FOR CONSIDERATION BY THE SCIENTIFIC COMMITTEE OF
THE INTERNATIONAL WHALING COMMISSION
MADEIRA, PORTUGAL JUNE 2009

Capture-recapture estimation of abundance for humpback whales of French Polynesia (Breeding Stock F) using photo-identification

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ABSTRACT

The abundance of humpback whales in French Polynesia was estimated using capture-recapture analysis of individual fluke photographs collected from 1999 to 2007. Photographs were reconciled annually and cross-matched for resights between years. The Usable Photos catalogue for these years contains 406 individual whales represented by photographs considered to be of usable quality. All Usable Photos were also reviewed according to five Quality Control criteria evaluating the clarity of the photos in five categories resulting in a catalogue of 256 individual whales defined as the Quality Control catalogue. Estimates of abundance were calculated for both the Usable Photos and Quality Control catalogues using CAPTURE, a closed population model, (adjusted for time and heterogeneity, but unadjusted for mortality) and JOLLY, an open population model (adjusted for time and survival). The CAPTURE and JOLLY estimates for the Usable Photos were 2,046 (CV 0.16) and 1,225 (CV 0.40) respectively. The CAPTURE and JOLLY Quality Control estimates were much smaller; 949 (CV 0.16) and 564 (CV 0.90) respectively. To alleviate the assumption of a closed population for nine years, an additional CAPTURE closed population estimate was calculated using only the years 2003-2007. For this 5-year period the estimate for the Usable Photos was 1,849 (CV 0.16), and the Quality Control estimate was 853 (CV 0.24).

INTRODUCTION

Although many humpback whale stocks appear to be recovering from whaling in the southern hemisphere, several small breeding stocks in Oceania in the South Pacific remain low despite an almost 50 year moratorium on whaling (Clapham *et al.* 2009). Monitoring abundance of these recovering populations is crucial, providing important information for the International Whaling Commission's Comprehensive Assessment on southern hemisphere humpback whales.

Mackintosh (1965) assumed the number of humpback whales in Oceania directly above Area VI was relatively small compared to Areas IV and V. French Polynesia is considered part of the International Whaling Commission breeding stock F in Oceania north of Antarctic Area VI. Historically French Polynesia was considered a transitory location, but more recently has been recognized as a breeding ground (Poole 2006). Although it has been established that French Polynesia is genetically differentiated from other Oceania breeding stocks (Olavarria *et al.* 2007) there has been a small degree of interchange documented by photo-identification between French Polynesia and Tonga (n=4 Garrigue *et al.* 2007) and between French Polynesia and American Samoa (n=4 Garrigue *et al.* 2007).

Fluke photo-identification has been collected consistently in French Polynesia since 1999. A preliminary estimate of Oceania, including French Polynesia, was first presented to the IWC by Baker *et al.* (2006) using a multi-year closed population model of fluke photograph catalogues compiled by the principal investigator from each Oceania region. In this study we seek to improve this abundance estimate for

French Polynesia humpback whales by using both open and closed population models. We compare results from two photo catalogues where one is a subset of the original principal investigator's photo catalogue that has passed additional quality criteria for the purpose of minimizing bias in the estimation of abundance (Garrigue *et al.* 2007).

METHODS

Field surveys

Fluke identification photographs were taken of humpback whales (Katona *et al.* 1979) on dedicated and opportunistic vessels throughout the breeding ground in various islands of French Polynesia. Collection of fluke photographs most often occurred around the island of Moorea in the Society Islands, less often around the island of Rurutu in the Austral Islands and rarely around smaller islands within the Society Islands (Poole 2006; Figure 1). Photographs were taken aboard one of two vessels between the months of July and November from 1999-2007. Some but not all years had similar sampling effort. Differences in sampling effort included opportunities lost due to weather and availability of volunteers.

Photograph matching procedure

The photographs were reconciled annually within and between years by the principal investigator in order to exclude all poor quality photographs and to record any possible recaptures identified from previous years. After photographs were reconciled the best fluke photograph per individual was chosen by the principal investigator to become a part of the Usable Photos catalogue. This catalogue currently consists of 406 individual humpback whales seen in French Polynesia waters for the years 1999-2007. Annually this catalogue is submitted to the South Pacific Whale Research Consortium's synoptic study of humpback whales in Oceania (Garrigue *et al.* 2007) for Quality Control analysis and assessment of possible matches between breeding regions.

All images of the Usable Photos catalogue were reviewed according to a standard set of quality control criteria that were originally developed for the SPLASH program in the North Pacific. This is a scoring system based on quality measures of the photos that are irrespective of distinctiveness of the fluke (Calambokidis *et al.* 2001, Garrigue *et al.* 2007). It consists of five quality criteria using a score between 1 and 5 in each category to accept or reject photographs (Figure 2). These five criteria categories were (i) proportion of the fluke visible, (ii) fluke angle, (iii) the lateral angle of the photographer, (iv) exposure quality, and (v) contrast quality as described in Calambokidis *et al.*, (2001). All the images were graded from the highest quality (1) to the lowest quality (5). A score of 4 or 5 in any of the five categories was considered to be of insufficient quality for a representative comparison of resight rates and was therefore excluded from the Quality Control catalogue (Garrigue *et al.* 2007). For a complete description of the implementation of the SPLASH criteria see Garrigue *et al.* (2007).

Data sets

As a result of the review two data sets, or photo catalogues, were used for this analysis (Table 1).

1) Usable Photos (N=406) included photographs of individuals of the primary investigator excluding those of extremely poor quality.
2) Quality Control catalogue (N=256) included photographs which scored between 1 and 3 for each of the SPLASH criteria.

Abundance estimation procedure

Lincoln-Petersen and Schnabel estimates

Pair-wise estimates were generated using the Chapman's modified Lincoln-Petersen model (Begon 1979; Amstrup *et al.* 2005). The weighted mean of the Petersen (Schnabel) model generated an estimate inclusive of all nine years of the study period (1999-2007). Like the Lincoln-Petersen estimate, the Schnabel model does not account for variation in capture probabilities (Begon 1979).

Program CAPTURE
We applied a series of models implemented in Program CAPTURE (Rexstad & Burnham, 1991) within Program MARK to generate the abundance covering the entire study period 1999-2007. To alleviate the violation of the closed population assumption in CAPTURE we ran an additional analysis including only the last five years 2003-2007. Different models were used for both study periods in Program CAPTURE to account for sources of variation in capture probabilities unique to humpback whales. These included but weren't limited to Darroch's model for time (M_t), and Chao's model for time in combination with individual heterogeneity (M_{th}) (Otis *et al.* 1979; Chao *et al.* 1992; Norris & Pollock 1996).

Program JOLLY
Program JOLLY operates as an open population model which allows for demographic changes in the population over time (Jolly 1965), and was implemented here to estimate abundance and survival for the years 1999-2007. In addition, program JOLLY performs a Likelihood Ratio Test (LRT) to determine if capture probabilities vary over time.

RESULTS
Between the years 1999-2007 humpback whales were identified in French Polynesia waters from distinct coloration patterns of the ventral side of the fluke. A series of capture-recapture models were used to determine abundance estimates for both the Usable Photos and Quality Control catalogues, and with the exception of the estimates generated by Program JOLLY all estimates assumed a closed population. Within-year sample sizes varied for both catalogues, ranging from 27-62 for the Usable Photos catalogue and 15-44 for the Quality Control catalogue (Table 1). Resighting rates were relatively low, with only 39 individuals sighted twice (34 individuals sighted twice for Quality Control) and 5 individuals sighted three times (for both Usable Photos and Quality Control catalogues) (Figure 3). Abundance estimates ranged from 1,225-2,046 for the Usable Photos catalogue and 564-949 for the Quality Control catalogue. All results are summarized in Table 2.

Catalogue Results
The Lincoln-Petersen estimate (not shown) gave a mean estimate of 1,000 individuals, but displayed wide variation between some years with 2-year population estimates ranging from 600 to 3,000 depending on the years calculated. A similar pattern was seen for the Quality Control catalogue with a mean of 400 individuals and 2-year estimates ranging from 200-850. The Schnabel weighted mean of the Petersen estimate for the entire study period was 1,679 (CV 0.15) for Usable Photos and 825 (CV 0.16) for Quality Control.

For the period 1999-2007, among the multiple-occasion closed population CAPTURE models the M_{th} Chao gave the largest estimate for both Usable Photos (2,046, CV 0.16) and Quality Control (949, CV 0.16). Similarly the model chosen by Program CAPTURE was M_t Darroch for both Usable Photos (1,824, CV 0.13) and Quality Control (861, CV 0.13). For the period 2003-2007 the largest estimate was M_{th} Chao for both Usable Photos (1,849, CV 0.16) and Quality Control (853, 0.24 CV). Once again the model chosen by Program CAPTURE was M_t Darroch (Usable Photos 1,724, CV 0.13; Quality Control 803, CV 0.20).

In the open population model, Program JOLLY mean results were much lower than the closed population model Usable Photos (1,225, CV 0.40) Quality Control (564, CV 0.90). These individual year results (not shown) contained large CVs (>0.40) and wide confidence intervals sometimes including zero. A Likelihood Ratio test in Program JOLLY was significant implying Model A (time dependent survival and capture) was the appropriate model to use compared to Model D (constant survival and capture). The survival rate calculated by Jolly for Usable Photos (0.82) and Quality Control (0.78) demonstrating about an 80% survival rate from one capture occasion to the next.

DISCUSSION

Closed population model five year study

There were several challenges in the analysis of these data including violations of a closed population assumption and limitations from sparse data. To assume a closed population of humpback whales for an extended study period is not biologically realistic (Calambokidis *et al.* 1990) and will have a positive bias on the abundance estimate (White *et al.*. 1982). An additional analysis with a shorter time period was used in Program CAPTURE (2003-2007). These results revealed similar abundance estimates to the nine year study, but larger standard errors most likely due to the reduction in captures and recaptures (Schwarz & Seber 1999). Despite this statistical quandary the results from the five year study period appear to be the most sensible to this study given that they address the heterogeneity issue and still have reasonable confidence intervals unlike the open model Program JOLLY.

Preferred model in Program CAPTURE

The model chosen by Program CAPTURE for both the Usable Photos and Quality Control catalogue was Darroch's M_t which assumes capture probability varies from one occasion to another (time) but do not vary in individual capture probabilities (heterogeneity). However, heterogeneity becomes apparent with large variability in capture probabilities (White *et al.* 1982) which was shown in our data to vary from 0.02 to 0.06. Our analysis revealed both time and heterogeneity to be factors as shown with a low number of recaptures (~10%) and sampling variability. Chao's model for both time and heterogeneity (Model M_{thChao}) has been shown to work well for sparse data and large variation in capture probability (Chao *et al.* 1989; Chao *et al.* 1992). Although models containing only time give reasonable estimates, if heterogeneity is present both of these models will have a negative bias (Otis *et al.*. 1978; Hammond & Anthony 2006). Both time and heterogeneity effects have been shown to be important in migratory animals including some cetacean species (Calambokidis *et al.* 1990; Gormley *et al.* 2007). Based on the information in Program CAPTURE and the known biology of the species, the appropriate model appears to be M_{th} Chao.

Limitation of open population model

The open population model requires more data per capture period (>100 captures) than the closed population models in order to provide equally as precise of estimates (White *et al*. 1982). Our number of individuals per capture occasion was < 60 resulting in large standard errors and high CVs. Although it is imperative that demographic changes are considered for both survival and capture probabilities to differ for each sampling period in studies of long lived species (Pollock *et al.*. 1990; Schwarz & Arneson 1996) in cetacean studies this has been found to be challenging due to sparse data (Cerchio *et al.* 2006). In this study a precise open population estimate could not be achieved.

Quality Control

Compared with the Usable Photo catalogue the Quality Control catalogue results were substantially smaller. The Quality Control criteria reduced the number of photographs by 156 from the Usable Photos catalogue, but also resulted in 5 individuals lost in recaptures (Figure 3). The loss of the large number of photographs could bias the abundance estimate if these are indeed animals that represent the population. The removal of marginal quality photographs should have reduced the probability of a 'missed match' (calling two sightings different when they were in fact the same) potentially improving the precision of the estimate (Perry *et al.* 1990; Stevick *et al.* 2001). However, this removal also reduces the sample size of both sightings and resightings, perhaps because of other underlying factors such as fluking behavior. In which case, the Quality Control could result in an unintended negative bias. A third possibility is that individuals represented by poorer quality photographs include a higher proportion of transients. The continued use of the Quality Control catalogue could assist in answering the question of transience. If after several years, there are still a large number of individuals only seen once in the population it is most likely

due to transience and not to low quality photographs. 'Double tagging' using genotypes would also provide information needed to evaluate these effects (Garrigue *et al.* 2004).

Summary and future direction

In summary, we have performed an extensive evaluation of humpback whale population abundance for breeding stock F2 in the South Pacific and discussed the advantage of using Quality Control photographs to carry out this evaluation. Sample size limitations and low capture probabilities resulted in low precision for open population models. However taking into consideration a variety of models and sample combinations the population is likely to be within the range of 850-1,850 individuals, suggesting potential vulnerability of a recovering population that is thought to have low interchange with other regions of Oceania (Garrigue *et al.* 2007).

Future surveys should include remote outlying areas within French Polynesia that are virtually unexplored for humpback whales, especially in the eastern Tuamotu Islands and northern Gambier Islands (Gannier 2004). If whales in outer islands are new individuals utilizing other habitat within the vast territory of French Polynesia they may need to be estimated independently. In contrast, if whales in outlying areas are also seen in well surveyed regions like Moorea or Rurutu within the same season this could provide critical data on residence times for some French Polynesia humpback whales.

ACKNOWLEDGEMENTS

The authors greatly appreciate Kirsten Thompson, Claire Garrigue and members of the South Pacific Whale Research Consortium who reviewed photographs tirelessly from the entire region of Oceania for Quality Control and interchange. We also wish to thank Dr. Robert Anthony for his time and efforts on various sections of this manuscript. His sound advice through meetings and emails was greatly appreciated. The International Fund for Animal Welfare graciously provided funding for the fieldwork in French Polynesia.

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Table 1: All photo-identification data representing yearly survey effort for capture-recapture analysis of French Polynesia humpback whales.

Synoptic Years	1999	2000	2001	2002	2003	2004	2005	2006	2007
Regions photographed	Moorea Rurutu	Moorea Rurutu	Moorea Rurutu	Moorea Rurutu	Moorea Rurutu	Moorea Rurutu Raiatea	Moorea Rurutu	Moorea	Moorea
Usable photos New sightings per year	46	29	27	42	59	62	52	28	61
Usable Photos Cumulative Catalogue Total	46	75	102	144	203	265	317	345	406
Usable photos Resights of individuals each year	0	1	2	1	3	18	5	6	9
Quality Control New sightings per year	22	15	19	31	44	41	20	21	43
Quality Control Cumulative Catalogue Total	22	37	56	87	131	172	192	213	256
Quality Control Resights of individuals each year	0	0	1	0	3	17	4	6	9

Table 2: Abundance estimates of Usable Photos and Quality Control tail fluke photo-identification catalogues for humpback whales of French Polynesia using the Schnabel estimate, closed models calculated by CAPTURE within Program MARK and an open model calculated by JOLLY.

	Usable Photos					**Quality Control**				
	N	SE	CV	95% CI	Model Selection	N	SE	CV	95% CI	Model Selection
Schnabel 1999-2007	1,679	254	0.15	1,181-2,177	--	825	132	0.16	566-1,084	--
Darroch's M(t) 1999-2007	1,824	235	0.13	1,437-2,389	1.0	861	112	0.13	678-1,124	1.0
Darroch's M(t) 2003-2007	1,724	112	0.13	678-1,124	1.0	803	160	0.20	561-1,203	1.0
M_{th} Chao 1999-2007	2,046	318	0.16	1,532-2,798	0.80	949	154	0.16	708-1,321	0.66
M_{th} Chao 2003-2007	1,849	439	0.16	1,197-2,970	0.73	853	206	0.24	556-1,392	0.72
Program Jolly 1999-2007	1,225	500	0.40	246-2,203	--	564	509	0.90	0-1,587	--
Survival Rate Φ	0.82	0.17	--	--	--	0.78	0.15	--	--	--

Figure 1: French Polynesia including the two locations (circled) humpback whale data has mostly been collected, Moorea in the Society Islands and Rurutu in the Austral Islands (Poole 2006).

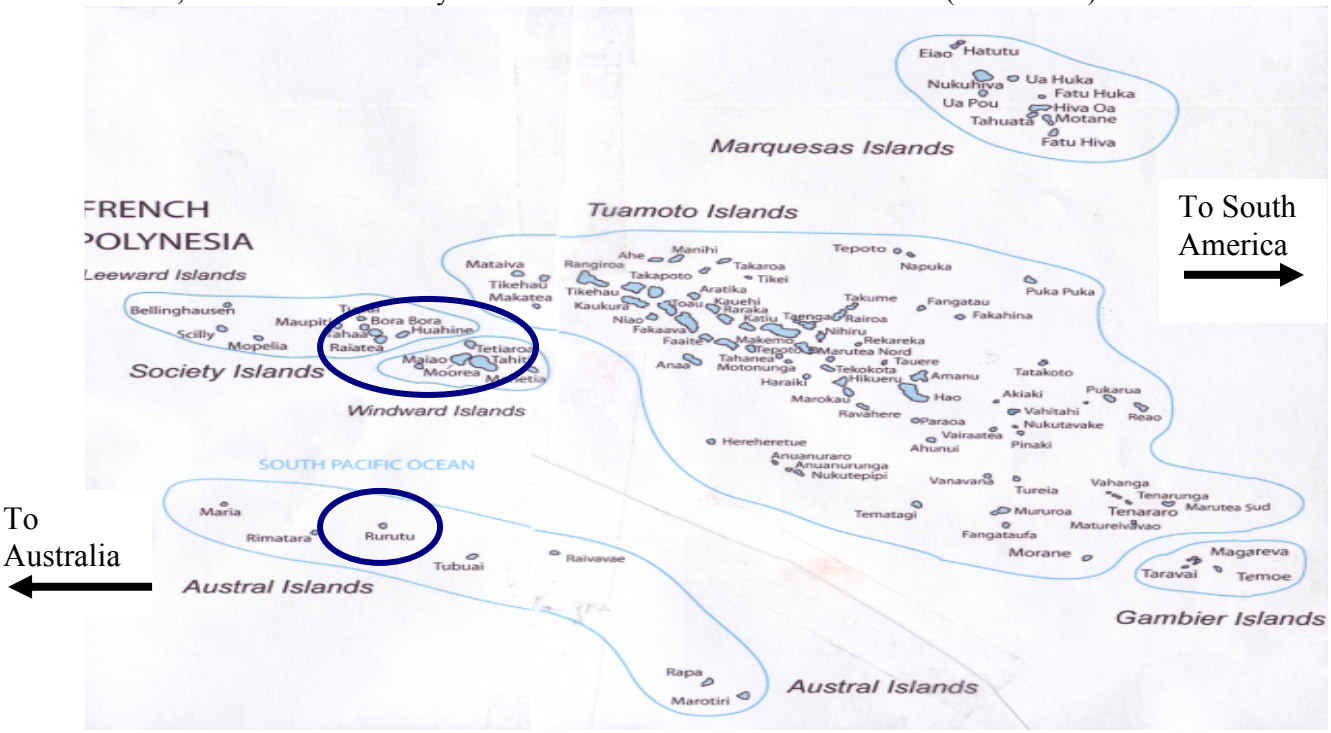

Figure 2: Examples of humpback whale fluke photos. The left photo was considered part of the Usable Photos catalogue due to the unique markings visible in the middle and to the right of center on the fluke, but was removed after Quality Control due to a score of 4 in the categories of % visible, fluke angle, and focus. The one on the right has passed all five Quality Control categories scoring a 3 or less for each.

a) 

b) 

Figure 3: The number of times individual humpback whales were sighted in French Polynesia 1999-2007.