The use of double marks to examine potential sources of capture heterogeneity in photographic identification features of humpback whales off west South Africa

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ABSTRACT

The ventral surface of the tail flukes (TF), especially its pigmentation and physical characteristics, is the most commonly used photographic identification feature for the individual identification of humpback whales. Such images from regional catalogues are used, *inter alia*, to estimate population size using capture-recapture models. The lateral view of the dorsal fin, although less distinctive than TF, may also be used to identify individuals whales, and microsatellites offer another alternative means of identification via skin biopsies. Use of these features for abundance estimation usually assumes a zero error rate in identification and equal capture probabilities of marked and unmarked individuals. In this paper we use resighted individuals that have been identified by more than one feature ('double-marked') to test for relative error rates and differences in capture probabilities. Tests for ID errors (using microsatellites as a control) indicate errors (missed matches) of 13.8% for left dorsal fins, 9.1% for right dorsal fins and 0% for tail flukes. The use of double-marked animals in a Chapman's modified Petersen population model, with the two ID features as independent recapture samples, suggests that estimates of abundance using TF may be substantially (34-50%) lower than those produced using other ID features after error-correction. Such apparent heterogeneity in TF capture probability may be site or operation-specific, but should be tested for in other situations.

KEYWORDS: CAPTURE-RECAPTURE; HUMPBACK WHALE; PHOTO-ID

INTRODUCTION

Humpback whales *Megaptera novaeangliae* are individually recognisable from the trailing edge, natural marks and the pigmentation of the ventral surface of their tail flukes (Katona and Whitehead 1981; Mizroch *et al.* 1990), the lateral view of their dorsal fins and knuckles on the caudal peduncle (Kaufman *et al.* 1987), and microsatellites from DNA samples (Palsbøll *et al.* 1997). Although dorsal fins are commonly used by researchers in the field to distinguish between different whales in a group while collecting data during boat intercepts, and have been proposed as a potentially more stable identification feature than ventral tail flukes (Blackmer *et al.* 2000), the more distinctive flukes are favoured for use in regional photo-ID catalogues. Such catalogues have been widely employed to identify migratory links (e.g. Stevick *et al.* 2004), examine regional movement patterns and population structure (e.g. Calambokidis *et al.* 2001), and calculate population sizes (e.g. Straley *et al.* 2008).

Apart from inter-regional differences in ventral fluke pigmentation (Rosenbaum *et al.* 1995), individual variation in the behaviour of exposing the ventral surface of the flukes ('fluking-up') on diving occurs that may relate to the prevalent behaviour at the given geographic location, i.e. breeding or feeding, the age or sex of an individual (Rice *et al.* 1987), or the size and composition of groups (Smith *et al.* 1999). Fluking rates may vary by more than an order of magnitude depending on these factors (Smith *et al.* 1999). Such individual variation in behaviour may introduce capture heterogeneity that would impact on population estimates calculated from capture-recapture models using this identification feature (Barlow *et al.* 2011). There are other known sources of capture heterogeneity when using tail flukes, such as photographic quality, or errors in correctly identifying individuals (Stevick *et al.* 2001), but in general these can be adequately corrected for by introducing some form of photographic quality control (Friday *et al.* 2008). It is however more difficult to quantify (and thus correct for) heterogeneity attributable to individual behaviour (Barlow *et al.* 2011).

Unlike tail flukes, dorsal fins are always exposed during surfacings; however, the extent to which photographic quality or distinctiveness affects the ability to match dorsal fins of humpback whales is unknown. A recent examination of individually identified humpback whales that feed around Saldanha Bay on the west coast of South Africa (Barendse *et al.* 2010a), showed that capture-recapture data from different identification features resulted in abundance estimates that varied considerably, and that estimates based on tail flukes (TF) were consistently lower than those derived from left and right dorsal fins (LDF, RDF) and microsatellites (MS) (Barendse *et al.* 2010b). These results suggested that fewer animals in the area tended to exhibit fluking-up behaviour, or that there was an

apparent difficulty in obtaining fluke pictures during boat intercepts, thus reducing the overall number of whales identified by this feature. While more individuals were identified by means of dorsal fins, it was apparent that these were more difficult to match, resulting in a number of instances where the same individuals were matched by other means (i.e. TF or MS) but not by dorsal fins, resulting in false-negatives that could inflate the abundance estimates. Estimates from MS recaptures were higher than those from TF, but lower that those derived from dorsal fins (Barendse *et al.* 2010b), bearing in mind that the use of genotypes is not completely free from error (e.g. Mills *et al.* 2000; Lukacs and Burnham 2005; Wright *et al.* 2009).

In this paper we examine potential sources of capture heterogeneity that may result from the use of different photographic identification features of humpback whales. The approach includes the use of various combinations of double marks available in the capture-recapture dataset described in Barendse *et al.* (2010b). Specifically, we try to assess the occurrence and effect of false negatives when using dorsal fins, and the possible capture heterogeneity introduced by the use of tail flukes for individual identification.

MATERIAL AND METHODS

Details of the study site, data collection, matching procedures and compilation of the sighting database are described in Barendse *et al.* (2010a, b). The capture-recapture data are comprised of a separate data set for each identification feature (TF, LDF, RDF, MS) collected during six 'capture occasions' or periods (j) of six months each from the years 2001 - 2007, starting on 1 September of one year and ending on 28 February the following year (i.e. the spring/summer season). These periods were selected on the basis of data availability and comparable collection effort and seasonal coverage (see Barendse *et al.* 2010b). All images used were graded for photographic quality and orientation on a 1 – 5 scale (1 = not useable, 2 = poor, 3 = fair, 4 = good, and 5 = excellent); only images with a quality and/or orientation rating of 3 or more (better than poor) were used for abundance estimation. Furthermore, no partial pictures of TF (i.e. showing one fluke or the trailing edge only) were used. Double-marked animals were included in the first sample when both mark types (of sufficient quality) were recorded and attributed to the same individual during the same intercept (sighting). For other tests, pictures of lesser quality may have been included (as stated) to increase sample sizes.

Wherever abundance estimates were used to test aspects of capture heterogeneity, the Chapman's modified Petersen (CMP) estimator (Seber 1982) was employed, due to its relative simplicity and the availability of five pairs of consecutive sampling periods. The CMP estimator has been used by others to calculate the size of feeding aggregations of humpback whales elsewhere (e.g. Larsen and Hammond 2004; Straley *et al.* 2008) and is considered an acceptable approach for a long-lived mammal with relatively low rates of natural mortality and recruitment, despite such populations not meeting the requirements of closed population models. The CMP estimator was calculated with the formula below (Seber 1982), using the following notation: N^* = CMP estimator; n_i = total number of individuals identified in first sampling period j_i; n_{i+1} = total number of individuals identified in following sampling period; m_{i+1} = number of individuals identified (i.e. matched) in both sampling periods (j_i and j_{i+1}).

$$N^* = \frac{(n_i + 1)(n_{i+1} + 1)}{(m_{i+1} + 1)} - 1$$

The variance and the coefficient of variation (CV) of N^* were calculated with the formulas provided in Seber (1982). Confidence intervals (95%) for the CMP estimator were calculated with the log-normal transformed method as proposed by Burnham *et al.* (1987).

Tests for false negative rates

Microsatellites were used as an independent (non-photographic) identification feature (the control) and all individuals (n = 32) that were identified by this feature and resighted on different days, were used as the sample. For each capture occasion (day) it was assessed whether a specific photographic feature of useable quality (>poor) was recorded; then, whether or not a specific feature confirmed the matches made by microsatellite. The sample size per ID feature was the number of times both a microsatellite match and a photograph of the feature in question were available ('matching opportunities'). Failure to detect a photographic match constituted a false negative. As a simple test to quantify the positive bias caused by the calculated false negative rate/s, the pair-wise CMP estimator was calculated for the LDF dataset but the numbers of individuals identified during the first and second sampling periods (n_i and n_{i+1}) were reduced by a factor based on detected error rates; this should compensate for the higher than actual numbers of whales identified due to missed matches within each sampling period. The number of individuals matched between these samples (m_{i+1}) was increased by the error factors to correct for missed matches

between n_i and n_{i+1}. The magnitude (%) of the resultant overestimation was calculated relative to uncorrected LDF estimates.

Variation in recording of tail flukes for resighted whales relative to other features
All whales resighted on different days were used as the sample, and the ID features collected during intercepts on these different days were compared. First, the number of times TF were recorded (of any photographic quality) during all intercepts of resighted whales was compared to other ID features. Second, the occasion on which TF were recorded in the case of multiple resightings was examined. Third, the duration of intercepts where TF were recorded was compared to those where no TF were recorded. Finally, the probability of recording TF or dorsal fins (left or right) for an individual whale was calculated by counting the number of intercepts during which the feature was recorded and expressing it as a fraction of the total number of times that the resighted whale was intercepted.

Use of double marks
Here we used TF as one type of mark, and LDF, RDF and MS respectively as alternative marks. For pairs of adjacent sampling periods, the n_i consisted of animals that were identified by both TF and the other mark in question, i.e. double marked animals. The n_{i+1} consisted of the total number of whales identified by either TF, or the alternative mark in the following sampling period, with recaptures (m_{i+1}) being those double marked animals that were identified by whatever feature was used for n_{i+1}. This approach is intended to compare the relative capture probabilities of the two marks used: if they are equal, then recapture rates (= population sizes) should be similar whichever feature is used for the second sample. During the calculation using the CMP estimator, a correction factor was applied to dorsal fins and microsatellites similar to that described above (i.e. n_{i+1} was adjusted downward, and m_{i+1} adjusted upward), but n_i was left unadjusted because the animals were already identified without error from the TF. The correction factors used for dorsal fins were those calculated from LDF and RDF false negative tests (see below), while the correction factor for microsatellites was the mean allelic error rate of 0.065 calculated for Breeding Stock B2 (Inês Carvalho pers. comm.).

RESULTS

False negatives
Assuming that the microsatellite identifications were correct, photographs of LDF and RDF when used alone as an identification feature resulted in 13.8% and 9.1% missed matches respectively, whereas no missed matches were detected for tail flukes (Table 1). To test for misidentifications using microsatellites, individuals resighted by tail flukes on different days using pictures of quality and/or orientation > 'poor' were used as a control (11 individuals, intercepted 24 times), and were compared to matches obtained by microsatellite (where biopsies were taken). No false negatives or positives were detected in seven matching opportunities. The values for N^* using the LDF dataset and bracketing the error rate between 0.09 and 0.14 as lower and upper values respectively, showed the average overestimation of abundance to range between 20% (at error rate 0.09) and 30% (at 0.14) (Table 2).

Individual variation in fluke exposure relative to other features
For 21.67% of the whales resighted on different days (n = 60), no pictures of TF were collected, for 20% no biopsies, 3.33% no RDF, and 1.67% no LDF (Figure 1). In the majority of cases, TF photographs (for the 47 whales) were obtained during the first intercept (65.96%), 27.66% during the second intercept, and 6.38% during the third and fourth. Furthermore, during all intercepts involving these resighted whales (n = 183 - some whales were in the same groups), TF pictures were collected during only 57.4% of intercepts, compared to 92.9% for dorsal fins. Duration of intercepts, where recorded (n = 178), ranged from 6 – 213 min with an overall mean of 63 minutes. There was no significant difference between the mean duration of intercepts where TF were photographed (73.84 min ± 3.88 SE, n=146) or not (83 min ± 11.14 SE, n = 31) (t = -0.93, df = 175, p = 0.35). The probability of recording a dorsal fin image (right or left) of an individual whale during all of its intercepts was high (Figure 2). This was not the case for TF, where for individual whales the probability of recording this feature during all, half, or none of their intercepts was very similar (28, 25 and 23 % respectively) (Figure 2).

Double mark models
With few exceptions, models in which the feature used for capturing the second sample was TF resulted in lower abundance estimates than when the alternative features were used (Table 3 and Figure 3). The highest estimates were calculated with RDF as alternative mark, while LDF and MS yielded very similar pair-wise estimates. Taking an average over all five sets of population estimates, those in which TF were used for n_{i+1} were 0.497, 0.658 and 0.517 of those using RDF, LDF and MS respectively for n_{i+1}. Apart from the detection of sources in heterogeneity attributable to the use of specific marks, the pair-wise abundance estimates also showed consistent variation that

appear to indicate different capture probabilities between the first two (*j*1-2) and last four (*j*3-6) capture periods, most likely as a result of known differences in sampling strategies between these (discussed in Barendse *et al.* 2010b). Except for RDF, the estimates by means of other ID features during the last *j*4-5 and *j*5-6 showed much less variation, although these were periods when very few humpback whales were identified. We do not believe that this variation should alter the conclusions about mark-specific heterogeneity (see below).

DISCUSSION

Assuming the microsatellite identifications were correct, dorsal fin photographs when used alone as an identification feature resulted in 9-14% missed matches, whereas none was detected for tail flukes. A reverse test for microsatellites (assuming a zero error rate for tail flukes) produced no missed matches, although the sample size was very small. Therefore, the use of dorsal fin photographs alone in mark recapture models can result in a small percentage of missed matches (false negatives), whereas this does not appear to be the case to the same extent for tail flukes or microsatellites. If left uncorrected, this may result in a substantial over-estimation (up to 30%) of abundance. This conclusion however may be case-specific, depending to a large extent on data collection, photographic quality and laboratory procedures. The differences between abundance estimates for RDF and LDF (although less pronounced compared to TF) during the same pairs of sampling periods (LDF estimates were always lower) suggests that there may have been a difference in the ability of photographers to obtain useable images of these two features. The reason for this is not immediately apparent, although it may relate, for example, to the orientation of whales relative to the shore, as more southbound whales were seen during late spring and early summer in 2001-2003, i.e. with their left sides turned towards the shore by (Barendse *et al.* 2010). Whether this or some other operational aspect of data collection influenced the approach by the boat, thus causing one side to be favoured over another, is unknown. Individual behaviour may also contribute to such a bias. Clapham *et al.* (1995) reported strongly lateralised behaviour by humpback whales that apparently favoured their right-side during feeding and flippering behaviour; it is possible that whales could preferentially present their right side to the boat. However, we are unable to test this with the available data.

That fluking as an individual behavioural trait could affect the probability of an individual being sampled is strongly suggested by the finding that for resighted whales, the probability of collecting TF pictures during all, half, or none of the intercepts was nearly equal. Although dorsal fin photographs (of sufficient quality) were not collected during all intercepts, there were no resighted individuals for which dorsal fin pictures were unavailable. There may be differences in the ability of researchers to obtain good quality images of these different features: during a typical approach from the rear, chances are good of obtaining a TF picture (provided that they are adequately exposed). For dorsal fins, a considerable amount of manoeuvring of the boat is required to position the photographer at a right angle to the whale, while still at the surface. The angle between the camera and the whale affects the quality of dorsal fin pictures to a greater extent than for TF (J. Barendse pers. obs.) and poor photo quality can be the source of substantial heterogeneity in capture probability when using dorsal fins in other species e.g. northern bottlenose whale *Hyperoodon ampullatus* (Gowans and Whitehead 2006). However, the fact that for all resighted whales, over 20% had no TF image collected at all during intercepts of similar mean duration, and that in the majority of cases (65%) flukes were photographed during the first intercept, suggests that fluking is an idiosyncratic feature for humpback whales in this area.

If some whales consistently fluke less often than others, or do not fluke at all, the resulting heterogeneity of capture probabilities will lead to under-estimation of population size, such as is strongly suggested by these data. In West Greenland such a bias was estimated as up to 10% of population size (Perkins *et al.* 1985), but presumably can vary with area, season, or photographic protocol. Based on the mean CMP abundance estimates for the double marked whales, those using TF recaptures and identifications during the second sampling period were 34 - 50 % lower than those when using an alternative feature. While this conclusion about the effects of individual fluking behaviour on population estimation is strictly only valid for the whales observed off Saldanha Bay, as humpback whale behaviour may differ (and sampling protocol vary) in different parts of its range, the effects shown here are certainly large enough to warrant similar investigations in other areas.

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TABLES

Table 1. False negative rates (no. missed matches as % of total no. of matching opportunities) detected for humpback whale photographic ID features, West South Africa, using microsatellite matches as a control. Pictures of quality and orientation > "poor" were used (as for abundance estimates).

ID feature	Sample occasions	Matching opportunities	Confirmed matches	Missed matches	False negative rate (%)
MS (control)	88	32	-	-	-
LDF	58	29	25	4	13.8
RDF	49	22	20	2	9.09
TF	30	13	13	0	0

Table 2. Calculation of positive bias attributable to occurrence of false negatives in West South Africa humpback whales, when using dorsal fins as photographic ID feature, using Chapman's modified Petersen estimator (N^*) and LDF capture-recapture data. Error rates derived from detected false negatives in Table 1 and % bias calculated relative to the uncorrected estimator.

Uncorrected									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	-
1-2	39	49	8	221	56.02	0.25	136	361	-
2-3	49	11	1	299	154.92	0.52	115	778	-
3-4	11	16	0	203	133.99	0.66	62	660	-
4-5	16	13	1	118	59.75	0.51	46	301	-
5-6	13	28	3	101	35.62	0.35	51	197	-
Error correction factor = 0.09									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	% bias
1-2	35.49	44.59	8.72	170	39.71	0.23	108	267	23
2-3	44.59	10.01	1.09	239	120.12	0.50	94	606	20
3-4	10.01	14.56	0	170	111.73	0.66	53	550	16
4-5	14.56	11.83	1.09	95	46.26	0.49	38	234	20
5-6	11.83	25.48	3.27	79	25.93	0.33	42	148	22
Error correction factor = 0.14									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	% bias
1-2	33.54	42.14	9.12	146	32.48	0.22	95	225	34
2-3	42.14	9.46	1.14	210	103.46	0.49	84	524	30
3-4	9.46	13.76	0	153	100.24	0.65	48	494	24
4-5	13.76	11.18	1.14	83	39.80	0.48	34	202	30
5-6	11.18	24.08	3.42	68	21.51	0.32	37	125	32

Table 3. Abundance estimates from the Chapman's modified Petersen estimator (N^*) for various model configurations using double marked (TF plus alternative mark) humpback whales identified during first sampling period, and recaptures based on TF or alternative mark during second sampling period. SE = standard error, CV = coefficient of variation, LCI and UCI = lower and upper 95% confidence intervals. Also shown is the mean (and SE of mean) of all pair-wise estimates for each model. An error correction of 0.065 for MS, 0.09 for RDF, and 0.14 for LDF was applied for n_{i+1} and m_{i+1}.

j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
{n_i=TF&RDF,n_{i+1}=RDF, m_{i+1}=RDF}									
1-2	10	52.72	3.27	137	45.19	0.33	73	257	
2-3	15	12.73	0	219	144.78	0.66	67	713	
3-4	9	18.18	0	191	125.26	0.66	59	617	
4-5	7	22.73	0	189	122.87	0.65	59	605	
5-6	9	24.54	1.09	121	59.21	0.49	49	300	171 ± 18
{n_i=TF&RDF, n_{i+1}=TF, m_{i+1}=TF}									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
1-2	10	16	3	46	14.58	0.32	25	84	
2-3	15	10	0	175	114.89	0.66	54	566	
3-4	9	7	1	39	17.89	0.46	17	92	
4-5	7	9	0	79	50.20	0.64	25	247	
5-6	9	16	1	84	41.23	0.49	34	209	85 ± 24
{n_i=TF&LDF, n_{i+1}=LDF, m_{i+1}=LDF}									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
1-2	11	42.24	3.41	117	38.06	0.33	62	218	
2-3	13	9.48	0	146	95.10	0.65	45	468	
3-4	8	13.79	0	132	85.70	0.65	41	422	
4-5	6	11.21	0	84	53.59	0.63	27	264	
5-6	8	24.14	1.14	105	49.89	0.48	43	254	117 ± 11
{n_i=TF&LDF, n_{i+1}=TF, m_{i+1}=TF}									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
1-2	11	16	3	50	16.28	0.33	27	93	
2-3	13	10	0	153	100.05	0.65	48	493	
3-4	8	7	1	35	15.87	0.45	15	82	
4-5	6	9		69	43.47	0.63	22	214	
5-6	8	16	1	76	36.59	0.48	31	186	77 ± 20
{n_i=TF&MS, n_{i+1}=MS, m_{i+1}=MS}									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
1-2	9	38.34	2.13	125	49.17	0.39	59	263	
2-3	8	17.77	0	168	109.55	0.65	52	539	
3-4	10	26.18	1.07	144	71.65	0.50	57	362	
4-5	6	20.57	1.07	72	33.35	0.46	30	171	
5-6	7	20.57	1.07	83	39.09	0.47	34	199	118 ± 18
{n_i=TF&MS, n_{i+1}=TF, m_{i+1}=TF}									
j_i - j_{i+1}	n_i	n_{i+1}	m_{i+1}	N^*	SE(N^*)	CV(N^*)	LCI	UCI	Mean N^*± SE
1-2	9	14.96	2.13	50	18.65	0.37	25	101	
2-3	8	9.35	0	92	59.02	0.64	29	291	
3-4	10	6.55	1.07	39	17.63	0.45	17	91	
4-5	6	8.42	0	65	40.79	0.63	21	201	
5-6	7	14.96	1.07	61	28.38	0.47	25	145	61 ± 9

FIGURES

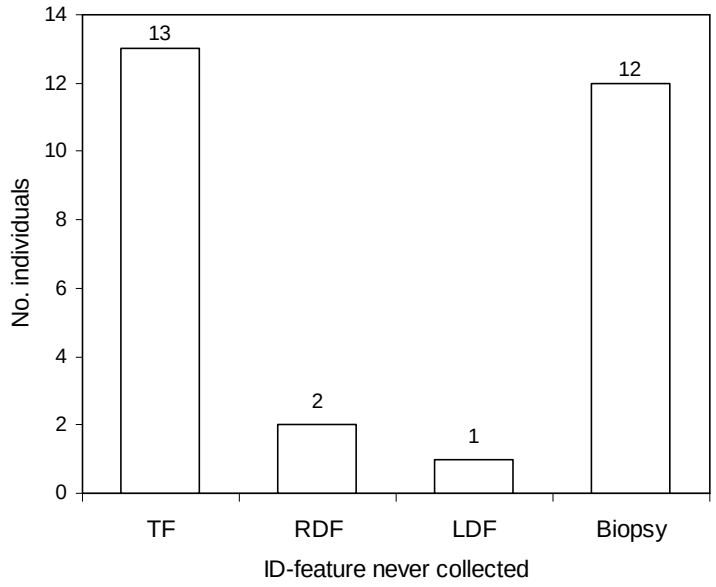

Figure 1. Numbers of resighted individual humpback whales (n = 60) for which specific identification features were not collected.

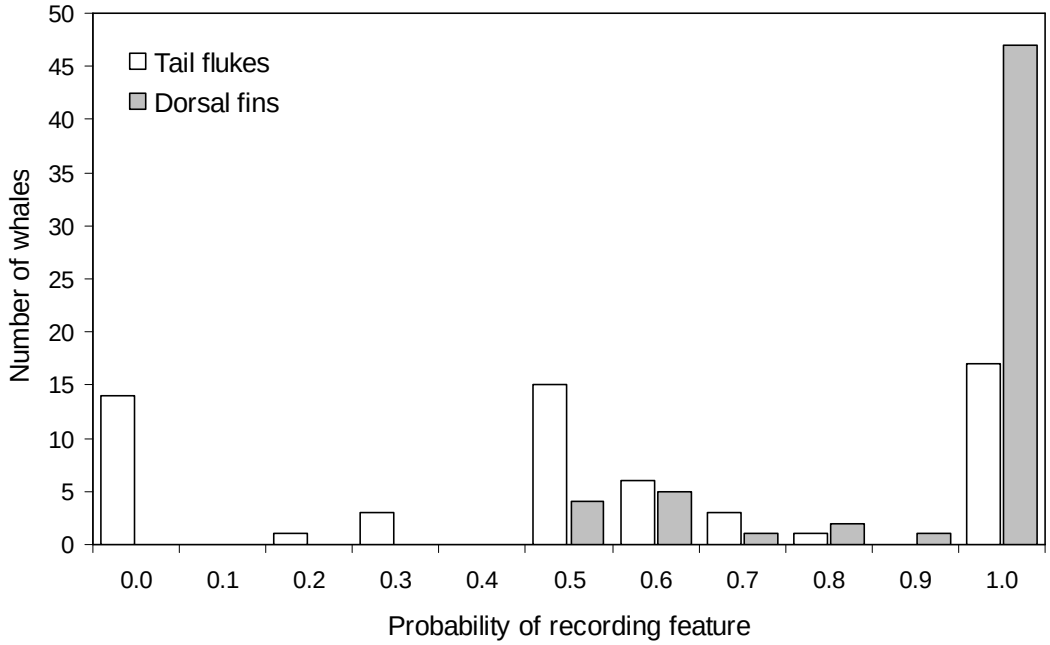

Figure 2. Probability for recording a photographic identification feature for individual (resighted) humpback whales, calculated as the number of times a feature (tail fluke or dorsal fin) was recorded as proportion of the total number of times that the whale was intercepted.

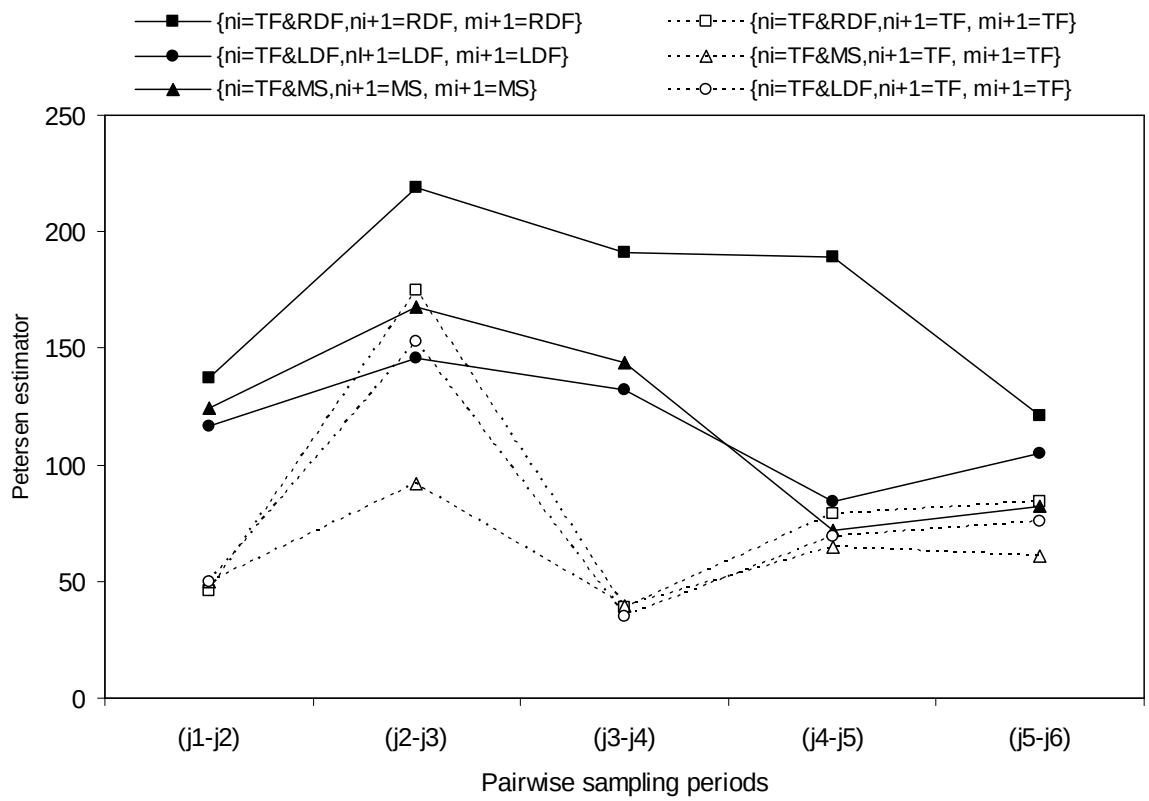

Figure 3. Chapman's modified Petersen abundance estimates between pairs of adjacent sampling periods based on double marks (TF plus alternative mark) during n_i and single mark (TF or alternative mark) for n_{i+1} and m_{i+1}. Dotted lines indicate models using TF as mark, and solid lines alternative mark used during j_{i+1}. Squares indicate RDF, circles LDF, and triangles MS used as the alternate (double) marks. Where applicable an error correction of 0.065 for MS, 0.09 for RDF, and 0.14 for LDF was introduced for n_{i+1} and m_{i+1}. Also see Table 3.