cradle. At the starboard bow station fish sometimes passed through several pairs of hands, and the anchor was an obstacle to fish release.

2.11. Length

Fish fork length was measured in the cradle during tagging to the nearest 1 cm, and aggregated into 5 cm groups for this analysis.

2.12. Species

Bigeye (BET), yellowfin (YFT) and skipjack (SKJ) tuna were included in the analyses.

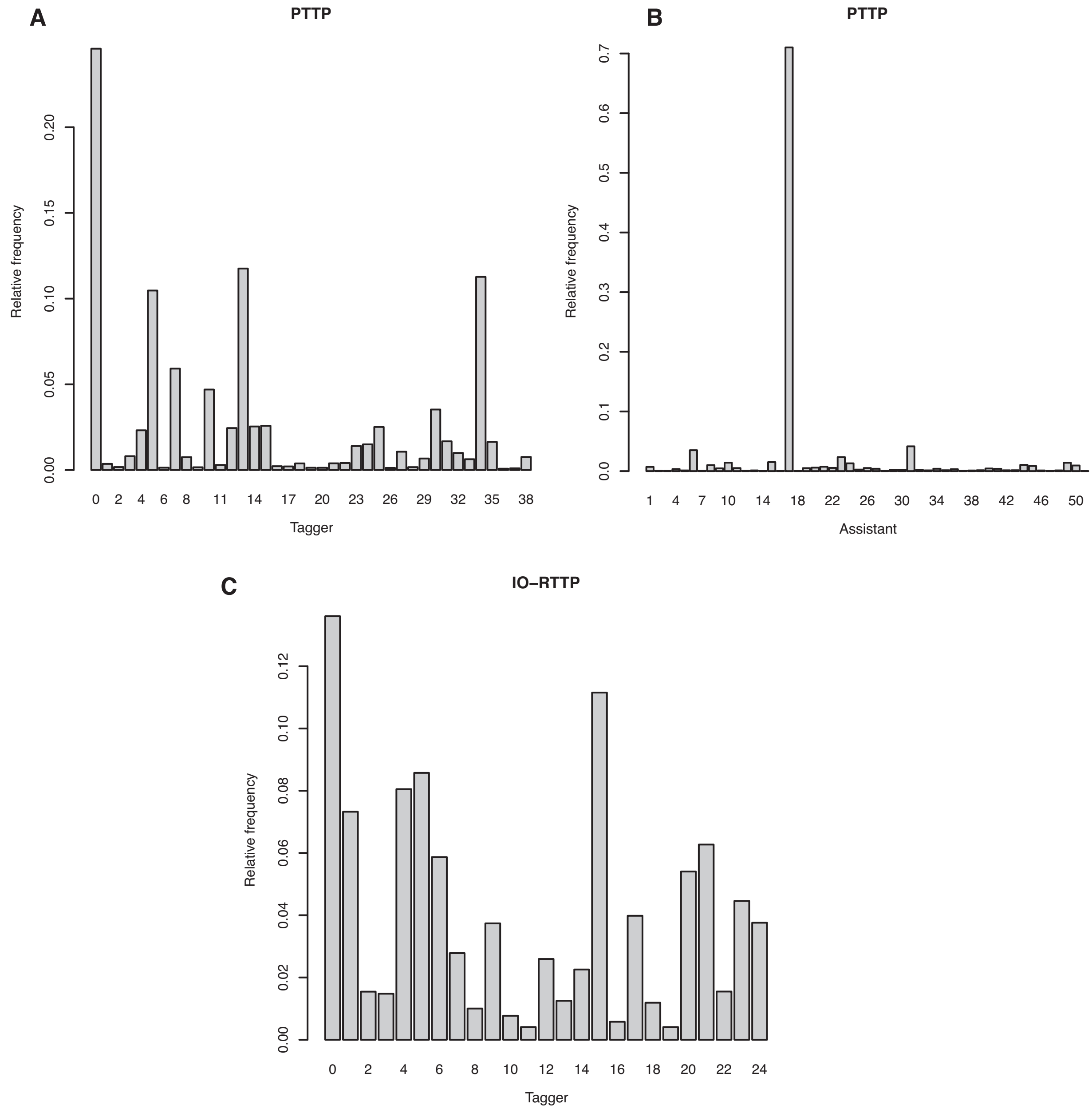

Fig. 2. Proportions of tags released by each (a) tagger and (b) tagging assistant in the PTTP and (c) each tagger in the IO-RTTP.

2.13. Data cleaning

Releases with the following characteristics were removed: length ≤15 cm, tag quality of 'tag lost', 'tag rejected', or 'unknown'. Data were included for taggers who had tagged at least 100 fish, and for all release events in which at least 20 (IO-RTTP) or 50 (PTTP) tags were released.

2.14. Analysis

The analysis was carried out with a generalized linear model in *R*, assuming a binomial response.

$$\log\left(\frac{\pi}{1-\pi}\right) \sim \beta_0 + \beta_1\text{event} + \beta_2\text{tagger} + \beta_3\text{experience} + \beta_4\text{tagtype} + \beta_5\text{spline}(\text{length}) \times \beta_6\text{species} + \beta_7\text{OTC} + \beta_8\text{condition} + \beta_9\text{quality} + \beta_{10}\text{station}$$

We fitted models to all parameters, compared models using the AIC, and removed parameters without significant support.

We modelled experience with a second order polynomial, and compared experience limits ranging from 100 to 4000 fish. Analyses of experience were initially carried out using only conventional tags, since the internal tag insertion process for archival and sonic tags requires different skills, and the experience would not be transferable. However, sample sizes for internal tags were far lower than for conventional tags and including both tag types in the model did not change the estimated limit experience level. Aside from tagger experience and tagging event, time variation was not included in the model.

Models were run for each species separately, for all species combined, and for bigeye combined with yellowfin. Model fits were compared using the AIC.

The contribution to tag recovery of the observed variation in each parameter was estimated from the ratio of predicted tag returns with observed parameter values versus predicted returns with that parameter set to the base level. The base levels represented a fish released in good condition by a highly experienced tagger and assistant, at the tagging station with the highest return rates. In the PTTP, the selected best levels were tagger 5, tagging assistant 8, and the port bow station for all tuna species. In the IO-RTTP the selected best levels were tagger 13 and the 'front' station. The following function was used, where k represents the parameter of interest and i represents the fish released: $\text{contrib}_k = \sum wt_i(\text{predtags}|\text{obspar}_{\text{all}})_i / (\text{predtags}|\text{obspar}_{\text{all but }k}, \text{basepar}_k)_i$. We also combined the base levels to infer an overall rate of tagging failure and estimate the number of effective releases in each program.

3. Results

Each variable in the model was examined for each tagging program. Initial tests combined all species within each dataset, and the best model for the PTTP included tagger, tag type, tagging event, tagger expertise, assistant, tagging station, length × species interaction, fish condition, and tag placement quality. The best model for the IO-RTTP differed from the PTTP in that it included OTC, but did not include tagger expertise, assistant, or station (Table 2).

3.1. *Species*

For the PTTP, separate analyses by species had a lower combined AIC than any fully pooled analysis (Table 2). A model with bigeye and yellowfin pooled, however, had more support than running these two species separately. In analyses for bigeye alone, sample sizes were comparatively small and fewer variables had significant support than for the other two species. Subsequent analyses were carried out for skipjack and for combined bigeye–yellowfin (YFT + BET). In the IO-RTTP analyses, in contrast, the AIC was lower for analysis pooled across all species. Significant interactions were apparent between species and the tagger, length, and OTC fields. Interaction terms for species with tag placement quality, condition and tag type were not statistically significant.

3.2. *Tagging event*

Return rates (pooled across species) varied substantially across tagging events (Fig. 3). There was more variability for the PTTP, which tagged within the fishing grounds, than for the IO-RTTP in which most releases were at some distance from the fishing effort and with longer times at liberty than the PTTP. Tagging event was statistically significant in PTTP models run for separate species, but this was not the case for the IO-RTTP (Table 2).

3.3. *Tagger and tag type*

Taggers and tag types were modelled in two ways: first as separate parameters and with all levels of the tag type variable; and second as an interaction between tagger and tag type. The first analysis for the PTTP showed that return rates varied by tag type for YFT + BET, and for skipjack. The conventional 11 cm and 13 cm tags had similar return rates, substantially higher than the archival and sonic tags which were similar to one another. For the IO-RTTP, the first tags of double tagged fish were returned at slightly higher rates than for single-tagged fish, and electronic tags had very low return rates (Fig. 4).

We re-ran the models with tag types pooled into either internal or conventional. For the PTTP across all species, the tagger × tag type model fitted the data better than the simpler tagger + tag type model, with ΔAIC of 18.2 (Table 2), whereas for the IO-RTTP the tagger + tag type model fitted better, with ΔAIC of 11.6. During the

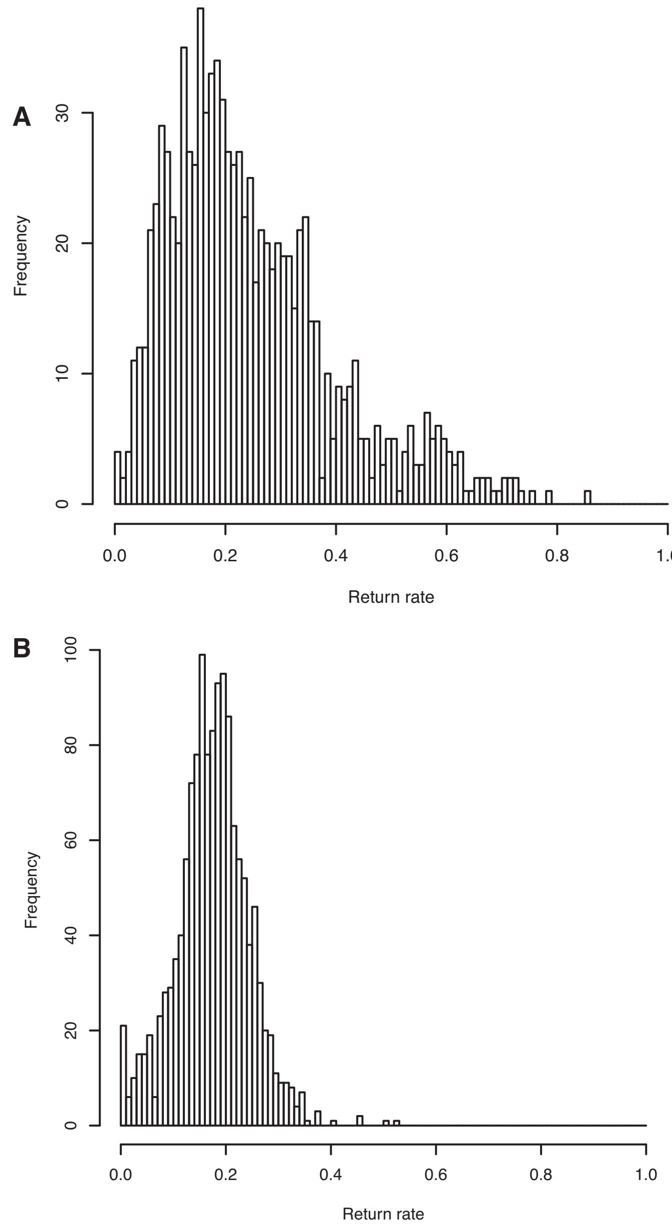

Fig. 3. Frequency distributions of the predicted return rate by tagging event for those events with sufficient releases to be included in the model. We predicted return rates for 50 cm yellowfin released in good condition by the base tagger and assistant, for (a) the PTTP and (b) the IO-RTTP.

IO-RTTP, 11 taggers applied internal tags, whereas there were 4 taggers for internal tags in the PTTP.

Return rates by tagger × tag type were modelled in comparison to the conventional tagger with the most releases. The analysis showed substantial variation among taggers, with return rates for some individuals considerably below the reference tagger (Fig. 5). The most prolific archival tagger in the PTTP (tagger 5) also had the highest archival tag return rate, with the return rate for archival tags 74% of the reference tagger's rate for conventional tags.

3.4. *Tagger experience*

For the PTTP, an experience level of 2500 fish was best supported as the level after which return rate stabilized for the model with all tags combined (Fig. 6). For PTTP BET + YFT, tag return rates started at about 65% of the rate for the most experienced taggers. For PTTP

Table 2
Akaike information criteria (AIC) for the full model, and differences in AIC from the full model for models removing individual parameters (ΔAIC) for each tagging programme. Analyses included data for both internal and conventional tags.

PTTP	BET_YFT_SKJ	BET_YFT	BET	YFT	SKJ
Full model	256,109.3	80,606.6	7809.3	73,087.9	173,994.0
Tag type	46.4	15.9	2.1	−0.9	17.4
Tagger	407.8	152.8	−5.2	131.4	229.8
Tagger:tagtype	18.2	−7.5	2.2	−11.4	2.4
Tagger × tagtype	434.8	182.4	−0.4	152.7	258.9
Tagger experience	53.6	27.0	−2.9	20.2	12.0
Tagging assistant	189.5	107.7	−39.0	97.3	66.8
Tagging station	112.7	25.7	−2.1	26.7	88.9
Tag placement quality	156.0	25.8	−1.6	24.7	136.1
Fish condition	289.4	116.8	9.1	102.2	165.3
Length			39.7	566.7	1323.8
Length:species	229.9	3.8			
Tagging event	21,256.9	6464.8	154.8	5847.1	15,454.6
IO-RTTP	BET_YFT_SKJ		BET	YFT	SKJ
Full model	144,888.4		30,072.2	49,271.2	67,035.7
Tag type	41.0		5.1	30.6	0.8
Tagger	69.0		10.7	11.4	29.9
Tagging station	4.9		−1.6	−0.8	4.4
Tag placement quality	1.3		3.3	−1.7	−4.6
Fish condition	10.3		−2.6	−1.0	−1.1
OTC	166.8		110.5	14.6	33.4
Length			86.3	117.8	186.5
Length:species	245.3				
Tagging event	571.2		−490.0	−182.6	−321.0

skipjack, tag return rates started at about 80% of the maximum, with the rate of improvement declining as experience approached the maximum value. For the IO-RTTP, including experience in the model was not supported.

3.5. Tagging assistant

The assistant's identity, which was recorded for 28% of releases in the PTTP but not at all for the IO-RTTP, explained a significant amount of variation in return rate, with ΔAIC of 108 for YFT + BET, and 67 for skipjack (Table 2). Average return rates varied more among assistants for YFT + BET than for skipjack (Fig. 7).

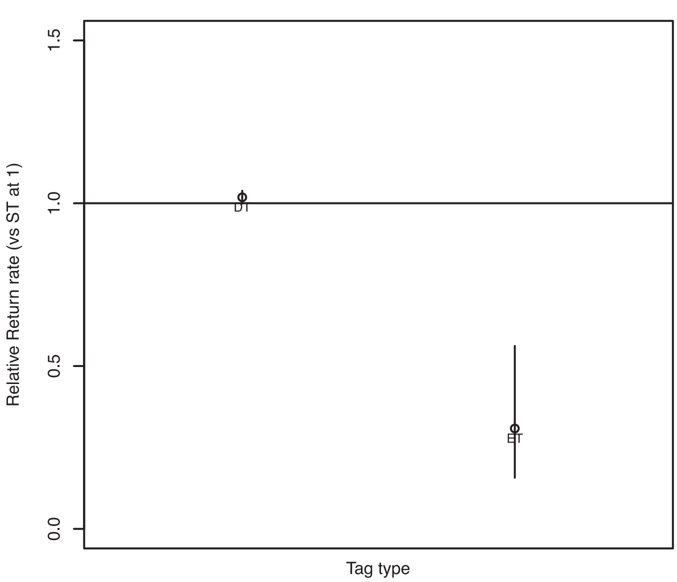

Fig. 4. The relative contribution of tag type to return rates of fish released in the IO-RTTP. Tag types are conventional double tags (DT) and electronic tags (ET) versus the base level of conventional single tags.

3.6. Station

The tagging station made a significant contribution to the variation observed, with ΔAIC of 26 for PTTP YFT + BET, 89 for PTTP skipjack, and 5 for the IO-RTTP (Table 2). In the PTTP, fish tagged at the port bow station had the highest return rates after taking into account other factors, with lower return rates from the other stations by between 6% and 18% (Table 3). The starboard bow and midships had the lowest return rates. Station effects were very similar for skipjack and BET + YFT. Return rates in the IO-RTTP varied only slightly among stations but were on average 4% higher in the front station than in the bow station.

3.7. Tagging quality

Tags recorded as badly placed were associated with substantially lower return rates in the PTTP (Table 3), by 27% for YFT + BET and 42% for skipjack. In the IO-RTTP, tags recorded as badly placed were also returned at a lower rate than other tags, but the difference was only 8%. In the PTTP, tags placed too slowly were associated with very low return rates, by 56% for YFT + BET and 63% for skipjack.

3.8. Fish condition on release

Suboptimal fish condition was well supported and associated with similarly lower return rates for both YFT + BET and skipjack in the PTTP, particularly for fish that were bleeding, had sustained eye damage, or experienced an impact such as hitting the side of the boat or being dropped on deck during capture (Fig. 8). Tail damage also appeared important though it applied to relatively few fish. Both mouth damage and cookiecutter shark bites were relatively common, but appeared to have little or no effect on return rates. Including fish condition in the PTTP models improved the fit significantly, with ΔAIC of 117 for YFT + BET and 165 for skipjack (Table 2). Modelling the more detailed categories was better supported than pooling 'impact' and 'fish damage' condition states.

For the IO-RTTP there were comparatively few reports of fish in poor condition on release, and it was more informative to pool

Table 3
Parameter estimates (in bold, and upper (U) and lower (L) 95% confidence limits) by tagging programme and species for the model variables tag placement quality, tagging station, and OTC use.

Programme and parameter	Value of variable	BET and YFT			SKJ		
PTTP		Ratio	L	U	Ratio	L	U
Quality	Badly placed	**0.73**	0.59	0.87	**0.58**	0.51	0.66
	Too slow	**0.44**	0.23	0.75	**0.37**	0.19	0.66
Station	Midships	**0.90**	0.70	1.10	**0.82**	0.72	0.92
	Starboard bow	**0.87**	0.83	0.92	**0.87**	0.84	0.90
	Stern	**0.94**	0.88	1.00	**0.94**	0.90	0.98

Programme and param	Value of variable	BET, YFT and SKJ			BET			YFT			SKJ		
IO_RTTP		Ratio	L	U	Ratio	L	U	Ratio	L	U	Ratio	L	U
Quality	Badly placed	**0.92**	0.85	0.98	**0.88**	0.54	1.25	**0.93**	0.81	1.06	**0.90**	0.83	0.98
Station	Front	**1.04**	1.01	1.07	**1.07**	0.99	1.16	**1.00**	0.95	1.05	**1.02**	0.98	1.06
	Mid	**1.01**	0.98	1.04	**1.10**	1.02	1.17	**0.98**	0.93	1.03	**1.00**	0.96	1.04
	Stern	**1.02**	0.97	1.06	**1.14**	1.05	1.23	**0.91**	0.82	1.00	**1.01**	0.93	1.10
OTC	With OTC	**0.69**	0.64	0.74	**0.54**	0.46	0.62	**0.81**	0.72	0.90	**0.70**	0.61	0.80

The ratio represents the relationship between tag return rates for fish released with the reported treatment, compared with those released in tag placement quality of 'good', at the port bow station, or without OTC.
Bold case as a way to identify the columns with estimates rather than confidence limits, and to visually separate the species.

into categories for impact and observed damage (ΔAIC of 10 vs. 9). Only damage during capture had a statistically significant effect on return rates. Of the individual damage effects only 'bleeding' was statistically significant.

3.9. OTC

In the IO-RTTP, fish with injected OTC and marked with white tags were returned at much lower rates than untreated fish (Table 3), and the OTC parameter was one of the best supported in the model (Table 2). In separate analyses by species, the effects of OTC were most severe for bigeye at 54% of base return rates, followed by skipjack (70%) and yellowfin (81%).

3.10. Species and length

Tag return rates varied by length at release for both IO-RTTP and PTTP (Table 2, Fig. 9). Within each program the patterns and

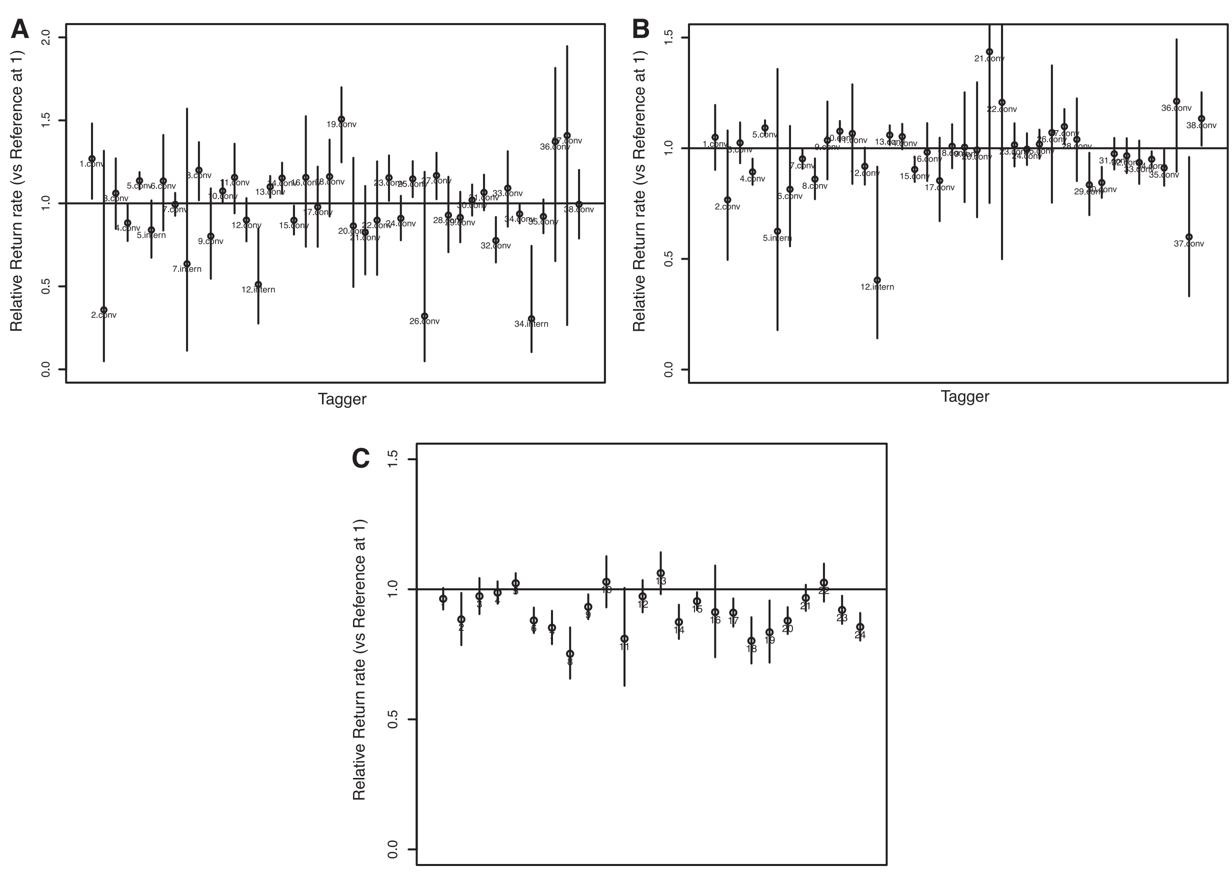

Fig. 5. The relative contribution of individual taggers to return rates of (a) bigeye and yellowfin and (b) skipjack released in the PTTP and (c) all species for the IO-RTTP. We use the tagger with the most conventional tag releases as the baseline for comparisons.

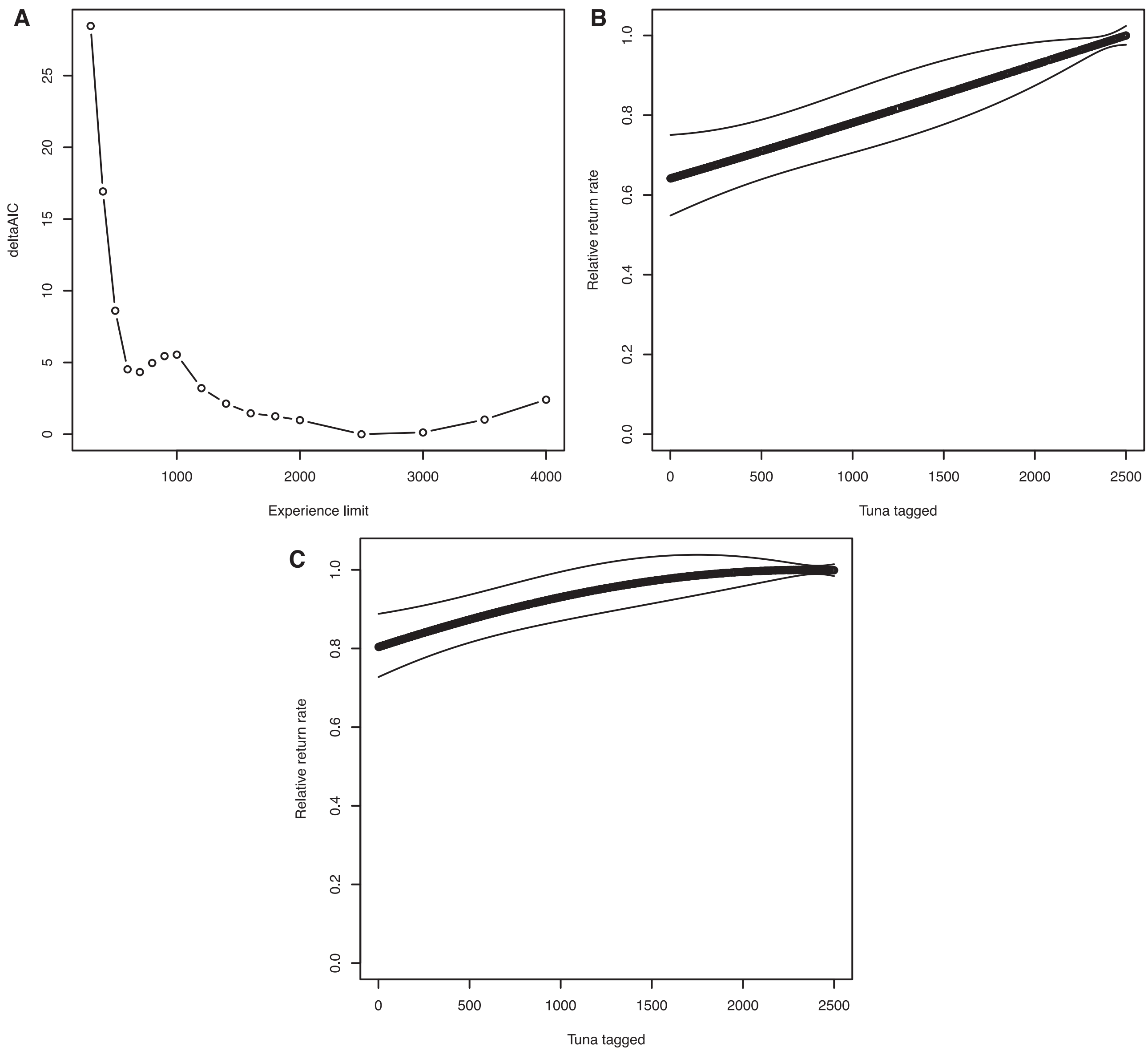

Fig. 6. (a) Comparison, using ΔAIC, of alternative assumptions about the number of fish after which further experience does not result in higher return rates in the PTTP. Estimated increase in relative return rate depending on the number of (b) bigeye and yellowfin or (c) skipjack previously tagged by an individual tagger in the PTTP. Relative return rate of 1 is applied to taggers once they have released more than 2500 fish.

maximum values varied by species, reflecting a combination of the selectivities and reporting rates of the fleets taking each species, and the post-release mortality and natural mortality at size of the fish. The reported return rates should not be compared among species and tagging programs, because each represents the return rate for a single tagging event.

Skipjack tag return rates were unimodal with respect to length at release (peaking at 50 cm for the PTTP and 45 cm for the IO-RTTP), which may reflect the size selectivity of purse seine fisheries (Hoyle et al., 2011). Bigeye return rates declined with length in the IO-RTTP, where purse seine fisheries had very high reporting rates, but in the PTTP showed an increase to about 45 cm and remained relatively high for larger lengths at release. In the IO-RTTP the yellowfin tag return rates had clearly separated peaks at release lengths of 45 cm and 85 cm, while there was a single broad peak for PTTP yellowfin at 45–70 cm, with a slight reduction for larger lengths at release. For all species the return rates of small fish were relatively lower in the PTTP than in the IO-RTTP, reflecting the shorter average time at liberty and less potential growth until recapture.

The contributions to tag recovery of the observed variation in each parameter varied strongly (Table 4), depending on the effect associated with each parameter level and its frequency of occurrence. For PTTP skipjack, the tagger, assistant, and station contributed similarly to tagging failure, but for YFT + BET the tagging assistant contributed substantially more than either tagger or station. For the IO-RTTP, differences among taggers contributed most to tagging failure. In both tagging programs, fish condition and tag placement quality made quite small contributions to overall tagging failure, because the vast majority of fish were released in the 'good' categories. Estimates of combined levels, which assume that all effects are independent of one another, were considerably higher for PTTP YFT + BET than for skipjack, based on higher rates of tagging failure associated with tagger, fish condition, expertise, and particularly tagging assistant.

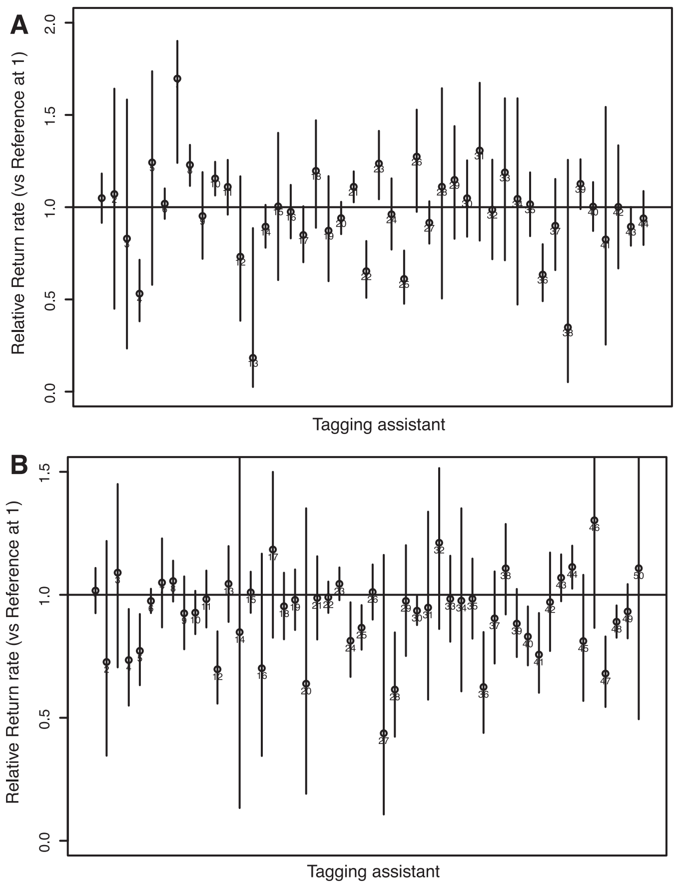

Fig. 7. The relative contribution of individual tagging assistants to return rates of fish released in the PTTP for (a) bigeye and yellowfin, and (b) skipjack. We use the assistant with the most conventional tag releases as the baseline for comparisons.

Table 4
For each tagging programme and model parameter, the ratio between the observed number of recaptures and the expected number of recaptures with the parameter at its best level.

Parameter	PTTP BET + YFT (%)	PTTP SKJ (%)	IO-RTTP, All (%)
Tagger	85.0	87.6	83.5
Tag type	99.7	100	100.4
Fish condition	98.5	99.0	100.0
Tag placement quality	99.7	99.5	99.8
OTC			98.5
Expertise	96.1	98.7	
Station	91.9	91.8	96.2
Tagging assistant	71.8	90.5	
All	55.1	71.6	79.5

4. Discussion

We provide evidence of significant tagging failure rates from two large-scale tuna tagging experiments in the Western Pacific and the Indian Ocean which have collectively tagged over 500,000 tuna. Analyses of tag returns demonstrated large differences in tagging failure rates among taggers, tagging assistants, and tagging stations, indicating overall levels of tagging failure that reduced the number of tagged fish in the population. Such tagging failure will affect the parameters estimated from tagging experiments unless taken into account. We suggest that more consistent treatment of fish and more diligent recording of fish treatment and condition will increase the reliability of tagging data used in assessments.

A significant cause of tagging failure may be predation associated with reduced ability to escape (Raby et al., 2013). Post-release predation has been observed in releases of tuna and other fish (Pepperell and Davis, 1999; Danylchuk et al., 2007), including during the PTTP (Leroy, personal communication). Recently-released fish may become easy targets for predators as they are significantly disoriented and physiologically impaired, and separated from their conspecifics. Blood associated with injuries may attract predators, which may also single out fish that behave differently (Danylchuk et al., 2007). Increased levels of chemical metabolites, as a result of physiological stress associated with capture and handling, may also increase the likelihood of predation (Danylchuk et al., 2007), especially by predators such as sharks that have strong chemoreception.

Factors that may have contributed to the variation among taggers and assistants include choices about which fish to tag and which to discard, inconsistencies in recording of covariates such as ‘too slow’ or ‘bleeding’, variation in speed of handling and tagging, and differences in treatment of the fish while handling or tagging. When recorded, damage to fish and delays in handling and tagging were associated with lower return rates. Different taggers and assistants inevitably make different choices about the levels of damage and signs of distress that should be recorded or that disqualify a fish from tagging, and these decisions are difficult to standardize. Increased post-release mortality and lower recapture rates have been associated with poor condition of fish upon release and increased handling time for several other fish species (e.g. Cooke and Philipp, 2004; Danylchuk et al., 2007; Sumpton et al., 2008).

As expected (Beverton et al., 1959), we observed that tuna released in less than optimal condition were returned at lower rates than fish released in good condition. Tail damage, bleeding, eye damage and impact against the vessel were each associated with 25–40% lower return rates, but mouth damage showed no effect. Tuna that had been bitten by cookiecutter sharks were also returned at the same rate as other fish. Fish that had been out of the water too long showed markedly lower return rates, though this was biased by the fact that fish were generally recorded as ‘too slow’ if they showed signs of asphyxiation (Leroy, personal communication). It may be useful in future to record time out of the water for a subset of fish, to permit estimation of the relationship between time out of water and return rate. The effect of time out of the water on survival is likely to vary with species, which have characteristic oxygen requirements (Brill et al., 2005), behaviour during tagging, and physiological responses to tagging (Barrett and Connor, 1962). This has parallels with the impact on stress and survival of angling duration (Skomal, 2007), which in pole and line fishing is minimal.

It is unclear how much difference in tagging failure rates is due to fish choice and how much to the technique of the tagger. Significant effects of individual taggers on recapture rates have been reported for sharks (Dicken et al., 2009) and coral reef fishes (Sumpton et al., 2010), but the effects of fish choice and tagger experience were not separated in these studies. Errors by inexperienced taggers include pushing the tag too far into the fish, placing the tag incorrectly, or taking longer to insert the tag. Variations in ability among individuals occur in virtually all activities and are to be expected, but they could be reduced by training and feedback. We observed that return rates for tuna increased with experience and levelled off after 2500 fish had been tagged.

The analysis method of standardizing by release event was powerful since the release event accounted for much of the variation in fish return rates, particularly for the PTTP. The release event accounts for variation in recapture rate, reporting rate, and tagging failure associated with oceanographic and weather conditions, location, and in particular local fishing effort. Some groups of fish were recaptured by purse seiners shortly after tagging occurred, particularly those released at anchored FADs. In the

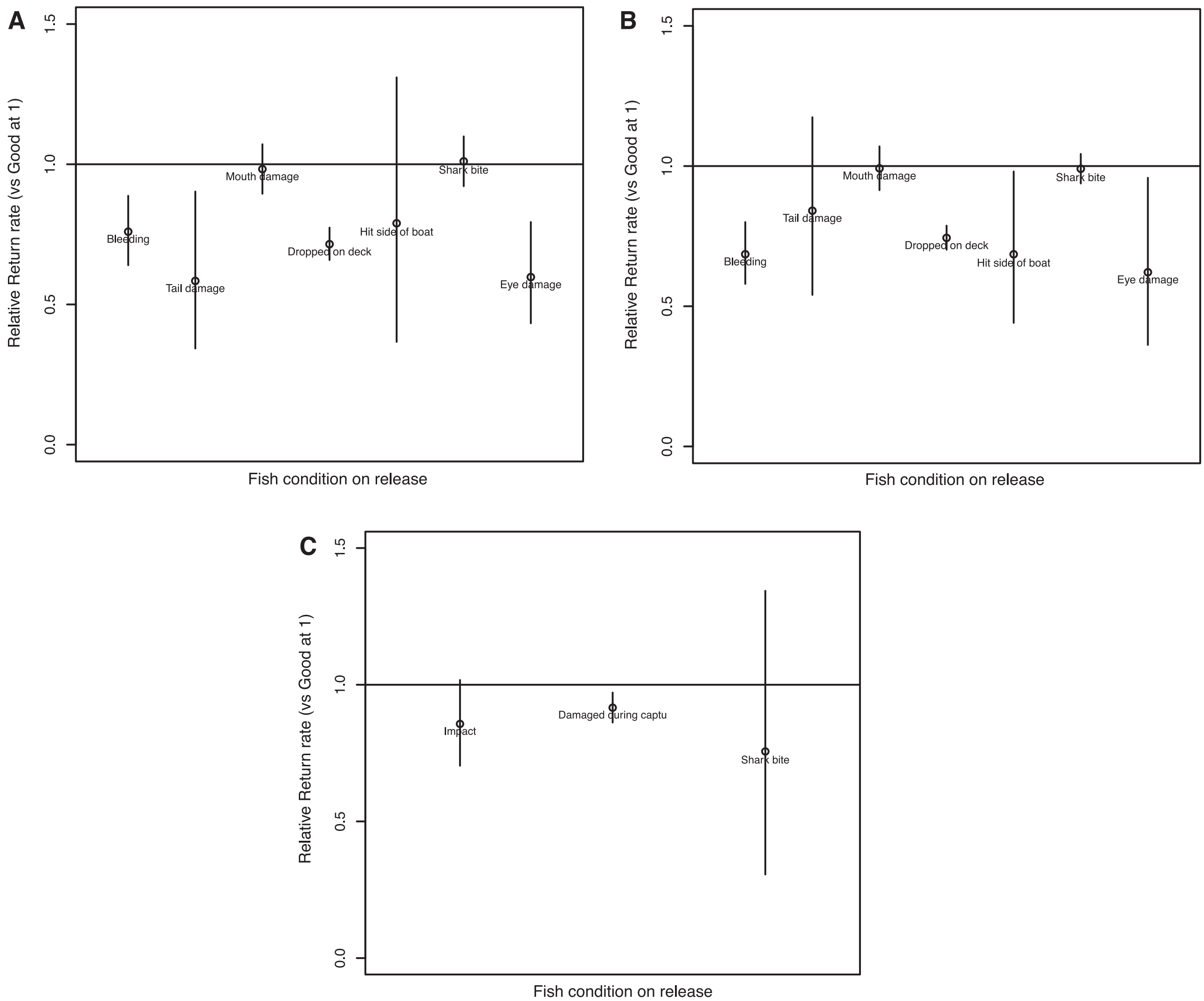

Fig. 8. The relative contribution of fish condition on release to return rates of (a) bigeye and yellowfin, and (b) skipjack released in the PTTP, and (c) all tuna species released in the IO-RTTP. Return rates are relative to fish release condition of 'good'.

IO-RTTP the tags were released far from the fishing grounds, with fewer short term recaptures and longer median time to recapture. This longer mixing period resulted in less variation in return rates among release events. Given the standardization by tagging event we were unable to estimate the effects on return rate of variables that were constant at the event level, such as ambient water temperature.

The tagger's experience had more impact on YFT + BET than on skipjack return rates. Similar differences between species were observed for tagger and assistant effects, which suggests that *Thunnus* may be more sensitive than skipjack to the effects of tagging, perhaps due to some feature of their physiology. This is surprising since skipjack are often highly active when landed, and might be expected to quickly deplete their oxygen reserves and accumulate lactic acid. However, skipjack movements involve mostly the tail, whereas bigeye and yellowfin tend to bend their whole body, and large yellowfin can be difficult and slow to handle. On the other hand, small yellowfin are relatively easy to handle and bigeye are the best 'behaved' of the three species on the tagging cradle. Taggers may have been less likely to reject bigeye and yellowfin because they were captured less often during the tagging programmes, and taggers may have been more disposed to maximising release numbers for these species. As a result, a greater proportion of bigeye and yellowfin may have been released in suboptimal condition. On the other hand, SKJ are relatively easy to tag in most cases so might arguably be preferred. Few studies have examined the effects of individual taggers on recapture rates across species. Sumpton et al. (2010) reported that the effect of tagger experience varied significantly between species of coral reef fish, though they did not offer an explanation for this observation.

Pooling of bigeye and yellowfin in the PTTP data was supported by the analysis, but we nevertheless caution that the majority of the tagged fish in the pooled analysis were yellowfin, and the results may be less reliable for bigeye. We recommend further work to analyse the two species separately as more data become available.

Additional variation occurred among the tagging assistants who supplied fish to the taggers. The individuals with the best return rates as assistants were also among the best performing taggers (assistant 8 and tagger 5 in the PTTP were the same individual), which suggests that fish selection may contribute significantly to reducing tagging failure. Nevertheless, given the observed level of variation with different fish handling and selection practices, there may be significant post-release mortality even among fish released by the best taggers.

Return rates of internal tags were on average between 30% and 50% of return rates for conventional tags. These lower return rates were apparent in both the IO-RTTP and PTTP tagging programs, for each species, and for individual taggers who employed both tag

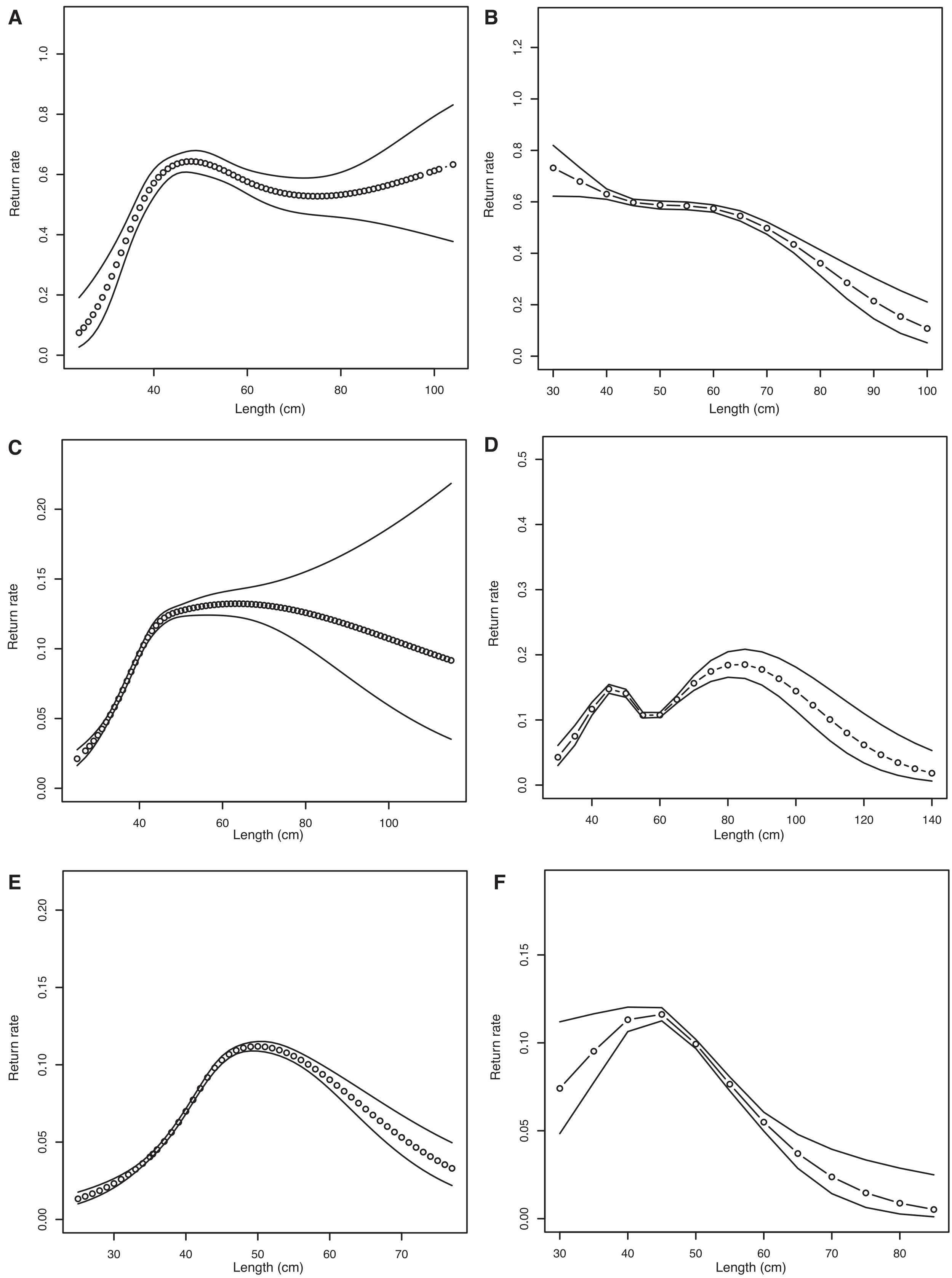

Fig. 9. The relative contribution of length to return rates by species of fish released in the PTTP ((a) bigeye, (c) yellowfin, (e) skipjack) and IO-RTTP ((b) bigeye, (d) yellowfin, (f) skipjack).

types. Internal tag return rates also varied substantially among taggers. Previous studies that have compared return rates for internal and conventional tags have had varying results (e.g. Clear et al., 1999; Schaefer et al., 2007; Schaefer and Fuller, 2009). However, these studies had relatively low sample sizes and made comparisons based on overall returns, without allowing for the substantial variation associated with covariates such as the tagging event and the size of the fish. Rewards were higher for electronic tags than for conventional tags (250 USD vs. 10 USD in the PTTP; by between 6 and 25 times in the IO-RTTP, depending on the country) which may have resulted in higher reporting rates (Pollock et al., 2001). On the other hand, the less familiar colour of dart tags associated with the rarer electronic tags may have reduced their reporting rate. Nevertheless similar recovery rate differentials between the tag types were seen in the PTTP and the IO-RTTP, at both moderate (PTTP) and very high (IO-RTTP) reporting rates (Hoyle, 2011; Hillary et al., 2014), suggesting that reporting rate was not a major factor.

Lower return rates for internal tags are expected since the surgery causes physical damage and carries a risk of infection. A number of recent studies have examined surgical technique and its effect on fish survival, but mostly for salmon and with relatively little research on the impact of surgical skill (Cooke et al., 2011; Wagner et al., 2011). A study in Chinook salmon found that fish surgeons differ in their tag suture retention, wound inflammation and ulceration, and incision openness (Deters et al., 2010), with better performance for taggers who had received feedback on their previous surgical technique. Given the high cost of internal tags, this result reinforces the need to invest in training, to prioritise releases by taggers who have demonstrated high return rates, and those with more experience and recent practise (Cooke et al., 2010). It may also be valuable to use dummy tags both for training and practice, and to investigate more thoroughly which approaches to internal tagging improve return rates.

For conventional tags also, most of the variation among taggers appeared to be due to mortality. Tag shedding rates do not appear to vary much among taggers (Gaertner and Hallier, 2013), and the expected rates for skipjack at mean recapture time in the IO-RTTP and PTTP are estimated to be 2.4% and 1.1%, respectively; rates far smaller than the differences observed here among taggers. A previous estimate of type 1 tag shedding for tunas was higher at 5.9% (Hampton, 1997), but again with no evidence of variation among taggers. The more recent estimate was based on more double tag recaptures (4500 vs. 525), and higher reporting rates (97% vs. 64%).

Station effects were significant, especially in the PTTP, where the port bow station had the highest return rates. Chumming occurs near the port bow station and densities of tuna are therefore higher, which may reduce the predation risk for fish released there. Due to the higher catch rates, the best and most experienced catchers, assistants, and taggers were assigned to the port bow, and catcher effects may be important. On the other hand, the greater fish supply sometimes led to more delay in tagging fish at the port bow station, which implies more need for taggers and assistants to reject fish unlikely to survive.

IO-RTTP tuna that were tagged with the antibiotic oxytetracycline (OTC) were returned at much lower rates than fish without OTC (0.68 of the non-OTC return rate, 95% CI 0.64–0.73). Although these fish were marked with white tags rather than the standard yellow, bias due to lower reporting of white tags (q.v. Schaefer et al., 1961) seems unlikely. A reporting rate for seeded yellow tags of 97% (Hillary et al., 2014) suggests that the catch was well examined, and it is unlikely that 32% of the white tags could have been missed. OTC may affect condition or behaviour e.g. (Monaghan, 1993) and thereby increase mortality in the wild. For example, injection at any dosage causes mortality in sablefish in the wild, though not in the laboratory (McFarlane and Beamish, 1987). Previous experiments with wild-tagged skipjack and yellowfin tuna at OTC dosages of 27 mg kg^{-1} have had variable return rates but no consistent evidence of mortality (Wild et al., 1995). In the Indian Ocean experiments, the dosages were not recorded, and some may have exceeded this level. The differences observed suggest that appropriate dosages for tunas should be estimated separately by species, and care taken in administering accurate doses in the field.

The three species have different size-related patterns of tag return. These patterns are similar to the selectivity patterns for the major purse seine fisheries, as estimated in the stock assessments for each species (Langley et al., 2011; Davies et al., 2011; Hoyle et al., 2011), although we cannot distinguish such effects from size-dependent tagging failure. Relative return rates for small tuna were higher in the IO-RTTP than the PTTP, presumably because the longer times at liberty in the IO-RTTP permitted these fish to grow into the selected length classes. Larger fish can also be slower to tag than small fish, and their greater mass may make them more vulnerable to damage during tagging.

Tagging failure introduces bias into stock assessments' estimates of fishing mortality. When there are fewer tagged fish in the population than assumed, fishing mortality estimates are biased downwards. The chief concern is whether post-release mortality is large enough to affect analyses. Ideally, estimated rates of tagging failure will be included in assessments by replacing observed releases with effective releases at the release event level, but this is only possible with assessment software that permits fractional releases. An alternative approach is to estimate an average rate of tagging failure across the entire tagging experiment, and apply this to the prior distribution of reporting rates. This approach has been applied to stock assessments in the Western and Central Pacific Ocean for bigeye, yellowfin, and skipjack (Langley et al., 2011; Davies et al., 2011; Hoyle et al., 2011).

The estimates of combined tagging failure presented here are very high at 45% for PTTP yellowfin and bigeye, 28% for PTTP skipjack, and 20% for IO-RTTP all species. The higher estimate in the PTTP analyses may largely reflect the availability of the tagging assistant parameter, rather than a higher failure rate. However, the combined estimates may be biased high if all the effects are not independent. An unknown proportion of the estimated effects may be due to fish selection, and in particular selection by taggers and assistants is not independent because a fish may be rejected by the tagger or the assistant, but not by both. In addition, if the process at the port bow station supplies fish in better condition, then fewer fish will need to be rejected and tagger effects will be less important.

Although we have no estimate of the base tagging failure rate, the results of this experiment allow us to make inferences about its distribution. The large variation among taggers and assistants and with suboptimal treatment indicates that rougher treatment and longer periods out of the water significantly increase fish mortality. Tagging has been found to reduce the condition of southern bluefin tuna (Hampton, 1986). Tagged tuna may be disoriented after release and subject to higher rates of predation (Schaefer et al., 1961). The currently assumed base level of post-release mortality in Western and Central Pacific tuna stock assessments is a normal distribution on the logit scale, with median of 7% and 95% CI from 3% to 16% (Langley et al., 2011; Hoyle, 2011; Davies et al., 2011; Hoyle et al., 2011). Direct estimates of base post-release mortality can be obtained by placing tagged fish in holding nets, by tagging released fish with pop-up or mortality-sensing tags, or by correlating survival of pop-up-tagged fish with post-tagging blood chemistry and then surveying the blood chemistry of large numbers of tagged fish. However, these approaches all have drawbacks since they omit potentially important mortality causes such as predation or change the nature of the tagging process, and most are impractical for tunas. It may be useful to test for a relationship between recovery rates and time out of the water, based on analysis of video and voice recordings, although this would still not provide an absolute estimate of tagging related mortality.

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