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PHOTOGRAPHIC IDENTIFICATION OF NORTHERN BOTTLENOSE WHALES (*HYPEROODON AMPULLATUS*): SOURCES OF HETEROGENEITY FROM NATURAL MARKS

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ABSTRACT

The use of natural marks in capture-recapture studies can lead to unequal capture probabilities. This paper examined a catalog of northern bottlenose whale (*Hyperoodon ampullatus*) photographs from the Gully, Nova Scotia, to identify potential sources of heterogeneity. This information can be used to select appropriate individuals and photographs to include in analyses. Individual northern bottlenose whales were sufficiently marked to uniquely identify individuals ($\bar{x}$ = 14.5 marks/individual; range 1–67), but not all mark types persisted over time. Reliable marks were defined as mark types that were not lost over the nine-year study period (notches, back indentation, and mottled patches). Individuals were considered reliably marked if they possessed at least one back indentation or mottled patch (located within one dorsal fin width, at the base of the dorsal fin) or a notch on the dorsal fin. Sixty-six percent (SE = 5%) of the population were reliably marked. Long-term analyses (months to years) should use only reliably marked individuals, and the results scaled to account for the rest of the population. Our results also showed that photographic quality affected an observer's ability to identify individuals. For this catalog, quantitative analysis indicated only photographs of $Q \geq 4$ (on a 6-point scale with 6 representing the highest quality) should be included in mark-recapture analyses sensitive to heterogeneity.

Key words: photo-identification, heterogeneity, mark-recapture, scarring, northern bottlenose whale, *Hyperoodon ampullatus*.

Photo-identification (photo-id) is commonly used in cetacean studies for many types of analysis including population estimates and social organization (see Hammond *et al.* 1990 for review). However, analysis of photo-id data can be problematic, especially when using models which require equal probabilities of capture and recapture (Hammond 1986). Behavioral differences may lead some individuals to be overrepresented in the catalog (*e.g.*, some individuals may be present in the sampling area for longer time periods, or may approach the boat more often). The marks on the animals may not be equally distributed throughout the population, such that some individuals are "clean" or unmarked even in high-quality photographs, while others have very large or obvious markings and can be identified even in the poorest photograph. Finally, the appearance of natural marks may change over time, such that not all individuals can be re-identified over long sampling intervals (Hammond 1986).

The object of this paper is to examine a photo-id catalog for sources of unequal capture probabilities, using a collection of photographs of northern bottlenose whales (*Hyperoodon ampullatus*) taken during a nine-year study. Behavioral sources of heterogeneity are not considered. Once the sources and degree of heterogeneity are identified in a specific catalog, researchers can set appropriate criteria by which photographs and individuals should be included in subsequent analysis to optimize the precision and accuracy of the results. For example, estimates of population size are sensitive to heterogeneity, thus it is important to carefully restrict the data set to minimize heterogeneity (Hammond 1986). This is often accomplished by selecting only high-quality photographs and individuals with persistent marks. Then the population estimate can be scaled to account for the remainder of the population which is considered unmarked (*e.g.*, Friday 1997, Whitehead *et al.* 1997, Wilson *et al.* 1999). Conversely, when using photo-id data to analyze association patterns between individuals, especially over short time scales, a great deal of valuable information would be lost if the same criteria were used to restrict the data set (*e.g.*, Gowans 1999).

Typically, photo-id catalogs have been assessed for heterogeneity for a specific analysis, especially when conducting population estimates. However, this process is time consuming, and it may be more efficient to assess a catalog once for the degree of heterogeneity caused by the various sources, and then to use this information to select appropriate selection criteria for each subsequent analysis.

To assess unequal capture probabilities in the northern bottlenose whale catalog, we describe the distribution of marks within the population to determine which types of marks are useful in identifying individuals and estimate the rate at which the mark types are gained and lost. Because large or obvious marks may be visible in poor quality photographs, and subtle marks may not be visible, we examine the visibility of marks in photographs of different qualities to assess the quality necessary to identify individuals accurately. Matches of photographs of bottlenose whale melons (from beak to blowhole) are used as a double tagging experiment to test the reliability of matches of dorsal fin photographs.

METHODS

Photographic Collection

Photographs of northern bottlenose whales were collected from the Gully, Nova Scotia (44°N, 59°W) during the summers of 1988–1997 from sailing

Table 1. Summary of photo-identification data (Q ≥ 2) by year.

Year	Number of frames	Number of individuals identified by left fin photographs	Number of individuals identified by right fin photographs
1988	123	18	19
1989	1,202	109	96
1990	3,116	171	167
1991	27	8	5
1993	549	46	53
1994	370	54	43
1995	82	14	17
1996	1,751	94	86
1997	1,531	99	90

vessels with auxiliary diesel engines. Field seasons varied in length from three months in 1990, 1996, and 1997, to only a few days in 1991 and 1992 (Table 1). When conditions permitted, photographs of the left or right dorsal fin and surrounding flank were taken of bottlenose whales <30 m from the vessel. Photographs were taken irrespective of any obvious markings on the individual, and photographs were taken throughout the encounter, whether or not photographs had already been taken of a particular individual. Most photographs were taken with Canon AE1, AT1 (manual focus), or Elan IIE 35-mm (automatic focus) SLR cameras equipped with 300-mm f4 lenses, using either Kodak T-max or Ilford HP5 400 ASA black-and-white film. Suites of photographs consisting of the melon and dorsal fin were taken whenever possible, however most identification work was conducted only on the single photograph containing the dorsal fin.

Black-and-white negatives were examined on a light table with a 10× magnifying loupe. All negatives were assigned a quality rating (*Q*-value) from 1 to 6 based on focus, exposure, angle of the fin relative to the negative plane, and the proportion of the frame filled by the fin (similar to Arnbom 1987), with Q-6 representing the highest quality photographs (Fig. 1). The Q-value was independent of the markings on the individual. Q-1 negatives were extremely poor and were not included in the collection. Sketches were made of the marks of each individual to assist in matching among negatives. The highest quality negative of each individual in each year was printed, and the photographs were compared with each other and to photographs from previous years. If a photograph matched an individual that was already known in the collection, the photograph and all other associated negatives were assigned the whale's identification number. If not matched, the individual was given a new number and added to the catalog. Photographic collections for left and right sides were maintained separately, although some identifications from different sides could be linked. The negative collection contained 8,751 negatives that were assigned an identification (Table 1). The catalog contained 140 individ-

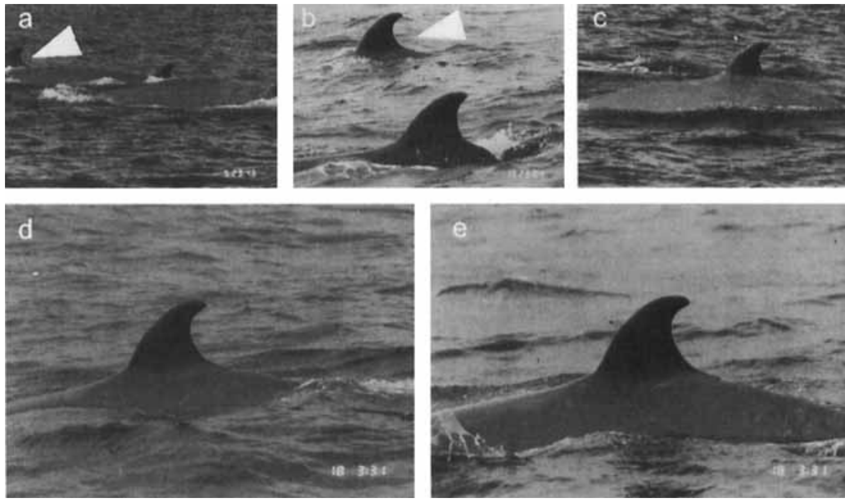

Figure 1. Examples of different photographic qualities (Q-2, through Q-6) used in this study of northern bottlenose whales. All photographs were of individual 45 in 1997. Arrows point to individual 45; (a) Q-2 very distant photograph with little of flank showing; (b) Q-3 distant photograph with little of flank showing; (c) Q-4 distant photograph but most of flank showing; (d) Q-5 close with good representation of flank; (e) Q-6 close with most of flank showing, well focused and exposed photograph.

uals identified by both left and right sides, 290 individuals identified only by left sides, and 252 individuals identified only by right sides. However, as these identifications were based on all mark types (not just mark types that persisted for years) some individuals were likely assigned more than one identification number.

Analyses

The analyses of marks in this study were similar to those used to establish the catalog. All marks were sketched, and the marks were categorized into mark types (Fig. 2, Table 2). In July 1998, 115 color slides (Kodachrome 200 ASA) were taken to determine mark color. All visible mark types were included in all analyses except those which were dark brown in color. Previous analysis indicated these marks were likely caused by diatoms and unsuitable for photo-id due to their rapid rates of change (Gowans 1999). All negatives were analyzed by the primary author, who had five years experience in photo-identification of bottlenose whales.

Mark distribution and the uniqueness of individuals—The distribution of marks within the population was analyzed to assess whether individuals were uniquely marked. To observe as many mark types as possible, only excellent-quality photographs ($Q \geq 5$) were selected for this analysis. One hundred individuals were randomly selected from the 268 individuals with excellent quality photographs. Only one negative ($Q \geq 5$) for each individual was analyzed to

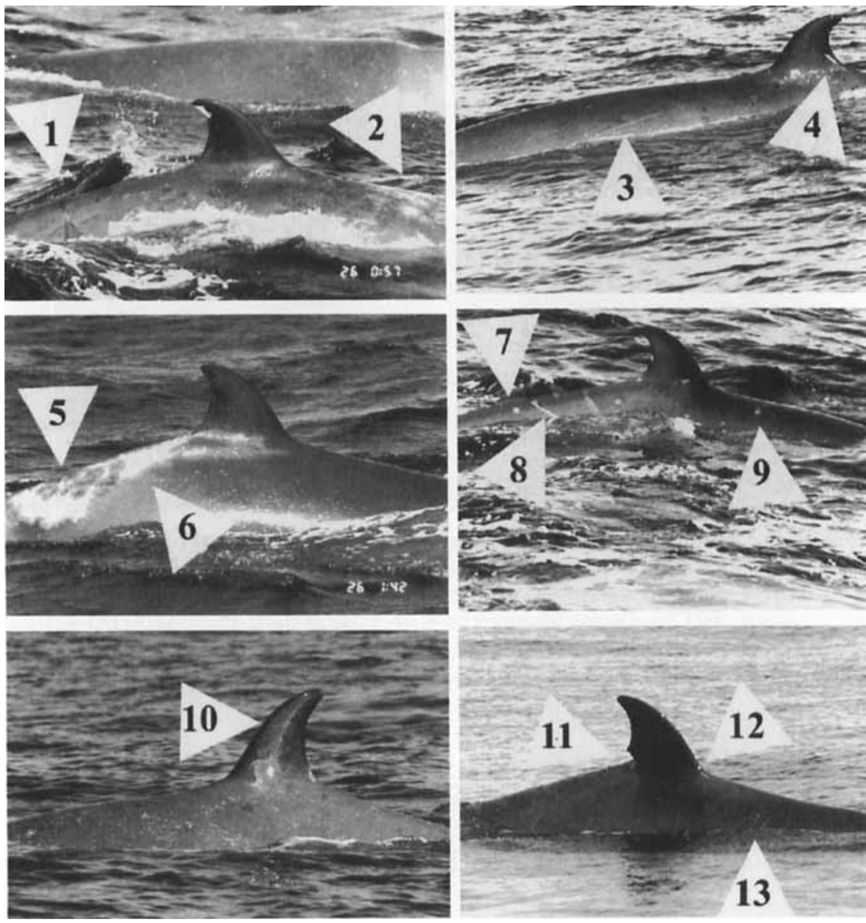

Figure 2. Examples of types of marks found on dorsal fins used to identify northern bottlenose whales. Mark types: (1) Attachment, (2) Mottled patches, (3) Single long linear scrape, (4) Short parallel linear scrape, (5) Back indentation, (6) Large scar, (7) Light band, (8) Short single linear scrape, (9) Large circular light patch, (10) Small white dot, (11) Notch on dorsal, (12) Non-circular light patch, (13) Long parallel linear scrape. Most of the other visible mark types were dark brown in color, believed to be caused by diatoms and found to be unreliable for photo-id.

examine whether a single photograph possessed sufficient marks to identify individuals. Marks on each negative were sketched and counted. As some individuals were identified from only a few marks, the possibility of two, different, poorly-marked individuals being matched was assessed by comparing the photographs of individuals with only one reliable mark (see below; mark types with no losses over the study period), to determine the likelihood of their being incorrectly matched as the same individual.

Because the sex of some individuals in the sample was known from melon photographs (Gray 1882, Gowans *et al.* 2000), *t*-tests were used to determine

Table 2. Description of mark types found on northern bottlenose whales.

Mark type	Color[a]	Size[b]	Description
Notch	may have white area surrounding missing tissue	vary in size from <1 cm to 10 cm	located on dorsal fin
Back indentation	May have white area surrounding missing tissue	<10 cm deep	located posterior to dorsal fin
Large scar	white	>10 cm	irregular shapes
Linear Marks			
Short single linear scrape	white	<5 cm	single line
Long single linear scrape	white	>5 cm	single line
Short parallel linear scrape	white	<5 cm	two parallel lines
Long parallel linear scrape	white	>5 cm	two parallel lines, longer than five cm
Tooth rake	white	usually <5 cm	multiple parallel lines
Attachment	white	disk <3 cm, trailing lines <10 cm long	circular disk 3–5 parallel lines trailing
Light band	cream	5–10 cm long	thin linear band
Patches			
Small white dot	white	<1 cm diameter	circular in shape
Circular light patch	cream	>5 cm diameter	circular shape—sometimes indented
Non-circular light patch	cream	>1 cm	irregular shape
Mottled patches	white and cream over light brown	Large—covering at least 25 cm^2	textured with light patches appearing raised

[a] From color slides taken in 1998.
[b] Size of mark estimated from width of dorsal fin (approximately 60 cm in adult female based on stranding measurements—Sergeant *et al.* 1970, Mitchell and Kozicki 1975).

whether males and females, or older mature males and younger subadult males, had distributions of different marks. G-tests determined whether the proportion of individuals with reliable marks differed between age and sex classes.

Photograph quality—To investigate the effect of photograph quality on the visibility of marks, we used individuals with at least one negative of a left fin of each quality (Q = 2–6) taken within the same year. Only 36 individuals met these criteria. If an individual met these criteria in more than one year, only negatives from the first year were used. If there was more than one negative of the same quality, the negative was randomly selected. Marks were sketched, categorized, and counted without reference to the previously assigned identification number and quality. The presence or absence of each mark was compared among negatives of different qualities for each individual. This analysis was repeated on the same set of negatives, using only reliable marks.

Mark change—To assess mark change, all individuals with negatives of Q $\geq$ 4 in three or more years were selected. The highest-quality negative of each individual in each year was analyzed. If there was more than one negative of the same quality, the negative for analysis was selected randomly. Pairs of negatives were simultaneously compared, and the marks were drawn on the same form. Presence or absence of each mark was compared to negatives from previous and subsequent years, so that multiple comparisons were made for each individual. As different proportions of the flank were recorded on the negatives, only marks located in areas shown in both negatives were counted. As there was no method other than photo-id to match individual bottlenose whales, individuals matched by photo-id were used to analyze the reliability of natural marks. This meant that instances in which a high proportion of marks on an individual had changed could have been missed, leading to underestimates in the rate of change of marks. To minimize such problems each mark was assessed separately.

The interval between the comparisons was calculated from the total number of years between first and last photograph. For example, an individual photographed in 1989, 1990, and 1997, was examined twice, from 1989–1990 (one-year interval as the photographs were taken roughly 365 d apart) and 1990–1997 (seven-year interval) over a total of eight-year intervals (following Dufault and Whitehead 1995). Gain and loss rates of each mark type per individual per year were calculated by dividing the total number of mark gains and losses by the number of year-intervals over which the comparisons were made. Gain and loss rates were compared for matches between photographs of different Q-values using G-tests. G-tests were conducted if there were $>$15 occurrences of gain or loss of that mark type (Sokal and Rohlf 1995).

Instantaneous mark-loss rates per mark per year were estimated by likelihood ratio methods, because some marks were lost rapidly and the comparisons were made over years. If marks were lost at an instantaneous rate of $\mu \cdot yr^{-1}$, then the probability that a mark seen at time t_1 was also present at time t_2 was:

$$e^{-\mu(t_2-t_1)}$$

μ was estimated by maximum likelihood methods and the hypothesis that μ varies between photographic quality was tested using likelihood ratio tests (Sokal and Rohlf 1995). Reliable mark types were defined as mark types with no losses over the nine- year study period. Because some mark types were rare and present in only a few photographs selected for this analysis, a mark type had to occur more than five times in the mark-change photographs to be considered reliable.

Identification photographs in this study were centered on the dorsal fin, and various sections of the flank appeared in the photographs. Thus, marks located closer to the dorsal fin were more likely to be photographed than marks located farther away. Marks, except for notches, were located on the dorsal fin or flank, so it was important to determine that this area of the body was routinely photographed. All photographs ($Q \geq 4$) of individuals with reliable marks were examined for the presence or absence of the reliable mark and the proportion of photographs in which the mark was visible was calculated for each individual.

The proportion of the population that was reliably marked was calculated by comparing the number of photographs ($Q \geq 4$) containing individuals with reliable marks with the total number of photographs (Williams *et al.* 1993), as photographs were taken throughout an encounter irrespective of individual markings. This analysis was performed for each year when more than one month was spent in the field (1989, 1990, 1996, and 1997) and for left and right sides separately. The overall mean and SE in the proportions were calculated from the mean and SE of annual estimates.

All occurrences of new reliable marks were counted, and the gain rate was calculated by dividing the number of occurrences by the interval of the comparison. Addition of a reliable mark sometimes changed the status of the individual (from unreliable to reliable), and this rate of change was also calculated.

The possibility that photographs of the same individual were not matched due to mark change was investigated by comparing the resighting rates for individuals between 1989–1990, 1996–1997, and 1990–1997 (long field seasons; Table 1), for reliably and unreliably marked individuals. These periods were selected to compare both short- and long-term resighting rates.

Double tag–melon matching—The melon profile of bottlenose whales is sexually dimorphic (Gray 1882; Gowans *et al.* 2000), so a catalog of melon photographs was also created. These photographs showed identifying marks (Fig. 3) and were used to independently test dorsal fin matches as a double-tagging experiment. If a photograph of a melon was linked in the field to a dorsal fin, then the melon was assigned the same identification number. If a melon was not linked to a dorsal fin, and the melon negative contained marks useful for matching, it was assigned a separate melon identification number. Each year, the highest-quality melon negative of an individual, including individuals with only a melon identification number, was printed. Melon pho-

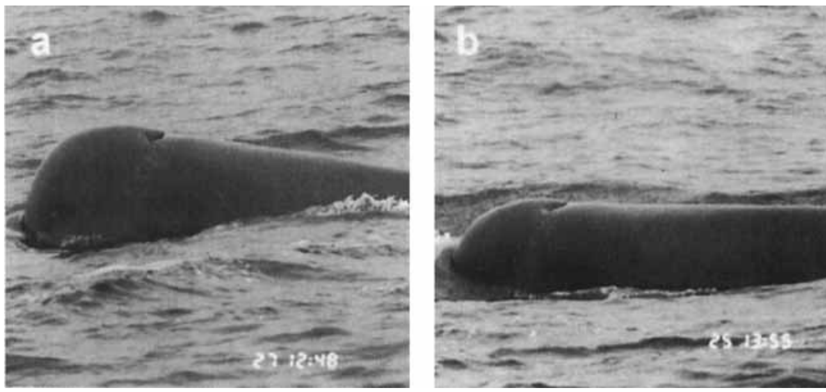

Figure 3. Examples of melon photographs of northern bottlenose whales matched between (a) 1996 and (b) 1997.

tographs were compared to each other without reference to the melon or fin identification numbers. Individuals that were matched based on melon photographs were compared to the matches based on dorsal fins to test the reliability of fin matches.

Results

Mark Distribution and the Uniqueness of Individuals

Bottlenose whales were well marked and possessed on average 14.5 different marks within a typical photograph (n = 100, SD = 12.8, range = 1–67, Table 3, Fig. 2). Common mark types (found on more than one third of the individuals) were notches, short and long single linear scrapes, large circular light patches, and non-circular light patches (Table 3).

Of the 100 negatives selected for analysis, 54 were assigned age or sex classes from melon photographs. There were no significant differences between the total number of marks found on female/immatures and on subadult or mature males, nor between subadult and mature males (Table 4a). Males were significantly more likely to be reliably marked than female/immatures, but there was no significant difference between the proportion of mature and subadult males which were reliably marked (Table 4b).

Forty-two of the sampled individuals had reliable marks ($\bar{x}$ number of reliable marks = 1.64, SE = 1.1, range 1–5). Seventeen individuals possessed only one reliable mark, and photographs of these individuals were compared to determine the possibility of matching to each other. Differences in mark shape, size, and location differentiated all but one of the potential matches. However, this pair could be differentiated by non-reliable marks as the photographs were taken in the same year.

Table 3. Distribution of mark types on 100 randomly selected individuals.

Mark type	Proportion of individuals with mark type	Mean number of marks per individual
Notch	0.37	0.48
Back indentation	0.04	0.05
Large scar	0.17	0.21
Linear Marks		
Short single linear scrape	0.54	1.45
Long single linear scrape	0.37	0.83
Short parallel linear scrape	0.03	0.06
Long parallel linear scrape	0.06	0.05
Tooth rake	0.06	0.07
Attachment	0.02	0.03
Light band	0.02	0.02
Patches		
Small white dot	0.19	2.30
Large circular light patch	0.89	7.34
Non-circular light patch	0.61	1.37
Mottled patches	0.13	0.24

Photograph Quality

While there was no clear cut-off point at which marks became visible, increasing the quality of the photograph increased the number of visible marks (Table 5). On average, less than 50% of the marks visible on high-quality

Table 4. Distribution of marks among age and sex classes.

(a) all mark types		
Age/sex category (n)	$\bar{x}$ number of marks per individual ± SE	Two sample t-test (P-value)
Male (21)	14.7 ± 2.5	Male *vs.* female/immature 0.223 (0.824)
Female/immature(33)	15.5 ± 2.7	
Mature male (11)	16.5 ± 3.5	Mature male *vs.* subadult male 0.744 (0.466)
Subadult male (10)	12.7 ± 3.7	
(b) reliable mark types only		
Age/sex category (n)	Proportion with reliable marks	G-test (df, P-value)
Male (21)	0.67	Male *vs.* female/immature 8.75 (1, >0.005)
Female/immature (33)	0.36	
Mature male (11)	0.55	Mature male *vs.* subadult male 2.58 (1, >0.10)
Subadult male (10)	0.8	

Table 5. Percentage of marks visible in first negative which were also visible in the second, for negatives of different photograph quality taken in the same year.

(a) All mark types (n = 36 individuals, 5 negatives per individual)

	2nd negative					
	Q	2	3	4	5	6
	2	—	48	66	63	67
1st	3	45	—	73	75	74
	4	46	54	—	77	82
	5	41	41	57	—	72
	6	29	36	48	57	—

(b) Reliable mark types (n = 36 individuals, 5 negatives per individual)

	2nd negative					
	Q	2	3	4	5	6
	2	—	91	100	100	100
1st	3	85	—	94	100	100
	4	78	79	—	96	96
	5	62	73	73	—	92
	6	56	63	72	83	—

photographs (Q < 4) were visible in Q-2 or Q-3 photographs (Table 5a). Reliable marks were more often visible in lower-quality photographs (Q < 4) than unreliable marks (Table 5). However, there was a decline in the number of reliable marks when Q-2 or Q-3 photographs were included in the sample. When comparing reliable marks, Q-5 photographs did not have more marks than Q-4 photographs (Table 5b).

Mark Change

To examine mark change 112 pairs of negatives were compared, involving 39 different individuals over 241 year-intervals (Table 6). No losses were recorded for notches, mottled patches, back indentation, or tooth rakes, although the number of comparisons containing tooth rakes was small (n = 2, Table 6). Reliable mark types, defined as ones with zero loss rates occurring in more than five samples, were notches, back indentation, and mottled patches. With the exception of long single linear scrapes and attachment marks, gain rates were higher than loss rates.

Gain and loss rates of some mark types were significantly different between comparisons of photograph qualities, although only unreliable mark types were affected (Table 6). Mark types did not appear to change from one type to another; instead, previously observed marks sometimes disappeared, and unmarked skin was visible in subsequent years. Individual marks lasted for variable lengths of time, but most non-reliable mark types were lost within one to three years of observation.

Although marks on the flanks may persist over years, they were not always photographed (Table 7). Reliable marks located less than one dorsal fin width

Table 6. Number of marks of each mark type gained and lost. Overall rates of gain and loss of marks per individual per year shown as well as estimated instantaneous loss rate (μ) of individual marks per year. Dashed lines represent mark types in which all marks were lost before resampling.

Mark type	Number of occurrences			Overall rates per animal year (marks/year)		Estimated loss (μ) per year
	Total	Gain	Loss	Gain	Loss	
Reliable Mark Types						
Notch	92	18	0	0.075	0	0
Back indentation	20	1	0	0.004	0	0
Mottled patches	7	0	0	0	0	0
Unreliable Mark Types						
Large scar	44	4	2	0.017	0.008	0.025
Short single linear scrape	164	80	55	0.332*	0.228*	0.519
Long single linear scrape	55	15	3	0.062	0.12	0.037
Short parallel linear scrape	6	2	1	0.008	0.004	0.288
Long parallel linear scrape	8	1	1	0.004	0.004	0.074
Tooth rake	2	0	0	0	0	0
Attachment	1	0	1	0	0.004	—
Light band	6	3	1	0.04	0.004	0.187
Small white dot	181	144	11	0.598*	0.046*	0.299
Large circular light patch	835	353	305	1.465*	1.266*	0.623
Non-circular light patch	240	87	74	0.361*	0.307*	0.344
Year intervals		241	241			

* Rates not comparable across different photograph qualities.

(at the base) from the anterior and posterior insertion points of the dorsal fin were routinely captured in photographs of the dorsal fin. Marks located farther than one dorsal fin width were included in only approximately half of the photographs of an individual. Thus, individuals were defined as reliably

Table 7. Proportion of photographs ($Q \geq 4$) of northern bottlenose whales in which back indentation or mottled patches was visible.

	Number of individuals	Negatives with mark	Total negatives	Percent of negatives with mark
Back Indentation				
All individuals	16	321	365	88
Mark closer than 1 dorsal fin	12	308	339	91
Mark farther than 1 dorsal fin	4	13	26	50
Mottled Patches				
All individuals	84	689	917	75
Mark closer than 1 dorsal fin	70	603	763	79
Mark farther than 1 dorsal fin	14	86	154	56

marked if they had a back indentation or mottled patch within at least one dorsal fin base width of the dorsal fin, or a notch on the dorsal fin.

The mean proportion of individuals in the population that were reliably marked was 0.66 (±0.05 SE) for all photographs (left side photographs 0.61 ±0.06 SE; right side photographs 0.69 ±0.03 SE). Addition of a reliable mark was relatively rare. Of 160 individuals with a reliable mark on the left side, only 13 individuals acquired another reliable mark (8% of total; gain rate = 3.3% per individual per year) within the nine-year study period. Of the 159 reliably marked right fins, 13 gained a reliable mark (8% of total, gain rate = 3.2% per individual per year). Five individuals (both left and right) changed status from unreliable to reliable (3% of total; change rate = 1.2% per individual per year).

Mark change hindered the ability to match photographs of the same individual and created unequal recapture rates. When comparing sets of photographs taken only one year apart, individuals with unreliable marks were still recaptured although at a lower rate than individuals with reliable marks (1989–1990: 61% reliably marked individuals recaptured, 15% unreliable; 1996–1997: 48% reliable, 18% unreliable). Over a seven-year period (1990–1997), no unreliably marked individuals were recaptured, while 20% of the reliably marked individuals sighted in 1990 were resighted in 1997.

Double Tag–Melon Matching

The melon catalog contained 253 left and 225 right melon photographs, which represented 173 and 149 individuals identified by dorsal fin identifications and 31 and 34 individuals with melon identifications alone, respectively. Few melon photographs matched other melon photographs. Only 7.9% of left melon photographs and 10.2% of right melon photographs were matched. Most of the matches were between melons where one of the pair of photographs was not linked to an identification number (48% of matches) or between pairs of melons linked to the same identification number (33% of matches). In four pairs, the melon photographs matched but the corresponding fin identifications did not match. In these cases, at least one photograph was of poor quality ($Q < 4$) or did not have a reliable mark.

Discussion

Mark Distribution

The dorsal fin and flanks of northern bottlenose whales were well marked and contained a variety of different mark types. In excellent-quality photographs ($Q \geq 5$) all individuals were marked, although not all possessed reliable marks. When conducting analyses with short sampling intervals (hours to days) all individuals should be considered uniquely marked. However, for long intervals (months to years) only the 66% of the population with reliable marks should be considered marked.

Because individuals accumulated marks over time, then the decision to include only reliably marked individuals might bias the data set to older animals. In this study, older mature males did not have a significantly higher proportion of reliable marks than subadult males, although females and immatures did have a significantly lower proportion of reliable marks than mature and subadult males (Table 4). However, sample sizes for these tests were small, so the results should be treated cautiously. Because few immatures were sexed, older individuals were likely to be overrepresented in the sample, which also limited the power of the test to determine whether older individuals possessed more reliable marks.

Most of the mark types found on bottlenose whales were similar to those found in other cetacean species and may have been caused by a variety of natural and anthropogenic sources (see Gowans 1999 for more details). Of the reliable mark types, notches and back indentations have been well documented and persist for many years (*e.g.,* Kraus 1990, Philo *et al.* 1992, Wells *et al.* 1998). Mottled patches did not appear to resemble any description of cetacean markings. In size and shape they were similar to the "blue-grey cloudy lesions" in bottlenose dolphins (*Tursiops truncatus*) (Wilson *et al.* 1997), although mottled patches on bottlenose whales were cream and white. The persistence of the mottled patches indicate they were unlikely to be active infections, although they may have been the result of previous infections.

Photograph Quality

Poor quality negatives (Q = 3) did not contain sufficient information to consistently identify individual northern bottlenose whales. Mark-type categorization also became more accurate in higher-quality negatives. Accurate mark-type categorization would be important in computer-assisted matching or when the process was based on the presence or absence of mark types (*e.g.,* Whitehead 1990). Some distinctive mark types, such as notches, were visible in poor-quality negatives and were matched to a known individual; however, other mark types were not visible in poor-quality negatives. Restriction of the data set to exclude poor-quality photographs (Q = 3) would minimize unequal capture probabilities. Exclusion of Q-4 photographs would reduce the sample size dramatically, with only minimal reduction in heterogeneity, and thus would not be warranted in most analyses.

Similarly, Agler (1992*b*) investigated the effect of photographic quality and the distinctiveness of an individual fin whale (*Balaenoptera physalus*) on the reliability of photograph matches. She found that fewer errors were made in photographic matches if individuals were distinctive and/or the photographs were of high quality.

Mark Change

If the rate of change of marks was sufficiently low, individuals with all mark types could be included in all analyses, as all individuals were likely to be recaptured. This was the case for marks on the trailing edge of sperm whale flukes (*Physeter macrocephalus*) (Dufault and Whitehead 1995, Childerhouse and Dawson 1996) but, in bottlenose whales, rates of mark change were highly variable. Some mark types (*e.g.*, linear marks) were gained and lost at rates that were unacceptable for use in individual identification for recaptures over periods of years. Reliable marks on bottlenose whales had similar gain and loss rates to marks on sperm whales, which had near zero loss rates and approximate gain rates of 2% per individual per year (Dufault and Whitehead 1995, Childerhouse and Dawson 1996). Photographs of reliably marked bottlenose whales could be re- identified over years. In long-term analyses (sampling intervals of months to years), the data set should be restricted to individuals that can be reliably re-identified. Similarly, Wilson et al. (1999) investigated the duration over which marks were visible on bottlenose dolphins to determine which individuals should be included for estimates of population size. Although calculating how long marks were visible gave some information about the reliability of mark types, these calculations may be biased by the yearly sampling regime. Therefore, the calculation of gain and loss rates, as in this study, likely results in a less biased estimate of mark longevity.

For most mark types, gain rates were higher than loss rates, indicating that marks accumulated over time. In bottlenose dolphins, minor wounds healed on average within 2.5 yr (Wilson *et al.* 1999) which was similar to the loss rate of scrapes and tooth rakes in this study. Notches and back indentations on bottlenose whales were probably caused by deep wounds and appeared to leave permanent scars. On fin whales, large scars persisted on average for three to four years although some scars, especially notches on the dorsal fin, persisted throughout the 16-yr study period (Agler 1992*a*). The light patches in our study had very high loss rates, and most were lost within one to three years. In bottlenose dolphins, similar colored marks tended to disappear within one year, although some lasted throughout the four-year study (Wilson *et al.* 1999).

In bottlenose whales, changes in markings that altered the classification of bottlenose whales from unreliably to reliably marked were relatively rare and were comparable with mark changes, which altered the classification of individuals in other photo-id catalogs. Dufault and Whitehead (1995) categorized individual sperm whales in their catalog based on the location of the largest mark on the trailing edge of the fluke. Changes in the categorization of flukes occurred in 9.5% of the comparisons in which mark change occurred, and individuals had a 1.3% probability per year of undergoing a change in categorization (Dufault and Whitehead 1995). Humpback whales (*Megaptera novaeangliae*) were identified by marks on the flukes and then categorized by the overall coloration of the fluke. Carlson *et al.* (1990) found a change in the coloration categorization in 4.6% of their comparisons. However, they did not calculate the rate of change and most of the changes involved individuals less than two years of age.

The estimated rate of addition of a reliable mark was low (3.3% per individual per year) and was lower than the gain rate for notches (Table 6). This discrepancy arose because individuals with notches (and other reliable marks) were overrepresented in the mark-change sample, because individuals had to be identified in three or more years to be included in the mark-change analysis. Therefore, the estimated gain rate, calculated by counting all occurrences of a gain of a reliable mark, was less biased than the rate of gain calculated from the mark change analysis. This bias did not affect the rate of gain of unreliable marks. The calculated rate of change of status from unreliable to reliable (1.2% per individual per year) must be viewed as a minimum rate. Other individuals may have been photographed before the acquisition of a reliable mark, but it was not possible to match the reliably marked photograph to the earlier photograph.

Double Tag–Melon Matching

Relatively few of the melon photographs contained marks that were matched over years. The photographs that were matched had scarring or multiple linear scrapes on the melon. When melon photographs matched, but fin identifications did not, at least one fin photograph of each pair either was of poor quality or did not contain a reliable mark. While the sample size was small, the matches that were found supported the suggestion that analyses sensitive to heterogeneity should be conducted on data sets consisting of high-quality photographs and reliably marked individuals.

While photo-id was an excellent technique for studying bottlenose whales, there were unequal capture probabilities due to differences in marking. Short-term capture histories (hours to days) were relatively unbiased; all individuals could be considered marked although not all individuals could be recaptured in poor-quality photographs. Long-term capture histories (months to years) were biased by mark change; only 66% (SE = 5%) of the population were reliably marked and the inclusion of poor-quality photographs would also contribute to heterogeneity.

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