J. CETACEAN RES. MANAGE. 21: 71–83, 2020

Photo-identification of individual humpback whales (*Megaptera novaeangliae*) using all available natural marks: implications for misidentification and automated algorithm matching technology

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ABSTRACT

As the ventral-tail fluke catalogues used to study humpback whales (*Megaptera novaeangliae*) increase in size, the time and cost involved with curation and manual photo-identification matching increases accordingly, and this is becoming a significant challenge for field researchers. In addition, misidentification errors in catalogue matching can seriously affect population dynamics parameter estimates and capture-mark recapture estimates of population size. In this study we used long-term photo-identification data, derived from an innovative matching system, which yielded a reconciled catalogue of 2,821 individual ventral-tail flukes and 578 resighting histories in Hervey Bay between 1992 and 2009. To investigate and examine the long-term stability and/or changes in natural marks on ventral-tail flukes, dorsal-fin shapes and lateral body marks, we used a sub-sample of 79 individual humpback whales, resighted in 2 to 11 years over timespans ranging from 2 to 21 years. A binary logistic mixed effects model was applied to a pair-matched sample of changes of marks in the 79 individual whales. The model found no significant difference between the proportion of changes in primary and secondary ventral tail fluke marks and the proportion of changes in primary dorsal-fin shape characteristics plus secondary lateral body marks ($F = 0.939$, $df = 1/156$, $p = 0.334$). The results of this study substantiate the value and reliability of using ventral-tail flukes together with dorsal-fin shapes and lateral body marks, as multiple complementary tags in the photo-identification process. The data were used to discuss minimisation and management of misidentification errors in the photo-identification matching process, and the use of multiple complementary tags in the development of automated algorithm matching technology for white-dominant Southern Hemisphere humpback whale ventral-tail flukes.

KEYWORDS: HUMPBACK WHALE; SOUTHERN HEMISPHERE; AUSTRALASIA; PHOTO-IDENTIFICATION; MARK-RECAPTURE; MODELLING; AUTOMATED ALGORITHM MATCHING TECHNOLOGY

INTRODUCTION

The use of photographs of natural markings on individual humpback whales (*Megaptera novaeangliae* [Borowski, 1781]) is a well established technique to study the biology, behaviour and ecology of both individuals and populations of humpback whales (Schevill and Backus, 1960; Emmel, 1976; Jurasz and Jurasz, 1979; Katona *et al.,* 1979; Katona and Whitehead, 1981; Baker *et al.,* 1986; 1992; Clapham and Mayo, 1990; Clapham, 1993, 2000; Whitehead, 1995; 2008; McGregor and Peake, 1998; Calambokidis *et al.,* 2008; Burns, 2010; Kniest *et al.*, 2010; Franklin *et al.,* 2011; 2012; 2018; Franklin, 2012; 2014; Burns *et al.*, 2013; 2014). The proportion of individuals that can be identified from natural marks varies between different cetacean species (Shane and McSweeney, 1990). In the case of humpback whales, double-tagging experiments using both genetic and photo-identification data have shown that almost 100% of individual humpback whales can be identified using natural marks, provided sufficient high-quality photographs of the natural marks can be obtained (Katona *et al.,* 1979; Stevick *et al.,* 2001; Calambokidis *et al.,* 2008; Garrigue *et al.,* 2011). However, natural marks can change over time, especially in immature whales (Carlson *et al.,* 1990; Blackmer *et al.,* 2000) leading to misidentification errors. Poorer quality photographs used in the process of individual identification and the photo-identification matching process can also give rise to misidentification errors (Friday *et al.,* 2000; Stevick *et al.,* 2001).

Capture-mark-recapture techniques, including the use of increasingly sophisticated modelling, are regularly used to estimate the size and population dynamics of humpback whale populations (Pollock, 1982; Kendall *et al*., 1995, 1997; Kendall and Nichols, 1995; Schwarz and Stobo, 1997; Kendall and Bjorkland, 2001; Franklin, 2014). In an early review of the use of capture-mark-recapture (CMR) techniques, Hammond (1986) suggested that the process of photo-identification with large numbers of photographs could be facilitated through the use of computers to digitise, store, categorise and catalogue individual whales by types of markings and by the utilisation of all available natural marks, for example ventral-tail flukes, dorsal-fin shapes and lateral body marks. Some statistical work has been done for other species to examine how multiple marks could be reconciled in a single CMR study (Madon *et al.,* 2011; Bonner and Holmberg, 2013).

Misidentification errors in capture-mark-recapture studies related to quality of photographs (non-evolving natural tags), and changes in natural marks (evolving natural tags), have been investigated and modelled (Yoshizaki, 2007). A simulation study, using a misidentification mechanism and

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a framework for modelling the effect of misidentification, showed that conventional estimators could upwardly bias population size estimates when errors due to misidentification are ignored (Yoshizaki *et al*., 2009).

Developments in recent decades related to digital photography and online data sharing have increased the availability of visual data and decreased its cost, allowing for the emergence of large, photo-based mark-recapture catalogues for multiple species (Burns, 2010; Holmberg *et al.,* 2018; Marshall and Holmberg, 2018). With increasing catalogue size and the limited scalability of data curation efforts, misidentification error concerns are growing. Emerging algorithms, such as the SIFT-based HotSpotter (Crall *et al*., 2013) and the neural network-based CurvRank (Weideman, 2017), have been successfully tested to match humpback ventral-tail flukes using differing and complementary visual parameters (Flynn *et al*., 2017). If provided with an accurate and representative baseline, these automated techniques can help quantify inherent error in matching. However, no automated system has yet been developed to accommodate the information provided by multiple marks (e.g. ventral-tail flukes, dorsal-fins and lateral body marks).

In this study we adopted an existing innovative, photo-identification matching system (Franklin, 2012) to obtain long-term photo-identification data of humpback whales in Hervey Bay. The long-term stability and/or changes in natural marks on individual humpback whales, including ventral-tail flukes, dorsal-fin shapes and lateral body marks were investigated using a sub-sample of the data. We discuss the stability of all natural marks on humpback whales, their use in the minimisation and management of misidentification in the photo-identification process, and the implications for the development of automated algorithm matching technology for white-dominant Southern Hemisphere ventral-tail flukes.

METHODS

Photo-identification survey in Hervey Bay

Hervey Bay, Queensland, Australia (25°S, 153°E) is neither a breeding ground nor feeding area but a stopover early in the southern migration for humpback whales after they leave the breeding and overwintering area north of Hervey Bay (Franklin *et al*., 2011). Mature females travelling and socially interacting with immature males and females use the Bay during August, while mothers-calf pods involved in maternal activities predominate during September and October. A female-biased sex ratio of 2.9:1 indicates that Hervey Bay is a preferential stopover for females (Franklin *et al*., 2018). We undertook vessel-based photo-identification of humpback whales in Hervey Bay during an annual ten-week period from 1992 to 2009. A summary of fieldwork effort, pods and whales observed is provided in Table 1. All pod and observation data were recorded daily in field notes and entered into a FileMaker Pro database each evening.

Photo-identification procedure

As well as high-resolution digital photography of ventral-tail flukes, systematic photography of dorsal-fin shapes and lateral body marks were also obtained for each of the individual humpback whales in each pod (Katona *et al.,* 1979; Katona and Whitehead, 1981; Hammond, 1986; Clapham and Mayo, 1990). To facilitate photographic analysis a marker-shot of Fraser Island was taken prior to commencement and after completion of photography on each pod. If sequential photographs of a dorsal-fin and lateral body were followed immediately by a ventral-tail fluke photograph of the same individual whale, a marker shot (of the ship's railings) was taken to verify that the preceding series of photographs were of the same individual whale. This protocol enabled the matching of dorsal-fin shapes, lateral body marks and ventral-tail flukes of the same individual whale.

Table 1

Summary of fieldwork, observations and photo-identification outcomes during vessel-based surveys in Hervey Bay from 1992 to 2009.

	Fieldwork effort and observations					Photo-identification outcomes		
	Fieldwork			Observations		Yearly catalogues		
Year	First day	Last day	Field days	Pods (n)	Whales (n)	Flukes (n)	Resighting histories	Cumulative resighting histories
1992	10 Aug.	09 Oct.	42	189	387	4	0	0
1993	06 Aug.	15 Oct.	53	229	442	5	7	7
1994	07 Aug.	14 Oct.	50	163	380	47	36	43
1995	06 Aug.	13 Oct.	51	172	374	47	27	70
1996	04 Aug.	11 Oct.	48	185	410	70	26	96
1997	01 Aug.	17 Oct.	64	300	693	140	52	148
1998	09 Aug.	16 Oct.	58	410	934	190	56	204
1999	28 Jul.	15 Oct.	63	399	929	210	43	247
2000	06 Aug.	13 Oct.	58	380	815	206	50	297
2001	12 Aug.	19 Oct.	57	432	954	234	43	340
2002	11 Aug.	17 Oct.	59	409	968	268	56	396
2003	10 Aug.	17 Oct.	56	390	928	270	42	438
2004	05 Aug.	15 Oct.	60	419	952	303	49	487
2005	30 Jul.	14 Oct.	61	448	1,050	376	43	530
2006	03 Aug.	13 Oct.	58	420	984	341	23	553
2007	30 Jul.	11 Oct.	60	399	945	297	14	567
2008	07 Aug.	17 Oct.	61	508	1,283	407	11	578
2009	06 Aug.	16 Oct.	55	396	901	317	0	578
		Totals	**1,014**	**6,248**	**14,329**	**3,732**	**578**	

Between 1992 and 2002, 35mm colour film photographs were taken with a Canon camera using a 100–300mm lens and from 2003 to 2009 with a Canon EOS digital camera using a 100–300mm lens. The 35mm slide photography selected for use in analysis was scanned and digitised prior to analysis. All photography used in analysis was digitally archived as high-resolution JPEG files at a standard ratio of 1,536 pixels by 1,024 pixels at 300 dpi, to enable the consistent display on Apple computers for photo-identification analysis and matching throughout the study.

After the completion of a season's fieldwork, field notes were imported into an integrated whale analysis FileMaker Pro database. All field photography was organised and archived by date, time and pod. The file name of each data image included frame number, pod identification, date and whether the image was of a ventral-tail fluke (USF), left or right-side lateral body (LSD, RSD) or gender information (GEN). Photography of each pod was reviewed in conjunction with field notes and archive numbers of photographs supporting identification of individual whales were recorded in the database. Ventral-tail fluke photographs were assessed for image quality (SPLASH; Calambokidis *et al.,* 2008) prior to inclusion in each yearly catalogue. Databases and photography files used in the photo-identification process are digitally stored, both on-site and off-site.

Photo-identification matching system

Annual ventral-tail fluke catalogues for the years 1992 to 2009 were compiled and analysed for intra- and inter-season resightings of individual humpback whales. To facilitate ventral-tail fluke matching we used a propriety photo-identification matching system based on discrete categorisation of ventral-tail flukes by applying an Array of Coded Discrete Characteristics (ACDC) to the file name of each image used in the photo-identification process (Franklin, 2012).

The ACDC categories were based on individually unique and stable patterns of black and white pigmentation on the ventral-tail flukes, as well as on dorsal-fin shapes and lateral body marks. The ACDC characteristics selected for the system were derived from an empirical visual analysis of photographs of ventral-tail flukes, dorsal-fin shapes and lateral body marks of humpback whales taken in Hervey Bay during the early years of the study. The selected ACDC characteristics and their filename codes are described and summarised in Table 2.

A consistent viewing protocol (see Table 3) was used to allocate ACDC codes to the filename of each ventral-tail fluke image. Dorsal-fin shape images and lateral body mark images were used as complementary tag information. A similar viewing protocol, from dorsal to ventral, was used to allocate ACDC codes to dorsal-fin shape and lateral body mark photographs.

The ACDC system allowed each ventral-tail fluke to be allocated to contiguous stratified categories, using the ACDC codes in the image filename, for visual display and organisation. This facilitated and expedited photographic analyses and ventral-tail fluke matching (see ventral-tail fluke photograph examples in *Supplementary Material Fig. 1*). The use of ventral-tail fluke natural marks in conjunction with dorsal-fin shapes and lateral body natural marks provided valuable information for use in the photo-identification analysis and matching process (see dorsal-fin, lateral body photograph examples in *Supplementary Material Fig. 2*).

Table 2

Array of Coded Discrete Characteristics (ACDC) for categorisation of ventral-tail flukes, dorsal-fin shapes and lateral body marks used for individual identification and photo-identification matching of humpback whales.

Ventral-tail flukes		Dorsal-fin shape and lateral body marks	
(A) Primary characteristics:		(A) Primary dorsal-fin shapes:	
TE	Trailing edge*	FH	Falcate high set
NT	Notch*	FL	Falcate low set
BB	Black border	FP	Falcate fine pointed
BC	Black centre	FR	Falcate rounded
BK	Black	RN	Rounded
		TC	Truncated
		TR	Triangular
		CP	Chipped
		WD	Wedge
		HK	Hook
		FT	Flat tops
(B) Secondary characteristics:		(B) Secondary lateral body characteristics:	
BS	Black stem	WP	White patches
DM	Damaged	WS	White sides
RK	Rake marks	DM	Damaged
HL	Hole	RK	Rake marks
CR	Curled		
WP	White patch		
BP	Black patch		
(C) Tertiary characteristics:		(C) Tertiary lateral body characteristics:	
SM	Scratch marks	SM	Scratch marks
DT	Dots	DT	Dots
RG	Rings	RG	Rings
		RM	Rub marks**
		GS	Grey spine**
		PK	Peduncle knobs[#]

*The TENT category is further categorised based on the thickness of black pigmentation along the trailing edge of the fluke as TENT-1 = thick, but less than the BB (black border category), TENT-2 = medium thickness and TENT-3 = fine thickness. All TENT ventral-tail flukes are predominantly white pigmentation (See Fig. 1 Supplementary Material). **These marks were usually observed on females with a calf present. [#]Peduncle knobs are observable on whales with reduced body mass.

Photo-identification analysis

When matching a ventral-tail fluke against a fluke catalogue it was pairwise matched with other photographs within its defined ACDC colour and pattern category and then if not matched within that category, it was then subsequently compared and pairwise matched to photographs in adjacent similar categories, until a clearly dissimilar category was reached. Photographs of available dorsal-fin shapes and lateral body marks were used to verify matches. As the majority of flukes were predominantly all white (87.6%, Table 4) the unique shape and colouration of the trailing edge and notch were very important characteristics in the matching process (Carlson *et al.*, 1990; Mizroch *et al.*, 1990; Blackmer *et al.,* 2000; Friday *et al.*, 2000). Because pigmentation patterns and marks of individual ventral-tail flukes may change over years (Carlson *et al.*, 1990), using a

Table 3

Array of Coded Discrete Characteristics (ACDC) applied to ventral-tail fluke image filenames, for photo-identification matching of intra- and inter-season resightings of individual humpback whales, and the protocol used for the ACDC code assignment and order in each filename.

Code	Description	Protocol used for code assignment[a]
(A) Primary characteristics:		
		Step I
BB	Black border	View and examine the ventral-tail fluke photo from posterior to anterior across the horizontal plane for primary characteristics.
BC	Black centre	
BK	Black	Step II
TE	Trailing edge	Compare to examples (Fig. 1 Supplementary Material) and assign primary code or codes. If BB and BC both present BB precedes BC. If BB, BC or BK not present, TE, will be the sole primary code. Separate each four digits of code by a hyphen.
NT	Notch	
(B) Secondary characteristics:		
BS	Black stem	Step III
DM	Damaged	View and examine the ventral-tail fluke photo from posterior to anterior across the horizontal plane for secondary characteristics.
RK	Rake marks	
HL	Hole	Step IV
CR	Curled	Compare to examples (Fig. 1 Supplementary Material) and assign secondary codes from posterior to anterior for characteristics present. Separate each four digits of code by a hyphen.
WP	White patch	
BP	Black patch	
(C) Tertiary characteristics:		Step V
		View and examine the ventral-tail fluke photo posterior to anterior across the horizontal plane for any tertiary characteristics present.
SM	Scratch marks	
DT	Dots	
RG	Rings	Step VI
		Compare to examples (Fig. 1 Supplementary Material) and assign tertiary codes posterior to anterior for characteristics present. If SM, DT and/or RG occur on in the same horizontal plane SM precedes DT and, DT precedes RG in the code array. Separate each four digits of code by a hyphen.

[a] Fig. 1 Supplementary Material (SM), uses example photographs to illustrate the stratification and computer display of ventral tail-flukes in discrete categories arising from the ACDC codes applied to each fluke photograph filename.

consistent viewing protocol (Table 3) in the assignment of ACDC characteristic codes minimised mismatch errors. If for example a resighting of a particular individual showed a change in marks, the ACDC filename reflects the change in that year.

Photographic analysis outcomes together with original field data were incorporated into a single FileMaker Pro relational database. Yearly ventral-tail fluke catalogues and resighting histories were compiled from the analyses of intra- and inter-season resightings of individual humpback whales.

To examine the stability and/or changes in natural marks on ventral-tail flukes as well as dorsal-fin shapes and lateral body marks, a sub-sample of 79 long-term resighting histories of individual humpback whales were selected, from the 1992 to 2009 resighting histories. The selection of individuals was primarily based on longevity of sightings over years, and that the samples be representative of the classes of whales using Hervey Bay (see Franklin *et al.*, 2018). The selected sample consisted of: 44 females (for method of sex identification see Franklin *et al.*, 2018) resighted in 5 to 12 different years, with resightings spanning 7 to 21 years; 20 males resighted in 4 to 10 different years, with resightings spanning 7 to 16 years; and 15 immature whales (3 females, 3 males and 9 of unknown gender) resighted in 2 to 4 different years, with resightings spanning 2 to 9 years. The 'immature' whales were identified based on resightings occurring predominantly during August or in early September when the immature cohort is present in Hervey Bay (Franklin *et al.,* 2018). The selected immature whales were first observed as either calves or yearlings. An experienced observer identified yearlings to be unambiguously small relative to adults, but too large to be calves of the year (Clapham *et al.*, 1999; Craig *et al.*, 2003). The resighting histories of some immature whales extended beyond their immature years. When available, some of the above resighting histories were extended with additional photography, obtained during the 2010, 2011 and 2012 seasons (see Tables 6a, 6b, 7 and 8).

The selected photographs of an individual whale's ventral-tail fluke, as well as left and/or right dorsal-fin shape and lateral body marks, for each sighting, from the first sighting to the last resighting, were placed in sequential order in *Preview* (an Apple Macintosh photo display program) (See *Supplementary Material Fig.1*). The ACDC filename for each sequential photograph was examined and any changes in the ACDC codes were noted and recorded. The photographs were then visually displayed in the program *Preview* in time-sequential order and systematically examined. Any observed changes in the ventral-tail fluke ACDC primary, secondary and tertiary characteristics were noted and recorded and any changes in the dorsal-fin shape and secondary and tertiary lateral body marks were also noted and recorded.

Data and modelling

The data on observed changes in the natural marks on 79 individual whales were reported for both (a) the marks on ventral tail flukes and (b) in primary dorsal-fin shapes plus marks on the lateral body. A binary logistic mixed effects model was fitted to assess the relative rate of change over time in primary and secondary marks on the ventral-tail fluke and in primary dorsal-fin shapes plus secondary lateral body marks. The model was binary because it compared changed to not changed, and mixed effects because there were two random effects, one for the residual variance from the sample of whales and one for the residual variance from the paired (a and b within whale) observed changes in natural marks of ventral tail flukes and dorsal-fin shape plus lateral body marks. Primary and secondary characteristics were combined to yield one measure of change (changed, not changed) in the natural marks in each of the ventral tail flukes and the dorsal-fin shape characteristics plus lateral body marks.

RESULTS

Long-term photo-identification

A total of 6,248 pods involving 14,329 whales were observed and photographed in Hervey Bay between 1992 and 2009. Yearly ventral-tail fluke catalogues and resighting histories obtained from the photo-identification analyses of intra- and inter-season resightings of individual humpback whales from 1992 to 2009 are summarised in Table 1.

The fully reconciled Hervey Bay ventral-tail fluke catalogue, using the ACDC matching system described above, for the period 1992 to 2009 consisted of 2,821 individual humpback whales. The number and percentage of ventral-tail flukes in each of the primary ACDC categories in the reconciled catalogue is reported in Table 4.

After photo-identification matching within and between each yearly ACDC ventral-tail fluke catalogue, using the matching system described above, a total of 578 resighting histories of individual humpback whales were obtained and are summarised in Table 1. The resighting histories ranged from 2 to 21 years. From those resighting histories a sub-sample of 79 long-term resighting histories of individual humpback whales were selected for the analysis of changes in natural marks.

Natural marks: overall summary and modelling of changes

The results of the analysis of natural marks of the 79 individual humpback whales are summarised in Table 5. The data for the analysis are summarised in Tables 6a and 6b (44 females), Table 7 (20 males) and Table 8 (15 immature whales).

Changes in primary characteristics of the ventral-tail flukes were observed in six of the 79 (7.6%) individual whales (Tables 6a and 6b, 7 and 8). Changes in secondary characteristics of the ventral-tail flukes were observed in four of the 79 (5.1%) individual whales (Tables 6a and 6b, 7 and 8). There were four of 79 (5.1%) cases where changes occurred to both the primary and secondary characteristics of the ventral-tail flukes of an individual whale (Table 5 below, also see Tables 6a and 6b, 7 and 8). Changes were observed in the tertiary marks of the ventral-tail flukes on 26 of 79 (32.9%) individual whales (Tables 6a and 6b, 7 and 8).

Changes in the primary dorsal-fin shape and/or secondary lateral body marks were observed in only two of the 79 (2.5%) individual whales (Table 5 below, also see Tables 6a and 6b, 7 and 8) while changes in the tertiary marks on the lateral body were observed in 36 of 79 (45.6%) individual humpback whales (Table 5 below, also see Tables 6a and 6b, 7 and 8). Changes in the natural marks of the 79 individual whales are summarised in Table 5.

Table 4

Number and % of ventral-tail flukes by primary ACDC categories in the reconciled 1992–2009 Hervey Bay ventral-tail fluke catalogue.

Primary ACDC categories[1]	Number of flukes	%
BBBC/BBDM/BBNT/BBRK (black borders plus)	51	1.8
BCBP/BCDM/BCCR/BCNT/BCRK (black centres plus)	214	7.6
BKDM/BKNT/BKRK/BKWP (black plus)	86	3.0
TEBB (trailing edge, black border)	311	11.0
TEBP/TECR (trailing edge, black patch or curled)	9	0.3
TEDM (trailing edge, damaged)	93	3.3
TEHL (trailing edge, holes)	52	1.8
TENT-1 (trailing edge (thick) and notch)	372	13.2
TENT-2 (trailing edge (medium) and notch)	722	25.6
TENT-3 (trailing edge (fine) and notch)	696	24.7
TERK (trailing edge, raked)	215	7.6
Total flukes 1992–2009	**2,821**	**100.0**

[1] The primary ACDC category is made-up of the first four digits of code in the filename, except for the TENT category; the TENT category is further categorised based on the thickness of black pigmentation along the trailing edge of the fluke as TENT-1 = thick, but less than the BB (black border category), TENT-2 = medium thickness and TENT-3 = fine thickness. All TENT ventral-tail flukes are predominantly white pigmentation (See Fig. 1 Supplementary Material).

Table 5

Summary of type and number of long-term changes in natural marks of 79 individual humpback whales between 1992 and 2009.

	Number of changes observed					
	Ventral-tail flukes			Dorsal-fin shape	Lateral body marks	
Whales	Primary	Secondary	Tertiary#	Primary	Secondary	Tertiary#
Females (44)	0	0	6	0	0	10
Males (20)	3	1	5	0	2	15
Immatures (15)	3	3	15	0	0	11

#Changes in tertiary marks do not affect individual identification.

Differences between the proportions of natural marks of ventral tail flukes and dorsal-fin shape plus lateral body marks that displayed changes over time were analysed using a binary logistic mixed effects model. The model found no significant difference between the proportion of changes in primary and secondary ventral tail fluke marks and the proportion of changes in primary dorsal-fin shape characteristics plus secondary lateral body marks (F = 0.939, df = 1/156, p = 0.334).

DISCUSSION

The results presented in this study from systematic long-term photo-identification of Southern Hemisphere humpback whales in Hervey Bay, using an innovative matching system, show how ventral-tail flukes, dorsal-fin shapes and lateral body marks can be used as 'complementary' tags in the photo-identification process. This outcome, and the matching system described, are designed to minimise the occurrence of misidentification errors in the photo-identification process and could be used to aid the development of automated algorithm matching technology for white-dominant Southern Hemisphere humpback whales.

White-dominant Southern Hemisphere ventral-tail flukes

Variation in white and black pigmentation on the ventral-tail fluke of humpback whales was reported during commercial whaling in the early 1900s (True, 1904; Lillie, 1915; Matthews, 1937; Omura, 1953). More recent studies have shown variation in pigmentations between humpback whale populations ranging from mostly black, predominantly in the Northern Hemisphere, to mostly white (Pike, 1953; Allen *et al.*, 1994; Rosenbaum *et al.*, 1995). Burns (2010) reported that both western and eastern Australian humpback whales showed the least amount of variation with over 80% of these whales being predominantly white, and suggested that categorisation into generic pattern types is more limited in its application for the Australian humpback whale populations. Furthermore, Burns (2010) argued that the use of a system that relies more on other characteristics, such as the shape of the ventral-tail fluke, the location of smaller marks and scars, and the shape of the notch would be more likely to increase efficiency in stratifying flukes for the Australian populations. The ACDC coding system presented in this study extensively utilises these 'other characteristics' to create an efficient and effective stratification and ventral-tail fluke matching system.

Data from this study demonstrate that 87% of the Hervey Bay ventral-tail flukes are predominantly white, suggesting that published match success rates for algorithms developed on data from mostly black-dominant, pigmented Northern Hemisphere ventral-tail flukes (e.g. 69% for HotSpotter, Flynn *et al.*, 2017; Moskvyak *et al.*, 2019) would be further suppressed. However, other algorithms use the trailing edge of the fluke (Jablons, 2016; Weideman *et al.*, 2017) and present no bias toward pigmentation.

The stratification of the Hervey Bay reconciled ventral-tail fluke catalogue reported here (Table 4) also provides holders of Southern Hemisphere humpback whale catalogues a baseline to evaluate if there is over- or under-representation of particular categories of ventral-tail flukes in their dataset, particularly of distinct categories.

Rake marks on ventral-tail flukes

Attempted predation of humpback whales by killer whales (*Orcinus orca*) results in teeth marks or rake marks on either the ventral-tail fluke, dorsal-fin or lateral body areas, which provides evidence of attacks (Clapham, 2000). Rake marked individual humpback whales are observed worldwide with occurrence ranging up to 40% in some populations (Mehta *et al.*, 2007). A recent study of the nature and scale of predatory interactions between killer whales and humpback whales off western Australia reported that the majority of kills were of calves (Pitman *et al.,* 2015). This study found that 8.2% of ventral-tail flukes exhibit rake marks, which is much less than the 17% reported earlier for eastern Australian humpback whales (Naessig and Lanyon, 2004). The lower levels of rake marks evident in Hervey Bay may be related to the high rate of population increase and recovery of the eastern Australian humpback whales over the last 15 years (Harrison and Woinarski, 2018; Noad *et al.*, 2016, 2019).

Changes in natural marks of various classes of humpback whales

Male humpback whales tend to have more marks than females on dorsal-fins and lateral bodies, most likely from intrasexual competition among males in competitive groups (Chu and Nieukirk, 1988). In Hervey Bay only 6.3% of pods are involved in competitive group behaviour (Franklin, 2012), and there is a female-biased sex ratio of 2.9:1 in Hervey Bay (Franklin *et al.,* 2018). Consistent with Chu and Nieukirk (1988) this study found significant changes in lateral body tertiary marks of male humpback whales (Table 5) observed over timespans of 7 to 16 years (see *Supplementary Material Figs 5, 6, 7, 8 and 9*); whereas relatively few changes in lateral body tertiary marks were seen on female humpback whales (see Table 5 and *Supplementary Material Figs 3 and 4*).

Acorn barnacles (*Coronula diadema* and *Coronula reginae*) can cause dots and ring marks on humpback whales (Felix *et al.,* 2006), leaving black marks on white pigmentation and white marks on black pigmentation. Such dots and ring marks on ventral-tail flukes can seriously alter natural pigmentation patterns (e.g. *see Supplementary Material Fig. 12* Whale UID 0665 [Moon E.T.] ventral-tail fluke patterns in 2001 and 2004). Cookie cutter sharks (*Isistius* spp.) (Wenzel and Lopez-Suarez, 2012; Best and Photopoulou, 2016) can cause holes and/or black dots in the ventral-tail flukes and crater marks on the lateral body (e.g. *Supplementary Material Fig. 1* ACDC Category TEHL). Substantial change in the tertiary marks (scratches, dots and rings), have been reported to occur with immature humpback whales (Carlson *et al.,* 1990; Blackmer *et al.,* 2000). Consistent with these reports, this study found substantial changes over time in the tertiary marks on ventral-tail flukes and lateral bodies of immature humpback whales (see Table 5).

Blackmer (2000) suggested that photographs of dorsal-fin shapes and the caudal peduncle knobs 'provide the most consistent way to re-identify humpback whales, particularly calves following weaning'. In this study, no changes were observed in dorsal-fin shapes of the immature whales (see Table 5 and Table 8), over time-spans ranging from 2 to 6 years. Three of the 79 humpback whales were observed from calf or yearling onwards – Whale UID 1116, [Hodda], Table 6a; Whale UID 0161, [Floppy], Table 7 and *Supplementary Material Fig. 9*, and Whale UID 1046, [Ninety Nine], Table 8 and *Supplementary Material Fig. 11*). The dorsal-fin shapes and secondary lateral body marks were crucial in re-identifying these whales in conjunction with ventral-tail flukes. Carlson *et al.* (1990) reported that where changes in natural marks occurred in immature whales, such changes stabilised within the first five years. The results reported in this study are consistent with the conclusions from Carson *et al.* (1990) (e.g. see Whale UID 0665 [Moon E.T.]; Whale UID 1046 ['Ninety-Nine'], Table 8 and *Supplementary Material Figs 10 and 11*; also see Whale UID 0161 ['Floppy'], Table 7 and *Supplementary Material Fig. 9*).

Management and minimisation of misidentification

Misidentification of individual whales in a humpback whale dataset can potentially arise from tag loss due to changes in natural marks (Carlson *et al.,* 1990; Blackmer *et al.,* 2000), evolving natural marks (Yoshizaki, 2007), or from the use of poor-quality photographs (Friday *et al.*, 2000) and/or non-evolving natural marks (Yoshizaki, 2007).

Two primary sources of misidentification can occur during the visual matching process. Firstly, if two matching ventral-tail fluke photographs are declared different individuals when in fact they are of the same individual, this creates a 'false negative', as the effective match count will be reduced. Secondly, if two photographs of different individuals are declared to be of the same individual this creates a 'false positive' as the effective match count will be increased (Yoshizaki, 2007; Burns, 2010). If such misidentification errors cannot be identified and/or resolved, the capture history of an individual can be split into multiple histories leading to 'ghost' histories in tandem with the individual's real history (Yoshizaki 2007; Yoshizaki *et al.,* 2009). Moreover, failure to eliminate such misidentification errors can lead to serious errors in estimation of population size and biases in other parameters using conventional estimators (Yoshizaki *et al.,* 2009; Link *et al.,* 2010; Morrison *et al.,* 2011, Winship *et al.,* 2012).

A total of 63.5% of the ventral-tail flukes in the Hervey Bay catalogue are categorised as either TENT-1, TENT-2 or TENT-3 (TENT – Trailing Edge and Notch, see Table 2 and *Supplementary Material Fig. 1*). In a large ACDC category such as TENT, the use of dorsal-fin shape and lateral body marks provide valuable additional identification information to minimise and manage potential misidentification. Application of the strict ACDC viewing protocol for ventral-tail flukes, dorsal-fin shapes and lateral body marks aids individual identification, while tertiary marks do not interfere with individual identification (Table 5). The results presented in this study show that use of ventral-tail flukes, dorsal-fins and lateral body marks as complementary 'tags' in the photo-identification process will significantly contribute to minimisation and management of misidentification errors.

The SPLASH study of humpback whales in the North Pacific tested the incidence of missed matches using several approaches and found that just over 90% of matches were found by a single matcher with success rate being largely a function of photographic quality ranging from 82 to 96% depending on quality (Calambokidis *et al.*, 2008). That study involved over 18,000 identification photographs representing just under 8,000 unique individuals so the current study with a more experienced single matcher and a smaller catalogue would be expected to have a higher success rate.

Implications for development of algorithm matching technology for white-dominant flukes

The importance and use of multiple marks as presented here and the successful application of multiple algorithms in tandem presented by Flynn *et al.* (2017) and now deployed in the *Flukebook.org* platform (Levenson, 2015) suggest an important new avenue forward for automated matching research: the employment of multiple algorithms for multiple marks and multiple types of marks (e.g. white-dominant versus black-dominant ventral tail flukes) and the use of ensembles of machine learning techniques (Zhou, 2012) to reconcile the application of multiple algorithms. Quantification of error of combined techniques will remain important, and exploration of independently quantified error for automated matching systems can also help the evaluation of CMR models with misidentifications error parameter estimates, either by reducing the number of parameters through specification of error values directly, or through comparison of estimated parameters against known system performance. Application of extant statistical tests for heterogeneity in capture probability and apparent survival (Choquet *et al.*, 2009) can also help check for confounding bias in matching system performance.

Importantly, if new, automated matching techniques are developed and trained using a trusted baseline of data from thorough and systematic manual matching efforts, such as that presented here, these advanced techniques could replace hundreds or thousands of hours of visual curation with just a few automated hours of computation (Flynn *et al.*, 2017). This is especially true if the fully automated pipelines can avoid the need for any pre-processing of imagery (Parham *et al.*, 2018) before ensembled matching techniques use all available data to accurately match individual humpback whales across multiple, collaborating research sites along their range. Our work here can not only provide the high quality data and justification needed to train the next generation of multi-mark, automated matching systems (e.g. using deep learning) for humpback whales, but it also provides a template for other species monitoring efforts to systematically move from fully manual 'by eye' curation of photos for population monitoring and to prepare for a new generation of machine algorithms that can quickly and with high accuracy answer the question 'Which individual animal is this?'

REFERENCES

Allen, J.M., Rosenbaum, H.C., Katona, S.K., Clapham, P.J. and Mattila, D.K. 1994. Regional and sexual differences in fluke pigmentation of humpback whales (*Megaptera novaeangliae*) from the North Atlantic Ocean. *Can. J. Zool.* 72(2): 274–79.

Baker, C.S., Herman, L.M., Perry, A., Lawton, W.S., Straley, J.M., Wolman, A.A., Kaufman, G.D., Winn, H.E., Hall, J.D., Reinke, J.M. and Ostman, J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar Ecol Prog. Ser.* 31: 105–19.

Baker, S.C., Straley, J.M. and Perry, A. 1992. Population characteristics of individually identified humpback whales in southeastern Alaska: Summer and Fall 1986. *Fish. Bull. US* 90(3): 429–47.

Best, P.B. and Photopoulou, T. 2016. Identifying the 'demon whale-biter': Patterns of scarring on large whales attributed to a cookie-cutter shark *Isistius* sp. *PLoS ONE* 11(4): e0152643. [doi: 10.1371/journal.pone.0152643].

Blackmer, A.L., Anderson, S. K. and Weinrich, M. T. 2000. Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). *Mar Mammal Sci.* 16(2): 338–54.

Bonner, S.J. and Holmberg, J. 2013. Mark-recapture with multiple, non-invasive marks. *Biometrics* 69: 766–75. [doi: 10.1111/biom.12045].

Burns, D. 2010. Population characteristics and migratory movements of humpback whales (*Megaptera novaeangliae*) identified on their southern migration past Ballina, eastern Australia. PhD Thesis, Southern Cross University, Lissmore, NSW, Australia. 265pp.

Burns, D., Brooks, L., Clapham, P. and Harrison, P. 2013. Between-year synchrony in migratory timing of individual humpback whales, *Megaptera novaeangliae*. *Mar. Mammal Sci.* 29(1): 228–235. [doi: 10.1111/j.1748-7692.2011.00557.x].

Burns, D., Brooks, L., Harrison, P., Franklin, T., Franklin, W., Paton, D. and Clapham, P. 2014. Migratory movements of individual humpback whales photographed off the eastern coast of Australia. *Mar. Mammal Sci.* 30(2): 562–578. [doi: 10.1111/mms.12057].

Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urban R, J., Weller, D., Witteveen, B.H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. 2008. *SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific.* US Dept. of Commerce, Western Administrative Center, Seattle, Washington. 57pp.

Carlson, C.A., Mayo, C.A. and Whitehead, W. 1990. Changes in the ventral fluke pattern of the humpback whale (*Megaptera novaeangliae*), and its effects on matching; Evaluation of its significance to photo-identification research. *Rep. Int. Whal. Commn* (Special Issue 12): 105–11.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.M. and Pradel, R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* 32(6): 1,071–74. [doi: 10.1111/j.1600-0587.2009.05968.x].

Chu, K. and Nieukirk, S. 1988. Dorsal fin scars as indicators of age, sex, and social status in humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* 66: 416–20.

Clapham, P.J. 1993. Social organization of humpback whales on a North Atlantic feeding ground. *Symposia of the Zoological Society, London* 66: 131–45.

Clapham, P.J. 2000. The humpback whale – Seasonal feeding and breeding in a baleen whale. pp.173–196. *In*: J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (eds.) *Cetacean Societies*: *Field Studies of Dolphins and Whales.* The University of Chicago Press, Chicago.

Clapham, P.J. and Mayo, C.A. 1990. Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. *Rep. Int. Whal. Commn.* (Special Issue 12): 171–75.

Clapham, P.J., Wetmore, S.E., Smith, T.D. and Mead, J.G. 1999. Length at birth and at independence in humpback whales. *J. Cetacean Res. Manage.* 1(2):141–46.

Craig, A.S., Herman, L.M., Gabriele, C.M. and Pack, A.A. 2003. Migratory timing of humpback whales (*Megaptera novaeangliae*) in the Central North Pacific varies with age, sex and reproductive status. *Behaviour* 140(8–9): 981–1,001.

Crall, J.P., Stewart, C.V., Berger-Wolf, T.Y., Rubenstein, D.I. and Sundaresan, S.R. 2003. HotSpotter – Patterned species instance recognition. Presented to the IEEE Workshop on Applications of Computer Vision (WACV 2013). 7pp. [Available at: *http://cs.rpi.edu/hotspotter/crall-hotspotter-wacv-2013.pdf*]

Emmel, T.C. 1976. Population size: Growth and dynamics. pp.89–99. *In:* T.C. Emmel (ed.) *Population Biology*. Harper and Row, New York.

Felix, F., Bearson, B. and Falconi, J. 2006. Epizoic barnacles removed from the skin of a humpback whale after a period of intense surface activity. *Mar. Mammal Sci*. 22(4): 979–84.

Flynn, K., Calambokidis, J., Weideman, H.J., Crall, J., Jablons, Z., Stewart, C., Kingen, C., Van Oast, J. and Holmberg, J. 2017. Testing of two new automated fluke identification algorithms and comparison to non-automated methods for humpback whales. Presented to the 22nd Biennial Conference on the Biology of Marine Mammals, Halifax, Nova Scotia, 22–27 October 2017. [Abstract]

Franklin, T. 2012. The social and ecological significance of Hervey Bay Queensland for eastern Australian humpback whales (*Megaptera novaeangliae*). PhD thesis, Southern Cross University, Lismore, NSW, Australia. 245pp. [Available at: *http://epubs.scu.edu.au/theses/357/*].

Franklin, W. 2014. Abundance, population dynamics, reproduction, rates of population increase and migration linkages of eastern Australian humpback whales (*Megaptera novaeangliae*) utilising Hervey Bay, Queensland. PhD Thesis, Southern Cross University, Lismore, NSW. 396pp. [Available at: *http://epubs.scu.edu.au/theses/422/*].

Franklin, T., Franklin, W., Brooks, L., Harrison, P., Baverstock, P. and Clapham, P. 2011. Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992–2005. *Mar. Mammal Sci.* 27(3): E134–E152 (July 2011) [doi: 10.1111/j.1748-7692.2010.00430.x].

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Harrison, P., Baker, S.C. and Clapham, P. 2012. Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australian (E(i) breeding group) humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manage.* 12(3): 321–27.

Franklin, T., Franklin, W., Brooks, L. and Harrison, P. 2018. Site-specific female-biased sex ratio of humpback whales (*Megaptera novaeangliae*) during a stopover early in the southern migration. *Can. J. Zool.* 96(6): 533–44. [doi: 10.1139/cjz-2017-0086].

Friday, N., Smith, T.D., Stevick, P.T. and Allen, J. 2000. Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. *Mar. Mammal Sci*. 16(2): 355–74.

Garrigue, C., Franklin, T., Constantine, R., Russell, K., Burns, D., Poole, M., Paton, D., Hauser, N., Oremus, M., Childerhouse, S., Mattila, D., Gibbs, N., Franklin, W., Robbins, J., Clapham, P. and Baker, C.S. 2011. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *J. Cetacean Res. Manage.* (Special Issue 3): 269–74.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. Int. Whal. Commn* (Special Issue 8): 253–82.

Harrison, P.L. and Woinarski, J.C.Z. 2018. Recovery of Australian subpopulations of humpback whale. Chapter 2, pp.5–12. *In*: S. Garnett, P. Latch, D. Lindemeyer and J. Woinarski, J. (eds) *Recovering Australian Threatened Species*. CSIRO Publishing, Australia. 360pp.

Holmberg, J., Arzoumanian, Z. and Pierce, S. 2018. Wildbook for Whale Sharks. Version 2018. [Available at: *https://www.whaleshark.org*, downloaded 22 March 2019]

Jablons, Z. 2016. Identifying humpback whale flukes by sequence matching of trailing edge curvature. MSc thesis, Rensselaer Polytechnic Institute, Troy, NY.

Jurasz, C.M. and Jurasz, V. 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Sci. Rep. Whales Res. Inst., Tokyo* 31: 69–83.

Katona, S.K., Baxter, B., Brazier, O., Kraus, S., Perkins, J. and Whitehead, H. 1979. Identification of humpback whales by fluke photographs. pp.33–44. *In:* H.E Winn and B.L. Olla (Eds) *Behaviour of Marine Animals – Current Perspectives in Research*. Plenum Press, New York.

Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Rec.* 20(128): 439–44.

Kendall, W.L. and Bjorkland, R. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57(4): 1113–22.

Kendall, W.L. and Nichols, J.D. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *J. Appl. Stat.* 22: 751–62.

Kendall, W.L., Pollock, K.H. and Brownie, C. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51:293–308.

Kendall, W.L., Nichols, J.D. and Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–78.

Kniest, E., Burns, D. and Harrison, P. 2010. Fluke Matcher: A computer-aided matching system for humpback whale (*Megaptera novaeangliae*) flukes. *Mar. Mammal Sci.* 26(3): 744–56. [doi: 10.1111/j.1748-7692.2009.00368.x].

Levenson, J., Gero, S., Van Oast, J., Blunt, D. and Holmberg, J. 2015. Flukebook: a cloud-based photo-identification analysis tools for marine mammal research. [Available at: *https://www.flukebook.org*, downloaded 22 March 2019]

Lillie, D.G. 1915. Cetacea. Vol. 1.3 *In*: *Natural History Reports: British Antarctic (Terra Nova) Expedition, 1910*. British Museum (Natural History). 39pp.

Link, W.A., Yoshizaki, J., Bailey, L.L. and Pollock, K.H. 2010. Uncovering a latent multinomial: Analysis of mark-recapture data with misidentification. *Biometrics* 66(1): 178–85. [doi: 10.1111/j.1541-0420.2009.01244.x].

Madon, B., Gimenez, O., McArdle, B., Scott Baker, C. and Garrigue, C. 2011. A new method for estimating animal abundance with two sources of data in capture recapture studies. *Methods Ecol. Evol.* 2: 390–400.

Marshall, A.D. and Holmberg, J. 2018. MantaMatcher Photo-identification Library. [Available at: *https://www.mantamatcher.org*, downloaded 22 March 2019]

Matthews, L.H. 1937. *The Humpback Whale*, Megaptera nodosa. University Press, Cambridge.

McGregor, P. and Peake, T. 1998. The role of individual identification in conservation biology. pp 31–55. *In*: Caro, T.M. (Ed.) *Behavioral Ecology and Conservation Biology*. Oxford University Press, New York.

Mehta, A.V., Allen, J.M., Constantine, R., Garrigue, C., Jann, B., Jenner, C., Marx, M.K., Matkin, C.O., Mattila, D.K., Minton, G., Mizroch, S.A., Olavarría, C., Robbins, J., Russell, K.G., Seton, R.E., Steiger, G.H., Víkingsson, G.A., Wade, P.R., Witteveen, B.H. and Clapham, P.J. 2007. Baleen whales are not important as prey for killer whales *Orcinus orca* in high latitude regions. *Mar. Ecol. Prog. Ser.* 348: 297–307.

Mizroch, S.A., Beard, J.A. and Lynde, M. 1990. Computer assisted photo-identification of humpback whales. *Rep. Int. Whal. Commn* 63–70.

Morrison, T.A., Yoshizaki, J., Nichols, J.D. and Bolger, D.T. 2011. Estimating survival in photographic capture–recapture studies: overcoming misidentification error. *Methods Ecol. Evol.* 2(5): 454–63. [doi: 10.1111/j.2041-210X.2011.00106.x].

Moskvyak, O., Maire, F., Armstrong, A.O., Dayoub, F. and Baktashmotlagh, M. 2019. Robust re-identification of manta rays from natural markings by learning pose invariant embeddings. arXiv:1902.10847v1 [cs.CV], 28 Feb 2019. 12pp.

Naessig, P.J. and Lanyon, J.M. 2004. Levels and probable origin of predatory scarring on humpback whales (*Megaptera novaeangliae*) in east Australian waters**.** *Wildl. Res.* 31(2): 163–70.

Noad, M.J., Dunlop, R.A., Bennett, L. and Kniest, H. 2016. Abundance estimates of the east Australian humpback whale population (BSE1): 2015 survey and update. Paper SC/66b/SH21 presented to the IWC Scientific Committee, June 2016, Bled, Slovenia (unpublished). 11pp. [Paper available from the Office of this Journal]

Noad, M.J., Kniest, E. and Dunlop, R.A. 2019. Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Popul. Ecol.*: 1–12. [doi: 10.1002/1438-390X.1014].

Omura, H. 1953. Biological study on humpback whales in the Antarctic whaling areas IV and V. *Sci. Rep. Whales Res. Inst.* 8: 81–102.

Parham, J., Stewart, C., Crall, J.P., Rubenstein, D., Holmberg, J. and Berger-Wolf, T. 2018. An animal detection pipeline for identification. Presented to the 2018 IEEE Winter Conference on Applications of Computer Vision (WACV). 9pp. [doi: 10.1109/WACV.2018.00123; Available from: *https://www.researchgate.net/publication/324996074_An_Animal_Detection_Pipeline_for_Identification*].

Pike, G.C. 1953. Colour pattern of humpback whales from the coast of British Columbia. *J. Fish. Res. Bd. Can.* 10(6): 320–25.

Pitman, R.L., Totterdell, J.A., Fearnbach, H., Ballance, L.T., Durban, J.W. and Kemps, H. 2015. Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Mar. Mamm. Sci.* 31(2): 629–57. [doi: 10.1111/mms.12182].

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* 46:757–60.

Rosenbaum, H.C., Clapham, P.J., Allen, J., Nicole-Jenner, M., Jenner, C., Florezgonzalez, L., Urban, J., Ladron, P., Mori, K., Yamaguchi, M. and Baker, C.S. 1995. Geographic variation in ventral fluke pigmentation of humpback whale *Megaptera novaeangliae* populations worldwide. *Mar. Ecol. Prog. Ser.* 124(1–3): 1–7.

Schevill, W.E. and Backus, R.H. 1960. Daily patrol of a *Megaptera*. *J. Mamm.* 41(2): 279–81.

Schwarz, C.J. and Stobo, W.T. 1997. Estimating temporary migration using the robust design. *Biometrics* 53:178–94.

Shane, S.H. and McSweeney, D. 1990. Using photo-identification to study pilot whale social organization. *Rep. Int. Whal. Commn* (Special Issue 12): 259–63.

Stevick, P.T., Palsbøll, P.J., Smith, T.D., Bravington, M.V. and Hammond, P.S. 2001. Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58(9): 1,861–70.

True, F.W. 1904. *The Whalebone Whales of the Western North Atlantic Compared with Those Occurring in European Waters; with Some Observations on the Species of the North Pacific*. Smithsonian Contributions to Knowledge, v.33, Smithsonian Institution Press, Washington, DC. 138pp. doi: *10.5962/bhl.title.25586* [Available from: *https://www.biodiversitylibrary.org/bibliography/25586#,*]

Weideman, H.J., Jablons, Z.M., Holmberg, J., Flynn, K., Calambokidis, J., Tyson, R.B., Allen, J.B., Wells, R.S., Hupman, K., Urian, K. and Stewart, C.V. 2017. Integral curvature representation and matching algorithms for identification of dolphins and whales. Presented to the 2017 IEEE International Conference on Computer Vision Workshop (ICCVW). arXiv:1708.07785 [cs.CV]. doi: 10.1109/ICCVW.2017.334 [Available at: *https://www.researchgate.net/publication/322649922_Integral_Curvature_Representation_and_Matching_Algorithms_for_Identification_of_Dolphins_and_Whales*]

Wenzel, F. and Lopez-Suarez, P. 2012. What is known about cookie cutter shark (*Isistius spp.*) interactions with cetaceans in Cape Verde seas? *Zoologia Caboverdiana* 3(2):57–66.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. *Behav. Ecol.* 6(6):199–208.

Whitehead, H. 2008. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. The University of Chicago Press, Chicago and London.

Winship, A.J., Jorgensen, S.J., Shaffer, S.A., Jonsen, I.D., Robinson, P.W., Costa, D.P. and Block, B.A. 2012. State-space framework for estimating measurement error from double-tagging telemetry experiments. *Methods Ecol. Evol.* 3(2): 291–302. [doi: 10.1111/j.2041-210X.2011.00161.x].

Yoshizaki, J. 2007. Use of natural tags in closed population capture-recapture studies: Modeling misidentification. PhD thesis, North Carolina State University, Raleigh, North Carolina. 178pp.

Yoshizaki, J., Pollock, K.H., Brownie, C. and Webster, R.A. 2009. Modeling misidentification errors in capture–recapture studies using photographic identification of evolving marks. *Ecology* 90(1): 3–9. [doi: 10.1890/08-0304.1].

Zhou, Z.-H. 2012. *Ensemble Methods: Foundations and Algorithms*. Chapman and Hall/CRC Press. xiv + 222pp.

[Figures are available in Supplementary Materials]

Table 6a

Changes in characteristics of ventral-tail flukes, dorsal fin shapes and lateral body marks in forty-four females sighted in five or more years.

						Ventral-tail flukes^ Array of Coded Discrete Characteristics (ACDC)				
Mnemonic name	UID*	Gender	Resightings (Number of years)	Years resighted **(Bold=with calf)**	Span of years	Primary	Secondary	Tertiary	Dorsals shape and lateral body marks	Scratches, dots, rings and rub marks on lateral body
1 Agathea	0326	Female	8	98, 99, **00, 02**, 03, **04, 07, 09**	12	NC	NC	NC	NC	NC
2 Alchemy[#]	1128	Female	5	**02, 04, 06, 08, 10**	9	NC	NC	NC	NC	NC
3 Alexandria	0559	Female	6	99, **03,** 0, **05, 07,** 09	11	NC	NC	C	NC	NC
4 Amity	0185	Female	6	97, **00, 02, 04, 06, 0S**	12	NC	NC	C	NC	C
5 Bluebell[#]	0232	Female	5	**97, 03, 05, 07, 11**	15	NC	NC	NC	NC	NC
6 Buttons[#]	0573	Female	6	**99, 01, 03, 07, 0, 12**	14	NC	NC	NC	NC	NC
7 Coda	0248	Female	11	**97,** 98, 99, **00, 01, 02,** 03, **04, 05,** 06, **07**	11	NC	NC	NC	NC	NC
8 Ester	0158	Female	6	**96, 98, 00, 03, 06, 09**	14	NC	NC	NC	NC	NC
9 Dover[#]	0865	Female	5	**01, 03, 05, 07, 12**	12	NC	NC	NC	NC	NC
10 Hodda	1116	Female	5	02, 03, 04, 06, 08	7	NC	NC	C	NC	C
11 Iceberg[#]	0221	Female	8	97, 98, 99, 03, **05, 07, 10, 12**	16	NC	NC	NC	NC	C
12 Ionus[#]	1101	Female	6	**02, 04, 06, 08, 10, 12**	11	NC	NC	NC	NC	NC
13 Italy[#]	0663	Female	5	99, 00, **06,** 08, **11**	13	NC	NC	NC	NC	C
14 Klina	1017	Female	5	02, 03, 04, **06, 08**	7	NC	NC	C	NC	NC
15 Lahaina	0293	Female	5	**97, 99, 01, 04, 08**	12	NC	NC	NC	NC	NC
16 Magenta[#]	0149	Female	9	**96, 98, 99, 01, 03, 04, 06, 08, 10**	15	NC	NC	NC	NC	NC
17 Mallard	0016	Female	6	94, **97, 01, 05, 08**	15	NC	NC	NC	NC	NC
18 My Auntie	0037	Female	7	94, **97,** 98, 01, **02,** 05, **06**	13	NC	NC	NC	NC	NC
19 Nala[#]	0007	Female	12	**92, 96,** 97, **98, 99, 02, 03, 06,** 08, **09, 10, 12**	21	NC	NC	NC	NC	C**
20 Nouveau	0164	Female	8	**96,** 98, 99, **04, 06,** 07, **08, 09**	14	NC	NC	NC	NC	NC
21 Numner	0574	Female	5	**99, 01, 04, 06, 08**	10	NC	NC	NC	NC	C
22 Papoose	0425	Female	9	**98,** 99, **00, 01, 02,** 03, **04, 06, 08**	11	NC	NC	NC	NC	NC

*UID = Universal identification number in fluke catalogue. ^NC = No change observed. C = Change observed. [#]Resight-history extended with sightings between 2010 and 2012. **Fig. 4 Supplementary Material.

Table 6b

Changes in characteristics of ventral-tail flukes, dorsal fin shapes and lateral body marks in forty-four females sighted in five or more years.

Mnemonic name	UID*	Gender	Resightings (number of years)	Years resighted **(Bold=with calf)**	Span of years	Ventral-tail flukes^ Array of Coded Discrete Characteristics (ACDC)			Dorsals shape and lateral body marks	Scratches, dots, rings and rub marks on lateral body
						Primary	Secondary	Tertiary		
23 Paulita[#]	1452	Female	6	04, 05, **06, 08, 09, 10**	7	NC	NC	NC	NC	NC
24 Pendant[#]	0654	Female	6	00, 03, 04, **06, 09, 12**	13	NC	NC	NC	NC	NC
25 Pele	0414	Female	5	**98,** 99, **00, 02, 08**	11	NC	NC	NC	NC	NC
26 Pinto[#]	0247	Female	6	97, 99, 02, **07, 09, 11**	15	NC	NC	C	NC	NC
27 Pixie[#]	1053	Female	5	**02, 06, 08,** 09, **12**	11	NC	NC	NC	NC	C
28 Quaver	0093	Female	5	**95,** 96, **97, 03, 07**	13	NC	NC	NC	NC	NC
29 Raindrop[#]	0089	Female	5	95, **96,** 97, 00, **11**	17	NC	NC	NC	NC	NC
30 Rama	0417	Female	6	**98,** 99, **00, 01, 02, 05**	8	NC	NC	NC	NC	NC
31 Reiki	0157	Female	8	**96, 98, 00,** 01, 06, **07, 08, 09**	14	NC	NC	NC	NC	NC
32 Ruby	0102	Female	8	**95, 97, 98, 00, 02, 03, 07, 08**	14	NC	NC	C	NC	C
33 Sapphire	0891	Female	5	**01, 03, 05, 07, 09**	9	NC	NC	NC	NC	NC
34 Sundance[#]	0165	Female	6	**96, 98, 02,** 05, **07, 11**	16	NC	NC	NC	NC	NC
35 Tasco[#]	0721	Female	6	00, 05, **06,** 09, 10,	11	NC	NC	NC	NC	C
36 Timantha	0092	Female	8	95, **96,** 99, **00, 01, 02, 04, 06**	12	NC	NC	NC	NC	NC
37 Tolerance	0022	Female	6	94, **98, 00, 03, 05, 09**	16	NC	NC	NC	NC	NC
38 Venus[#]	0114	Female	6	**95, 98, 99, 01, 05, 10**	16	NC	NC	NC	NC	C
39 Wedgewood	0152	Female	7	**96, 98, 00, 02, 04, 06, 08**	13	NC	NC	NC	NC	NC
40 Wendy[#]	0409	Female	8	**98,** 00, **01, 02, 03, 05, 08, 11**	14	NC	NC	NC	NC	NC
41 White Wings	0428	Female	6	**98, 00, 02, 04, 08, 09**	12	NC	NC	NC	NC	NC Figure 3, SM"
42 White Wolf[#]	**0006**	Female	11	**92,** 94, **97, 98,** 99, **01, 04, 05, 07, 09, 12**	21	NC	NC	NC	NC	NC
43 Yolanda	0160	Female	8	**96, 98, 00, 02, 03, 05,** 06, **07**	12	NC	NC	NC	NC	NC
44 Zipper	0014	Female	5	94, **97, 01, 04, 09**	16	NC	NC	NC	NC	NC

*UID = Universal identification number in fluke catalogue. ^NC = No change observed. C = Change observed. [#]Resight-history extended with sightings between 2010 and 2012. **Fig. 3 Supplementary Material.

Table 7

Changes in characteristics of ventral-tail flukes, dorsal fin shapes and lateral body marks in twenty males sighted in four or more years.

						Ventral-tail flukes^ Array of Coded Discrete Characteristics (ACDC)				
Mnemonic name	UID*	Gender	Resightings (number of years)	Years resighted	Span of years	Primary	Secondary	Tertiary	Dorsals shape and lateral body marks	Scratches, dots, rings and rub marks on lateral body
1 Excalibur	0074	Male	5	94, 95, 96, 98, 01	8	NC	NC	C	NC	C
2 Floppy	0161	Male	10	96, 97, 99, 01, 02, 03, 04, 0S, 06, 07	12	NC	NC	NC	C	NC*
3 Gatch	0040	Male	8	94, 96, 97, 98, 99, 02, 04, 0S	12	NC	NC	NC	NC	C
4 Glen QC	0352	Male	8	98, 02, 03, 04, 05, 07, 08, 09	12	NC	NC	NC	NC	C
5 Hockey Stick#	0300	Male	3	98, 99, 10	13	C	C	NC	NC	NC**
6 Jambo	0012	Male	5	93, 95, 99, 01, 04	12	NC	NC	NC	NC	NC
7 Kristallos	0278	Male	8	97, 98, 99, 00, 02, 03, 07, 08	12	NC	NC	NC	NC	NC
8 Matra#	0400	Male	6	98, 00, 01, 05, 07, 11	14	NC	NC	NC	NC	C
9 Moon Shark#	0586	Male	10	99, 00, 01, 02, 04, 05, 06, 07, 08/11	13	NC	NC	C	C	C***
10 Orsen Welles	0418	Male	5	98, 99, 03, 05, 06	9	NC	NC	C	NC	NC
11 Owl Claw	0043	Male	8	94, 95, 96, 97, 98, 00, 03, 0S	12	NC	NC	NC	NC	C
12 Peru#	0715	Male	9	00, 01, 02, 04, 05, 06, 07, 09, 11	12	C	NC	NC	NC	C****
13 Picollo	0984	Male	4	02/06/07/08	7	NC	NC	C	NC	C
14 Rune	0420	Male	5	98, 00, 01, 03, 06	9	NC	NC	C	NC	C
15 Scorpio#	0730	Male	7	00, 01, 02, 03, 04, 10, 12	13	C	NC	NC	NC	C*****
16 Spiral	0049	Male	5	94, 96, 97, 98, 00	7	NC	NC	NC	NC	C
17 Trident#	0470	Male	4	99, 00, 02.12	14	NC	NC	NC	NC	C
18 Two Forks#	0237	Male	6	97, 01, 04, 05, 06, 12	16	NC	NC	NC	NC	C
19 Velo#	0531	Male	4	99, 00, 01, 11	13	NC	NC	NC	NC	C
20 Zephyrus#	1507	Male	5	04, 05, 08, 09, 10	7	NC	NC	NC	NC	C

*UID = Universal identification number in fluke catalogue. ^NC = No change observed. C = Change observed. #Resight-history extended with sightings between 2010 and 2012.
*Fig. 9 Supplementary Material. **Fig. 5 Supplementary Material. ***Fig. 7 Supplementary Material. ****Fig. 6 Supplementary Material. *****Fig. 8 Supplementary Material.

Table 8

Changes in characteristics of ventral-tail flukes, dorsal fin shapes and lateral body marks in fifteen immature whales[1] sighted in two or more years.

Mnemonic name	UID*	Gender	Resightings (number of years)	Years resighted **(Bold=with calf)**(1)	Span of years	Ventral-tail flukes^ Array of Coded Discrete Characteristics (ACDC)			Dorsals shape and lateral body marks	Scratches, dots, rings and rub marks on lateral body
						Primary	Secondary	Tertiary		
1 Atoll	0966	Unknown	4	01/00, 02/08, 03/08, 04/08	4	NC	NC	C	NC	NC*
2 Ayla	0944	Female	2	02/08, **05/10**	4	NC	NC	C	NC	C
3 Crowe	0723	Unknown	2	00/09, 01/08	2	NC	NC	C	NC	C
4 Gemini	1063	Unknown	2	02/09, 04/08	3	NC	NC	C	NC	C
5 Hitch	0767	Unknown	2	01/08, 03/09	3	NC	NC	C	NC	NC
6 Marcus	0536	Inferred M	2	99/09, 04/09	6	NC	NC	C	NC	C
7 Moon E.T.	0665	Female	3	00/08, 01/08, **04/09**	5	C	C	C	NC	C**
8 Moon Mist	1182	Unknown	2	03/08, 04/08	2	NC	NC	C	NC	NC
9 Ninety Nine[#]	1046	Inferred M	3	02/00, 04/08, 10/09	9	C	C	C	NC	C***
10 Santa Maria	1392	Female	3	02/00, 04/08, 06/08	5	NC	NC	C	NC	C
11 Solstice	0965	Unknown	2	02/08, 03/09	2	NC	NC	C	NC	C
12 Strike Two	1180	Unknown	2	02/09, 03/08	2	NC	NC	C	NC	C
13 Tom	0617	Male	3	00/08, 01/08, 02/08	3	NC	NC	C	NC	C
14 Ustinov	1166	Unknown	3	03/08, 04/08, 05/08	3	NC	NC	C	NC	C
15 Ziggy	0524	Unknown	2	99/09, 00/08	2	C	C	C	NC	NC****

[1] Some resight histories extend beyond immaturity. *UID = Universal Identification Number in fluke catalogue. ^NC = No change observed. C = Change observed. [#] Resight-history extended with sightings between 2010 and 2012. *Fig. 10 Supplementary Material. **Fig. 12 Supplementary Material. ***Fig. 11 Supplementary Material ****Fig. 13 Supplementary Material.