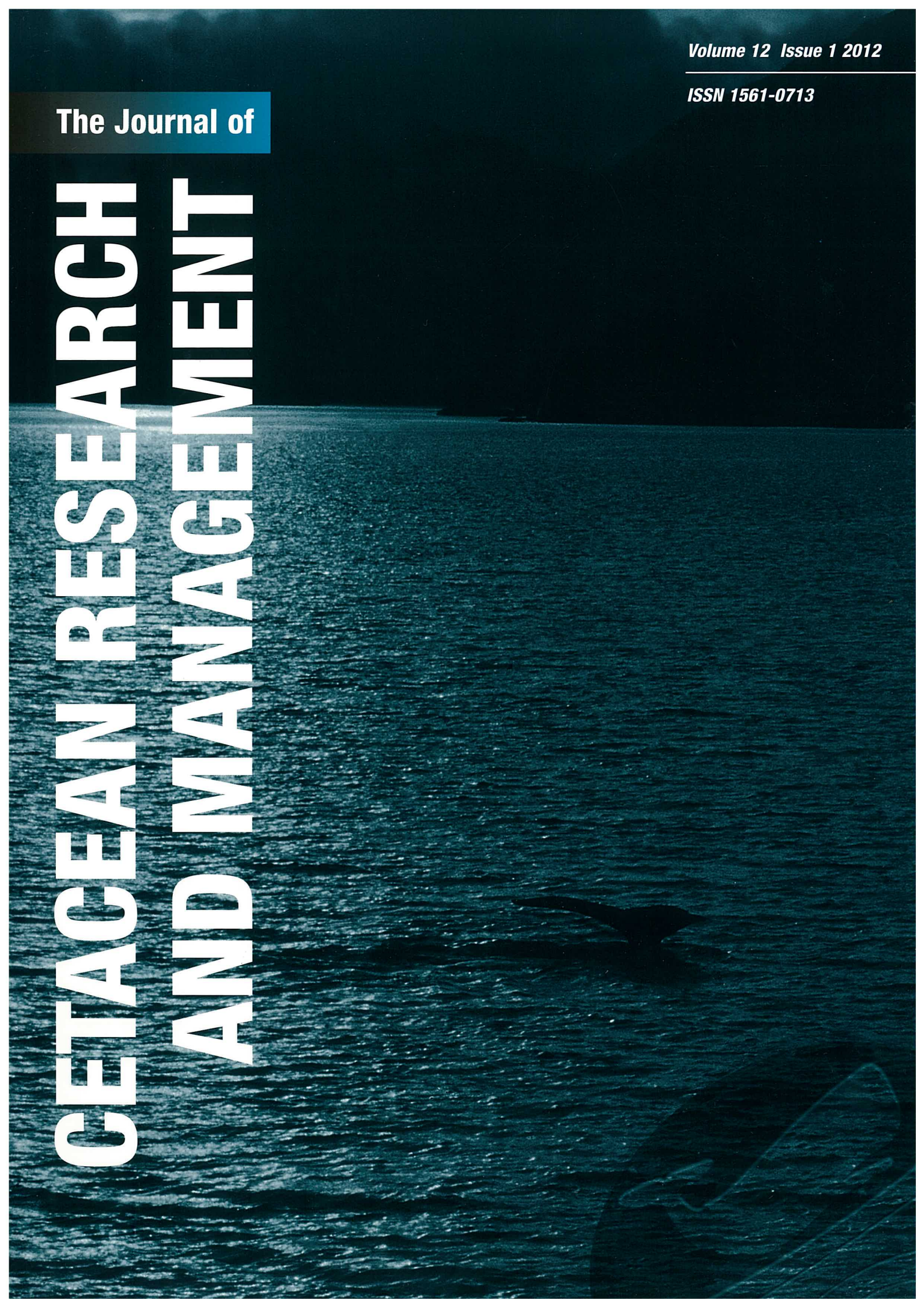


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# **CETACEAN RESEARCH AND MANAGEMENT**





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## Editorial

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Welcome to this the first issue of the twelfth volume of the *Journal of Cetacean Research and Management*. This volume contains fifteen papers covering a wide range of conservation and management issues.

I would like to draw your attention to the *Guide for Authors* included at the end of this issue. Please read these

carefully before submitting manuscripts. Not following the guidelines may result in considerable delay in the consideration of your manuscript!

G. P. DONOVAN  
*Editor*

# Rate of increase and current abundance of humpback whales in West Greenland

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## ABSTRACT

Aerial line transect surveys of the density of humpback whales (*Megaptera novaeangliae*) conducted off West Greenland eight times between 1984 and 2007 were used to estimate the rate of increase on the summer feeding ground. Only surveys in 1993, 2005 and 2007 had enough sightings to construct independent density estimates, whereas the surveys in 1984–85 and 1987–89 had to be merged and treated as two surveys. The annual rate of increase was  $9.4\% \text{ yr}^{-1}$  (SE = 0.01) between 1984 and 2007. This rate of increase is higher than the increase estimated at the breeding grounds in the West Indies, but is of the same magnitude as the observed rate of increase at other feeding grounds in the North Atlantic. A matrix model based on observed life history parameters revealed that the theoretical growth rate of a humpback whale population ranged between 1 and 11%. This confirms that the observed growth in West Greenland is within the plausible values. The survey in 2007 was used to make a fully corrected abundance estimate including corrections for whales that were submerged during the passage of the survey plane. The line transect estimate for 2007 was 1,020 (CV = 0.35). When the estimate was corrected for perception bias with mark-recapture distance sampling (MRDS) methods, the abundance increased to 1,505 (0.49). A correction for availability bias was developed based on time-depth-recorder information on the time spent at the surface (0–4m). However, used directly this correction leads to a positively-biased abundance estimate and instead a correction was developed for the non-instantaneous visual sighting process in an aircraft. The resulting estimate for 2007 was 3,272 (CV = 0.50) for the MRDS analysis. An alternative strip census estimate deploying a strip width of 300m resulted in 995 (0.33) whales. Correction for perception bias resulted in 991 (0.35) whales and corrected for the same availability bias as for the MRDS method resulted in a fully corrected estimate of 2,154 (0.36) humpback whales in West Greenland in 2007.

KEYWORDS: HUMPBAC WHALE; ABUNDANCE ESTIMATE; SURVEY-AERIAL; SATELLITE TAGGING; WEST GREENLAND; MARK-RECAPTURE; DISTANCE SAMPLING

## INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) undertake long migrations between high latitude, productive feeding grounds during summer and warmer oligotrophic mating/breeding grounds at low latitudes during winter (Kellogg, 1929; Norris, 1967). The main breeding grounds in the North Atlantic are located in the West Indies and the feeding grounds are primarily located in northern Norway, around Iceland, in West Greenland, in eastern Canada, and in the Gulf of Maine (Stevick *et al.*, 2003).

The large catches of North Atlantic humpback whales during the commercial whaling époque nearly exterminated the population and as an effect commercial whaling of humpback whales has been banned since 1955 (Smith and Reeves, 2002). To document the recovery of such long-lived, slowly reproducing migratory species long time series of abundance estimates covering the distributional range of the population is needed. Such time series of abundance have been collected in most of the core areas and there seem to be a general increase in the population. In the West Indies the instantaneous rate of increase between 1979 and 1993 has been estimated at 3.1% (Stevick *et al.*, 2003).

Increases in abundance of humpback whales have also been detected at several of these feeding grounds. For

example, annual increases of 11% from 1970 to 1988 (Sigurjónsson and Gunnlaugsson, 1990) and 12% during 1986 and 2001 (Pike *et al.*, 2009) around Iceland, 5.5% in the Gulf of Maine (Barlow and Clapham, 1997) and 9.4% in the Western North Atlantic (Katona and Beard, 1990) have been observed or estimated. Until now, no estimates of changes in abundance have been developed for the West Greenland feeding ground.

Aerial surveys for common minke (*Balaenoptera acutorostrata*) and fin whales (*Balaenoptera physalus*) have been conducted at regular intervals in West Greenland since 1984. Estimates of abundance of humpback whales from these surveys have only been presented for 2005 (Heide-Jørgensen *et al.*, 2008) mostly due to the low number of sightings in the previous years.

In this study the aerial survey data from 1984 to 1993 were re-examined and used to construct a time series of the relative abundance of humpback whales using eight surveys from 1984, 1985, 1987, 1988, 1989, 1993, 2005, and 2007. These estimates are then used together with recent abundance estimates to estimate the rate of increase of humpback whales on the West Greenland feeding ground since 1984. The observed rate of increase is compared to a theoretical model of the plausible range of growth based on

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Table 1

Effort and sightings distributed by year and strata that are comparable between years for the aerial surveys of West Greenland. Only effort and sightings in Beaufort sea state <5 is included.

Year/strata	Effort (km)	Area (km <sup>2</sup> )	Transects	Effort/area	Sightings	Mean pod size (SE)	Sighting rate
<b>1984</b>							
1: 71°20'–70°N	491	24,516	5	0.0200			
2: 70°–68°30'N	435	17,872	3	0.0243			
3A: 68°30'–67°N inshore	224	14,913	3	0.0150			
3B: 68°30'–67°N offshore	735	19,305	7	0.0381			
4A: 67°–66°N inshore	442	9,446	5	0.0468			
4B: 67°–66°N offshore	398	8,311	6	0.0479			
5A: 66°–65°N inshore	174	6,431	3	0.0271			
5B: 66°–65°N offshore	644	10,900	7	0.0591			
6: 65–64°N	2,145	17,107	15	0.1254	3		
7: 64–63°N	699	11,122	7	0.0628	1		
8: 63°–62°N	410	11,748	4	0.0349	1		
Sum	6,797	151,671	65	0.0448	5	2.14 (0.27)	0.00074
<b>1985</b>							
1: 71°20'–70°N	791	24,516	7	0.0323			
2: 70°–68°30'N	321	17,872	2	0.0180			
3A: 68°30'–67°N inshore	337	14,913	4	0.0226			
3B: 68°30'–67°N offshore	424	19,305	4	0.0220			
4A: 67°–66°N inshore	444	9,446	5	0.0470	1		
4B: 67°–66°N offshore	462	8,311	7	0.0556			
5A: 66°–65°N inshore	829	6,431	9	0.1289	2		
5B: 66°–65°N offshore	1,156	10,900	12	0.1061	1		
6: 65–64°N	1,007	17,107	7	0.0589	3		
7: 64–63°N	298	11,122	3	0.0268			
8: 63°–62°N	772	11,748	6	0.0657			
Sum	6,841	151,671	66	0.0451	7	2.14 (0.27)	0.00102
<b>1987</b>							
1A: 71°30'–69°15'N	1,915	14,779	13	0.1296			
1B: Disko Bay and Vaigat	729	5,358	11	0.1361			
2: 69°15'–67°N	1,153	39,883	7	0.0289			
3: 67°–64°15'N	1,417	42,400	8	0.0334	4		
4: 64°15'–60°40'N	1,673	25,165	9	0.0665	1		
5: 60°40'–58°45'°N	1,118	16,518	8	0.0677	2		
Sum	8,005	144,103	56	0.0556	7	1.9 (0.14)	0.00087
<b>1988</b>							
1A: 71°30'–69°45'N	703	24,560	10	0.0286			
1B: Disko Bay and Vaigat	404	13,876	12	0.0291			
2A: 69°45'–68°N	820	29,228	5	0.0281			
2B: 68°–66°30'N	1,077	19,488	10	0.0553			
3: 66°30'–64°15'N	1,399	41,660	9	0.0336	7		
4: 64°15'–60°45'N	648	50,742	6	0.0128	2		
5: 60°45'N–58°45'N	605	34,283	8	0.0176			
Sum	5,656	213,837	60	0.0265	9	1.1 (0.14)	0.00159
<b>1989</b>							
2A: 69°45'–68°00'N	428	29,228	4	0.0146			
2B: 68°–66°30'N	836	19,488	5	0.0429			
3: 66°30'–64°15'N	706	41,660	11	0.0169	1		
4: 64°15'–60°45'N	1,218	50,742	19	0.0240	2		
5: 60°45'–58°45'N	72	34,283	2	0.0021			
Sum	3,260	175,401	41	0.0186	3	2.7 (0.7)	0.00092
<b>1993</b>							
1A: 71°30'–69°45'N	138	25,130	5	0.0055			
1B: Disko Bay and Vaigat	392	13,110	8	0.0299			
2A–C: 69°45'–68°00'N	1,635	15,160		0.1078			
2B–C: 68°–66°30'N	94	15,700	5	0.0060			
3 offshore: 66°30'–64°15'N	185	26,680	2	0.0069	1		
3 coast: 66°30'–64°15'N	828	23,100	10	0.0358	6		
4 offshore: 64°15'–60°45'N	348	24,320	4	0.0143			
4 coast: 64°15'–60°45'N	2,341	27,410	29	0.0854	9		
5 offshore: 60°45'–58°45'N	436	18,450	6	0.0236	1		
5 coast: 60°45'–58°45'N	881	14,920	11	0.0590	3		
Sum	7,140	178,850	75	0.0399	20	3.2 (0.60)	0.00280
<b>2005</b>							
CF: 59°–58°N	293	11,523	4	0.0254			
CW: 67°30'–64°N	1,958	74,798	30	0.0262	4		
Disko Bay	556	12,312	12	0.0452	1		
SG: 61°–59°N	1,106	19,491	19	0.0567	4		
SH: 68°30'–67°30'N	577	15,669	7	0.0368			
SW: 64°–61°N	1,968	29,781	31	0.0661	13		
Sum	6,458	163,574	103	0.0395	22	8.3 (0.38)	0.00340

Cont.

Table 1 cont.

Year/strata	Effort (km)	Area (km <sup>2</sup> )	Transects	Effort/area	Sightings	Mean pod size (SE)	Sighting rate
<b>2007</b>							
1: Uummannaq Fjord	191	8,404	3	0.0227			
2: 71°30'–69°45'N	502	22,631	5	0.0222			
3: Disko Bay and Vaigat	532	14,653	9	0.0363			
4: 69°45'–68°N	545	34,272	4	0.0159	1		
5: 68°–66°30'N offshore	862	16,226	9	0.0531	3		
6: 68°–66°30'N inshore	973	14,902	9	0.0653			
7: 66°30'–64°N offshore	551	22,085	6	0.0249	2		
8: 66°30'–64°N inshore	1,345	20,264	12	0.0664	5		
9: 64°–62°N	998	20,334	12	0.0491	4		
10: 62°–60°30'N	932	15,951	10	0.0584	3		
11: 60°30'–59°N	1,194	24,085	16	0.0496	2		
14: coastal 67–66°30'N	45	189	6	0.2381	1		
Sum	8,670	213,996	101	0.0405	21	1.5 (0.21)	0.00242

life history observations from North Atlantic and North Pacific humpback whale populations.

## MATERIAL AND METHODS

### Construction of abundance estimates for 1984 and 1985

Aerial surveys of the West Greenland banks north of 62°N were conducted in June–July 1984 and 1985 (Figs 1a and 1b). East-west going transects separated by two nautical miles were chosen randomly and were flown in a twin-engine high winged *Partenavia Observer P68* at a target altitude and speed of 183m (600ft) and 160km hr<sup>-1</sup> (100 knots), respectively. Three observers participated and the right front observer also acted as data recorder. Distance to sightings was estimated with *Suunto* inclinometers and was together with information on size of humpback whale groups recorded on tape recorders. The number of sightings from the surveys in 1984 and 1985 were too low to develop reliable detection functions. Instead the detection function from the surveys in 1987–1989 was used with a left truncation at 200m to take into account the effects of the flat windows used in the 1984–85 surveys (cf. Richard *et al.*, 2010).

### Construction of abundance estimates for 1987–89 and 1993

Aerial line transect surveys covering the West Greenland banks were completed in July–August 1987–1989 and 1993 (Figs 1c to 1f) and were conducted with a twin engine *Partenavia Observer P68* with two observers in rear seats with bubble windows and one observer in the right front seat with a flat window. Information on size of humpback whale groups and declination angle to sightings measured with *Suunto* inclinometers were recorded.

Due to the low number of sightings, a common detection function was developed for the surveys between 1987 and 1989. These surveys all used the same aircraft, the same target altitude (229m or 750ft), same speed (160km hr<sup>-1</sup>) and in some cases, the same observers. The surveys were also completed in weather conditions that were similar between years. The survey in 1993 had a sufficient number of sightings to develop an independent detection function.

### Construction of abundance estimate for 2005

An aerial survey in 2005 covering most of West Greenland (Fig. 1g) essentially used the same aircraft and techniques as previous surveys and the details of the survey were presented

in Heide-Jørgensen *et al.* (2008). The survey provided several sightings of large groups (>10 whales) which caused problems for the line transect estimation. Instead a line transect estimate for all groups <10 whales was derived and added to a strip census estimate of all groups >10 whales (discussed in detail in Heide-Jørgensen *et al.*, 2008).

### Construction of abundance estimates for 2007

An aerial line transect survey of humpback whales in West Greenland was conducted between 25 August and 30 September 2007. The survey platform was a *Twin Otter*, with long-range fuel tank and two pairs of independent observers all with bubble windows. Sightings and a log of the cruise track (recorded from the aircrafts GPS) were recorded on a Redhen msDVRs system that also allowed for continuous video recording of the trackline as well as vertical digital photographic recordings. Declination angle to sightings was measured with *Suunto* inclinometers. Target altitude and speed was 213m and 167km hr<sup>-1</sup>, respectively.

Survey conditions were recorded by the primary observers at the start of the transect lines and whenever a change in sea state, horizontal visibility and glare occurred. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf

Table 2

Estimates of relative abundance of humpback whales in West Greenland. Numbers in parenthesis indicate the coefficient of the variation. Photo-id estimates from 1982 from Perkins *et al.* (1984; 1985) and from 1988–92 from Larsen and Hammond (2004). Aerial line-transect estimates from 1984–85 and 1987–93 from this study, from 2005 from Heide-Jørgensen *et al.* (2008) and from 2007 from this study. The ship-based line transect estimate is from Heide-Jørgensen *et al.* (2007). \*=partial coverage.

Year	Aerial line transect abundance	Ship-based line transect abundance	Photo-id
1982	–	–	271 (0.13)
1984	99 (0.46)*	–	–
1985	177 (0.44)*	–	–
1987	220 (0.62)	–	–
1988	200 (0.74)	–	–
1989	272 (0.75)	–	357 (0.16)
1990	–	–	355 (0.12)
1991	–	–	376 (0.19)
1992	–	–	566 (0.42)
1993	873 (0.53)	–	348 (0.12)
2005	1,158 (0.35)	1,306 (0.42)	–
2007	1,020 (0.35)	–	–

break (i.e. the 200m depth contour). Transect lines were placed in an east-west direction except for south Greenland where they were placed in a north-south direction. The surveyed area was divided into 12 strata (Fig. 1h).

### Conventional line transect abundance estimation for all the surveys

Declination angles to sightings were converted to perpendicular distance of the animal to the trackline from:  $distance\ (m) = 213 * \tan(90 - angle)$ . Using conventional distance sampling (CDS) methods, animal abundance in each stratum was estimated by

$$\hat{N} = \frac{n}{2L\hat{\mu}} \hat{E}[s]A$$

where  $A$  is the area of the stratum,  $L$  is the total search effort in the stratum,  $n$  is the number of unique groups detected in the stratum by either observer and  $\hat{\mu}$  was the estimated effective strip width of perpendicular distances to detected groups and  $\hat{E}[s]$  was the estimated mean group size estimated using a regression of log group size against estimated detection probability (cf. Buckland *et al.*, 2001).

### Mark-recapture distance sampling correction for perception bias for the 2007 survey

The search method deployed during the 2007 survey used an independent observer configuration where the primary and secondary observer teams acted independently of each other. Detections of animals by the primary observer served as a set of binary trials in which a success corresponded to a detection of the same group by the secondary observer in the same side of the aircraft. The converse was also true because the observers were acting independently; detections by secondary observers served as trials for the primary observers. Analysis of the detection histories using logistic regression allowed the probability that an animal on the trackline was detected by an observer to be estimated, and thus, abundance could be estimated without assuming  $g(0)$  was one. These methods combine aspects of both mark-recapture (MR) techniques and distance sampling (DS) techniques and so they are known as mark-recapture distance sampling (MRDS) methods (Laake and Borchers, 2004).

Although observers were acting independently, dependence of detection probabilities on unmodelled variables (called unmodelled heterogeneity) can induce correlation in the detection probabilities. Laake and Borchers (2004) and Borchers *et al.* (2006) developed estimators

which assumed that detections were independent at zero perpendicular distance only (called point independence estimators) that are well suited for aerial surveys where no responsive movements are expected.

The effects of the correlation in detections can be reduced by modelling the effects of variables which cause the correlation. Variables, additional to perpendicular distance, can be included in the MRDS models using a model selection criteria to select the best model. Detection probability was estimated using the independent observer configuration implemented in Distance 6.0 (Thomas *et al.*, 2009).

Group abundance was estimated in each stratum using:

$$\hat{N}_G = \frac{A}{2wL} \sum_{i=1}^n \frac{1}{\hat{p}(\underline{z}_i)}$$

where  $w$  is the truncation distance,  $\underline{z}_i$  is a vector of explanatory variables for group  $i$  (possibly including the group size,  $s_i$ ) and  $\hat{p}(\underline{z}_i)$  is the estimated probability of detecting group  $i$  obtained from the fitted MRDS model. Individual animal abundance is estimated by

$$\hat{N} = \frac{A}{2wL} \sum_{i=1}^n \frac{s_i}{\hat{p}(\underline{z}_i)}$$

The estimated mean group size in the stratum is given by

$$\hat{E}[s] = \frac{\hat{N}}{\hat{N}_G}$$

### Strip census estimation of the survey in 2007

Most of the humpback whale sightings were made within 300m from the trackline and at relatively short distances. The detection function dropped beyond 300m and it was therefore decided to assume a constant probability of detecting a group of humpback whales in a 300m strip on each side of the aircraft. The mark-recapture line transect analysis indicates that no variables other than distance and observer affect detection probability (see later). Thus in addition to the CDS estimates a strip census estimate was also obtained using a simple arithmetic mean of the group size across all strata ( $\bar{s}$ ). To correct for perception bias ( $p'$ ) by the observers Chapman's (1951) modification of the Petersen estimator was used to estimate group abundance within  $w = 300$ m of the trackline (the 'covered region') over all strata:

$$\hat{N}_{G,strip} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

Table 3

Humpback whale abundance estimates in 2007 using CDS methodology showing the encounter rate ( $n/L$ ), effective strip width ( $esw$ ) and estimates for pod size  $E[s]$ , pod density  $D_G$ , pod abundance  $N_G$ , animal density  $D$  and animal abundance  $N$ . Strata without sightings are not shown although the total densities take all strata into account. CV are given in parentheses.

Stratum	$n/L$ (pods/km)	$esw$ (km)	$E[s]$	$D_G$ (pods/km <sup>2</sup> )	$N_G$ (pods)	$D$ (whales/km <sup>2</sup> )	$N$ (whales)
4	0.0018 (0.81)			0.0030 (0.83)	101 (0.83)	0.0041 (0.84)	141 (0.84)
5	0.0035 (0.77)			0.0056 (0.79)	91 (0.79)	0.0078 (0.80)	127 (0.80)
7	0.0036 (0.96)			0.0058 (0.97)	129 (0.97)	0.0081 (0.98)	180 (0.98)
8	0.0037 (0.61)			0.0060 (0.64)	121 (0.64)	0.0083 (0.65)	169 (0.65)
9	0.0050 (0.38)	0.311 (0.19)	1.394 (0.12)	0.0081 (0.43)	164 (0.43)	0.0112 (0.44)	228 (0.44)
10	0.0021 (0.68)			0.0035 (0.71)	55 (0.71)	0.0048 (0.72)	77 (0.72)
11	0.0017 (0.60)			0.0027 (0.63)	65 (0.63)	0.0038 (0.64)	90 (0.64)
14	0.0223 (0.85)			0.0358 (0.87)	7 (0.87)	0.0500 (0.88)	9 (0.88)
Total	0.0022 (0.20)			0.0033 (0.33)	732 (0.33)	0.0046 (0.35)	1,020 (0.35)



Table 4

MRDS point independence model fitted to the data from 2007 survey.

Distance sampling model	Mark recapture model	AIC	$\Delta AIC$
Uniform	Petersen	205.34	0
Half Normal: Distance	Distance	296.03	90.69
Hazard rate: Distance	Distance	296.55	91.21
Half normal: Distance	Distance + Observer	292.97	87.63
Hazard rate: Distance	Distance + Observer	293.49	88.15

where  $n$  is the total number of sightings,  $n_1$  and  $n_2$  are the total number of sightings by the primary and secondary observers and  $m_2$  is the number of sightings by both pairs of observers.

The abundance in stratum  $v$  ( $v = 4, 5, 7, 8, 9, 10, 11, 14$ ) was estimated as follows:

$$\hat{N}_{G,v} = \frac{n_v A_v}{\hat{p}' 2wL_v}$$

where  $n_v$  is the number of groups detected in stratum  $v$ ,  $L_v$  is the total length of transect in stratum  $v$ ,  $A_v$  is the surface area of stratum  $v$  and the combined detection probability for both observers ( $\hat{p}'$ ) across all strata was estimated as follows:

$$\hat{p}' = \frac{n}{\hat{N}_{G,strip}} = \frac{n}{\frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1}$$

The variance of  $\hat{p}'$ ,  $\hat{N}_{G,v}$  and  $\hat{N}_{G(Chapman)} = \sum_v \hat{N}_{G,v}$  was estimated using a nonparametric bootstrap with transect as the sampling unit. Transects were sampled with replacement, separately in each stratum, until the total number of sightings was at least as large as the original number of sightings in the stratum ( $n_v$ ).

The mean group size  $\bar{s}$  and its coefficient of variation,  $cv(\bar{s})$  was estimated across all strata and estimated individual abundance and its CV was obtained by

$$\hat{N}_{(Chapman)} = \hat{N}_{G(Chapman)} \bar{s}$$

and

$$cv(\hat{N}_{(Chapman)}) = \sqrt{cv(\hat{N}_{G(Chapman)})^2 + cv(\bar{s})^2}$$

### Correction for availability bias of the survey in 2007

The above estimates of abundance from aerial surveys are negatively biased if some animals were underwater and hence undetectable during the passage of the plane. To correct for this availability bias satellite-linked time-depth recorders were deployed on five humpback whales off Central West Greenland (Fyllas Bank 64°N, 52°W) in June–July 2000 to estimate the probability of an animal being available for detection. The satellite transmitters (SDR-T16) produced by Wildlife Computers (Redmond, Washington) were fitted with a harpoon spear for attachment. The transmitter had a length of 10cm and a diameter of 2.5cm and was sitting on the outside of the whale while an anchoring spear of 14.5cm was partly or fully inside the whale. The tags were programmed to collect and summarize measurements of the time spent at or above 4m depths in four 6hr periods and the data were transmitted through Service Argos. The tags were deployed from the stern of a MK II Zodiac powered by a 40 Hp engine.

Table 5

Number of sightings seen by each observer and the number of duplicates (seen by both) during the 2007 survey. The total column shows the number of sightings seen by observer 1 plus observer 2 minus sightings seen by both.

Pod size	Primary observer	Secondary observer	Seen by both	Total
1	14	11	10	15
2	4	1	1	4
3	1	1	1	1
5	1	1	1	1
Total	20	14	13	21

A person fixed with a harness deployed the transmitter with a 6.8m aluminum pole (diameter 33mm).

As humpback whales are available for more than an instant during aerial surveys and some whales may even be seen ahead of the plane, the probability that an animal is available is not simply the probability that it is available at a randomly-chosen instant in its dive cycle. McLaren (1961) derived an equation, used by others, including Barlow *et al.* (1988) for estimating the average probability that an animal is available (at the surface) at least some of the time within a time interval of length  $t$ :

$$\Pr(\text{available}) = (s+t)/(s+d)$$

where  $s$  is the average time the whale is at the surface,  $d$  is the average time it is below the surface and  $t$  is the window of time the whale is within visual range of the observers. However, this equation is inappropriate if  $t$  is not very small relative to  $d$ , as is clear by noting that when  $t > d$  the probability is greater than 1. A more appropriate estimator of the probability that an animal is available within time  $t$  was provided by Laake *et al.* (1997):

$$\hat{a} = \frac{E[s]}{E[s] + E[d]} + \frac{E[d](1 - e^{-t/E[d]})}{E[s] + E[d]}$$

where  $E[s]$  is the average time the whale is at the surface,  $E[d]$  is the average time it is below the surface and  $t$  is the window of time the whale is within visual range of the observers.

It was assumed that the whales were available for detection when within 4m of the surface and the times spent at above and below this measurement from 7 June through 18 July from the satellite-linked time-depth recorders were used to estimate this probability.

Abundance (corrected for availability bias) was then estimated as

$$\hat{N}_c = \frac{\hat{N}}{\hat{a}}$$

with estimated CV

$$cv(\hat{N}_c) = \sqrt{cv(\hat{N})^2 + cv(\hat{a})^2}.$$

### Construction of time series

A time series of indices of relative abundance of humpback whales was constructed from previous photo ID mark-recapture studies and from aerial and ship-based surveys presented previously (Heide-Jørgensen *et al.*, 2007; Larsen and Hammond, 2004), re-analysed in this study (Heide-



Table 6

Humpback whale abundance estimates in 2007 using MRDS methodology showing the encounter rate ( $n/L$ ), estimates for pod size  $E[s]$ , pod density  $D_G$ , pod abundance  $N_G$ , whale density  $D$  and whale abundance  $N$ . Strata without sightings are not shown although the total densities take all strata into account. CV's are given in parentheses.

Stratum	$n/L$ (pods/km)	$D_G$ (pods/km <sup>2</sup> )	$N_G$ (pods)	$D$ (whales/km <sup>2</sup> )	$N$ (whales)	$E[s]$
4	0.0018 (0.81)	0.0040 (0.90)	136 (0.90)	0.0040 (0.90)	136 (0.90)	1.00 (00.0)
5	0.0035 (0.77)	0.0075 (0.86)	122 (0.86)	0.0125 (0.96)	203 (0.96)	1.67 (0.21)
7	0.0036 (0.96)	0.0078 (1.03)	173 (1.03)	0.0157 (1.03)	346 (1.03)	2.00 (00.0)
8	0.0037 (0.61)	0.0080 (0.72)	163 (0.72)	0.0080 (0.73)	163 (0.73)	1.00 (00.0)
9	0.0050 (0.38)	0.0108 (0.54)	220 (0.54)	0.0238 (0.60)	484 (0.60)	2.20 (0.34)
10	0.0021 (0.68)	0.0046 (0.78)	74 (0.78)	0.0046 (0.78)	74 (0.78)	1.00 (0.24)
11	0.0017 (0.60)	0.0036 (0.71)	87 (0.71)	0.0036 (0.71)	87 (0.71)	1.00 (00.0)
14	0.0223 (0.85)	0.0482 (0.93)	9 (0.93)	0.0489 (0.94)	9 (0.94)	1.00 (00.0)
Total	0.0022 (0.20)	0.0045 (0.47)	985 (0.47)	0.0068 (0.49)	1,505 (0.49)	1.53 (0.14)

Jørgensen *et al.*, 2008; Larsen, 1995; Larsen *et al.*, 1989) or presented for the first time here. The trend in abundance or instantaneous rate of increase ( $N_t = N_0 e^{rt}$ ) was estimated by weighted (weight =  $1/cv(N_t)^2$ ) regression through the log transformed estimates of relative abundance ( $N_t$ ) with jack-knifed standard error.

### Population dynamics model

An age based Leslie-matrix model was created (Caswell, 2001; Leslie, 1945; 1948) using life-history data obtained from literature (Barlow and Clapham, 1997; Clapham, 1992; Gabrielle *et al.*, 2001; Mizroch *et al.*, 2004). This model was used to calculate the growth rate at a stable age structure as

the dominant positive eigenvalue of the matrix. The matrix only projects female individuals, and due to this, the fertility used is half of that reported in the literature, since there is no evidence of a strongly biased sex ratio at birth.

## RESULTS

### Construction of estimates of relative abundance

In all years, the aerial surveys covered the coastal areas of West Greenland from 60°N (in 1984 and 1985 from 62°N) to 70°N with the maximum effort between 62° and 66°N (Figs 1a–h). The total survey effort however ranged between 3,260 and 8,670km (Table 1). The average ratio between survey effort and stratum area was 0.04 (SD = 0.01). However this fluctuated in the first five years between 0.02 and 0.06, but remained constant around 0.04 after 1989. The seven abundance estimates were not significantly correlated with the survey effort ( $p = 0.42$ ). There was an increasing trend in sighting rate in the aerial surveys with  $r = 0.06$  (CV = 0.28,  $r^2 = 0.69$ ) for the period 1984 to 2007.

The combined detection function for humpback whales for the surveys in 1987–89 was fitted with a half-normal function with a left truncation at 200m to construct a detection function for the surveys in 1984–85 that used flat windows. The sample size was 10 and the effective search width was 587m (CV = 0.37) (Fig. 2a). The distribution of perpendicular distances to the 15 humpback whale sightings were combined for the surveys in 1987–1989 and a half-normal model was selected to fit the sightings distance data (Fig. 2b). The effective search width was estimated at 708m (CV = 0.20). The survey in 1993 had 18 sightings that were fitted to the half-normal model to derive an effective search width of 503m (CV = 0.43, Fig. 2c). A simple mean of the group sizes was used for each of the years.

In 2005, 22 sightings within the truncation distance of 3km were used for deriving a half-normal detection function model with an effective search width of 664m (CV = 0.12, Fig. 2d), similar to that found in previous years (see Heide-Jørgensen *et al.*, 2008). A regression of log group size against estimated detection probability was used to estimate mean group size across all strata.

In 2007, the distribution of perpendicular distances of sightings shows some sightings close to the trackline indicating the absence of a blind spot for observers beneath the plane (Fig. 2e). However, in the distributions for both observers there was a peak in sightings between 200–250m after which detection declined substantially. In 2007 all

Table 7

Proportion of time spent at surface (0–4m) for four humpback whales instrumented on Fyllas Bank in June 2006.

Whale	Date	6 hr period	Percentage time at 0–4m
21809	8/6/2000	03–09	47.92
20158	7/6/2000	03–09	19.80
20158	8/6/2000	03–09	25.59
			31.10
21801	10/6/2000	09–15	37.17
21801	20/6/2000	09–15	42.51
21802	10/6/2000	09–15	34.35
21802	17/6/2000	09–15	68.42
21802	18/6/2000	09–15	71.75
21802	22/6/2000	09–15	32.04
			47.71
21801	10/6/2000	15–21	33.52
21801	14/6/2000	15–21	26.57
21801	15/6/2000	15–21	40.67
21801	16/7/2000	15–21	34.94
20160	9/6/2000	15–21	26.53
21802	14/6/2000	15–21	37.73
21802	17/6/2000	15–21	57.77
21802	19/6/2000	15–21	39.58
			37.16
21801	9/6/2000	21–03	31.79
21801	11/6/2000	21–03	26.35
21801	14/7/2000	21–03	44.44
21801	18/7/2000	21–03	42.62
20158	5/6/2000	21–03	48.89
20158	7/6/2000	21–03	30.72
21802	16/6/2000	21–03	57.64
21802	23/6/2000	21–03	35.30
			39.72
Average	All days all whales	09–21	41.68
SD			14.24
$n$			14.00
SE			3.81
CV			0.09

Table 8

Humpback whale estimates in 2007 using strip census methodology and estimated detection probability  $\hat{p}' = 0.98$  (cv = 0.03) with esw = 300m showing the encounter rate ( $n/L$ ) and simple estimate of pod size  $\bar{s}$ , pod density  $D_G$ , pod abundance  $N_G$ , animal density  $D$ , and  $N$  animal abundance. Strata without sightings are not shown. CV's are given in parentheses.

Stratum	$n/L$ (pods/km)	$\bar{s}$	$D_G$ (pods/km <sup>2</sup> )	$N_G$ (pods)	$D$ (animals/km <sup>2</sup> )	$N$ (animals)
4	0.002 (0.81)	1.42 (0.16)	0.003(0.81)	105 (0.81)	0.004 (0.82)	149 (0.83)
5	0.004 (0.77)		0.006 (0.77)	94 (0.77)	0.008 (0.78)	134 (0.78)
7	0.004 (0.96)		0.006 (0.96)	134 (0.96)	0.009 (0.97)	190 (0.97)
8	0.003 (0.75)		0.005 (0.75)	100 (0.75)	0.007 (0.77)	143 (0.77)
9	0.004 (0.47)		0.007 (0.47)	136 (0.47)	0.010 (0.49)	193 (0.49)
10	0.002 (0.68)		0.004 (0.68)	57 (0.68)	0.005 (0.70)	81 (0.70)
11	0.002 (0.60)		0.003 (0.60)	67 (0.60)	0.004 (0.62)	96 (0.62)
14	0.002 (0.85)		0.037 (0.85)	7 (0.85)	0.053 (0.86)	10 (0.86)
Total	0.002 (0.22)		0.003 (0.29)	700 (0.29)	0.005 (0.33)	995 (0.33)

sightings were within 500m from the trackline which is very different from the distribution in 2005 where most sightings were beyond 500m. The difference is due to a combination of a different type of survey planes and observer instruction in 2007 to concentrate on covering the trackline. Both hazard rate and half normal functional forms were considered for the 2007 distribution of sightings, but based on AIC the half-normal model was chosen. The effective search width was 311m (CV = 0.19). The survey region in the 2007 survey included an area of 213,996km<sup>2</sup> with 8,670km tracklines covered in Beaufort sea states less than 5 (Fig. 1h and Table 1). The group sizes varied between 1 and 5 whales and all the 21 humpback whale sightings were seen in strata 4 to 11 with the exception of one sighting in stratum 14.

### Trends in abundance

The uncorrected estimates from the aerial surveys are smaller than the estimates from the photo identification study except for 1993 where the survey abundance estimate was about twice the estimate from the photo ID study (Fig. 3). It is however not straightforward to compare the estimates as the aerial surveys covered a much larger area and they are not corrected for the time the whales were not available at the surface to be seen by the observers. The aerial survey estimate from 2005 (1,158 95% CI 595–2,255) is similar to a ship-based line transect survey in 2005 (Fig. 3).

The time series of aerial line transect surveys provides an index of the changes in relative abundance (i.e. uncorrected for perception and availability bias) of humpback whales in West Greenland from 1984 through 2007 (Table 2). If it is assumed that the bias remains constant, the rate of increase of humpback whales on the feeding ground in West Greenland can be estimated. The abundance estimates from 1984–1985 and 1987–1989 used the same detection function and were therefore averaged for the purpose of estimating the rate of increase. The overall exponential rate of increase from 1984 to 2007 was 0.09 or 9.4% per year (SE = 0.01,  $p = 0.010$ ).

### Current abundance

The CDS estimate of 1,020 (CV = 0.35) humpback whales for 2007 does not include animals that were submerged or missed by the observers (Table 3). Both the conventional DS model and the MRDS models were fitted to the data without truncation. The final MRDS model included a term for observer in the MR model (Table 4). This indicated that the secondary observers had a much smaller probability of

detection on the trackline than the primary observers (Table 5); 0.66 (CV = 0.43) for the primary observers compared to 0.22 (CV = 0.76) for the secondary observers (Fig. 4). The estimate for both observers combined was 0.73 (CV = 0.34). The abundance of humpback whales was 1,505 animals (CV = 0.49; 95% CI 581–3896) when using MRDS methods to correct for perception bias (Table 6).

Data on surface time obtained from the satellite-linked time-depth-recorders indicate that humpback whales in West Greenland spend on average 42% (CV = 0.09) of their time during daylight periods (09–21hr) at depths <4m (Table 7). In the relatively productive waters of West Greenland, 4m is probably the maximum depth to which humpback whales can be reliably detected on the trackline from an aircraft passing at 213m altitude. Humpback whales are known to have long dive cycles with average dive times lasting several minutes and with average time spent at the surface (<4m) mostly lasting >40 seconds (Winn and Reichley, 1985). Both the dive time and the at-surface-time are considerably longer than the average time the whales are visible from an aircraft. In this survey the time between first sighting of the whales and the time when the whales passed abeam was on average 3.21s (CV = 0.38). If the probability of detecting a whale at the surface given the observation time of 3.21s and the ratio between dive and surface times is compared to an instantaneous correction of whales at the surface then the most severe positive bias can be expected for short durations of surfacings and dives (Fig. 5). For surface times >30s the positive bias from using an instantaneous correction of availability ranges between 7 and 15% for observation times between 2 and 7s, or 10% for an average 3.21s observation period. This positive bias can be eliminated by increasing the availability correction factor to 0.46. Applying this correction to the MRDS estimate gives a fully corrected abundance estimate of 3,272 (CV = 0.50, 95% CI 1,300–8,233) humpback whales in West Greenland in 2007.

The Chapman estimate of perception bias was 0.98 (CV = 0.03) and correcting for this bias results in an abundance of 995 (0.33) humpback whales in 2007 from the strip census analysis (Table 8). In comparison the CDS estimate was 1,020 (0.35) and the MRDS estimate was 1,528 (0.51). Further correction of the strip census analysis with  $\hat{a}$  46% (CV = 0.09) gives an estimate of 2,154 (CV = 0.36, 95% CI 1,087–4,270) humpback whales corrected for whales that were submerged during the passage of the plane or a slightly lower but more precise estimate than the MRDS estimate.

Table 9  
Life history data used to calculate plausible growth rates for North Atlantic humpback whales.

	Lower CI	Average	Upper CI	Geographical region	Reference
Fertility (females)	0.20	0.21	0.22	North Atlantic	Barlow and Clapham (1997)
Age at sexual maturity	6.4	5.9	5.4	North Atlantic	Clapham (1992)
Calf survival	0.797	0.805	0.813	North Pacific	Gabriele <i>et al.</i> (2001); Zerbini <i>et al.</i> (2010)
Juvenile survival	0.797	0.895	0.995		Estimated
Adult survival	0.954	0.984	0.995	North Pacific	Mizroch <i>et al.</i> (2004)
Growth rate	0.9964	1.0578	1.1070		Calculated

### Population dynamics

Age at first parturition is reported in decimal numbers in the literature and was included in the age based matrix by adding partial fertility at age 5 (Upper 95% CI and average models in Table 9) or 6 (Lower CI model, based on the 95% CI for the individual life history traits used) corresponding to the deviation from the closest higher integer, i.e. 60% fertility at age 5 (Upper) and 6 (Lower) for the CI models and 10% fertility at age 5 for the average model. Calf survival was multiplied by the fertility to obtain the chance of birth and survival to age 1. Due to uncertain data in the literature, juvenile survival (up to an age of first parturition of 5 or 6, depending on model) was set as the average of calf and adult survival in the average model, as the same value as calf survival in the Lower CI model and as the same value as adult survival in the Upper CI model. These widely ranging numbers were used to avoid under- or over-estimation of the extreme lambdas. The effect of juvenile survival was tested within the average model where juvenile survival was stepwise changed from calf survival values to the adult survival values (0.8 to 0.96) which consequently affected the growth rate linearly from 3% to 8% with all other parameters kept constant. Survival estimates and fertility affected the theoretical growth rates in a linear fashion whereas earlier age of first parturition increased the growth exponentially (Fig. 6). Estimates of the longevity of the whales had relatively little effect on the theoretical growth rate.

### DISCUSSION

Humpback whales have generally been protected in the North Atlantic since 1955 although a low level of exploitation (total catch 1955–85; 24) continued in West Greenland until 1985 (IWC, 2003). After 1985, they were completely protected although a few whales were taken as bycatch in fishery operations (total 1986–2001; 7, IWC, 2003). Considering this low level of exploitation and the fact that the number of humpback whales have clearly increased on their breeding ground (i.e. the West Indies) and feeding grounds in other areas of the North Atlantic, it is not surprising that the abundance on the West Greenland feeding ground has also increased. The detected increase is considerably larger than the increase of 3.1% per year observed in the West Indies (Stevick *et al.*, 2003). However, it is of the same magnitude as some of the estimates of increase from other North Atlantic feeding grounds (Katona and Beard, 1990; Pike *et al.*, 2009; Sigurjónsson and Gunnlaugsson, 1990).

The analysis of the dynamics of a hypothetical humpback whale population in the North Atlantic shows that the observed growth in West Greenland is within the upper range of plausible growth rates based on an age structured model

with life history parameters from observed populations of humpback whales. Both the age at first parturition and subadult survival had a profound effect on the dynamics of the population and population specific determination of these life history parameters is required to narrow the range of plausible growth rates. The values used in the model were from the Gulf of Maine (Clapham, 1992), an area considered to be part of the range of the western North Atlantic humpback whale breeding population that also is found in West Greenland.

The use of upper and lower CI models should not be interpreted as the 95% CI of population growth, since it is based on the assumption that all life history traits are at their own individual 95% CI border values. This leads to an over- and under-estimation for the possible 95% CI for the whole population growth since the probability of all life history traits to be at their maximum/minimum values at the same time is low. The matrix model does not discern between calf survival for first time mothers and experienced mothers, something that can have significant impact on other mammal species (for example rabbits (Rödel *et al.*, 2009) and cheetahs (Durant *et al.*, 2004)). A recent study on Hawaiian humpback whales also show that larger females attract more male suitors (Pack *et al.*, 2009), which could have a significant impact on young female fertility rates.

The estimates of humpback whale abundance derived from the photo-identification study in West Greenland in 1989–1993 (Larsen and Hammond, 2004) may provide a correct magnitude of the occurrence of humpback whales in the areas where the photo-identification work was concentrated at that time. However, the photo-identification work covered a smaller area of West Greenland than the aerial surveys and it is reasonable to expect that an increasing humpback whale population will also expand its distribution. Satellite tracking studies in 2001 and 2002 demonstrated that some humpback whales do not spend time within the area used for the photo-identification study (Heide-Jørgensen and Laidre, 2007; GINR, unpubl. data). In recent surveys humpback whales were found more widely in West Greenland than in previous surveys and there are now frequently records of observations far north in West Greenland (e.g. in Uummannaq 71°N; GINR, unpubl. data).

If detection probability varies with distance within the first 300m (and the CDS and MRDS analyses strongly suggest it does), then the strip transect estimate is negatively biased because it neglects heterogeneity due to distance. If some animals at distance zero are missed (and the MRDS analysis suggests that this is the case), then the CDS estimate is negatively biased. If the detection function does in reality initially increase with distance from the transect line, the



MRDS estimator of abundance might be positively biased, because while the MR component of the model allows this, the CDS component does not (i.e. the CDS detection function is monotonically decreasing) – see Fig. 4. While it is difficult to say whether or not the MRDS estimate of abundance is positively biased, it is probable that both the strip transect and CDS estimates are negatively biased.

The best estimate of the abundance of humpback whales in 2007 was 3,299 whales, with a relatively large coefficient of variation (0.57). Even the lower bound of this estimate (1,170 whales) is substantially higher than any previous estimates. The estimate is based on a visual aerial line transect survey that covered a larger part of West Greenland than in previous surveys. However coverage was still partial with poor coverage west of Disko Bay and humpback whales were often observed at the westernmost point of the transects indicating that the West Greenland feeding ground may extend over deeper water (>200m) west of the shelf area into areas not covered in any of the surveys.

The observed rate of increase and the estimates of current abundance of humpback whales on the summering ground in West Greenland change the status of this stock and allows for the resumption of a low level of harvesting which was abandoned in 1985.

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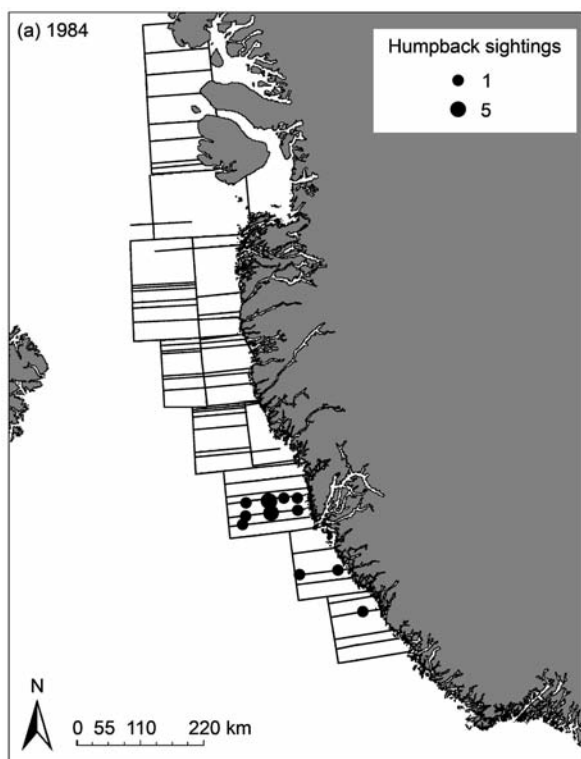


Fig. 1a. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1984.

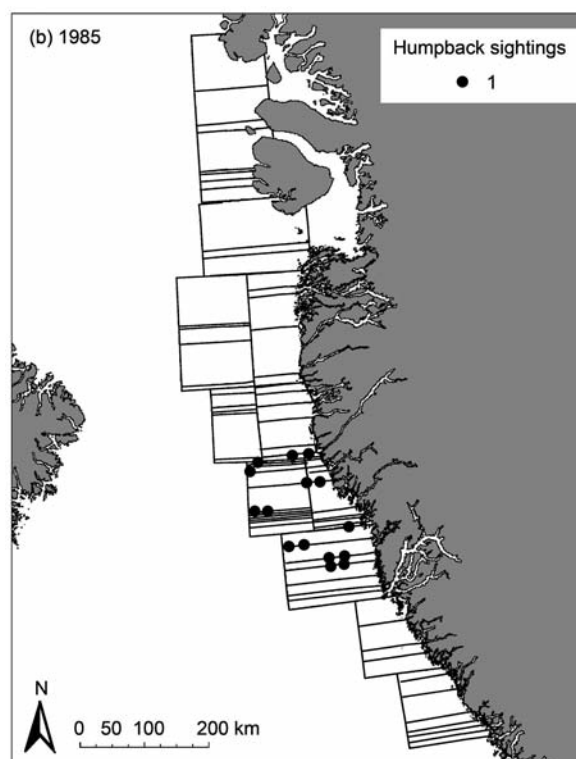


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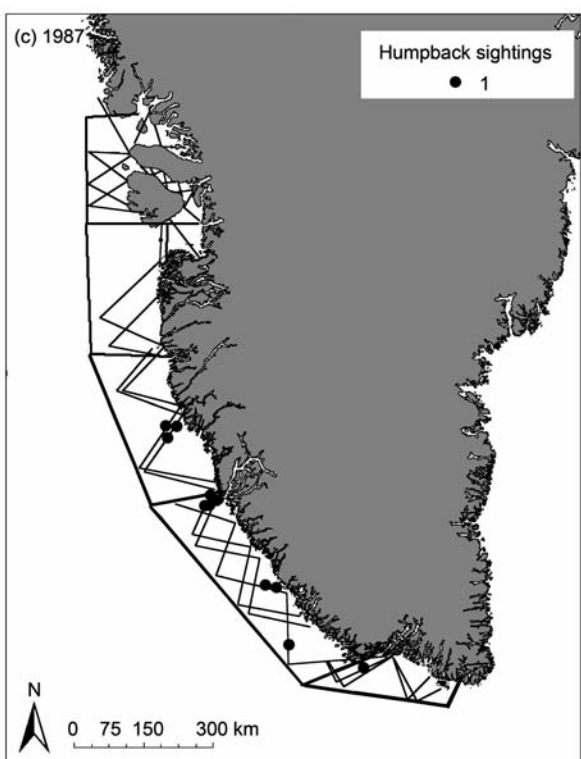


Fig. 1c. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1987.

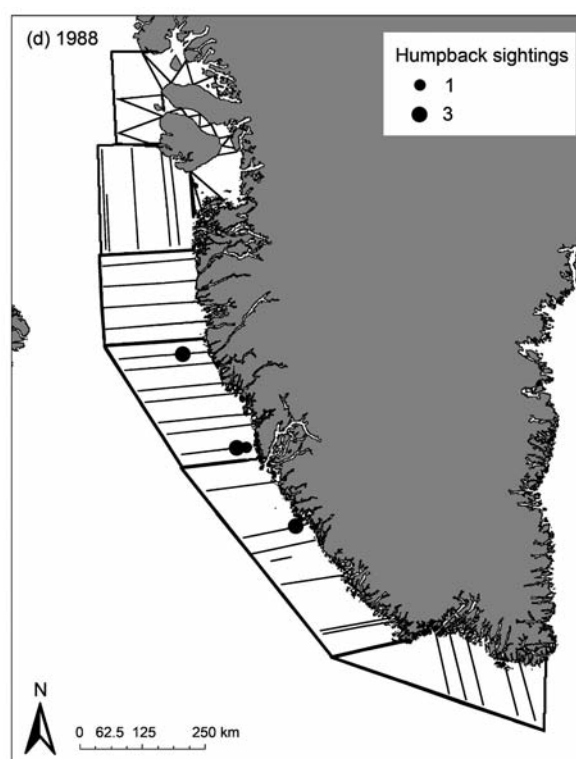


Fig. 1d. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1988.

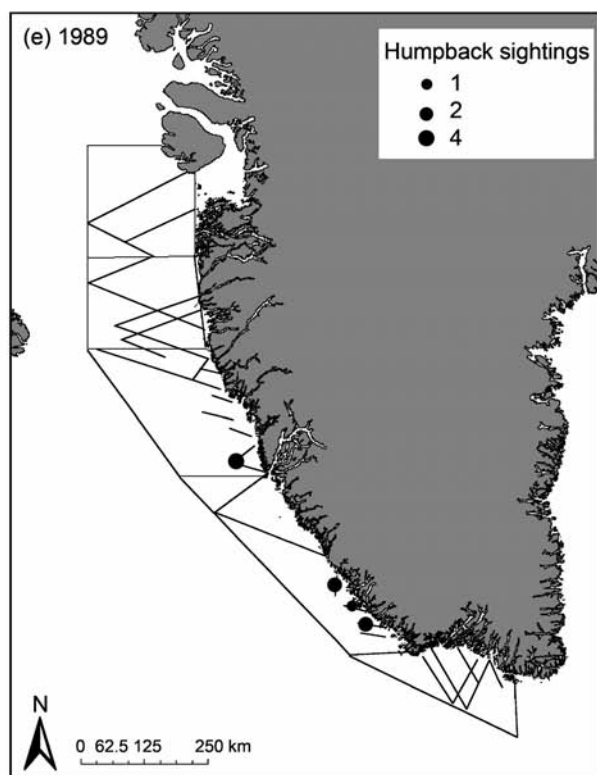


Fig. 1e. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1989.

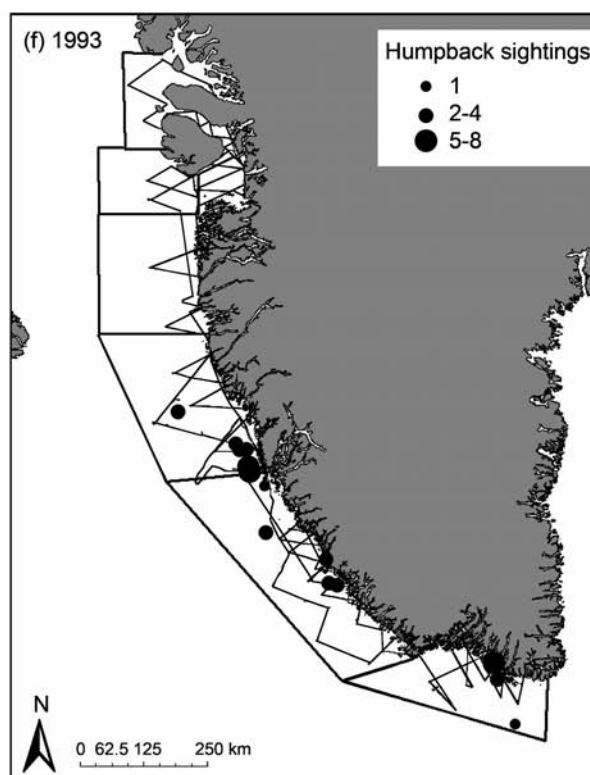


Fig. 1f. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1993.

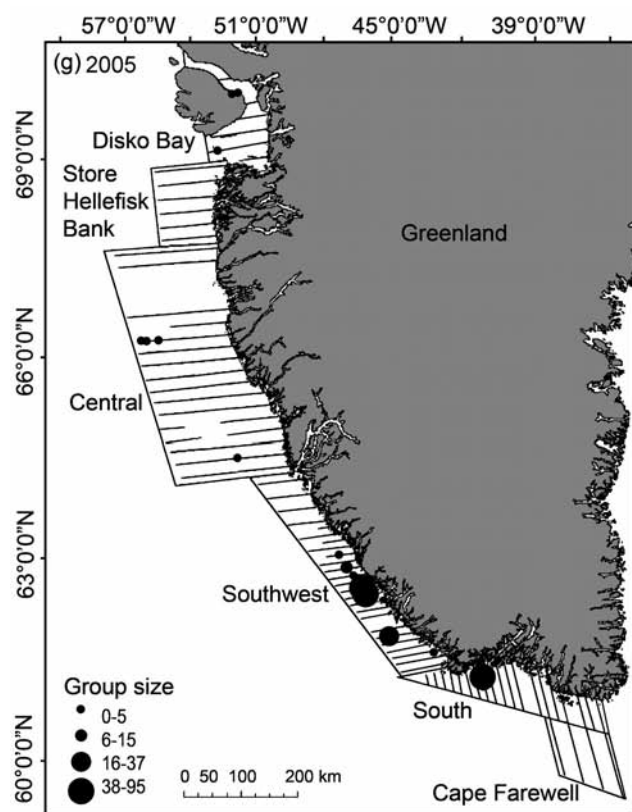


Fig. 1g. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 2005.

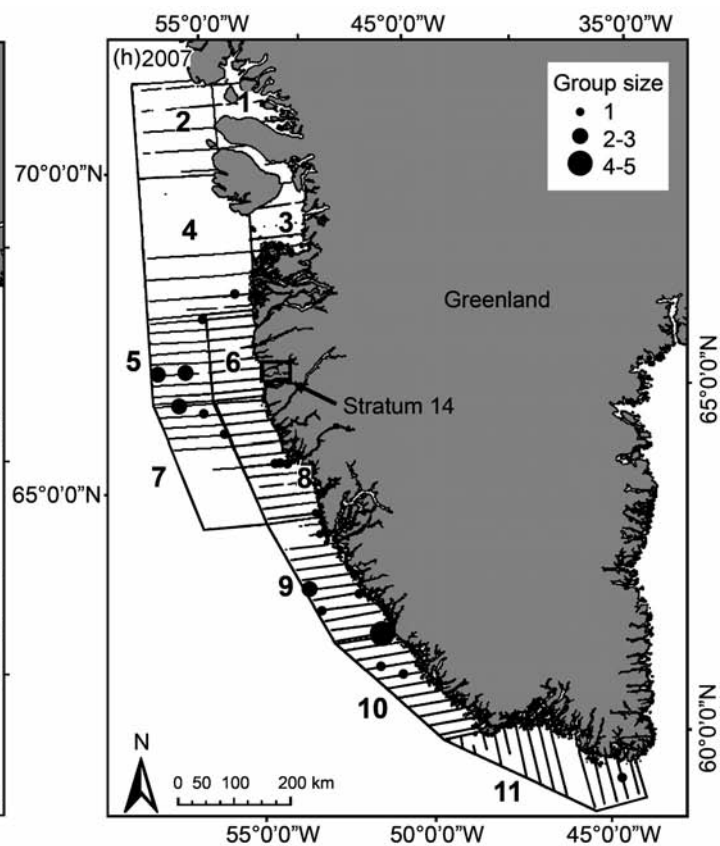


Fig. 1h. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 2007. Note that stratum 14 is inside coastal fjords.



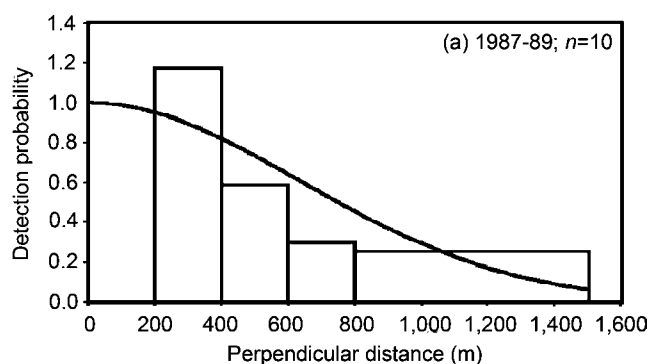


Fig. 2a. Distribution of humpback whale sightings at various distances from the trackline during the surveys in 1987–89 with a left truncation at 200m to allow the detection function to be applied to the surveys in 1984 and 1985 that used flat windows instead of the bubble windows that were used in subsequent surveys. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1,500m and the effective search width was 587m (CV = 0.37).

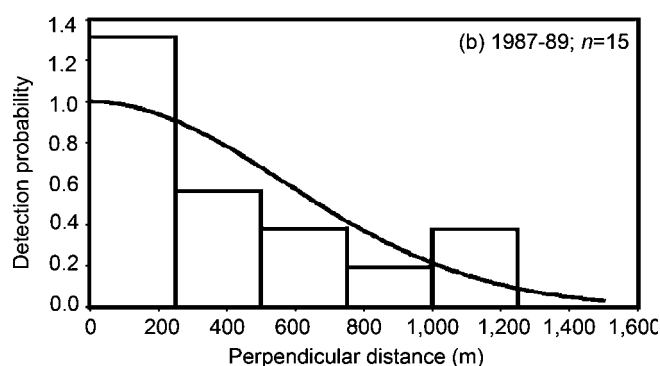


Fig. 2b. Distribution of humpback whale sightings at various distances from the trackline during the surveys in 1987–89. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1,500m and the effective search width was 708m (CV = 0.20).

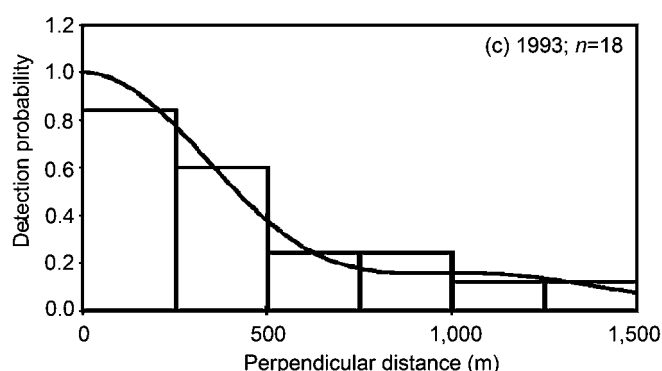


Fig. 2c. Distribution of humpback whale sightings at various distances from the trackline during the survey in 1993. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1500 m and the effective search width was 503m (CV = 0.43).

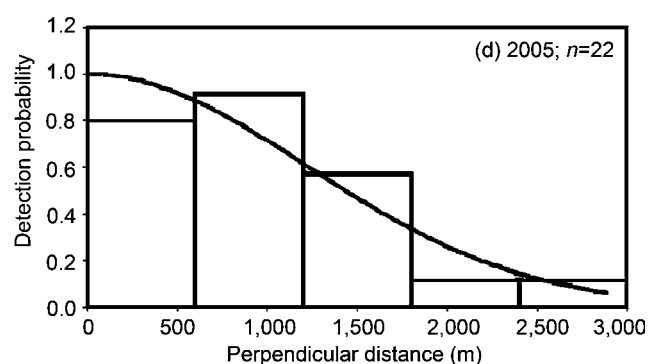


Fig. 2d. Distribution of humpback whale sightings at various distances from the trackline during the survey in 2005. Data has been fitted to the hazard rate function and the fitted curve shows the expected number of sightings. The effective search width was 1,506m (CV = 0.17) (see also Heide-Jørgensen *et al.*, 2008).

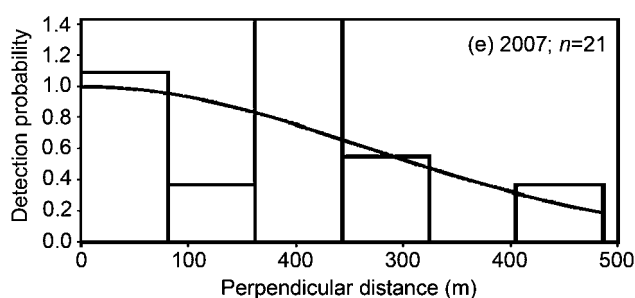


Fig. 2e. Distribution of humpback whale sightings at various distances from the trackline during the survey in 2007. Data has been fitted to the hazard rate function and the fitted curve shows the expected number of sightings. The effective search width was 311m (CV = 0.19).

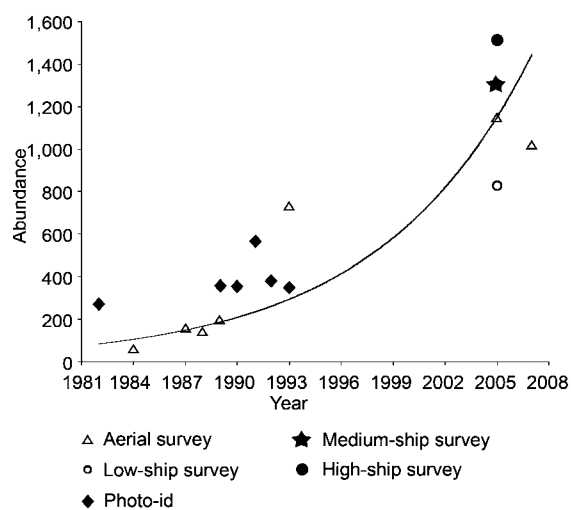


Fig. 3. Trends in relative abundance of humpback whales in West Greenland 1982–2007. The exponential growth model is fitted to the estimates from the aerial surveys. Details of the three abundance options from the ship-based survey in 2005 are given in Heide-Jørgensen *et al.* (2007).

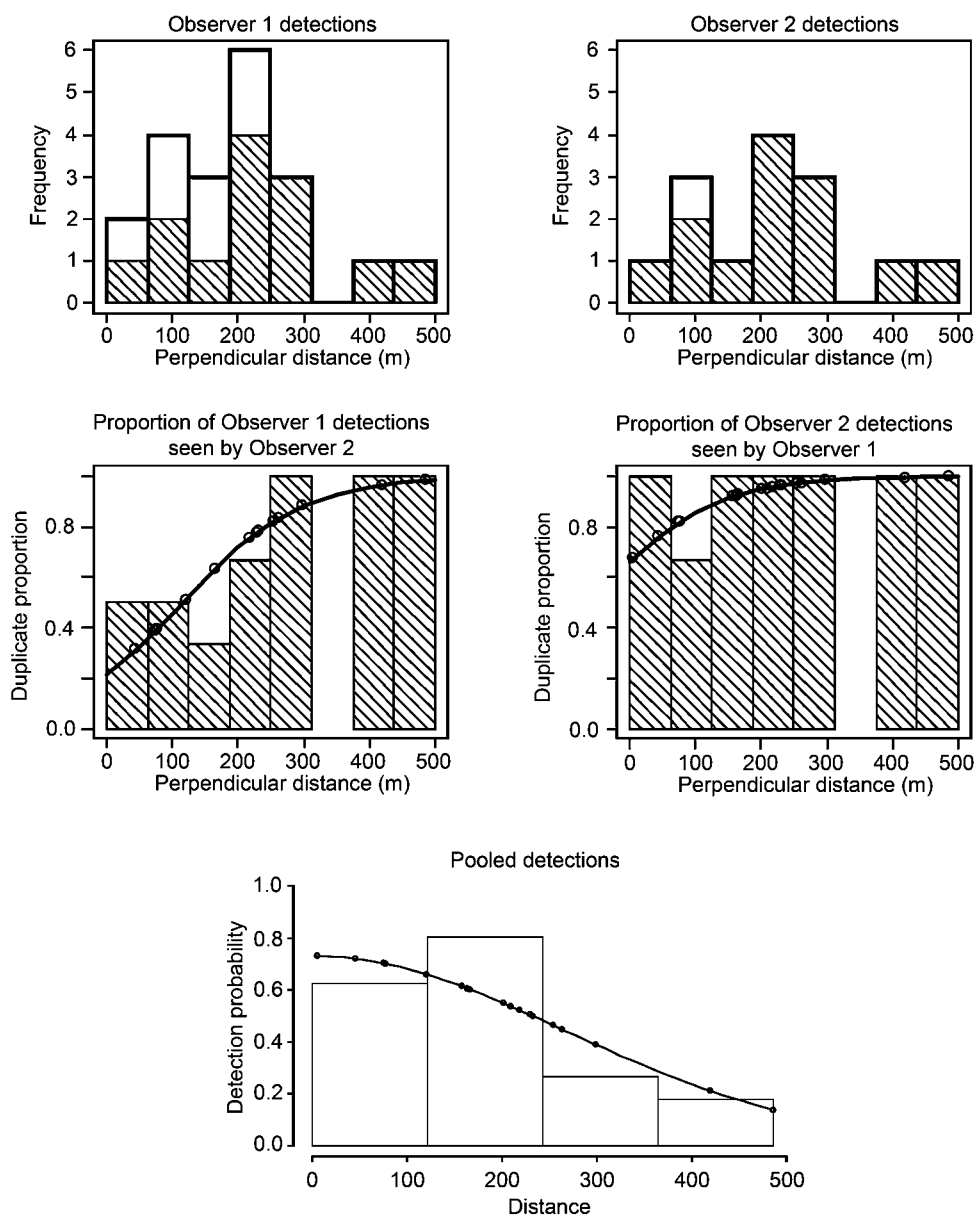


Fig. 4. Detection function plots for the MRDS analyses. Duplicate detections are indicated in the shaded areas; as a number in the top plots and as a proportion in the middle plots. The points are the probability of detection for each sighting given its perpendicular distance. The lines are the fitted models (in the pooled detection plot, the line is a smooth function fitted to the points).

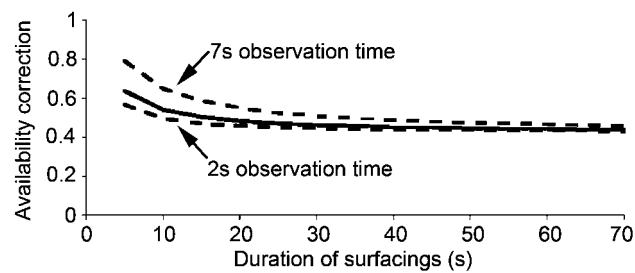


Fig. 5. Estimation of the positive bias in instantaneous availability correction factors compared to correction based on the probability of detecting a whale given surface-dive patterns with 42% of time at surface and average observation times of 2, 3.1 and 7 seconds.

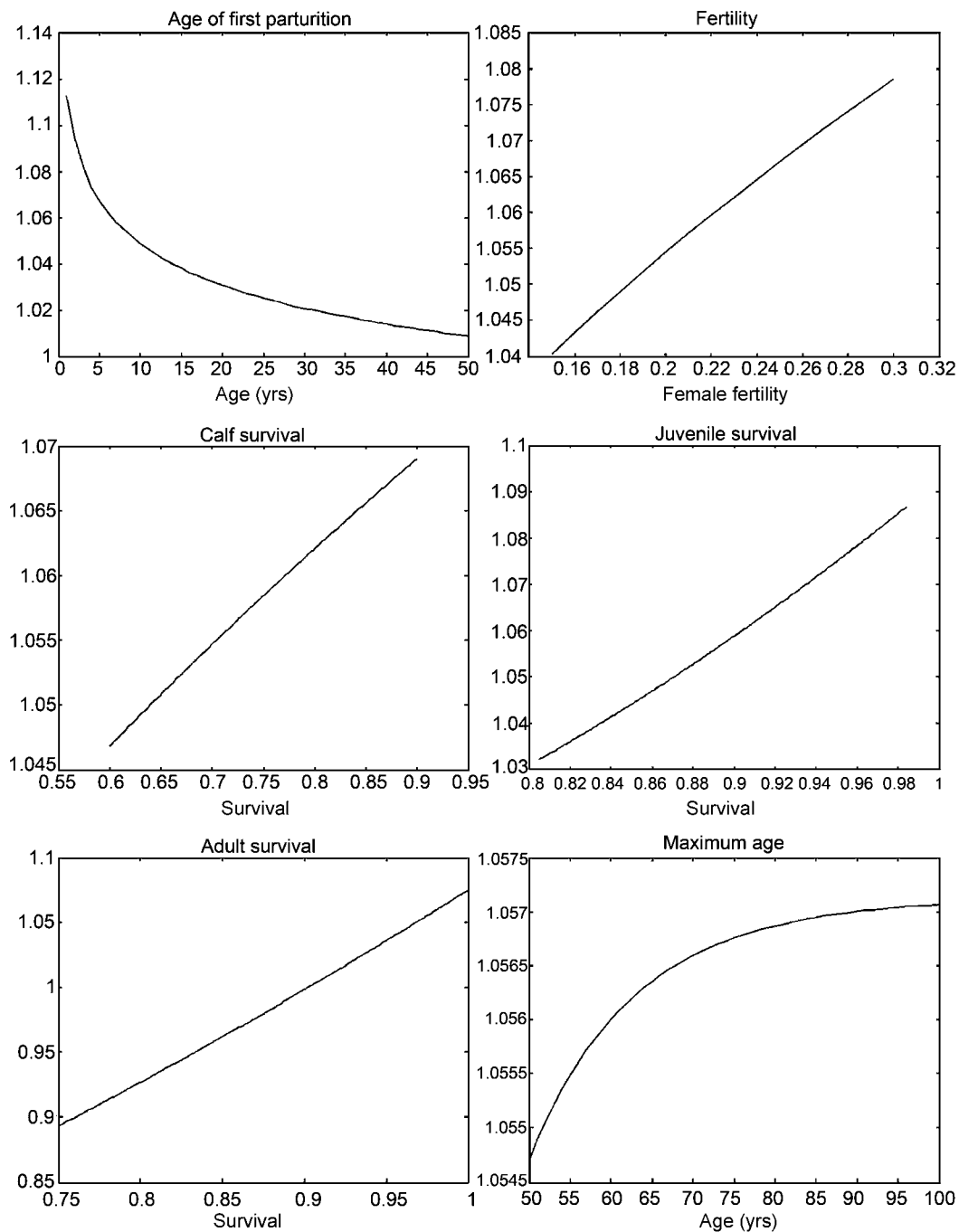


Fig. 6. Changes in lambda ( $\lambda$ -axis) due to changes in different life history traits ( $x$ -axis). Base values used for the life history traits are not changed: Age of first parturition = 6, Fertility = 0.21, Calf survival = 0.805, Juvenile survival = 0.894, Adult survival = 0.984, Max age = 100 years. Based on Barlow and Clapham (1997), Clapham (1992), Gabriele *et al.* (2001) and Mizroch *et al.* (2004).



# Population status of the eastern North Pacific stock of gray whales in 2009

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## ABSTRACT

An age- and sex-structured population dynamics model is fitted using Bayesian methods to data on the catches and abundance estimates for the Eastern North Pacific (ENP) stock of gray whales. The prior distributions used for these analyses incorporate revised estimates of abundance for ENP gray whales and account explicitly for the drop in abundance caused by the 1999–2000 mortality event. A series of analyses are conducted to evaluate the sensitivity of the results to different assumptions. The model fits the available data adequately, but, as in previous assessments, the measures of uncertainty associated with the survey-based abundance estimates are found to be negatively biased. The data support the inclusion of the 1999–2000 mortality event in the model, and accounting for this event leads to greater uncertainty regarding the current status of the resource. The baseline analysis estimates the ENP gray whale population to be above the maximum sustainable yield level (MSYL) with high probability (0.884). The posterior mean for the ratio of 2009 (1+) abundance to MSYL is 1.29 (with a posterior median of 1.37 and a 90% probability interval of 0.68–1.51). These results are consistent across all the model runs conducted. The baseline model also estimates the 2009 ENP gray whale population size (posterior mean of 20,366) to be at 85% of its carrying capacity (posterior mean of 25,808), and this is also consistent across all the model runs. The baseline model estimate of the maximum rate of increase,  $\lambda_{\max}$ , is 1.062 which, while high, is nevertheless within the range of estimates obtained for other baleen whales.

KEYWORDS: ASSESSMENT; GRAY WHALES; WHALING – ABORIGINAL

## INTRODUCTION

The eastern North Pacific (ENP) gray whale (*Eschrichtius robustus*) population has been hunted extensively by both commercial and aboriginal whalers. Indigenous peoples of both North America and Russia have hunted gray whales in some locations for centuries and possibly for 2000 years or more (Krupnik, 1984; O’Leary, 1984). The winter breeding grounds of the ENP gray whale (lagoons and adjacent ocean areas in Baja California, Mexico) were discovered by Yankee whalers in the early 19<sup>th</sup> century, and two commercial whaling vessels first hunted gray whales (in Magdalena Bay) in the winter of 1845–46 (Henderson, 1984). This began a period of intense hunting with large catches of ENP gray whales by Yankee whalers from 1846 until 1873 which decimated the population. Whaling ships and shore-based whalers continued to catch gray whales for the next two decades which drove the population to apparent commercial extinction by 1893. In the 20<sup>th</sup> century, modern commercial pelagic whaling of ENP gray whales began in 1910 and ended in 1946 when gray whales received full protection under the International Convention for the Regulation of Whaling (Reeves, 1984). Aboriginal catches of ENP gray whales along the Chukotka Peninsula of Russia have continued since 1946 until the present.

From 1846 to 1900 recorded commercial kills numbered nearly 9,000 gray whales, and it is roughly estimated that about 6,500 gray whales were killed by aboriginal hunters during this same period, for a total of more than 15,500 whales caught (Table 1). Since 1900, about 11,500 additional ENP gray whales have been killed by commercial and aboriginal whalers for a total since 1846 of more than 27,000

whales caught (Table 1). The magnitude of the catches, particularly for the period of high exploitation during the 1800s, gives some information on the likely pre-exploitation population size. For example, Jones *et al.* (1984) state that ‘most whaling historians and biologists believe the pre-exploitation stock size was between 15,000 and 24,000 animals’.

ENP gray whales migrate along the west coast of North America, and the US National Marine Fisheries Service (NMFS) has taken advantage of this nearshore migration pattern to conduct shore-based counts of the population in central California during December–February from 1967–68 to 2006–07. These survey data have been used to estimate the abundance of the ENP gray whale stock over the survey period (Buckland *et al.*, 1993; Hobbs *et al.*, 2004; Laake *et al.*, 1994; Reilly, 1981; Rugh *et al.*, 2008a; 2005). The resulting sequence of abundance estimates has also been used to estimate the population’s growth rate (Buckland and Breiwick, 2002; Buckland *et al.*, 1993), as well as its status relative to the maximum sustainable yield level (MSYL)<sup>1</sup> and carrying capacity (*K*) (Cooke, 1986; Lankester and Beddington, 1986; Punt and Butterworth, 2002; Reilly, 1981; Wade, 2002). However, attempts to model the gray whale population from 1846 until the present, accounting for the catch record and assuming that the stock was at its carrying capacity in 1846, have run into difficulties because the catch history cannot be reconciled with a population that increased at the observed rate from 1967/68 to 1979/80 (Cooke, 1986; Lankester and Beddington, 1986; Reilly, 1981). The

<sup>1</sup> MSYL expressed in terms of 1+ component of the population.

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Table 1a

Historical (pre-1944) aboriginal catches from the eastern North Pacific stock of gray whales (C. Allison, IWC Secretariat, pers. comm.).

Years	Annual kill
1600–1675	182
1676–1750	183
1751–1840	197.5
1841–1846	193.5
1847–1850	192.5
1851–1860	187
1861–1875	111
1876–1880	110
1881–1890	108
1891–1900	62
1901–1904	61
1905–1915	57
1916–1928	52
1929–1930	47
1931–1939	10
1940–1943	20

explanation for this is simple; if one assumes a relatively low maximum growth rate, the ENP gray whales would not have been able to increase between 1967/68 and 1979/80 because of the catches during that time, and if one assumes a high maximum growth rate, the population would not be increasing then because it would have already returned to carrying capacity. Butterworth *et al.* (2002) investigated the inability to fit a standard population dynamics model to the data for the ENP gray whales extensively and concluded that the catch history and the observed rate of increase could be reconciled in one of three different ways, which were not mutually exclusive: (1) a 2.5X increase in  $K$  between 1846 and 1988, (2) a 1.7X increase or more in the commercial catch between 1846 and 1900, and (3) a 3X increase or more in aboriginal catch levels prior to 1846 compared to what was previously assumed (Butterworth *et al.*, 2002).

Given these difficulties, recent gray whale assessments have been conducted by modelling the population since 1930 or later, rather than trying to model the population since 1846 (e.g. Punt and Butterworth, 2002; Wade, 2002). These analyses differed from the earlier assessments by not assuming that the population size in 1846 was  $K$ . Instead,  $K$  is essentially estimated by the recent trend in abundance, where a growing population implies that  $K$  has likely not yet been reached, and a roughly stable population implies the population is at or near  $K$ . Based on abundance surveys through 1995–96, point estimates of  $K$  from these analyses ranged from 24,000 to 32,000, but these estimates were relatively imprecise because they had broad probability intervals (Punt and Butterworth, 2002; Wade, 2002). In particular, the results did not exclude the possibility that  $K$  could be much larger than this range. However, these analyses did suggest that the population was probably close to  $K$  and at or above its MSYL. For example, Wade (2002) estimated a probability of 0.72 that the population was above MSYL<sup>1+</sup> in 1996. Punt and Butterworth (2002) also conducted analyses projecting the population from the year 1600 under various assumptions that historic commercial and aboriginal catches were underestimated (as in Butterworth *et al.*, 2002). Those analyses resulted in point estimates of  $K$  that ranged between 15,000 and 19,000. In those analyses, it was estimated the population was at a very high fraction of

$K$  in 1996 and had a very high probability of being above MSYL<sup>1+</sup>.

Recently, Rugh *et al.* (2008b) evaluated the accuracy of various components of the shore-based survey method, with a focus on pod size estimation. They found that the correction factors that had been used to compensate for bias in pod size estimates were calculated differently for different sets of years. In particular, the correction factors estimated by Laake *et al.* (1994) were substantially larger than those estimated by Reilly (1981). Also, the estimates for the surveys prior to 1987 in the trend analysis were scaled based on the abundance estimate from 1987–88. This meant that the first 16 abundance estimates used one set of correction factors, and the more recent 7 abundance estimates used different (and larger) correction factors which would influence the estimated trend and population trajectory. In addition, there were other subtle differences in the analysis methods used for the sequence of abundance estimates. Thus, a revaluation of the analysis techniques and of the abundance estimates was warranted to apply a more uniform approach throughout the years. Laake *et al.* (In press) derived a better, more consistent, approach to abundance estimation, and incorporated it into an analysis to re-estimate abundance for all 23 shore-based surveys. These new revised abundance estimates led to the present re-assessment of the ENP gray whale population.

The population is assessed by fitting an age- and sex-structured population model to these revised abundance estimates, using methods similar to those of Wade (2002) and Punt and Butterworth (2002); recent abundance estimates from 1997/98, 2000/01, 2001/02, and 2006/07 that were not available in previous assessments are also used. As in Punt and Butterworth (2002), sensitivity tests are performed to examine various assumptions or modelling decisions.

The analyses also incorporate new information about the biology of the ENP gray whales from recent studies. In particular, it is now recognised that the population experienced an unusual mortality event in 1999 and 2000. An unusually high number of gray whales were stranded along the west coast of North America in those years (Gulland *et al.*, 2005; Moore *et al.*, 2001). Over 60% of the dead whales were adults, and more adults and subadults stranded in 1999 and 2000 relative to the years prior to the mortality event (1996–98), when calf strandings were more common. Many of the stranded whales were emaciated, and aerial photogrammetry documented that migrating gray whales were skinnier in girth in 1999 relative to previous years (Perryman and Lynn, 2002; W. Perryman, SWFSC, pers. comm.). In addition, calf production in 1999 and 2000 was less than one third of that in the previous years (1996–98). In 2001 and 2002, strandings of gray whales along the coast decreased to levels that were below their pre-1999 level (Gulland *et al.*, 2005) and average calf production in 2002–2004 returned to the level seen in pre-1999 years (Table 2). A US Working Group on Marine Mammal Unusual Mortality Events (Gulland *et al.*, 2005) concluded that the emaciated condition of many of the stranded whales supported the idea that starvation could have been a significant contributing factor to the higher number of strandings in 1999 and 2000. Perryman *et al.* (2002) found a

Table 1b

Commercial and recent aboriginal (post-1943) catches from the eastern North Pacific stock of gray whales (C. Allison, IWC Secretariat, pers. comm.).

Year	Male	Female	Year	Male	Female	Year	Male	Female	Year	Male	Female
1846	23	45	1889	7	13	1932	3	7	1975	58	113
1847	23	45	1890	7	13	1933	36	69	1976	69	96
1848	23	45	1891	7	13	1934	64	92	1977	86	101
1849	23	45	1892	7	13	1935	48	96	1978	94	90
1850	23	45	1893	0	0	1936	74	114	1979	57	126
1851	23	45	1894	0	0	1937	5	9	1980	53	129
1852	23	45	1895	0	0	1938	18	36	1981	36	100
1853	23	45	1896	0	0	1939	10	19	1982	56	112
1854	23	45	1897	0	0	1940	39	66	1983	46	125
1855	162	324	1898	0	0	1941	19	38	1984	59	110
1856	162	324	1899	0	0	1942	34	67	1985	55	115
1857	162	324	1900	0	0	1943	33	66	1986	46	125
1858	162	324	1901	0	0	1944	0	0	1987	47	112
1859	162	324	1902	0	0	1945	10	20	1988	43	108
1860	162	324	1903	0	0	1946	7	15	1989	61	119
1861	162	324	1904	0	0	1947	0	1	1990	67	95
1862	162	324	1905	0	0	1948	6	13	1991	69	100
1863	162	324	1906	0	0	1949	9	17	1992	0	0
1864	162	324	1907	0	0	1950	4	7	1993	0	0
1865	162	324	1908	0	0	1951	5	9	1994	21	23
1866	79	159	1909	0	0	1952	15	29	1995	48	44
1867	79	159	1910	0	1	1953	19	29	1996	18	25
1868	79	159	1911	0	1	1954	13	26	1997	48	31
1869	79	159	1912	0	0	1955	20	39	1998	64	61
1870	79	159	1913	0	1	1956	41	81	1999	69	55
1871	79	159	1914	6	13	1957	32	64	2000	63	52
1872	79	159	1915	0	0	1958	49	99	2001	62	50
1873	79	159	1916	0	0	1959	66	130	2002	80	51
1874	79	159	1917	0	0	1960	52	104	2003	71	57
1875	17	33	1918	0	0	1961	69	139	2004	43	68
1876	17	33	1919	0	0	1962	53	98	2005	49	75
1877	17	33	1920	1	1	1963	60	120	2006	57	77
1878	17	33	1921	13	25	1964	81	138	2007	50	82
1879	21	42	1922	6	4	1965	71	110	2008	64	66
1880	17	34	1923	0	0	1966	100	120			
1881	17	33	1924	1	0	1967	151	223			
1882	17	33	1925	70	64	1968	92	109			
1883	19	39	1926	25	17	1969	93	121			
1884	23	45	1927	7	25	1970	70	81			
1885	21	41	1928	4	8	1971	62	91			
1886	17	33	1929	0	3	1972	66	116			
1887	7	13	1930	0	0	1973	98	80			
1888	7	13	1931	0	0	1974	94	90			

significant positive correlation between an index of the amount of ice-free area in gray whale feeding areas in the Bering Sea and their estimates of calf production for the following spring for the years 1994 to 2000; the suggested mechanism is that longer periods of time in open water provides greater feeding opportunities for gray whales. Whether or not heavy ice cover was ultimately the mechanism that caused the 1999–2000 event, it is clear that ENP gray whales were substantially affected in those years; whales were on average skinnier, they had a lower survival rate (particularly of adults) and calf production was dramatically lower. Given that this event may have affected the status of the ENP gray whale population relative to  $K$ , an additional model parameter (‘catastrophic mortality’) has been specified in the model that allowed for lower survival in the years 1999 and 2000 to investigate this effect.

## METHODS

### Available data

A variety of data sources are available to assess the status of the ENP stock of gray whales. These data sources are used when developing the prior distributions for the parameters

of the population dynamics model, when pre-specifying the values for some of the parameters of this model, and when constructing the likelihood function. Table 1 lists the time-series of removals. It should be noted that the catches for the years prior to 1930 are subject to considerable uncertainty, and evaluating these catches remains an active area of research. However, the uncertainty associated with these early catches is inconsequential for this paper because the population projections do not start before 1930.

The key source of information on the abundance of the ENP gray whales is data collected from the southbound surveys that have been conducted since 1967/68 near Carmel, California (Laake *et al.*, In press; Table 2). Information on trends in calf numbers are also available from surveys of calves during the northbound migration (Perryman *et al.*, 2002; W. Perryman, pers. comm.; Table 2). The calf abundance data are not included in the baseline analyses, but are considered in one of the tests of sensitivity.

### Analysis methods

#### *The population dynamics model*

An age- and sex-structured population dynamics model is used that assumes that all whaling takes place at the start of



Table 2

Baseline estimates of 1+ abundance (and associated standard errors of the logs) from southbound surveys (Laake *et al.*, In press), the estimates of 1+ abundance used in previous assessments, two alternative series of abundance estimates ('Hi' and 'Lo', see footnote 7 for details), and estimates of calf numbers from northbound surveys (W. Perryman, SWFSC, pers. comm.).

1+ abundance					1+ abundance							
Laake <i>et al.</i> (In press)		Unrevised estimates		Calf counts	Lo series				Hi series			
Year	Estimate	CV	Estimate	CV	Year	Estimate	SE	Year	Estimate	SE	Estimate	SE
1967/68	13,426	0.094	13,776	0.078	1994	945	68.2	1967/68	12,961	0.094	14,298	0.095
1968/69	14,548	0.080	12,869	0.055	1995	619	67.2	1968/69	14,043	0.080	15,493	0.081
1969/70	14,553	0.083	13,431	0.056	1996	1,146	70.7	1969/70	14,049	0.082	15,498	0.084
1970/71	12,771	0.081	11,416	0.052	1997	1,431	82.0	1970/71	12,328	0.081	13,601	0.082
1971/72	11,079	0.092	10,406	0.059	1998	1,388	92.0	1971/72	10,695	0.092	11,799	0.093
1972/73	17,365	0.079	16,098	0.052	1999	427	41.1	1972/73	16,763	0.079	18,493	0.080
1973/74	17,375	0.082	15,960	0.055	2000	279	34.8	1973/74	16,772	0.081	18,503	0.083
1974/75	15,290	0.084	13,812	0.056	2001	256	28.6	1974/75	14,760	0.084	16,283	0.085
1975/76	17,564	0.086	15,481	0.060	2002	842	78.6	1975/76	16,955	0.086	18,705	0.087
1976/77	18,377	0.080	16,317	0.050	2003	774	73.6	1976/77	17,739	0.079	19,570	0.081
1977/78	19,538	0.088	17,996	0.069	2004	1,528	96.0	1977/78	18,860	0.088	20,806	0.089
1978/79	15,384	0.080	13,971	0.054	2005	945	86.9	1978/79	14,850	0.080	16,383	0.081
1979/80	19,763	0.083	17,447	0.056	2006	1,020	103.3	1979/80	19,077	0.082	21,046	0.083
1984/85	23,499	0.089	22,862	0.060	2007	404	51.2	1984/85	22,684	0.089	25,025	0.090
1985/86	22,921	0.081	21,444	0.052	2008	553	53.0	1985/86	22,126	0.081	24,409	0.082
1987/88	26,916	0.058	22,250	0.050	2009	312	41.9	1987/88	25,661	0.057	28,692	0.056
1992/93	15,762	0.067	18,844	0.063				1992/93	14,785	0.065	17,879	0.072
1993/94	20,103	0.055	24,638	0.060				1993/94	19,468	0.057	21,124	0.056
1995/96	20,944	0.061	24,065	0.058				1995/96	20,636	0.063	22,314	0.063
1997/98	21,135	0.068	29,758	0.105				1997/98	20,426	0.063	22,378	0.065
2000/01	16,369	0.061	19,448	0.097				2000/01	16,051	0.063	17,145	0.062
2001/02	16,033	0.069	18,178	0.098				2001/02	15,162	0.066	16,883	0.067
2006/07	19,126	0.071	20,110	0.088				2006/07	18,775	0.071	20,129	0.072

the year, and that all animals are 'recruited' to the hunted population by age 5 (i.e. hunting only occurs on animals age 5 and older) (Punt, 1999; Punt and Butterworth, 2002). The dynamics of the population are assumed to be governed by the equations:

$$N_{t+1,a}^s = \begin{cases} 0.5P_{t+1}^M f_{t+1} & \text{if } a = 0 \\ N_{t,a-1}^s (1 - F_{t,a-1}^s) S_{a-1}^s \tilde{S}_t & \text{if } 1 \leq a \leq x-1 \\ N_{t,x}^s (1 - F_{t,x}^s) S_x^s \tilde{S}_t + N_{t,x-1}^s (1 - F_{t,x-1}^s) S_{x-1}^s \tilde{S} & \text{if } a = x \end{cases} \quad (1)$$

where

$N_{t,a}^s$  is the number of animals of age  $a$  and sex  $s$  (m/f) at the start of year  $t$ ,

$S_a$  is the annual survival rate of animals of age  $a$  in the absence of catastrophic mortality events (assumed to be the same for males and females),

$\tilde{S}_t$  is the amount of catastrophic mortality (represented in the form of a survival rate) during year  $t$  (catastrophic events are assumed to occur at the start of the year before mortality due to whaling and natural causes; in general  $\tilde{S}_t = 1$ , i.e. there is no catastrophic mortality),

$F_{t,a}^s$  is the exploitation rate on animals of sex  $s$  and age  $a$  during year  $t$ ,

$P_t^M$  is the number of females that have reached the age at first parturition by the start of year  $t$ ,

$$P_t^M = \sum_{a=a_m+1}^x N_{t,a}^f \quad (2)$$

$a_m$  is the age-of-maturity,

$f_t$  is pregnancy rate (number of calves of both sexes per 'mature' female) during year  $t$  (note that Equation (1) assumes an equal male : female sex ratio at birth), and

$x$  is the maximum age-class, which for convenience is lumped across older age-classes (i.e. individuals stay in this age-class until they die).

Density dependence on fecundity can be modelled by writing the pregnancy rate,  $f_t$ , as follows:

$$f_t = \max \left( f_{eq} \left[ 1 + A \left\{ 1 - \left( \bar{S}_{t-2}^{1+} / K^{1+} \right)^z \right\} \right], 0 \right). \quad (3)$$

Where  $f_{eq}$  is the pregnancy rate at the pre-exploitation equilibrium,  $f(F=0)^2$ :

$$f(F) = 2 \left\{ \sum_{a=a_m+1}^x \tilde{N}_a^f(F) \right\}^{-1} \quad (4)$$

$A$  is the resilience parameter:

$$A = \frac{f_{max} - f_{eq}}{f_{eq}} \quad (5)$$

$f_{max}$  is the maximum (theoretical) pregnancy rate,

$z$  is the degree of compensation,

$P_t^{1+}$  is number of animals aged 1 and older at the start of year  $t$ :

$$P_t^{1+} = \sum_s \sum_{a=1}^x N_{t,a}^s \quad (6)$$

$K^{1+}$  is the (current) pre-exploitation equilibrium size (carrying capacity) in terms of animals aged 1 and older, and

$\tilde{N}_a^s(F)$  is the number of animals of sex  $s$  and age  $a$  when the exploitation rate is fixed at  $F$ , expressed as a fraction of the

<sup>2</sup>The pregnancy rate at the pre-exploitation equilibrium can be considered to be the equilibrium pregnancy rate when the exploitation rate,  $F$ , is fixed at zero.

number of calves of the same sex  $s$  (see appendix 1 of Punt (1999) for details).

Although these equations are written formally as if only the pregnancy rate component of ‘fecundity’ as defined here is density-dependent, exactly the same equations follow if some or all of this dependence occurs in the infant survival rate (Punt, 1999). Catastrophic mortality is assumed to occur before density-dependence because many of the deaths in 1999 and 2000 occurred before mating was likely to have occurred. Non-catastrophic natural mortality does not appear in Equation 3 because it cancels out. The time-lag in Equation 3 is specified to match the reproductive cycle of gray whales; mature female gray whales mate and become pregnant in early winter, have a gestation period of slightly longer than one year, and give birth at the start of the next year (on average in January) (Rice and Wolman, 1971; Shelden *et al.*, 2004). Their body condition at the end of the summer feeding season will help determine their probability of becoming pregnant the following winter and producing a calf a year later. Therefore, the density-dependent effect on calf production is assumed to be determined by the population size during the feeding season two time-steps prior (approximately 1.5 years earlier).

Following past assessments of the ENP stock of gray whales (e.g. Butterworth *et al.*, 2002; Punt *et al.*, 2004; Punt and Butterworth, 2002), the catch (by sex) is assumed to be taken uniformly from the animals aged five and older, that is:

$$F_{t,a}^s = C_t^s / \sum_{a=5}^x N_{t,a}^s \quad (7)$$

Where  $C_t^s$  is the catch of animals of sex  $s$  during year  $t$ .

The population is assumed to have had a stable age-structure at the start of the projection period (year  $t_{INIT}$ ).

$$N_{t_{INIT},a}^s = N_{t_{INIT}}^{Tot} \tilde{N}_a^s(F_{INIT}) / \sum_{s'} \sum_{a'=0}^x \tilde{N}_{a'}^{s'}(F_{INIT}) \quad (8)$$

Where  $N_{t_{INIT}}^{Tot}$  is the size of the total (0+) component of the population at the start of year  $t_{INIT}$ . The value of  $F_{INIT}$  is selected numerically so that:

$$N_{t_{INIT},a}^{Tot} = 0.5 N_0(F_{INIT}) / \sum_s \sum_{a=0}^x N_a^s(F_{INIT}) \quad (9)$$

Where  $N_0(F_{INIT})$  is the number of calves (of both sexes) at the start of the year when  $F = F_{INIT}$ :

$$N_0(F_{INIT}) = \left( 1 - \frac{1}{A} \left[ \frac{f(F_{INIT})}{f_{eq}} - 1 \right] \right)^{1/z} \frac{K^{1+}}{\tilde{P}^{1+}(F_{INIT})} \quad (10)$$

$\tilde{P}^{1+}(F)$  is the size of the 1+ component of the population as a function of  $F$ , expressed as a fraction of the number of calves (of both sexes).

### Parameter estimation

Catastrophic mortality is assumed to be zero (i.e.  $\tilde{S}_y = 1$ ) except for 1999 and 2000 when it is assumed to be equal to a parameter  $\tilde{S}$ . This assumption reflects the large number of dead whales observed stranded along the coasts of Oregon and Washington during 1999 and 2000 relative to numbers

stranding there annually historically (Brownell *et al.*, 2007; Gulland *et al.*, 2005).

The parameters of the population dynamics model are  $a_m$ ;  $\tilde{S}$ ;  $K^{1+}$ ; the 1+ population size at the start of 1968,  $P_{1968}^{1+}$ ;  $MSYL^{1+}$  (the maximum sustained yield level for the 1+ population, which is the population size at which maximum sustained yield (MSY) is achieved when hunting takes place uniformly on animals aged 1 and older, relative to  $K^{1+}$ );  $MSYR^{1+}$  (the ratio of MSY to  $MSYL^{1+}$ );  $f_{max}$ ; and the non-calf survival rate,  $S_{1+}$ . The analysis does not incorporate a prior distribution for the survival rate of calves ( $S_0$ ) explicitly. Instead, following Wade (2002), an implicit prior distribution for this parameter is calculated from the priors for the five parameters  $a_m$ ,  $f_{max}$ ,  $S_{1+}$ ,  $MSYR^{1+}$  and  $MSYL^{1+}$ . For any specific draw from the prior distributions for these five parameters, the value for  $S_0$  is selected so that the relationships imposed by the population model among the six parameters are satisfied. If the resulting value for  $S_0$  is less than zero or greater than that of  $S_{1+}$ , the values for  $S_{1+}$ ,  $a_m$ ,  $f_{max}$ ,  $MSYR^{1+}$  and  $MSYL^{1+}$  are drawn again<sup>4</sup>. Thus, the prior for  $S_0$  is forced to conform to the intuitive notion that the survival rate of calves must be lower than that for older animals and must be larger than zero (Caughley, 1966).

Under the assumption that the logarithms of the estimates of abundance based on the southbound surveys are normally distributed, the contribution of these estimates to the negative of the logarithm of the likelihood function (ignoring constants independent of the model parameters) is:

$$-\ln L = 0.5 \ln |V + \Omega| + 0.5 \sum_i \sum_j (\ln N_i^{obs} - \ln \hat{P}_i^{1+}) [V + \Omega]^{-1}_{i,j} (\ln N_j^{obs} - \ln \hat{P}_j^{1+}), \quad (11)$$

Where  $N_i^{obs}$  is the  $i^{th}$  estimate of abundance<sup>5</sup>,

$\hat{P}_i$  is the model-estimate corresponding to  $N_i^{obs}$ ,

$V$  is the variance-covariance matrix for the abundance estimates, and

$\Omega$  is a diagonal matrix with elements  $CV_{add}^2$  (this matrix captures sources of uncertainty not captured elsewhere; termed ‘additional variance’ in Wade (2002)).

A Bayesian approach is used to estimate the ‘free’ parameters of the model based on the prior distributions in Table 3 and the sampling/importance resampling (SIR) algorithm (Rubin, 1988).

- Draw values for the parameters  $S_{1+}$ ,  $a_m$ ,  $f_{max}$ ,  $MSYR^{1+}$ ,  $MSYL^{1+}$ ,  $K^{1+}$ ,  $P_{1968}^{1+}$ ,  $\tilde{S}$ , and  $CV_{add}$  from the priors in Table 3.
- Solve the system of equations that relate  $S_0$ ,  $S_{1+}$ ,  $a_m$ ,  $f_{max}$ ,  $MSYR^{1+}$ ,  $MSYL^{1+}$ ,  $A$  and  $z$  (Punt, 1999; Eqs. 18–21) to find values for  $S_0$ ,  $A$ , and  $z$ , and find the population size in year  $t_{INIT}$  and the population rate of increase in this year, so that, if the population is projected from year  $t_{INIT}$

<sup>4</sup>The implications of different treatments of how to handle situations in which the calculated value for  $S_0$  is outside of plausible bounds is examined by Brandon *et al.* (2007).

<sup>5</sup>The abundance estimate for year  $y/y+1$  is assumed to pertain to abundance at the start of year  $y+1$ .

<sup>3</sup>The 1968 population size is taken to be a measure of initial abundance so that the analyses based on different starting years are comparable in terms of their prior specifications.

to 1968, the total (1+) population size in 1968 equals the generated value for  $P_{1968}^{1+}$ .

- (c) Compute the likelihood for the projection (see Equation 11).
- (d) Repeat steps (a)–(c) a very large number (typically 5 million) of times.
- (e) Select 5,000 parameter vectors randomly from those generated using steps (a)–(d), assigning a probability of selecting a particular vector proportional to its likelihood

The above formulation implies that the year for which a prior on abundance is specified (1968) is not necessarily the same as the first year of the population projection ( $t_{\text{INIT}}$ , baseline value 1930). Starting the population projection before the first year for which data on abundance are available allows most of the impact of any transient population dynamics caused by the assumption of a stable age-structure to be eliminated. Therefore, the model population should mimic the real population more closely by allowing the sex- and age-selectivity of the catches to correctly influence the sex- and age-distribution of the population once the trajectory reaches years where it is compared to the data (i.e. 1967/68 and beyond).

Table 3  
The parameters and their assumed prior distributions.

Parameter	Prior distribution
Non-calf survival rate, $S_{1+}$	U[0.950, 0.999] <sup>a</sup>
Age-at-maturity, $a_m$	U[6, 12] <sup>b</sup>
Maximum pregnancy rate, $f_{\text{max}}$	U[0.3, 0.6] <sup>a</sup>
Carrying capacity, $K^{1+}$	U[10,000, 70,000] <sup>c</sup>
Population size in 1968, $P_{1968}^{1+}$	U[5,000, 20,000] <sup>c</sup>
Maximum Sustainable Yield Level, $\text{MSYL}^{1+}$	U[0.4, 0.8] <sup>a</sup>
Maximum Sustainable Yield Rate, $\text{MSYR}^{1+}$	U[0, 0.1] <sup>a</sup>
Catastrophic mortality, $\delta$	U[0.2, 1.0] <sup>c</sup>
Additional variance, 1+ abundance estimates, $\text{CV}_{\text{add}}$	U[0, 0.35] <sup>a,c</sup>
Additional variance, calf counts, $\text{CV}_{\text{add-2}}$	U[0.2, 0.8] <sup>a,d</sup>
Constant of proportionality, $\ell n q$	U[ $-\infty$ , $\infty$ ] <sup>d,e</sup>

<sup>a</sup>Equal to the prior distribution used in the most recent assessments (Punt *et al.*, 2004); <sup>b</sup>Bradford *et al.* (2010); <sup>c</sup>preliminary analyses provided no evidence of posterior support for values outside this range; <sup>d</sup>not used in the baseline analysis; <sup>e</sup>the non-informative prior for a scale parameter (Butterworth and Punt, 1996).

### Output statistics

The results are summarised by the posterior medians, means and 90% credibility intervals for  $\text{MSYR}^{1+}$ ,  $\text{MSYL}^{1+}$ ,  $S_{1+}$ ,  $S_0$ ,  $\delta$ , and  $K^{1+}$  and the following management-related quantities:

- (a)  $P_{2009}^{1+}$  is the number of 1+ animals at the start of 2009;
- (b)  $P_{2009}^{1+} / K^{1+}$  is the depletion level, or the number of 1+ animals at the start of 2009, expressed as a percentage of that corresponding to the equilibrium level;
- (c)  $P_{2009}^{1+} / \text{MSYL}^{1+}$  is the *MSYL ratio*, the number of 1+ animals at the start of 2009, expressed as a percentage of that at which MSY is achieved; and
- (d)  $\lambda_{\text{max}}$  is the maximum rate of increase (given a stable age-structure and the assumption of no maximum age; Breiwick *et al.*, 1984)

$P_{2009}^{1+} / K^{1+}$  is termed the *depletion level* because it provides a measure of how depleted the population is relative to the carrying capacity, as the equilibrium level in a density-dependent model is equivalent to carrying capacity.  $P_{2009}^{1+} / \text{MSYL}^{1+}$  is referred to as the *MSYL ratio* because it provides a measure of whether the population is above  $\text{MSYL}^{1+}$ . Note that  $\lambda_{\text{max}}$  can be equated to  $r_{\text{max}}$  (e.g. as in Wade, 1998) through the equation  $r_{\text{max}} = \lambda_{\text{max}} - 1.0$ .

### Sensitivity tests

Our baseline assessment includes the baseline estimates of 1+ abundance (Table 2) and allows for a catastrophic mortality event in 1999–2000. The sensitivity of the results of the analyses is explored to:

- (a) varying the first year considered in the population projection (1940, 1950 and 1960);
- (b) replacing the estimates of abundance for the southbound migration by the values used in the previous assessment (Table 2, ‘Unrevised estimates’);
- (c) replacing the abundance estimates with the ‘Lo’ and ‘Hi’ series (Table 2)<sup>6</sup>;
- (d) ignoring the catastrophic event in 1999–2000 (abbreviation ‘No event’);
- (e) basing the analysis on the generalised logistic equation (see Appendix 1 for details; abbreviation ‘Gen Logist’)<sup>7</sup>;
- (f) splitting the abundance series after 1987/88 (abbreviation ‘Split series’), where the first abundance series is treated as a relative index of abundance scaled to absolute abundance through a constant of proportionality, and the second series is treated as an absolute index of abundance; and
- (g) including the calf counts at Point Piedras Blancas, California (Perryman *et al.*, 2002; Perryman, pers. comm.) in the analysis (abbreviation ‘With calf counts’).

For the last sensitivity test, the contribution of the data on calf counts to the negative of the logarithm of the likelihood function (ignoring constants independent of the model parameters) is based on the assumption that the calf counts are relative indices of the total number of calves and are subject to both modelled and unmodelled sources of uncertainty:

$$-\ell n L = 0.5 \sum_i \ell n (\sigma_i^2 + \text{CV}_{\text{add-2}}^2) + 0.5 \sum_i \frac{(\ell n A_i^{\text{obs}} - \ell n (q(N_{i,0}^m + N_{i,0}^f)))^2}{\sigma_i^2 + \text{CV}_{\text{add-2}}^2} \quad (12)$$

<sup>6</sup>The sequence of gray whale abundance estimates depends in part on the estimates of observer detection probability that were measured with the double observer data. Assessment of matches amongst the pods detected by the observers depends on the weighting parameters for distance and time measurements (Laake *et al.*, In press). The weighting parameters used for the baseline abundance estimates were selected such that 95% of the observations of the same pod would be correctly matched. Sensitivity is explored to matching weighting parameters that gave 98% and 90% (table A2; Laake *et al.*, In press).

<sup>7</sup>This sensitivity test is provided because the generalised logistic model has been the basis for some previous management advice for this stock (for example, Wade, 2002).

where

$A_i^{obs}$  is the estimate of the number of calves during year  $i$  based on the surveys at Point Piedras Blancas;

$q$  is the constant of proportionality between the calf counts and model estimates of the number of calves;

$\sigma_i$  is the standard error of the logarithm of  $C_i^{obs}$ ; and

$CV_{add-2}^2$  is the additional variance associated with the calf counts.

### Prior distributions

The prior distributions (Table 3) are generally based on those used in recent International Whaling Commission (IWC) assessments of ENP gray whales. The prior distributions for  $S_{1+}$ ,  $K^{1+}$ ,  $\tilde{S}$ ,  $CV_{add}$ ,  $CV_{add-2}$ , and  $\ln q$  were selected to be uniform over a sufficiently wide range so that there is effectively no posterior probability outside of that range.

The prior for the age-at-maturity differs from that used in previous assessments, Uniform[5,9], based on the review by Bradford *et al.* (2010) who could find no basis for that range in the literature. They concluded that the most relevant data set for age-at-maturity was that of Rice and Wolman (1971), corrected by Rice (1990) for the underestimation of whale ages by one year in the original study, resulting in a median age of 9, and lower and upper bounds of 6 and 12. Bradford *et al.* (2010) note that the only observation of the age-at-first-reproduction (AFR) in ENP gray whales (a known whale observed with a calf for the first time) was 7 years for a whale first seen as a calf in a lagoon in Mexico. In the western Pacific population of gray whales, there have been observations of AFR of 7 and 11 years for the only two whales whose first calving has been documented to date (Bradford *et al.*, unpublished ms). The prior for the maximum pregnancy rate,  $f_{max}$ , was set equal to the prior selected for recent assessments (Punt and Butterworth, 2002;

Wade, 2002). This prior implies a minimum possible calving interval between 1.67 and 3.33 years.

The prior for the population size (in terms of animals aged 1 and older) in 1968 differs from that used in previous assessments. Rather than combining a uniform prior on 1968 population size with the abundance estimate for 1968 to create an informative prior for  $P_{1968}^{1+}$  as was the case in previous assessments, this assessment assumes a broad uniform prior for 1968 population size, and includes all of the estimates of abundance in the likelihood function. This is because the previous approach cannot be applied because all of the estimates of abundance are correlated (Laake *et al.*, In press).

The prior for  $MSYR^{1+}$  is bounded below by the minimum possible value and above by a value which is above those supported by the data. This prior is broader than those considered in previous assessments because those assessments assigned a prior to  $MSYR^{1+}$  when this parameter is expressed in terms of removals of mature animals only. The prior for  $MSYL^{1+}$  has been assumed to be uniform from 0.4 to 0.8. The central value for this prior reflects the common assumption when conducting IWC assessments of whale stocks that maximum productivity occurs at about 60% of carrying capacity. The upper and lower bounds reflect values commonly used to bound  $MSYL$  for whale stocks (e.g. those used in the tests that evaluated the IWC's catch limit algorithm).

### RESULTS

The baseline assessment estimates that ENP gray whales increased substantially from 1930 until 1999 when a substantial reduction in population size from close to carrying capacity (in terms of median parameter estimates) occurred (Fig. 1). This reduction was associated with an estimated decline in non-calf survival from 0.982 to 0.847 (posterior means, where  $0.981 \times 0.863 = 0.847$ ) in each of 1999 and 2000. The population is estimated to have been

Table 4

Posterior distributions for the key model outputs (posterior mean, posterior median [in square parenthesis], and posterior 90% intervals) for the baseline analysis and the sensitivity tests.

	Baseline	$t_{INIT}=1940$	$t_{INIT}=1950$	$t_{INIT}=1960$	Unrevised estimates	No event	Gen logist	With calf counts
$K^{1+}$	25,808 [22,756] (19,752 49,639)	25,450 [22,506] (19,537 49,109)	24,681 [22,282] (19,454 43,887)	24,396 [22,047] (19,212 43,307)	41,046 [37,889] (24,214 66,564)	21,640 [20,683] (18,301 25,762)	21,146 [20,668] (18,229 24,292)	27,716 [24,194] (20,387 51,775)
$MSYR^{1+}$	0.046 [0.048] (0.022 0.064)	0.047 [0.048] (0.022 0.067)	0.049 [0.049] (0.024 0.068)	0.048 [0.049] (0.024 0.070)	0.035 [0.034] (0.025 0.050)	0.052 [0.053] (0.026 0.068)	0.065 [0.066] (0.034 0.096)	0.040 [0.040] (0.022 0.057)
$MSYL^{1+}$	0.656 [0.669] (0.532 0.725)	0.664 [0.677] (0.535 0.741)	0.677 [0.689] (0.541 0.762)	0.691 [0.702] (0.545 0.786)	0.611 [0.611] (0.506 0.706)	0.672 [0.684] (0.577 0.730)	0.630 [0.640] (0.441 0.786)	0.632 [0.638] (0.514 0.725)
$P_{2009}^{1+} / K^{1+}$	0.849 [0.919] (0.393 1.006)	0.865 [0.933] (0.403 1.016)	0.885 [0.946] (0.451 1.022)	0.899 [0.959] (0.453 1.043)	0.615 [0.598] (0.334 0.948)	0.956 [0.977] (0.872 0.987)	0.964 [0.976] (0.922 0.989)	0.775 [0.816] (0.372 0.984)
$P_{2009}^{1+} / MSYL^{1+}$	1.288 [1.366] (0.681 1.508)	1.295 [1.362] (0.701 1.522)	1.302 [1.355] (0.775 1.516)	1.296 [1.343] (0.786 1.513)	1.002 [0.992] (0.580 1.459)	1.423 [1.424] (1.303 1.583)	1.541 [1.515] (1.252 2.091)	1.217 [1.284] (0.681 1.494)
$P_{2009}^{1+}$	20,366 [20,447] (17,515 23,127)	20,489 [20,511] (19,628 23,274)	20,583 [20,648] (17,726 23,247)	20,678 [20,705] (17,856 23,497)	22,773 [22,701] (19,910 25,865)	20,247 [20,127] (17,726 22,993)	20,213 [20,090] (17,827 22,910)	19,892 [19,863] (16,872 22,723)
$\lambda_{max}$	1.062 [1.063] (1.032 1.088)	1.063 [1.063] (1.033 1.094)	1.063 [1.062] (1.035 1.094)	1.062 [1.060] (1.035 1.092)	1.054 [1.052] (1.036 1.081)	1.068 [1.069] (1.038 1.091)	1.017 [0.088] (0.042 0.242)*	1.057 [1.057] (1.033 1.080)
$S_{1+}$	0.981 [0.982] (0.957 0.997)	0.981 [0.982] (0.957 0.997)	0.980 [0.982] (0.957 0.997)	0.980 [0.982] (0.957 0.997)	0.978 [0.980] (0.956 0.997)	0.983 [0.985] (0.960 0.998)	N/A	0.972 [0.972] (0.954 0.993)
$S_0$	0.711 [0.732] (0.423 0.950)	0.716 [0.734] (0.426 0.949)	0.713 [0.727] (0.426 0.952)	0.706 [0.720] (0.425 0.949)	0.662 [0.666] (0.400 0.926)	0.730 [0.747] (0.437 0.955)	N/A	0.722 [0.751] (0.428 0.943)
$\tilde{S}$	0.863 [0.865] (0.772 0.951)	0.866 [0.867] (0.778 0.951)	0.868 [0.870] (0.779 0.960)	0.870 [0.870] (0.781 0.961)	0.814 [0.809] (0.725 0.915)	1	N/A	0.847 [0.840] (0.749 0.949)

\* $r$  rather  $\lambda_{max}$ .



Table 4 (continued).

	Baseline	Split series	Lo series	Hi series	Unrevised no event	Calf counts no event
$K^{1+}$	25,808 [22,756] (19,752 49,639)	27,489 [22,870] (19,640 55,929)	25,826 [22,030] (19,129 52,878)	26,902 [24,181] (21,043 48,118)	24,162 [23,044] (20,946 29,554)	21,501 [20,887] (18,439 24,793)
$MSYR^{1+}$	0.046 [0.048] (0.022 0.064)	0.046 [0.047] (0.024 0.062)	0.046 [0.048] (0.021 0.064)	0.046 [0.048] (0.023 0.063)	0.047 [0.048] (0.032 0.061)	0.049 [0.050] (0.028 0.065)
$MSYL^{1+}$	0.656 [0.669] (0.532 0.725)	0.648 [0.663] (0.529 0.721)	0.654 [0.670] (0.520 0.725)	0.654 [0.664] (0.537 0.725)	0.663 [0.673] (0.568 0.722)	0.668 [0.676] (0.577 0.733)
$P_{2009}^{1+} / K^{1+}$	0.849 [0.919] (0.393 1.006)	0.819 [0.908] (0.358 1.003)	0.837 [0.917] (0.355 1.008)	0.855 [0.913] (0.428 1.005)	0.957 [0.975] (0.881 0.985)	0.958 [0.974] (0.906 0.984)
$P_{2009}^{1+} / MSYL^{1+}$	1.288 [1.366] (0.681 1.508)	1.253 [1.357] (0.642 1.502)	1.270 [1.361] (0.632 1.504)	1.301 [1.366] (0.748 1.512)	1.446 [1.442] (1.344 1.608)	1.438 [1.436] (1.314 1.607)
$P_{2009}^{1+}$	20,366 [20,447] (17,515 23,127)	20,380 [20,372] (17,708 23,139)	19,752 [19,817] (16,925 22,432)	21,654 [21,594] (18,607 24,683)	22,781 [22,456] (20,432 26,047)	20,337 [20,283] (17,912 23,050)
$\lambda_{\max}$	1.062 [1.063] (1.032 1.088)	1.063 [1.064] (1.037 1.088)	1.062 [1.063] (1.032 1.088)	1.063 [1.064] (1.034 1.089)	1.063 [1.062] (1.043 1.087)	1.065 [1.065] (1.037 1.090)
$S_{1+}$	0.981 [0.982] (0.957 0.997)	0.981 [0.982] (0.957 0.997)	0.980 [0.982] (0.957 0.997)	0.981 [0.982] (0.957 0.998)	0.982 [0.984] (0.959 0.997)	0.980 [0.982] (0.958 0.997)
$S_0$	0.711 [0.732] (0.423 0.950)	0.711 [0.729] (0.420 0.949)	0.710 [0.728] (0.420 0.949)	0.708 [0.725] (0.425 0.949)	0.705 [0.716] (0.420 0.950)	0.720 [0.732] (0.426 0.954)
$\tilde{S}$	0.863 [0.865] (0.772 0.951)	0.860 [0.862] (0.763 0.958)	0.862 [0.862] (0.775 0.950)	0.855 [0.857] (0.772 0.939)	1	1

increasing since 2000. The model fits the data well, although, as in previous IWC assessments, the analyses suggest that the coefficients of variation for the abundance estimates are underestimated (by 14% median estimate). The baseline assessment estimates that this stock is currently well above  $MSYL^{1+}$  (posterior mean for  $P_{2009}^{1+} / MSYL^{1+}$  of 1.29) (Table 4). The posterior probability that the stock is currently greater than  $MSYL^{1+}$  is 0.884.

The posterior probability that the stock is currently above  $MSYL^{1+}$  is less for the baseline analysis and for the analysis in which the original abundance estimates are used ('Unrevised estimates' in Table 4) than in some earlier assessments. The reasons for this are explored using the analyses in which no allowance is made for survival having dropped in 1999–2000 ('No Event' and 'Unrevised, No event' in Table 4, see also Fig. 2) because the previous assessments did not explicitly account for the mortality event. This comparison suggests that allowing for the possibility of a catastrophic mortality event in 1999–2000 has reduced the ability to constrain the upper bound for carrying capacity because the lower 5% limit for  $P_{2009}^{1+} / MSYL^{1+}$  is notably higher for the analyses which ignore this event (Table 4). Bayes factors comparing the analyses which

include a 1999–2000 catastrophic mortality event and those which do not provide support for estimating a parameter for the 1999/2000 event. For example, in the baseline analysis the  $\ln$  (Bayes factor) value is 3.00 compared to the 'No event' model. This is interpreted as strong, but not definitive, support (Kass and Raftery, 1995) for including the catastrophic mortality parameter in the model.

The results are insensitive to changing the first year of the analysis (Table 4, Fig. 3). The key management-related results are also not sensitive to splitting the series in 1987–88, using the calf count estimates and using the 'Lo' and 'Hi' abundance estimates (Fig. 4). The results for the generalised logistic model are most comparable with the two 'No event' analyses because no account is taken of a catastrophic mortality event in 1999–2000 when fitting the generalised logistic model (see Appendix 1). While not entirely comparable, the qualitative conclusions from the generalised logistic model are identical to those from the age-structured model.

Fig. 5 shows the posterior distributions for the parameters for the baseline analysis. These posteriors show that the data update the priors for  $MSYR^{1+}$  and  $MSYL^{1+}$  to a substantial extent. The posterior for  $MSYL^{1+}$  emphasises higher values for  $MSYL^{1+}$ , which is not unexpected given that the rate of

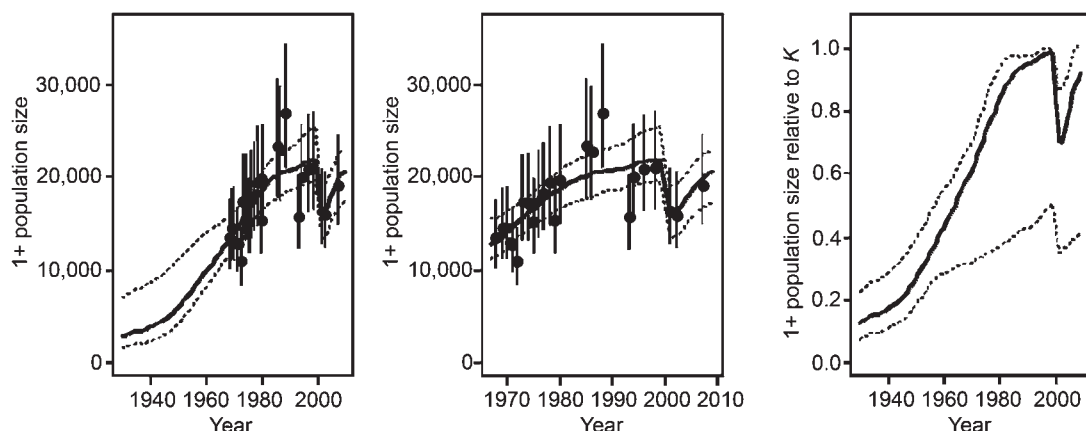


Fig. 1. Posterior distributions (medians and 90% credibility intervals) for the time-trajectories of 1+ population size (left and centre panels) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis.

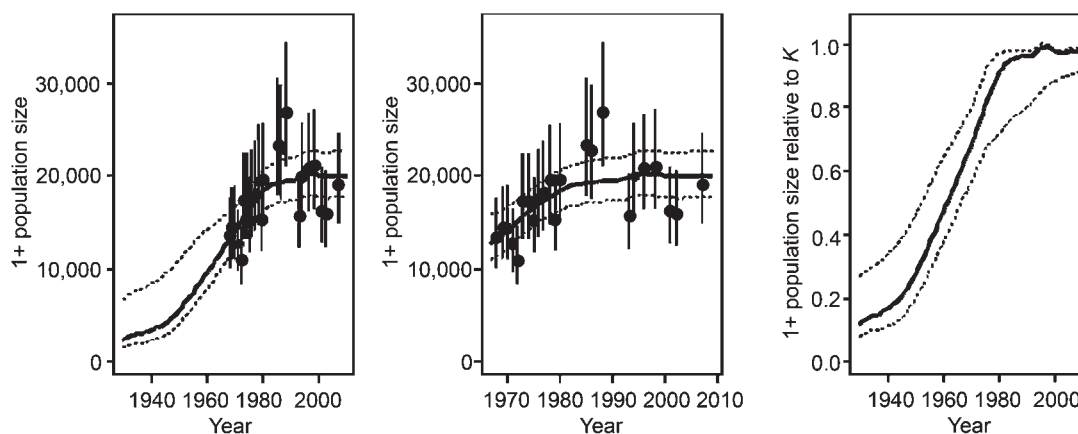


Fig. 2. Posterior distributions (medians and 90% credibility intervals) for the time-trajectories of 1+ population size (left and centre panels) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the 'No Event' analysis.

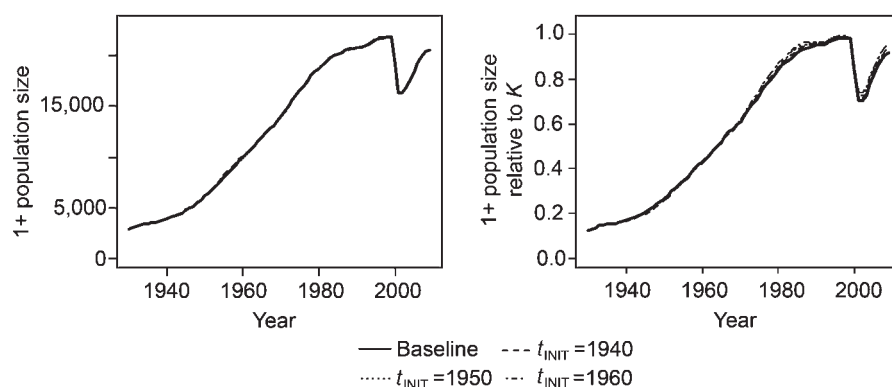


Fig. 3. Posterior median time-trajectories of 1+ population size (left panel) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis and the sensitivity tests which vary the value for  $t_{INIT}$ .

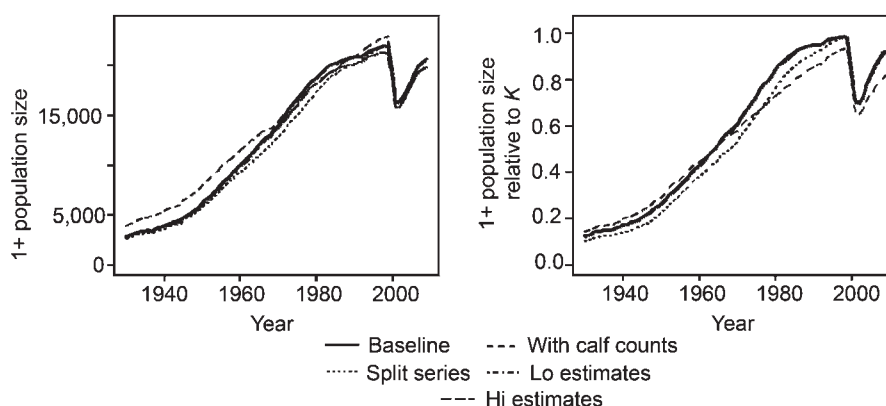


Fig. 4. Posterior median time-trajectories of 1+ population size (left panel) and 1+ population size expressed relative to (current) carrying capacity (right panel) for the baseline analysis and a subset of the sensitivity tests.

increase for the ENP gray whales is assessed to have been high until just before this population (almost) reached its current carrying capacity. The posteriors for the age-at-maturity, maximum fecundity, and adult survival place greatest support on low, high, and high values, respectively. This is consistent with the fairly high growth rates and values for  $MSYR^{1+}$ . The posterior for the survival multiplier is also updated substantially, with both high (close to 1) and low

values (below 0.7) assigned low posterior probability. Sensitivity tests in which the bounds for the priors were widened (results not shown) did not lead to outcomes which differed noticeably from the baseline assessments.

The maximum rate of increase,  $\lambda_{max}$ , is well-defined in all of the analyses. The posterior mean estimates of this quantity range from 1.057 to 1.068 and are fairly precisely determined (Table 4).

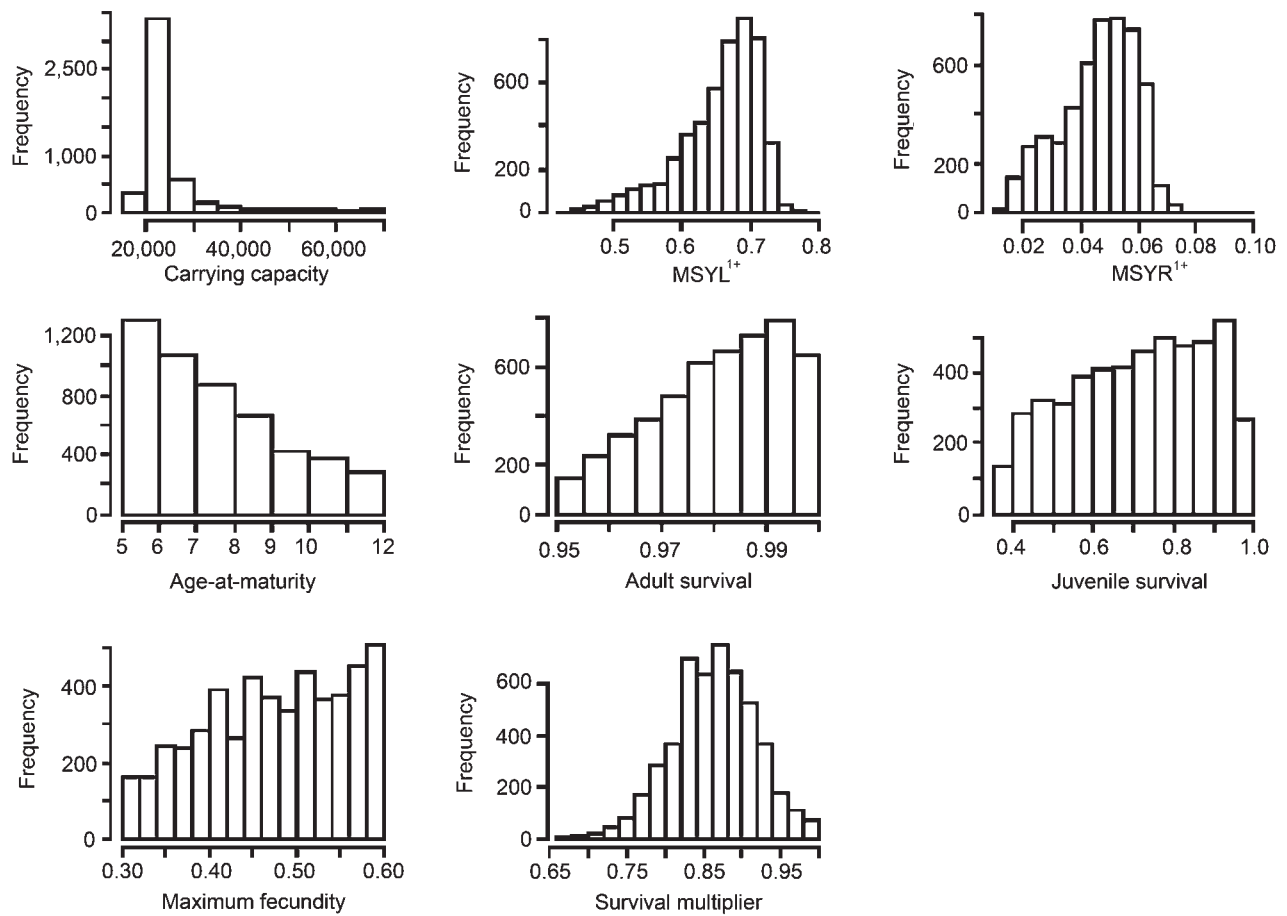


Fig. 5. Posterior distributions for the parameters of the baseline analysis.

## DISCUSSION

The sensitivity tests were designed to examine the effect of various assumptions on the assessment results and to examine the effect of changes in the methods that have occurred, particularly related to abundance estimation. Overall, the results are consistent across most of the sensitivity tests with some exceptions. In particular, the baseline model fit to the unrevised abundance estimates had relatively different results from the other analyses. Leaving aside that analysis for the moment, the posterior medians for the parameters of interest were relatively consistent. Across all the other analyses, posterior means for  $K^{1+}$  ranged from 21,146 to 27,716, for the *depletion level* ranged from 0.76 to 0.96, and for the *MSYL ratio* ranged from 1.22 to 1.54. Therefore, as in previous assessments, the ENP gray whale population is estimated to be above  $MSYL^{1+}$  and approaching or close to  $K$ . The estimates of *depletion level* and *MSYL ratio* in Wade (2002) and in Punt and Butterworth (2002) are very similar to the results presented here, although our current estimates of  $K$  are lower. The results in Wade and Perryman (2002) and Brandon (2009), which were the only previous assessments to use abundance estimates from the 1997/98 and subsequent surveys, gave higher and more precise estimates for *depletion level* and *MSYL ratio* than estimated here. However, in common with previous assessments, those results are superseded by this new assessment because it uses the revised abundance estimates of Laake *et al.* (In press).

The posterior means for the life history parameters were very consistent as well, with the posterior means for  $\lambda_{\max}$

ranging from 1.057 to 1.068, non-calf survival ranging from 0.972 to 0.983, and calf survival ranging from 0.706 to 0.730. The parameter  $MSYL^{1+}$  was updated to strongly emphasise higher values in the baseline analysis. There are theoretical arguments for why  $MSYL$  should be relatively higher in marine mammals than, say, marine fishes (Eberhardt and Siniff, 1977; Fowler, 1981; Taylor and DeMaster, 1993), but, in general, there has not been empirical data of sufficient quantity and quality to estimate this parameter well for marine mammals (Gerrodette and DeMaster, 1990; Goodman, 1988; Ragen, 1995). Empirical evidence that is available for large, long-lived mammals has shown convex nonlinear density-dependence in life history parameters such as age-specific birth and mortality rates (Fowler, 1987; 1994; Fowler *et al.*, 1980), which suggest  $MSYL > 0.5K$ . A relatively long time-series of abundance estimates has documented the recovery of harbour seal (*Phoca vitulina*) populations in Washington state, and Jeffries *et al.* (2003) estimated  $MSYL$  to be greater than  $0.5K$  for these populations. In the ENP gray whale analysis here, values from 0.40 to 0.54 for  $MSYL^{1+}$  have low probability in the posterior distribution (Fig. 5, Table 4) which is consistent with the conclusions of Taylor and Gerrodette (1993) that  $MSYL$  was likely to be greater than  $0.5K$ . Thus, the posterior distribution for  $MSYL^{1+}$  estimated here (posterior means for the baseline analysis of 0.656, range of posterior means 0.611–0.691), suggests that the ENP gray whale population experienced a decrease in population growth only when it was relatively close to  $K^{1+}$ .

The results did not vary much for a large number of the sensitivity tests, providing assurance that the assumptions made for the baseline analysis did not have a substantial influence on the results. Changing the initial year from which the model was projected had little effect on the results, which is similar to the results seen in Punt and Butterworth (2002) for initial years ranging from 1930 to 1968, as used here. The results for the ‘Lo’ and ‘Hi’ series of abundance estimates are very similar to the baseline results, suggesting that assumptions made in calculating the abundance estimates do not have a strong influence on the results of the assessment. Additionally, splitting the abundance time series in 1987/88 did not have a substantial effect. This is particularly reassuring, because some changes in the field methods happened at that time, notably the use of a second independent observer during that and subsequent surveys (Laake *et al.*, In press). The generalised logistic model provided similar results to the ‘No-event’ analysis, with some small differences. This was similar to results seen in Wade (2002), where the quantitative values for some parameters were somewhat different for the generalised logistic, although the qualitative results are nearly identical in this case. That the quantitative results differ between the generalised logistic and our baseline analyses is to be expected because the analysis based on the generalised logistic did not account for the dynamics of sex- and age-structure, and also ignored time-lags in the dynamics.

The baseline analysis fits the abundance data better than in the ‘No-event’ analysis because it includes the catastrophic mortality event in 1999–2000 (Figs 1 and 2). Furthermore, the Bayes factor confirms that there is strong, but not definitive, evidence supporting the use of a model including the catastrophic mortality. The model estimates that 15.3% of the non-calf population died in each of the years with catastrophic mortality, compared to about 2% in a normal year. In that 2-year period, the model estimates of the population size relative to  $K^{1+}$  fell from being at 99% of  $K^{1+}$  in 1998 to 83% in 1999 and 71% in 2000, before increasing back up to 91% by 2009. In contrast, the ‘No-event’ analysis estimates the population had reached a level very close to  $K^{1+}$  by ~1995 and has remained there since, which clearly does not match the evidence regarding the biological effects on the population in 1999 and 2000. In the baseline analysis, the estimate of the number of whales that died in 1999 and 2000 was 3,303 (90% interval 1,235–7,988) and 2,835 (90% interval 1,162–6,389), respectively, for a combined total for the two years of 6,138 (90% interval 2,398–14,377). In comparison, the ‘No-event’ analysis estimates that the number of whales that died in 1999 was 587 and in 2000 it was 447. Comparing the number of strandings (from Mexico to Alaska) reported in Gulland *et al.* (2005) in the years around the mortality event to these estimates of total deaths from the baseline model indicates that only 3.9–13.0% of all ENP gray whales that die in a given year end up stranding and being reported.

The baseline analysis is more conservative regarding status relative to  $K^{1+}$  than the ‘No-event’ analysis. On the other hand, it can be argued that the ‘No-event’ analysis provides a more accurate estimation of current average  $K^{1+}$ . In other words, the baseline analysis does a better job of modelling the actual time-course of the population by

including the mortality event, but it might provide an overestimate of the average recent  $K^{1+}$  by essentially considering high abundance estimates to be near  $K^{1+}$ , but lower abundance estimates to be lower than  $K^{1+}$ . The different interpretations hinge on whether  $K^{1+}$  is viewed as relatively fixed, with the 1999–2000 mortality event considered to be unrelated to density-dependence (and therefore  $K^{1+}$ ), or whether  $K^{1+}$  is viewed as something that can vary from year to year, with the 1999–2000 years viewed as an event when  $K^{1+}$  itself was low. As populations increase in density, the impact of density-independent factors on population dynamics probably becomes more pronounced (Durant *et al.*, 2005; Wilcox and Eldred, 2003). The actual carrying capacity of the environment, in terms of prey available for the ENP gray whale population, is likely to vary from year to year to a greater or lesser extent due to oceanographic conditions affecting primarily benthic production. In terms of the model, the parameter  $K^{1+}$  that is being estimated is interpreted as the average carrying capacity in recent years. In the baseline analysis, the estimated  $K^{1+}$  is approximately (though not exactly) the average recent  $K^{1+}$  for the years before 1999–2000, whereas in the ‘No-event’ analysis, the estimate of average recent  $K^{1+}$  includes all the recent years, including 1999–2000, and is lower. This is clear from the results, where the baseline estimate of  $K^{1+}$  is 25,808 (90% interval 19,752–49,639), whereas the ‘No-event’ estimate of  $K^{1+}$  is substantially lower, 21,640 (90% interval 18,301–25,762).

The analysis using the original unrevised estimates is not a sensitivity test in the usual sense. Those results are provided simply to aid in interpretation of the results of the other analyses relative to past results using the unrevised estimates. For example, no previous analyses other than Brandon (2009) had used the 2006/07 abundance estimate, so this sensitivity test provides a comparison in which both analyses use that estimate. In the ‘No-event’ model, the analyses using the original and revised abundance estimates are nearly identical for estimates of *depletion level* and *MSYL ratio*.  $K^{1+}$  was estimated to be higher in the analysis that used the original abundance estimates, but even though  $K^{1+}$  is lower using the revised abundance estimates, overall the entire time-series is shifted such that the estimates of status relative to  $K^{1+}$  are unchanged.

In contrast, in the baseline model, the original abundance estimates give a fairly different result from any other analysis. From the discussion of how correction factors for the abundance estimates were calculated in different years in Laake *et al.* (In press), it is clear that the revised abundance estimates should be more accurate, and there were shifts of certain sequences of abundance estimates relative to one another that influence the results. For example, the three estimates from 1993/94 to 1997/98 are the three highest estimates in the original time-series, whereas the three estimates from 1984/85 to 1987/88 are the three highest estimates in the revised time-series. This has an effect on the baseline analysis results because the model is trying to fit the drop in abundance that occurred after the 1997/98 abundance estimate. That drop is substantially larger in the unrevised data set than it is in the revised data set, and therefore the results for the baseline model differ somewhat between the revised and unrevised data sets.



The only previous assessment that modelled the 1999–2000 mortality event was that of Brandon (2009), whose point estimates of total natural mortality in those years ranged from 1,300 to 5,200, depending upon a variety of assumptions he explored, lower than the 6,138 estimated here in the baseline model. The difference presumably arises because Brandon (2009) modelled mortality as a function of a sea-ice index for the Bering Sea, following the relationship found between calf production and sea-ice (Perryman *et al.*, 2002). This constrains the dynamics of the mortality in Brandon (2009) to reflect the dynamics of the index to some extent. In contrast, the 1999–2000 mortality was unconstrained in the baseline analysis here and is essentially estimated by what value fit the drop in abundance estimates best. Brandon (2009) noted this difficulty in his analysis, stating it was not possible in his analysis to fit the strandings data for the 1999–2000 mortality event without allowing for some additional process error in the survival rates during those years.

$\lambda_{\max}$  is estimated to be 1.062 (90% interval 1.032–1.088) in the baseline analysis. This is similar to, but a little lower than, the estimate from Wade (2002) of 1.072 (90% interval 1.039–1.126) and the estimates from Wade and Perryman (2002). The posterior for  $\lambda_{\max}$  from the ‘No-event’ analysis is very similar to this, as is that from the ‘No-event’ analysis using the unrevised abundance estimates, indicating the lower estimates of  $\lambda_{\max}$  seen here are not due entirely to the revision of the abundance estimates but are instead partly due to the additional four abundance estimates used here (1997/98 to 2006/07) that were not available at the time the Wade (2002) analysis was conducted. To get an estimate of  $\lambda_{\max}$  of 1.062, the posterior distribution favoured a low age-of-maturity, a high maximum fecundity, and a high adult survival.  $\lambda_{\max}$  appears to be well-defined, as the posterior medians from most of the sensitivity tests are very similar. It should be noted that these are theoretical estimates of the population growth rate at a very low population size, based upon the density-dependent assumptions of the population model; the ENP gray whale has not been observed to actually grow this rapidly because the population was estimated to be approaching  $K$  by the time its growth rate was monitored; consequently, the observed population growth rate was less than its theoretical maximum.

The small and endangered western North Pacific population of gray whales has been estimated to have an annual population increase that is between 2.5% and 3.2% per year, but there is concern that this growth rate is low because of possible Allee effects and from ongoing human-caused mortality (Bradford *et al.*, 2008). Best (1993) summarised the growth rates of eight severely depleted baleen whale populations (other than gray whales) and the values ranged from 3.1% to 14.4%. Some of these estimates were not very precise, and Zerbini *et al.* (2010) suggested that the higher rates are implausible given life-history constraints for (at least) humpback whales (*Megaptera novaeangliae*). In more recent studies of other species, a number of estimates of trend have been similar to the estimates of  $\lambda_{\max}$  reported here. In a simulation study based on empirical estimates of life history parameters for humpback whales, Zerbini *et al.* (2010) estimated maximum rates of increase of 7.5%/year (95% CI 5.1–9.8%) using one

approach and 8.7%/year (95% CI 6.1–11.0%) using a second approach. Calambokidis *et al.* (2008) calculated point estimates of 4.9% to 6.7% for the North Pacific humpback whale population using data from a recently completed North Pacific study of humpback whale abundance. Zerbini *et al.* (2006) used line transect data from sequential surveys to estimate an annual rate of increase for humpback whales in shelf waters of the northern Gulf of Alaska from 1987 to 2003 of 6.6% per year (95% CI 5.2–8.6%), and for fin whales of 4.8% (95% CI 4.1–5.4%). On the other hand, Mizroch *et al.* (2004) estimated a rate of increase for North Pacific humpback whales in Hawaii using mark-recapture methods for the years 1980–1996 of 10% per year, but the confidence limits were wide (95% CI 3–16%). Other unpublished estimates are available spanning essentially a similar range as originally reported by Best (1993) (i.e. see IWC, 2010)). In summary, the estimates of  $\lambda_{\max}$  reported here are similar to trend estimates seen in other species, but there are also lower and higher values that have been recorded.

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## Appendix 1

### ANALYSES BASED ON THE GENERALISED LOGISTIC EQUATION

The dynamics of the population are assumed to be governed by the generalized logistic model:

$$N_{y+1} = N_y + rN_y(1 - (N_y / K)^z) - C_y \quad (\text{App.1})$$

where  $N_y$  is the number of animals at the start of year  $y$ ;

$r$  is the intrinsic rate of growth;

$z$  is the extent of compensation;

$K$  is the (current) carrying capacity; and

$C_y$  is the catch (in numbers) during year  $y$ .

The parameters of Equation (App.1) are  $r$ ,  $z$ , and  $K$  while the data available to estimate these parameters are the estimates of abundance and their associated variance-covariance matrix. The analysis is based on the same likelihood function (Eqn (11) of the main text) and priors as the baseline analysis using the age- and sex-structured model.

# Southern Hemisphere Breeding Stock D humpback whale population estimates from North West Cape, Western Australia

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## ABSTRACT

Estimates of the abundance of Breeding Stock D humpback whales (*Megaptera novaeangliae*) are key to the conservation and management of what is thought to be one of the largest populations of the species. Five years (2000, 2001, 2006, 2007 and 2008) of aerial surveys carried out over an eight-year period at North West Cape (Western Australia) using line transect methodology allowed trends in whale numbers to be investigated, and provided a base for comparison with estimates made approximately 400km south at Shark Bay (Western Australia). A total of 3,127 whale detections were made during 74 surveys of the 7,043km<sup>2</sup> study area west of NWC. Pod abundance for each flight was computed using a Horvitz-Thompson like estimator and converted to an absolute measure of abundance after corrections were made for estimated mean cluster size, unsurveyed time, swimming speed and animal availability. Resulting estimates from the migration model of best fit with the most credible assumptions were 7,276 (CI = 4,993–10,167) for 2000, 12,280 (CI = 6,830–49,434) for 2001, 18,692 (CI = 12,980–24,477) for 2006, 20,044 (CI = 13,815–31,646) for 2007, and 26,100 (CI = 20,152–33,272) for 2008. Based on these data, the trend model with the greatest  $r^2$  was exponential with an annual increase rate of 13% (CI = 5.6%–18.1%). While this value is above the species' estimated maximum plausible growth rate of 11.8%, it is reasonably close to previous reports of between 10–12%. The coefficient of variation, however, was too large for a reliable trend estimate. Perception bias was also not accounted for in these calculations. Based on a crude appraisal which yielded an estimated  $p(0)$  of 0.783 (from independent observer effort, CV = 0.973), the 2008 humpback population size may be as large as 33,300. In conclusion, the work here provides evidence of an increasing Breeding Stock D population, but further surveys are necessary to confirm whether the population is indeed increasing at its maximum rate.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY-AERIAL; MIGRATION; MODELLING; TRENDS

## INTRODUCTION

The population of humpback whales (*Megaptera novaeangliae*) known as Southern Hemisphere Breeding Stock D (IWC, 1998) migrates annually from Antarctica to the Kimberley region (northwestern Australia) along the Western Australian (WA) coastline (Jenner *et al.*, 2001). This population has one of the longest records of study and management in the Southern Hemisphere, due to its long history of exploitation from the whaling industry (Bannister, 1964; 1991; 1994; Bannister *et al.*, 1991; Chittleborough, 1953; 1965). Assessment of its size, however, has been a more recent undertaking and thus far, three 'best estimates' of 11,500 for surveys in 1999, 12,800 for surveys in 2005, and 33,850 for surveys in 2008 have been produced at Shark Bay, WA (Bannister and Hedley, 2001; Hedley *et al.*, 2011; Paxton *et al.*, 2011). Whilst these previous works provide a framework from which to begin trend estimation, the wide confidence intervals (typical of cetacean population estimates) and limited data points (three years) point towards the need for supplementary monitoring. Consequently, the general aim of this study was to: (1) supplement existing knowledge with data gathered from the same population but at a location approximately 400km north of Shark Bay (at North West Cape) over five years; and (2) define a possible trend in the abundance of Breeding Stock D humpback whales based on combined North West Cape (NWC) and Shark Bay survey results. The work presented here provides significant information on the current status of Breeding

Stock D – information essential for the effective long-term conservation and management of the population.

## METHODOLOGY

Steps taken to fulfil the objectives of this study were: (1) for each survey, daily abundance was estimated; (2) a migration model was fitted for each year; (3) annual population abundance using the migration models were estimated; and (4) the population abundance trend between 2001 and 2008 was estimated.

### Daily survey abundance estimates

#### Survey area and design

Aerial surveys were conducted between June and November west of NWC during 2000, 2001, 2006, 2007, and 2008, in an area where humpback whales travel within close proximity to the shore (Chittleborough, 1953; Jenner *et al.*, 2001; Fig. 1). A total of eight tracks 10km apart and taking about four hours to complete were surveyed consistently every year in a direction against that of the general whale migration during the northern migration (from transect 1 to 8; Fig. 1) and in the direction of the migration during the southern migration. The travel speed of the aircraft (~20km hr<sup>-1</sup>) in the direction of southerly migrating whales was much greater than the travel speed of the whales (~4km hr<sup>-1</sup>), hence sampling the same animals on adjacent transects was highly improbable. The eight tracks resulted in a total region surveyed of 7,043km<sup>2</sup>. The timing of the first and last flights of each field

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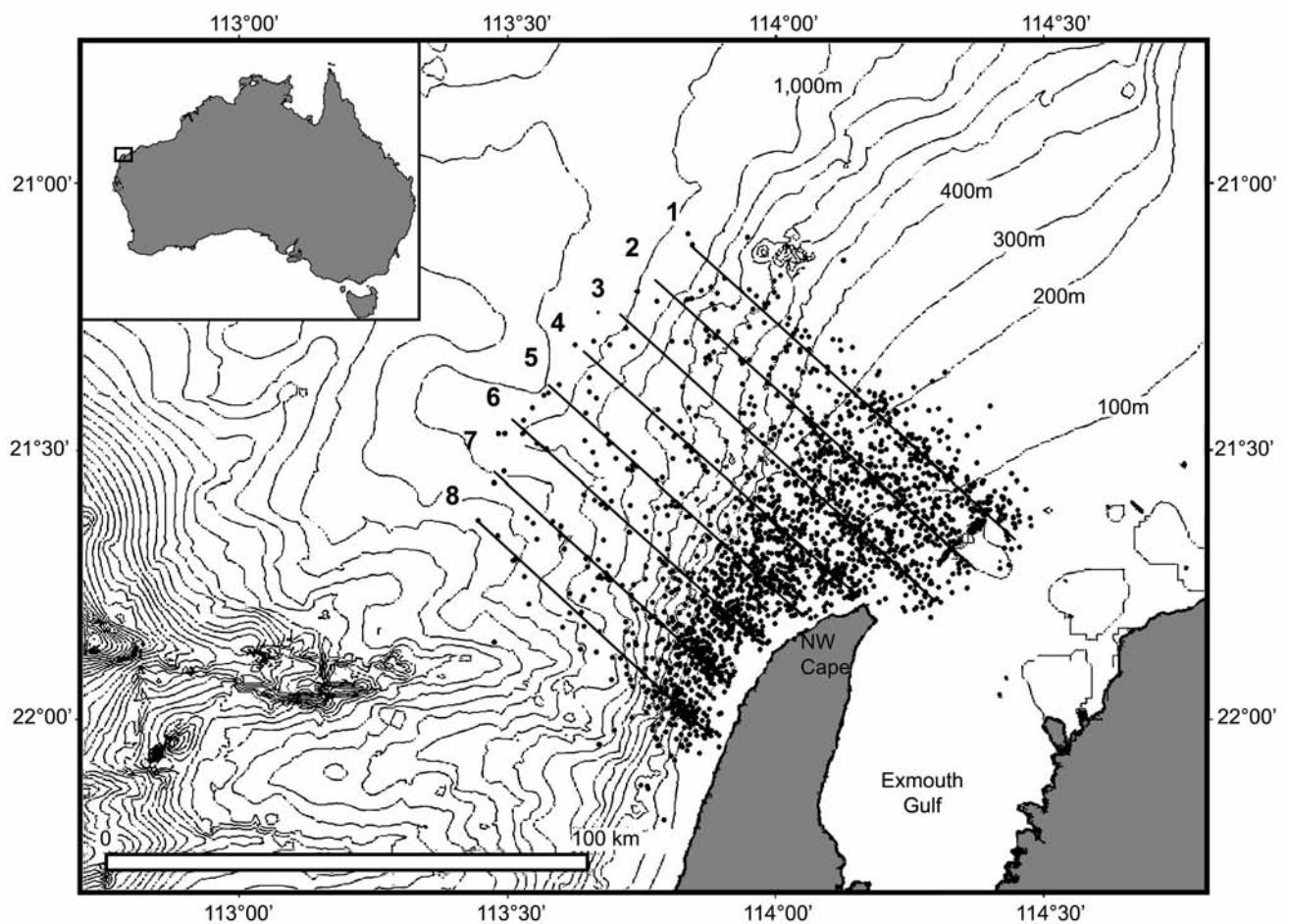


Fig. 1. Aerial survey tracks conducted during 2000, 2001, 2006, 2007, and 2008 west of North West Cape, Western Australia, with positions of all pod detections overlaid on the map (black circles).

season varied among years, but most were spaced 5 to 10 days apart (Table 1). Surveys were designed to cover the whales' northern migration (June to August) and southern migration (August to November), with the exception of the survey in 2008 which only covered the northern migration. During the five years, a total of 74 flights were carried out: 17 in 2000, 17 in 2001, 14 in 2006, 13 in 2007, and 13 in 2008.

#### Data collection and analysis

Aerial surveys were flown at an altitude of 305m (1,000ft) and a speed of 222km hr<sup>-1</sup> (120 knots) using a *Cessna 337*, or a *Partenavia P68B* aircraft (twin engine, overhead wing aircraft) fitted with bubble windows (to maximise viewing under the plane) or with standard windows (depending upon aircraft availability). The type of platform used remained consistent

Table 1  
Number of humpback whale pod detections for 2000, 2001, 2006, 2007 and 2008 North West Cape aerial surveys.

2000		2001		2006		2007		2008	
Date	Number detected	Date	Number detected	Date	Number detected	Date	Number detected	Date	Number detected
11 Jun.	1	10 Jun.	2	13 Jun.	1	24 Jun.	4	24 Jun.	8
12 Jun.	1	11 Jun.	4	19 Jun.	5	01 Jul.	5	27 Jun.	23
19 Jun.	10	17 Jun.	3	26 Jun.	16	08 Jul.	38	01 Jul.	27
20 Jun.	5	30 Jun.	8	08 Jul.	23	14 Jul.	44	05 Jul.	23
03 Jul.	26	07 Jul.	21	15 Jul.	22	29 Jul.	54	11 Jul.	70
12 Jul.	30	20 Jul.	28	29 Jul.	40	05 Aug.	59	15 Jul.	98
22 Jul.	20	29 Jul.	15	06 Aug.	77	19 Aug.	44	28 Jul.	88
23 Jul.	15	12 Aug.	50	20 Aug.	72	31 Aug.	75	01 Aug.	27
04 Aug.	31	24 Aug.	121	25 Aug.	41	09 Sep.	37	08 Aug.	63
13 Aug.	60	11 Sep.	27	09 Sep.	19	23 Sep.	13	09 Aug.	72
25 Aug.	92	22 Sep.	27	20 Sep.	6	08 Oct.	11	16 Aug.	71
17 Sep.	30	08 Oct.	23	29 Sep.	12	14 Oct.	7	19 Aug.	54
24 Sep.	9	21 Oct.	3	07 Oct.	4	25 Oct.	3	27 Aug.	68
20 Oct.	9	30 Oct.	7	15 Oct.	2				
29 Oct.	3	10 Nov.	4						
12 Nov.	1	30 Oct.	1						
26 Nov.	3	10 Nov.	5						

throughout any single season, except in 2000, where the first eleven flights were completed with a *Partenavia* fitted with bubble windows, and the last six with a *Partenavia* with standard windows. The plane followed box-end line transects (Fig. 1) which were surveyed in passing mode (e.g. no deviation from the flight path). Survey tracks were 10km apart and were designed to be perpendicular to bathymetric contours and to the known humpback whale migratory path.

Personnel for all surveys before 2006 included two pilots, two observers and a data recorder. The observers and data recorder were linked via a separate intercom system from the pilots, and the data were logged with a time code to a digital tape recorder. Observers measured vertical and horizontal angles from the plane to each sighted pod (using *Suunto* PM-5/360PC clinometers and a compass board), while the pilots recorded the angle of drift of the aircraft from the flight path (for diagram of angles see Lerczak and Hobbs, 1998). All relevant animal data (i.e. group size, migratory heading) were entered into a palm-top computer by the data typist. GPS coordinates and altitudes were logged in a laptop computer for every second of the flight, and subsequently used to link the palm-top computer with the digital tape recorder. Each device was calibrated to  $\pm 1$ sec accuracy at the beginning of each flight. Whales' travel direction were categorised as 'north', 'south', or 'milling' for each observed pod. Groups reported as 'milling' were generally surface lying at the time of sighting with no obvious signs of swimming activity or were swimming slowly in different directions at each surfacing. Observers who were unable to determine the nature of the whales' movements and/or surface behaviour classified their direction of travel as 'undetermined'.

From 2006 onwards, a time-coded Mini-Disk recorder (Sony Mini Disk Recorder NH900), which was synchronised to the GPS prior to takeoff, was used (instead of a data typist) to record animal data and the time that waypoints were

marked on the GPS for each detection.

True angles from the aircraft to the animals were later calculated with the following formula:  $AW = AC + MHA \pm DA$ , where  $AW$  is the angle to the whale,  $AC$  the aircraft course,  $MHA$  the measured horizontal angle and  $DA$  the angle of drift of the aircraft, which was either subtracted or added depending upon the side of the aircraft the animal was sighted on (as defined and described in Lerczak and Hobbs, 1998). Radial distances were calculated using equations detailed in Lerczak and Hobbs (1998). In 2008, an independent observer (or 'double blind') configuration was used every other survey, and required in a total of 5–6 personnel (including four observers, two on each side of the aircraft).

#### Detection function and abundance estimation

All analyses described here forward were run using R v2.9.2 (The R Foundation for Statistical Computing 2006) and DISTANCE 6.0 release 2 (Thomas *et al.*, 2010).

Conventional Distance Sampling techniques (Buckland *et al.*, 2001; 2004) were used to estimate the abundance of humpback whales migrating past NWC. First, estimates of pod abundance ( $\hat{N}_{pods}$ ) were computed using a Horvitz-Thompson like estimator:

$$\hat{N}_{pods} = \frac{n}{p(x)} \frac{A}{2Lw} \quad (1)$$

where  $n$  is the number of detections made during any one flight,  $A$  is size of study region,  $p(x)$  is the average probability of detection (estimated for each survey; fit shown for pooled data in Fig. 2),  $L$  is the total survey effort, and  $w$  is the perpendicular right-truncation distance.

A right-truncation distance of  $w = 13$ km was chosen since smaller values dramatically reduced the number of available observations for surveys at the beginning and at the end of the migration seasons, thereby compromising the estimation

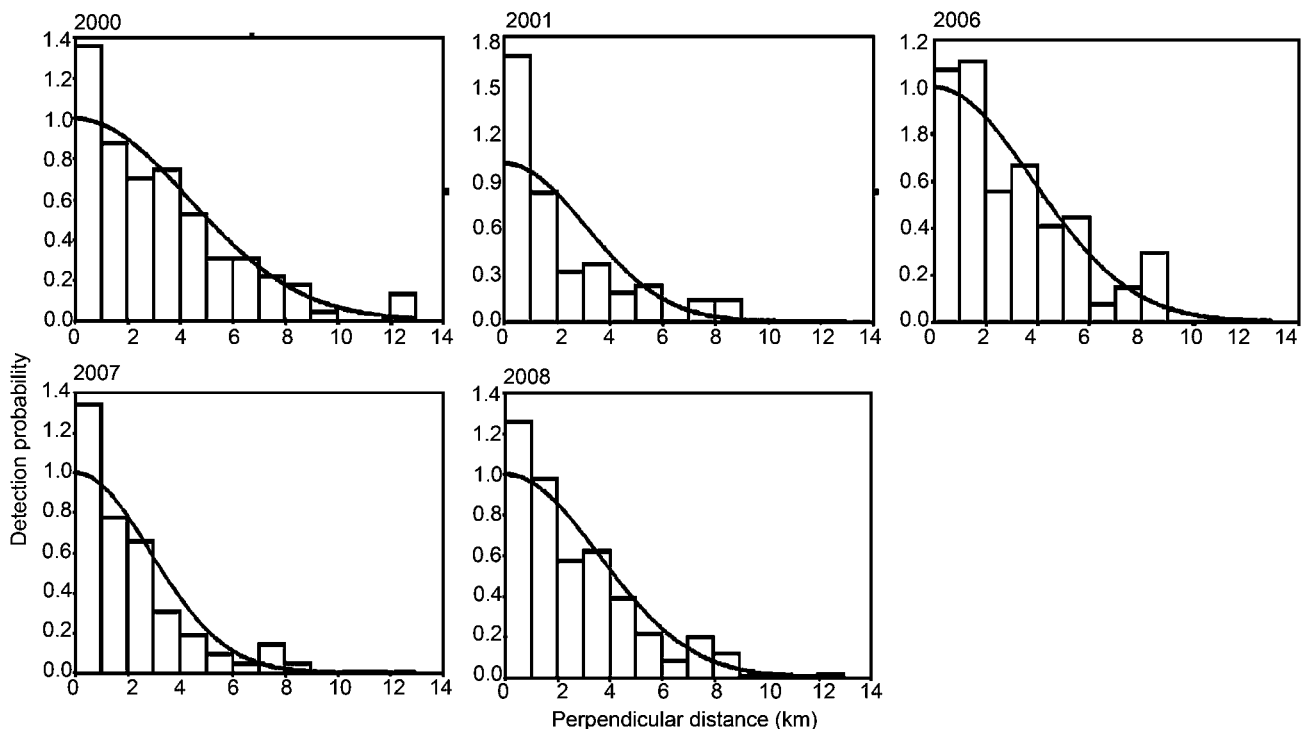


Fig. 2. Detection probability (pooled by year) as function of perpendicular distance from flight line for the northern migration using Approach no. 2 during 2000, 2001, 2006, 2007 and 2008.

of daily abundance and lowering the number of surveys which could be incorporated into the final migration model. Approximately one to two surveys at the beginning and at the end of the migration would have had to have been removed from the annual migration models if a right-truncation distance of  $w = 10\text{km}$  had been used. In a model where the greatest source of variation is from the migration model itself, it is important to elevate the number of surveys informing the migration model as much as possible. Violating the assumption of independence between transects (by having a right truncation distance larger than the inter-transect distance) was considered to be a less significant problem than the uncertainty associated with inferences made from a limited number of data points. By having the covered area of transects overlap, there is a possibility that some animals may be detected from  $>1$  transect. This has no effect upon the point estimate which is calculated as a function of encounter rate, but the estimated variance of the density estimate may be too small. The inclusion of the small number of detections at large distances, however, allowed for a detection function to be fitted to surveys where only a handful of whales were detected (surveys with too few detections were not included since corresponding detection functions were either unreliable or could not be fitted).

Observers' viewing ranges were restricted between  $10^\circ$  and  $140\text{--}160^\circ$  of the nose of the airplane, and visual obstruction by the fuselage and wheels only permitted maximum declination angles of  $84^\circ$  when using bubble, or  $38^\circ$  when using flat windows (with  $0^\circ$  at the horizon). These conditions gave blind strips of  $31\text{m}$  ( $0.02\text{ n.miles}$ ) or  $390\text{m}$  ( $0.21\text{ n.miles}$ ) either side of the path for the elevated height considered here. The different results due to visibilities offered by both flat and bubble windows were tested and deemed equivalent (Bouchet, 2009), and availability computations were made by choosing the angular margins of the view-field as the minimum and maximum bearings recorded in each year. In this way the time windows for observing pods were estimated for each year. Data were left-truncated at  $0.75\text{km}$  as it was assumed that complete detection ought to have been achieved at this distance (Bouchet, 2009).

The probability of detecting a whale  $p(x)$  can be regarded as the outcome of two contiguous events; namely (1) the animal is or becomes available to be seen and (2) it is spotted by an observer. This can be described mathematically by:

$$\int_0^w p(\text{seen} | a, x) p(a | x) \frac{1}{w} dx \quad (2)$$

where  $p(\text{seen} | a, x)$  is the probability of being seen given that the pod is available ( $a$ ) for detection (at the surface) and  $p(a = 1 | x)$  is the probability of the pod being available for detection.  $p(\text{seen} | a, x)$  was determined based on the fitting of a constrained half-normal key function inside Distance 6.0 (this was the best fitting function of those available within Distance 6.0):

$$p(\text{seen} | a, x) = e^{-\frac{x^2}{2\sigma^2}} \quad (3)$$

The integration of covariates associated with each observation such as glare, sea state, cloud cover, and observer into the model was explored. While cloud cover was not correlated with detections, glare, sea state, and to a

lesser extent observer appeared to have some effect, although this effect did not change the AIC scores significantly. Because the correlations were inconsistent in their nature and the AICs did not improve significantly, integrating these covariates into the model was deemed inappropriate.

To estimate  $p(a = 1 | x)$  the following equation developed by Laake *et al.* (1997) was applied:

$$\hat{p}(a | x) = \frac{E[s]}{E[s] + E[d]} + \frac{E[d](1 - e^{-\frac{t}{E[d]}})}{E[s] + E[d]} \quad (4)$$

where  $E[s]$  is the expected time a whale spends at the surface,  $E[d]$  is its expected dive duration, and  $t$  is the time the animal is within detectable range (given the physical constraints of the aircraft). The time that a humpback stays in view is a function of the viewing angle forward and aft of the perpendicular line to the aircraft's centreline (Fig. 3) and of the aircraft's velocity, and was computed by:

$$t = \frac{d_1 + d_2}{v} \quad (5)$$

where  $v$  represents the plane's cruising speed ( $120\text{ n.miles hr}^{-1}$ ), and  $d_1 + d_2$  is the distance covered by the animal within the detection range of the observer ('time window'). Distances varied since they depended upon the position of the pod relative to the aircraft, and were calculated trigonometrically (Fig. 3). The expected surfacing time and expected dive duration ( $E[s]$  and  $E[d]$ , respectively) were estimated by obtaining the average of randomly sampled dive-surface pairs (with replacement) from observations made of 44 pods during 22 dedicated boat-based focal follows conducted within the same area as the aerial surveys, between 22 July and 18 September 2002. These vessel-based surveys consisted of closing mode approaches conducted from a 6m centre console, inflatable Zodiac, with a crew comprising of a driver, a note-taker and a marksman/photographer. The surveys were carried

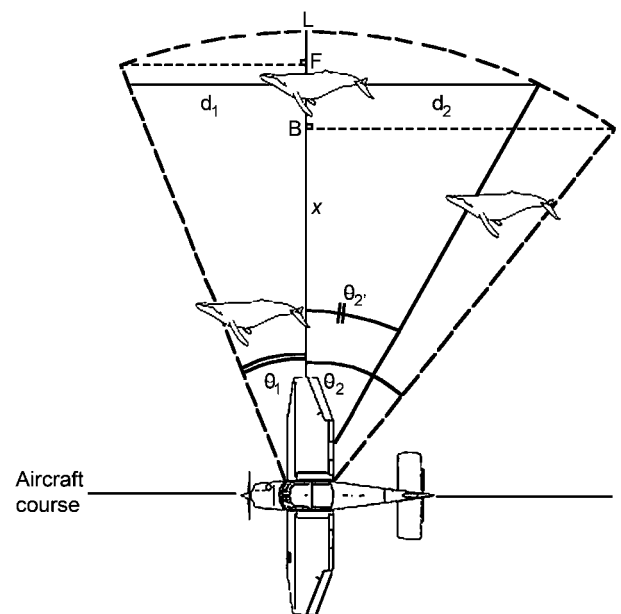


Fig. 3. Diagram of the view-field and detection range available to observers onboard an aircraft, where  $L$  = outer limit of the viewing range,  $\theta_1$  = fore angle of view,  $\theta_2$  = aft angle of view,  $\theta_1'$  = aft angle to the whale when it comes into view,  $x$  = sighting distance (relative to the aerial track), and  $d_1 + d_2$  = time window.



out haphazardly within the study region and were aimed at gathering behavioural information on movements and travelling speeds, and collecting biopsy samples and photo-identification images. The latter two data types were collected as part of an independent study and are not discussed here. Only those observations made prior to biopsy sampling have been included in the analyses presented here, in an effort to only rely on information reflecting conditions of minimum observer disturbance. Dive times were measured as the time between surfacing events (of the last individual of the pod to dive and the first individual of the pod to surface), while surfacing intervals were defined as the time from the first individual of the pod to blow (after a dive) to the last individual of the pod to blow (before the following dive).

Estimates of pod abundance ( $\hat{N}_{pods}$ ) for each flight were converted to estimates of individual abundance ( $\hat{N}_{individuals}$ ) by multiplying the former by the estimated mean cluster size. This was obtained by regressing the log of the observed cluster size against the estimated detection probability for each survey, thereby accounting for the potentially greater visibility of larger pods with increasing distance from the track line to produce an unbiased estimate of the average size of pods in the population.

The daily number of individual animals migrating past NWC was then estimated by multiplying the above individual abundance by the mean whale speed (km/hr) and the number of hours in a day (24), and dividing it by the total latitudinal length of the survey area in km (80km). The method applied is roughly consistent with that described in Buckland *et al.* (2004). This approach assumes that there is a constant rate of migration through the area over the period of a day, and that the estimate derived from each survey is an ‘instantaneous’ abundance estimate. Pod speed was obtained from the 2002 boat surveys by marking GPS waypoints and recording the time taken and distance covered from the beginning of a surfacing event to the beginning of the subsequent one. Average whale speed was found to be 5.65 km hr<sup>-1</sup> (SE = 0.33) for northerly migrating whales, and 4.07 km hr<sup>-1</sup> (SE = 0.24) for southerly migrating whales.

#### Perception bias

While estimates of availability bias were achieved for all surveys, estimates of perception bias were only possible for surveys undertaken in 2008 (since this was the only year when an independent observer setup was in place). As a consequence, these are presented separately to the overall population size estimates (described below), so that trend estimation is based on results derived from comparable methods.

To evaluate the extent of perception bias, data were left-truncated at 0.75 km to remain consistent with previous analyses and then imported into Distance 6.0 to be analysed using the available Mark-Recapture Distance Sampling (MRDS) tools. A set of 75 contending mark-recapture models was examined with various combinations of covariates which affect detectability (i.e. perpendicular distance, sea state, glare intensity, minimum and maximum glare angles, angle of drift from the plane, wind speed, wind direction, survey date, cluster size and observer). Cluster size, observer, glare, Beaufort sea state, and survey date were treated as factor variables. The models were tested under the

assumption of full independence (FI) only (Buckland *et al.*, 2004), and the model of best fit was selected based on its Akaike Information Criterion (AIC) score.

#### Annual population abundance estimates using the migration models

To extrapolate estimates to days when surveys could not be completed, a smooth line was fitted to abundance estimates for the days in which surveys were completed during each year, resulting in an estimated number of whales migrating past NWC each day of the year. The smooth line represents the migration model. Several migration models consisting of either one (unimodal) or a mixture of two or three normals, whose parameters  $\mu$  (mean) and  $\sigma$  (variance) were found by Maximum Likelihood Estimation (MLE; Borchers *et al.*, 2002), were tested for best fit (using Akaike Information Criterion values). Integrating the area under the entire density function then provided an estimate of the total number of whales filing through the region during their migration. Because whales migrate past NWC twice (once on their way north to their breeding grounds, and a second time south during their return to polar feeding grounds), assessments of the population size must be based on one of these phases. Three approaches were taken to tackle this issue, and their respective results compared.

- (1) Northerly and southerly travelling whales were separated according to their recorded direction of travel. Here, northerly travelling whales were assumed to be migrating north, and southerly travelling whales were assumed to be migrating south. Those entered as ‘milling’ or ‘unknown’ were randomly allocated ‘north’ or ‘south’, proportionally to the observed ratio of northerly to southerly travelling whales. This was done for blocks of time equivalent to the maximum time interval between surveys in any one year. Depending upon the year, the blocks ranged from 16 to 20 days.
- (2) Northerly and southerly travelling whales were separated as above (1), but in addition survey dates which fell outside the expected end of the northern and beginning of the southern migrations were excluded. The expected end of the northern migration was deemed to be the time at which the proportion of northbound whales fell to less than 0.2 and the proportion southbound rose to above 0.8, corresponding to the 15–20 August. Similarly, the expected beginning of the southern migration was regarded as the time at which the percentage of observed southbound whales exceeded 0.2, which coincided with 10–15 August. The rationale behind this strategy is that humpback whales are known to spend a considerably greater amount of time milling during their southbound migration, leading to an elevated risk of recording a southbound whale as migrating north (when in fact the animals are only temporarily moving north during their southbound migration). By truncating the data early, an attempt was made at excluding data at the tails of the migration curve which were prone to errors in recording the migration direction (of milling southbound animals), and instead to allow the migration models to estimate the expected tails (in the absence of migration direction errors).



- (3) Northerly and southerly travelling whales were incorporated into one single model, and the resulting estimate was halved.

In all circumstances, the tails of the migration curves were required to be ‘pinned down’ so as to ensure better performance. This was done on a case-to-case basis by adding zero counts at the onset and end of the migration pulses.

To quantify the uncertainty inherent to the final abundance estimate, each working parameter (namely encounter rate, probability of detection (adjusted for availability), travelling speed, pod size, and migration model fit was bootstrapped (with replacement,  $B = 1,000$  pseudo samples). The distribution of replicates allowed coefficients of variation (CV) to be produced and 95% confidence intervals to be calculated using the percentile method. Individual coefficients were then combined into an overall CV based on the Delta method (Buckland *et al.*, 2004).

$$CV_{\hat{N}_{pop}} = \sqrt{(CV_{\frac{n}{L}})^2 + (CV_{p(x)})^2 + (CV_{speed})^2 + (CV_{cluster})^2 + (CV_{MLE})^2} \quad (6)$$

where  $CV_{\hat{N}_{pop}}$  is the coefficient of variation of the final abundance estimate,  $CV_{\frac{n}{L}}$  is the coefficient of variation of encounter rate,  $CV_{p(x)}$  is the coefficient of variation of detection probabilities (adjusted for availability),  $CV_{speed}$  is the coefficient of variation of swimming speeds,  $CV_{cluster}$  is the coefficient of variation of pod size, and  $CV_{MLE}$  is the coefficient of variation of the migration models.

### Population abundance trend estimation

For trend estimation, annual abundance estimates from NWC and from Shark Bay (from Bannister and Hedley, 2001; Hedley *et al.*, 2011; Paxton *et al.*, 2011) were integrated into a single data set and fitted with linear and exponential models. Model selection was based on the largest  $r^2$ . Since there were two estimates for 2008 (one from Shark Bay and one from NWC), models were fit to a data set containing the Shark Bay 2008 estimate, and then to a data set containing the NWC 2008 estimate. Trend detection reliability was then tested using TRENDS (Gerrodette, 1993).

## RESULTS AND DISCUSSION

In this section, the models are first evaluated and the ‘best models’ selected based on the credibility of their assumptions and model fit (discussed below). Following model selection, the details of the models considered as the ‘best models’ are then presented in the same order as in the methods, thereby eliminating the lengthy presentation of parameter estimates from improbable models.

### Model selection

A total of 3,127 whale detections were made during 74 surveys conducted over the five years (Table 1). The number of whale detections varied substantially amongst survey days (Table 1), which resulted in highly variable daily abundance estimates. As a consequence of the high variability, the migration models also varied widely in how well they fit the daily estimates.

The three migration model functions (i.e. the normal, and the mixtures of 2 and 3 normals) delivered similar results in

most cases, at least when all could be plotted (e.g. there were too few surveys to fit mixture models of 2 and 3 normals for some years and migration directions, as this would have resulted in over-parameterising the model; Table 2). Overall, the mixed migration models (of 2 and 3 normals), yielded the best fit according to the corresponding AIC scores (Table 2). There was no consistency in the shape of the mixed model curves among years, however, which begged the question of whether a model with multiple modes in the migration was realistic. Furthermore, in evaluating the credibility of selecting mixed models over unimodal models for the migration of whales in any one direction, no strong support in the literature was available. Rather, there was more support for the selection of a unimodal model from a land-based study (with a relatively high sampling effort) conducted on migrating humpback whales at a similar latitude on the east coast of Australia (Noad *et al.*, 2005). In this study, the migration followed an overall unimodal shape with variability in daily counts occurring across the entire migratory season (Noad *et al.*, 2005). In the absence of strong evidence for a multimodal migration and given the high variability expected among daily counts, mixed models (i.e. multi-modal models) were assumed to be overfitting the underlying data rather than representing the true shape of the migration. Hence, for any single migration direction, unimodal models (i.e. single normal models) were considered to be more suited for capturing the change in densities of humpback whales over their migration past NWC.

With regard to models fitted to the entire northern and southern migratory cycle, a bimodal fit could potentially be a true reflection of the shape of the migration cycle (in which the first mode represents the northbound migration, and the second mode represents the southbound migration; as in Noad *et al.*, 2005). If there is no lag in the crossover period between north and southbound whales at NWC however, then the true shape of the migratory cycle could arguably be unimodal. As a result of a lack of strong evidence for either case, here the ‘best’ models are considered to be those with the best fit (lowest AIC), regardless of whether they are unimodal or multimodal.

In comparing the results from the three approaches taken, approaches (1), (2) and (3) gave widely conflicting estimates, particularly during the last three survey years (Table 2). Similarly, models resulting from data collected during either migration direction (northern and southern) also produced different values, especially during the last three field seasons (Table 2). For example, models based on the northern migration component of approach (1) (un-truncated dataset) returned larger population estimates than their equivalents under approach (2) (truncated data set). There are several potentially contributing factors to this discrepancy. The first, and possibly most likely cause, is the inclusion of surveys conducted during the period considered to be the main southbound migration for the northern migration estimates, where southbound milling whales if temporarily travelling north, might have been erroneously classified as northbound whales. During the southbound migration, the proportion of milling animals is by far greater than during the northbound migration (Salgado Kent *et al.*, 2010). The increased milling behaviour during the southbound migration may be

Table 2

Estimated population size and 95% confidence intervals (CI) based on migration models with a single normal, 2-normals, and 3-normals fit to each aerial survey year, and for: (a) a migratory direction filter applied; (b) a migratory filter and truncation at the expected end of the northern and beginning of the southern migration applied; and (c) the entire migratory cycle (no filter applied).

Model	2000	2001	2006	2007	2008
<b>(a) Migratory direction filter only</b>					
<i>North</i>					
Normal	10,828 (CI=7,714–14,816)	21,712 (CI=12,772–75,778)	15,118 (CI=10,745–20,906)	28,217 (CI=20,635–38,875)	31,172 (CI=24,188–39,345)
2-normals	11,444 (CI=7,616–17,896)	22,455 (CI=12,171–67,189)	16,888 (CI=11,297–27,258)	28,628 (CI=20,558–40,241)	33,022 (CI=25,190–44,438)
3-normals	11,761* (CI=9,104–15,827)	21,518* (CI=12,627–68,811)	16,244* (CI=11,509–23,344)	28,290* (CI=19,849–42,389)	33,869* (CI=25,937–44,798)
<i>South</i>					
Normal	8,662 (CI=5,952–11,366)	10,003 (CI=6,230–17,931)	8,127 (CI=5,265–13,979)	7,727 (CI=4,961–12,065)	–
<b>(b) Migratory direction filter and truncation at the expected end of the northern and beginning of the southern migration</b>					
<i>North</i>					
Normal	<b>7,276</b> (CI= <b>4,993–10,167</b> )	<b>12,180</b> (CI= <b>6,830–49,434</b> )	<b>18,692</b> (CI= <b>12,980–24,477</b> )	<b>20,044</b> (CI= <b>13,815–31,646</b> )	<b>26,100</b> (CI= <b>20,152–33,272</b> )
2-normals	9,345* (CI=6,529–15,484)	–	18,483* (CI=9,511–55,176)	27,009* (CI=14,595–50,390)	28,497* (CI=18,341; 39,092)
<i>South</i>					
Normal	8,914 (CI=6,130–12,983)	–	6,445 (CI=3,478–14,502)	6,766 (CI=4,069–10,969)	–
<b>(c) Entire migratory cycle (no filter applied)</b>					
Normal	20,551 (CI=15,519–26,806)	37,304 (CI=22,916–114,047)	23,172 (CI=17,047–31,337)	36,743 (CI=28,019–48,323)	–
2-normals	25,446 (CI=17,997–35,570)	49,493 (CI=22,112–192,832)	24,954 (CI=17,637–34,917)	37,263 (CI=27,724–53,783)	–
3-normals	26,308* (CI=19,293–35,636)	39,511* (CI=19,831–123,984)	24,459* (CI=17,355–34,447)	36,942* (CI=27,567–50,577)	–
Best fit halved	13,154	19,756	12,230	18,471	–

Key: \*Best fit model. **Bold** indicates estimates used in the estimation of the trend in abundance.

associated with the use of Exmouth Gulf, just east of NWC, as a resting area for whales migrating south (Jenner *et al.*, 2001). It is quite possible that the area west of NWC, where surveys for this study were conducted, may be an extension of this resting area or used as a transitional area between resting and migrating. The consistently small abundance estimates throughout the southbound migration in comparison to the northern migratory estimates (when Exmouth Gulf is not used by whales and there is less milling), and the sudden rise in numbers of northbound whales at the very end of the northern migration and at the beginning or middle of the southern migration (Fig. 4) are further indicators that there is an erroneous classification of northbound whales. Another factor that may have contributed to the discrepancy between the northern and southern migration estimates is that a greater number of whales, particularly cow-calf pairs as a means of protection from predators, migrate close to surf break along Ningaloo Reef during their migration south. Whales surfacing near the surf break may be more difficult to detect. A third factor that may have contributed in the discrepancy between the northern and southern migration population estimates, is the inconsistent number of surveys conducted during the two migration periods. This is particularly true during later years of the study (2006, 2007 and 2008) when the discrepancy is more pronounced. In years with the lowest estimates (2006 and 2007) field work ended in mid October, whereas 2000 and 2001 field work ended in mid November. All factors identified here as potential contributors to the inconsistencies observed in northern and southern migration estimates are artifacts that have arisen during the data collection phase.

While it is not possible to correct field-based artifacts *post hoc* by, for example, adding further surveys or correcting miss-recorded migration directions, placing constraints to exclude data prone to high error rates can return more reliable model based estimates.

As a result of the discrepancies from likely erroneously classified northbound whales at the end of the northern migration, the limited surveys conducted during the southern migration, and the possible lower detectability of southbound whales migrating near the surf break of Ningaloo reef, the models selected as representing the best and most credible estimates for this study were considered to be those based on the northern migration truncated at the expected end of the migration period, as per approach (2), and fitted with a single normal migration model.

### Abundance estimates

For the models selected, bootstrap estimates of availability at 0.75km distance (the point considered to be the best estimate of  $\hat{g}(0)$ ) varied among years, and resulted in values of 0.58 (SE = 0.04) in 2000, 0.58 (SE = 0.04) in 2001, 0.40 (SE = 0.03) in 2006, 0.42 (SE = 0.03) in 2007, and 0.64 (SE = 0.03) in 2008.

The resulting integral of the product of the probabilities of detection and availability were similar among surveys (Fig. 5). The half normal detection function increases with perpendicular distance because the rate at which availability increased with distance outpaced the decrease in detectability given availability. This peaked at 1km perpendicular distance for all years and migratory directions, and then diminished.

The mean pod size ranged from 1.21 to 1.62 (Table 3).

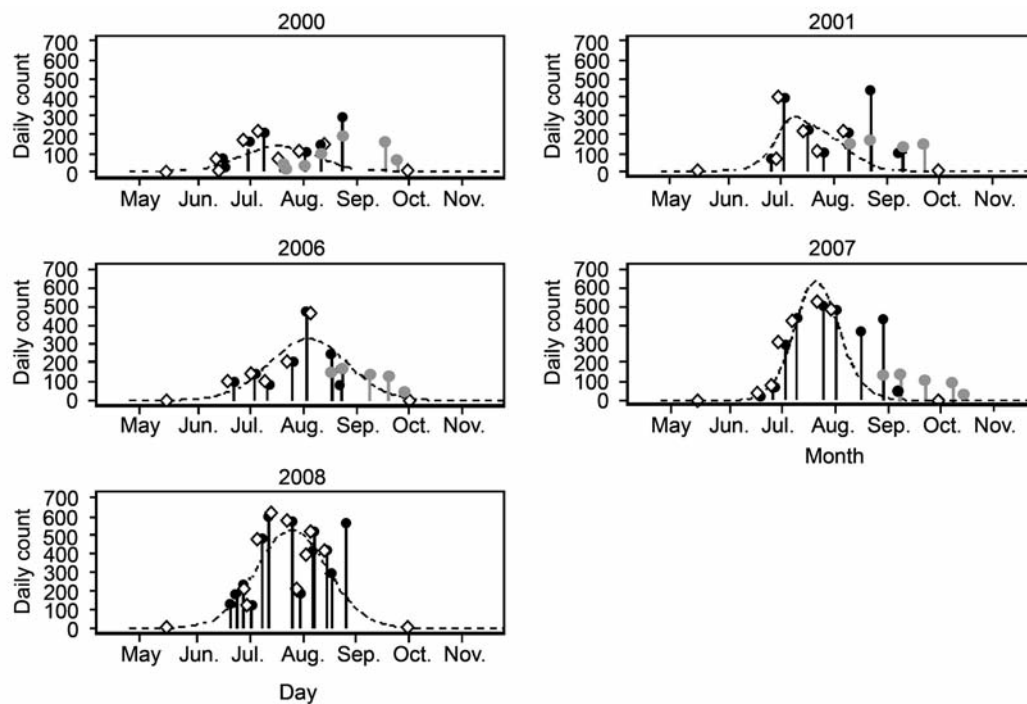


Fig. 4. Abundance estimates for the northern and southern migration using Approach no. 1 (black and grey circles, respectively), and abundance estimates and fitted migration curves (single normal) for the northern migration using Approach no. 2 (open diamonds) during 2000, 2001, 2006, 2007, and 2008. The southern migration was not surveyed in 2008, so does not appear on the corresponding plot.

Although in most cases there were no significant differences between measured pod sizes and expected pod sizes (Table 3) based on regression, corrections were applied. Since there were a few cases where there were significant differences and because adjusted pod sizes in all cases but one had slightly wider confidence intervals than the unadjusted pod sizes, we chose to adjust pod size to increase accuracy and to be conservative in our assessment of uncertainty.

Table 3

Mean pod size and adjusted mean pod size ( $\pm$  SE) for used for estimating abundance from surveys conducted in 2000, 2001, 2006, 2007, 2008.

Year	Mean pod size	Adj. mean pod size
2000	1.21 $\pm$ 0.04	1.26 $\pm$ 0.05
2001	1.52 $\pm$ 0.13	1.54 $\pm$ 0.14
2006	1.43 $\pm$ 0.05	1.56 $\pm$ 0.04
2007	1.62 $\pm$ 0.04	1.77 $\pm$ 0.04
2008	1.42 $\pm$ 0.02	1.60 $\pm$ 0.03

#### Annual population abundance estimates using the migration models

The single normal migration models based on the truncated northern migration and model parameters listed above resulted in the following population estimates: 7,276 (CI = 4,993–10,167) for 2000, 12,280 (CI = 6,830–49,434) for 2001, 18,692 (CI = 12,980–24,477) for 2006, 20,044 (CI = 13,815–31,646) for 2007 and 26,100 (CI = 20,152–33,272) for 2008. These estimates were not corrected for perception bias. Based on a preliminary assessment of perception bias for the 2008 surveys which yielded a  $p(0)$  of 0.783 (CV = 0.973), the 2008 humpback population size could be crudely estimated to be as large as 33,333. If estimates in 2000, 2001, 2006 and 2007 accounted for perception bias, they could also

be expected to be greater than the values reported above (e.g. crude predictions based on the 2008 perception bias estimates result in 9,292 for 2000, 15,683 for 2001, 23,872 for 2006, and 25,598 for 2007). The large CV associated with perception bias, however, suggests that future work should aim at reducing the uncertainty of its estimation.

#### Population abundance trend estimation and comparison to Shark Bay population estimates

The function for trend estimation (for population estimates uncorrected for perception bias) for the NWC data with the highest  $r^2$  (0.92) was exponential with an increase rate of 13%  $\text{yr}^{-1}$  (SE = 2.3%, Equation:  $x(t) = x_0 e^{0.1314t}$ ). While this increase rate is probably not biologically possible (Zerbini *et al.*, 2010), it is only just above previous estimates of between 10–12%  $\text{yr}^{-1}$  and has a high associated standard error. For the NWC and Shark Bay data combined, the highest  $r^2$  (0.78) was an exponential fit of 11.9 (SE = 2.6%, Equation:  $x(t) = x_0 e^{0.1186t}$ ) which is at the upper limit of what is considered to be biologically possible. Based on a power analysis (using TRENDS and setting  $\alpha = 0.05$  and power,  $1 - \beta$ , = 0.8) 5 more consecutive survey years would be required to reliably detect a 10%  $\text{yr}^{-1}$  change, and 9 to reliably detect a 5%  $\text{yr}^{-1}$  change. If survey years were staggered, then 3 over 6 years, and 7 over 13 years would be required for the same levels of detectable change (respectively).

In comparing NWC estimates to those from approximately 400km south at Shark Bay (Bannister and Hedley, 2001; Hedley *et al.*, 2011; Paxton *et al.*, 2011) modelling approaches varied greatly, however, no major anomalies (data points that would appear to be outliers) were detected in an integrated NWC and Shark Bay trend estimate, except for a difference in population estimates in 2008 (33,850 for

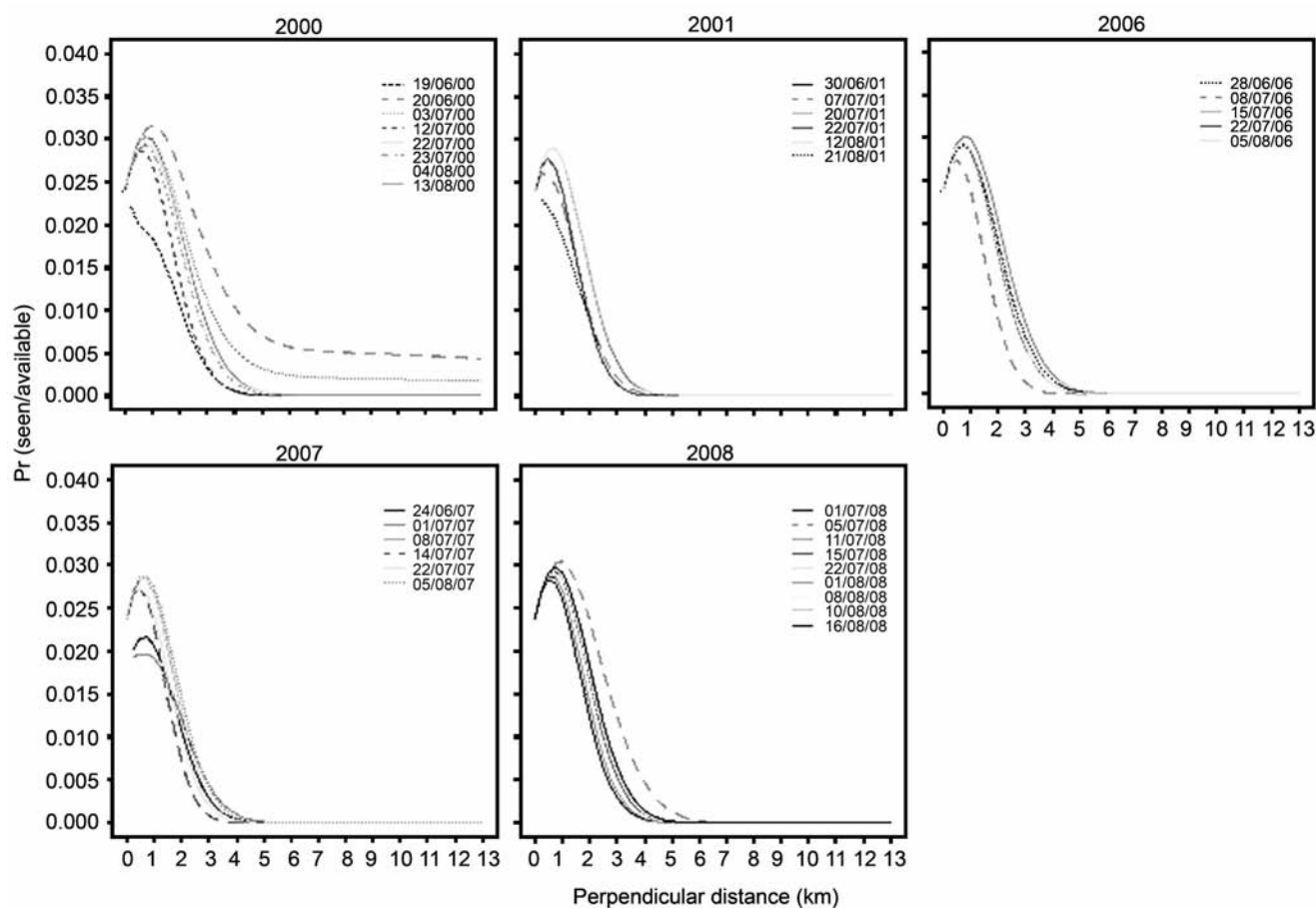


Fig. 5. Probability of detection of a humpback pod given perpendicular distance from flight line (adjusted for availability) for the northern migration. Lines represent separate detection function fitted to each survey, using a 13km right truncation distance.

Shark Bay and 26,100 for NWC). It is worth noting that the crude NWC estimate (33,333) which accounts for perception bias is much more similar to the 2008 Shark Bay estimate of approximately 34,000 (which also accounts for perception bias). An exponential function was again associated with the lowest  $r^2$  for the combined NWC and Shark Bay trend estimate. The exponential increase rate was 12.3%  $\text{yr}^{-1}$ , which is a value closer to the calculated maximum plausible increase rate (Zerbini *et al.*, 2010). While the increase rate estimate is similar to previous estimates, the large coefficient of variation associated with the estimates, again, is too large

to conclusively determine the population growth rate (Fig. 6). The work here, however, can be said to confidently provide evidence of an increasing Breeding Stock D humpback whale population, and brings us closer to reliable trend detection.

#### Uncertainty

Overall, the greatest source of variation was found to reside in the MLE migration models themselves (Table 4; and most notable for the 2001 data). This uncertainty stems from the limited number of samples (aerial surveys) at hand, but may

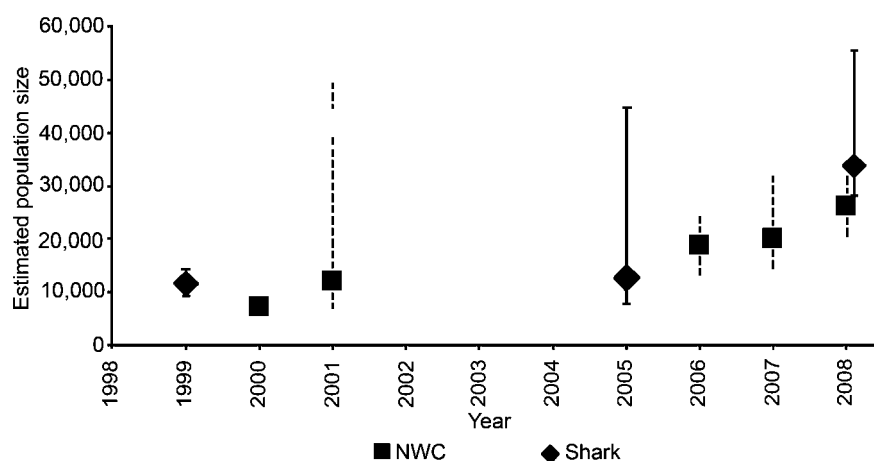


Fig. 6. Trend in population size based on the best available estimates from North West Cape and Shark Bay, Western Australia.



Table 4

Coefficients of variation for all parameters used for estimating the population size from surveys conducted in 2000, 2001, 2006, 2007, 2008.

Source of variation	2000	2001	2006	2007	2008
Coefficient of variation of encounter rate ( $CV \frac{N}{L}$ )	0.127	0.131	0.130	0.123	0.066
Coefficient of variation of detectabilities (adjusted for availability) ( $CV_{p(x)}$ )	0.238	0.107	0.091	0.102	0.077
Coefficient of variation of swimming speeds ( $CV_{speed}$ )	0.058	0.057	0.056	0.061	0.059
Coefficient of variation of pod size ( $CV_{cluster}$ )	0.070	0.207	0.047	0.050	0.031
Coefficient of variation of the migration models ( $CV_{MLE}$ )	0.181	0.939	0.17	0.185	0.123
Coefficient of variation of the final abundance estimate ( $CV_{N_{pop}}$ )	0.34	0.97	0.24	0.26	0.17

also be influenced by the probable field based errors made in identifying whales' travel directions. Adjusted detection probabilities also constituted a significant source of variability, which was most likely a function of the accuracy in  $\hat{g}(0)$  estimates. To address these limitations and improve future estimates, double platform surveys (preferably aerial and land-based platforms) with a major overlap in whales sampled is recommended if possible, and either land or aerial survey sample size increased. Land based surveys would provide a non-instantaneous record of migration direction (as opposed to aerial surveys), and would provide an alternative and potentially more accurate method for estimating  $\hat{g}(0)$ . Depending upon the practicality of land-based surveys, however, alternative methods such as using a vessel as an alternative platform or tagging whales with packages that provide information on whale movement and surfacing patterns, may help reduce some of the sources of uncertainty and increase the accuracy of the models.

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# Quantifying spatial characteristics of the Bowhead Whale Aerial Survey Project (BWASP) survey design

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## ABSTRACT

The Bowhead Whale Aerial Survey Project (BWASP) has been conducted annually since 1979 in the Alaskan Beaufort Sea to monitor the distribution and relative abundance of the Bering-Chukchi-Beaufort (BCB) stock of bowhead whales (*Balaena mysticetus*) during their autumn migration. BWASP was created to specifically address broad-scale research and management questions related to bowhead whale ecology, with particular interest in the potential effects of oil and natural gas exploration, development and production activities on the BCB bowhead whales. With elevated concerns about climate change, increasing oil and gas activities and the forecasted increase in vessel traffic, it is expected that interest in the BWASP dataset will also increase in order to evaluate effects of these anthropogenic activities on BCB bowhead whales and indigenous whaling. The following analysis quantified the spatial characteristics of the BWASP survey design and provided guidelines for the types of investigations that the BWASP data can potentially address. Sampling lags (transect spacing) in the BWASP survey design of approximately 20km along the east/west axis of the study area limit the spatial scale of phenomena that can be detected using data from a single BWASP survey. Therefore, BWASP data are relatively uninformative for studying variability in distribution or relative abundance along the east/west axis over short time scales (one survey) and within small areas measuring less than approximately 20km. In addition, computer simulations showed spatial heterogeneity in the long-term survey coverage probability (the probability that a given location will be included in a survey having an assumed effective search width under the BWASP survey design). Pooled transects created from simulated surveys resulted in a repeating diamond pattern in which coverage probability was low. Analyses incorporating data from many BWASP surveys should account for this spatial heterogeneity, via either the survey coverage probabilities or quantification of survey effort; otherwise estimates of variables such as relative density, density, or habitat use may be biased. The BWASP surveys have increased understanding of the broad-scale patterns of bowhead distribution, relative abundance and behaviour. The utility of this dataset in informing other questions will depend upon the scale of the ecological phenomena under investigation and the analytical scales used to address the questions.

KEYWORDS: BOWHEAD WHALE; ARCTIC; SURVEY – AERIAL; MODELLING; DISTRIBUTION; BEAUFORT SEA; LINE TRANSECT; NORTHERN HEMISPHERE

## INTRODUCTION

The Bering-Chukchi-Beaufort (BCB) stock of bowhead whales (*Balaena mysticetus*) undertakes spring migrations northward and eastward from the Bering Sea, following the receding seasonal sea ice across the Chukchi Sea to the eastern Beaufort Sea; in the autumn, these whales return via the Chukchi Sea to winter in the Bering Sea (Moore and Reeves, 1993). Understanding the ecology of the BCB bowhead whales is of concern to many including indigenous subsistence whalers, scientists, representatives of the oil and natural gas industry, and natural resource managers. Aerial surveys can be a valuable source of insight into BCB bowhead whale ecology, especially their distribution and relative abundance, and the spatial and temporal variability therein (e.g. Givens, 2009; Moore, 2000; Moore *et al.*, 2000; Schweder *et al.*, 2010). The utility of data from a given aerial survey for addressing a specific question is largely determined by details of the survey's design (transect layout and number) and field protocol (data collection methods). Matching the spatiotemporal scale of the question to the sampling resolution of the data is critical.

Bowhead Whale Aerial Survey Project (BWASP) surveys and their predecessors have been consistently conducted in the Alaskan Beaufort Sea annually from 1979 to the present and they coincide with the westward autumn migration of BCB bowheads (late August through late October or early November). BWASP was created to address broad-scale

research and management questions related to bowhead whale ecology, with particular interest in the effects of oil and natural gas exploration, development and production activities on the BCB bowhead stock. When developing the BWASP survey design, 'particular emphasis was placed on regional surveys to assess large-area shifts in the migration pathway of bowhead whales and on the coordination of effort and management of data necessary to support seasonal offshore-drilling and seismic-exploration regulations' (Treacy, 2002). The ongoing goals of BWASP are as follows (Monnett and Treacy, 2005).

- (1) Define the annual fall migration of bowhead whales, significant inter-year differences, and long-term trends in the distance from shore and water depth at which whales migrate;
- (2) Monitor temporal and spatial trends in the distribution, relative abundance, habitat, and behaviours (especially feeding) of endangered whales in arctic waters;
- (3) Provide real-time data to MMS [the US Minerals Management Service, now the Bureau of Ocean Energy Management] and NMFS [the National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA)] on the general progress of the fall migration of bowhead whales across the Alaskan Beaufort Sea, for use in protection of this Endangered Species;

- (4) Provide an objective wide-area context for management interpretation of the overall fall migration of bowhead whales and site-specific study results;
- (5) Record and map beluga whale distribution and incidental sightings of other marine mammals; and
- (6) Determine seasonal distribution of endangered whales in other planning areas of interest to MMS.

The BWASP survey design and protocol were based on line transect methods, and have not changed substantially since 1982. BWASP has collected a wealth of data over nearly three decades. Heightened interest by the oil and gas industry to explore and extract resources from the Arctic, in addition to heightened awareness of the pressures of climate change and other anthropogenic activities on Arctic ecosystems, has provided increased motivation to identify, predict and quantify the potential effects of these factors on bowhead whales.

Dungan *et al.* (2002) provided an overview of the importance of scale in spatial statistical analyses. They identified three components to which the concepts of spatial scale pertain: (1) the phenomenon (system) under investigation; (2) the sampling units used to acquire information about the phenomenon; and (3) the analysis used to summarise information or make inferences. The phenomenon being studied can be characterised by its physical structure (patch size or patterns of objects) and the dynamic processes that act upon it. A process can be described by measures of the distance across which it can act (its range of action) and the area over which it can or does act (its potential or actual extent, measured in two dimensions) (Dungan *et al.*, 2002). The authors highlight four elements used to describe fundamental spatial characteristics of phenomena, sampling units or analyses: size; shape; lag (the spacing or interval between neighbouring phenomena, sampling or analysis units); and extent (the total length, area or volume that exists, is observed or is analysed).

The concepts outlined by Dungan *et al.* (2002) were applied to examine issues of spatial scale relevant to BCB bowhead whales and the BWASP survey design. The phenomena of interest were the spatial distribution and relative abundance of bowhead whales in the Alaskan Arctic, including the associated variability. The spatial scales that are relevant for understanding bowhead whale ecology span three orders of magnitude, from ocean basins (thousands of kilometers) to mesoscale features such as eddies, canyons, and fronts (tens to hundreds of kilometers) to prey patches (tens to hundreds of meters). Examples of processes acting upon the Arctic ecosystem that potentially affect bowheads include oceanic circulation (currents, eddies, upwelling and downwelling, and the energy and objects that these features transport); sea ice dynamics; movements of predators and prey; generation and transmission of sound from marine organisms, wind, ice, vessels, drilling, acoustic (seismic) surveys, etc., that contribute acoustic signals or noise which may help bowhead whales interpret their environment or hinder their ability to function in their environment (e.g. via masking communication or, in extreme cases, causing temporary or permanent hearing loss); and physical

disturbances due to the movement of vessels. The objectives were as follows:

- (1) Quantify the spatial characteristics of the BWASP survey design. To do this, the magnitude and spatial distribution of the long-term survey coverage probability was investigated, which is the probability that a given location will be included in a survey having an assumed effective search width under the BWASP survey design. This aspect of the BWASP survey design has not been examined until now. The spatial lags that are inherent in the BWASP survey design were also examined;
- (2) Inform researchers and resource managers about some of the ecological questions and analytical scales to which the BWASP data can be appropriately applied.

## METHODS

The BWASP study area is located in the Alaskan Beaufort Sea, stretching from 140°W to 157°W, and from the northern coast of Alaska (located within a latitudinal range of approximately 69.5° to 71.5°N) to 72°N (Fig. 1). It encompasses 107,500km<sup>2</sup>, including the continental shelf and slope, and extending into the Arctic Ocean basin with depths approaching 3,600m. The isobaths in the study area tend to parallel the coastline; one prominent exception is Barrow Canyon, which cuts across the shelf near 71.5°N, 155°W (Fig. 1).

### BWASP survey design

The BWASP study area was divided into geographic blocks of variable size and shape (Fig. 1), upon which the survey design was based (Treacy, 2002). The BWASP survey design comprised six to eight transects per block, depending on the width of the block. The northern and southern endpoints of each transect were randomly placed at minute marks along the survey block boundaries, independent of each other and of all other transects, within a fixed 0.5° longitudinal bin (Fig. 2). Paired northern and southern endpoints were connected by linear transects so that adjacent transects never crossed. Transects were generally oriented along a north/south axis, but the exact orientation for each transect depended upon the location of the randomly generated northern and southern endpoints (Fig. 2).

### Simulation exercise to compute long-term survey coverage probabilities

The simulation procedure developed for this analysis comprised four basic steps.

- (1) Define the study area, including the shoreline and boundaries of the BWASP survey blocks.
- (2) Create a fine-scale grid (500m × 500m) overlaying the entire study area.
- (3) Generate transects for the study area using the BWASP survey design. Transform transect lines into strips 2,000m wide and centred on the transect line. (A 2,000m strip width was chosen because preliminary analyses suggested that the effective search half-width for these surveys was close to 1km.) Overlay the fine-scale grid (produced in step 2) onto the transect strips to determine



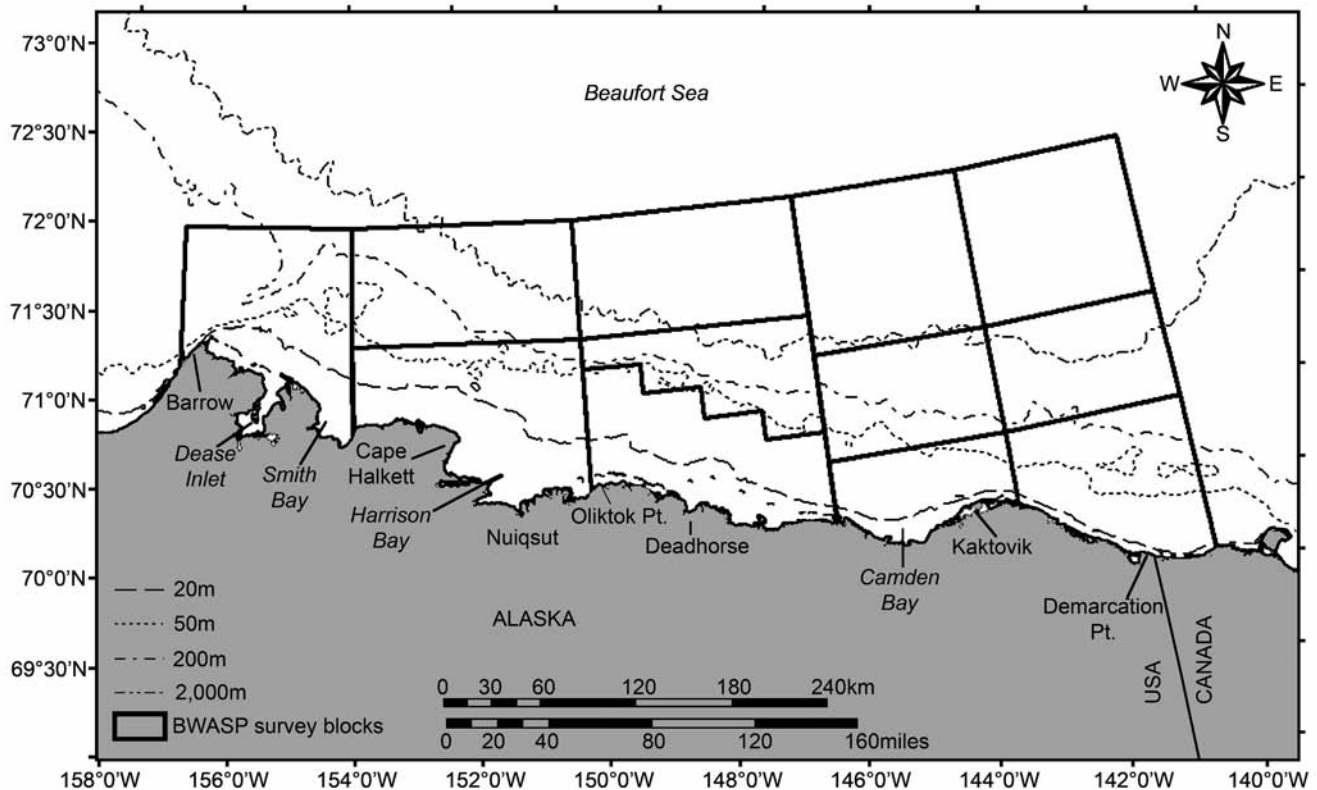


Fig. 1. Study area for the BWASP aerial surveys in the western Beaufort Sea. Solid lines represent the survey block boundaries; dashed and dotted lines represent the 20, 50, 200, and 2,000m isobaths.

which grid cells contain transect segments. Repeat this step 5,000 times.

- (4) Compute the cumulative number of times (across all iterations) that the midpoint of each cell in the study area was found within a strip of transect. Divide these cumulative counts for each cell by the total number of iterations in the simulation (5,000 in this case) to compute cell-specific long-term survey coverage probabilities.

Survey blocks and associated  $0.5^\circ$  longitudinal bins used for the simulation were identical to those used to generate transects for actual BWASP surveys. During each iteration, one transect was placed inside each  $0.5^\circ$  bin by drawing random numbers from a uniform distribution to determine attachment points along the northern and southern boundary of the survey block within which the transect was located. Random numbers were independently drawn for each attachment point throughout the BWASP study area. The southern attachment points for transects in survey blocks bordering the Alaskan coastline were located on a 'modified coastline' having 52 straight-line segments that approximate the actual coastline (Fig. 2). This is the same modified coastline used to generate transects for an actual BWASP survey.

All analyses for this investigation were coded in R version 2.10.1 (R Development Core Team, 2009), using the packages *maptools* (Lewin-Koh *et al.*, 2009), *rgdal* (Keitt *et al.*, 2010) and *sp* (Pebesma and Bivand, 2005). Spatial analyses were computed only after re-projecting the spatial objects into a Lambert Azimuthal Equal Area projection as defined by the PROJ.4 projection library by the following parameterisation:

- Latitude at projection center:  $70.0^\circ\text{N}$ , Longitude at projection center:  $154.5^\circ\text{W}$
- False Easting: 0, False Northing: 0.

An equal area projection was chosen for the spatial analyses because fidelity to the true surface area covered by each of the fine-scale grid cells in the simulation exercise was important for computing accurate estimates of survey coverage. R code for the analysis is available from the author upon request.

## RESULTS

The long-term survey coverage probabilities across the BWASP study area were spatially heterogeneous (Fig. 3), ranging from 0.0 to 0.238 with a mean of 0.109 and CV of 0.432 (Fig. 4). Transects could not cross any of the borders of the  $0.5^\circ$  bins. In addition, the probability of a transect cutting at any angle across the bin was greater than the probability of a transect being oriented along a straight north/south axis at the edges of a bin, producing long-term survey coverage probabilities in the eastern and western margins of the bins that were at least half as large as those towards the interiors of the bins. As a result, when transects for many simulated surveys were pooled, the sampling coverage exhibited a pattern of repeating diamonds (associated with the longitudinal boundaries of the  $0.5^\circ$  bins used for transect placement) in which coverage probability was relatively low (Fig. 3).

Examination of the spatial lags inherent in the BWASP survey design was also informative. Sampling along the north/south axis of the study area could be considered continuous because transects cut across the bathymetric



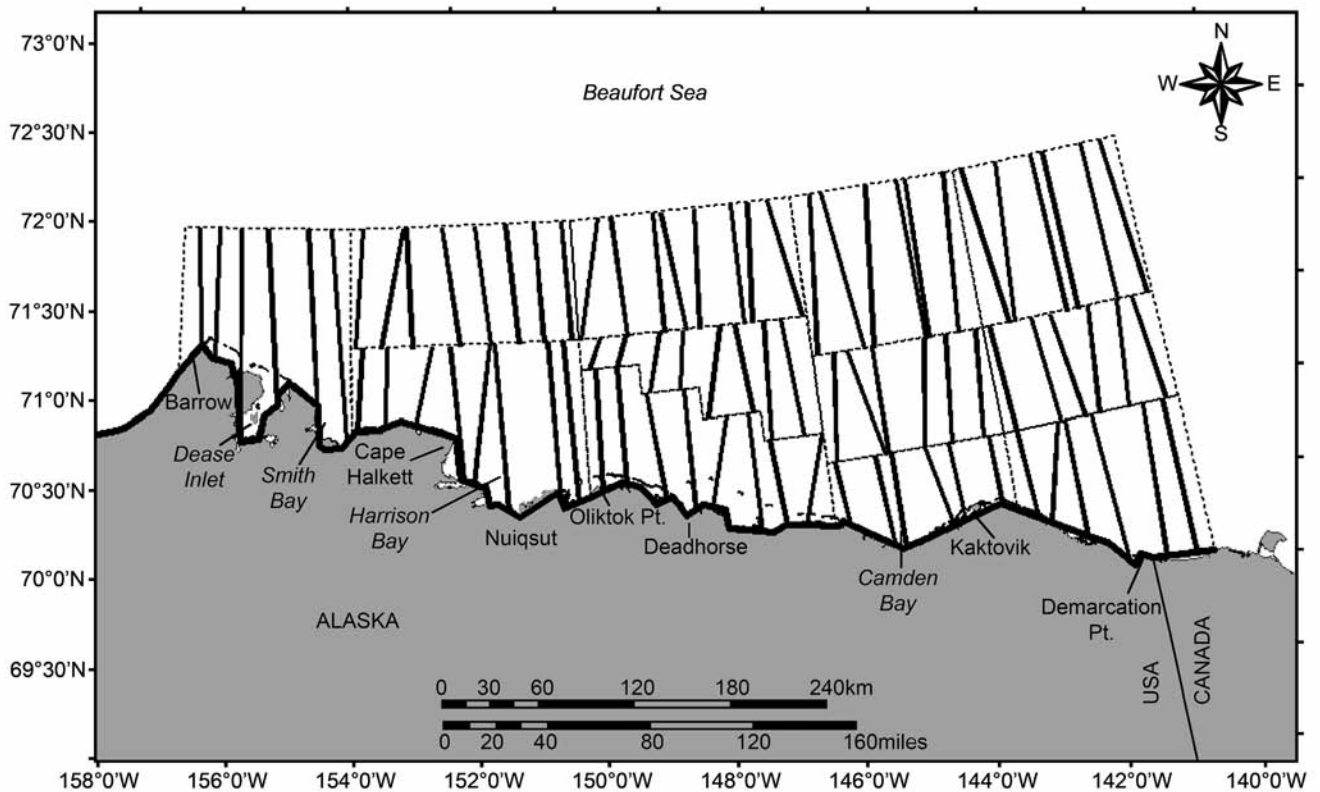


Fig. 2. Example of BWASP transects from one iteration of the simulation exercise, which corresponds to one complete survey. Bold line represents the modified coastline used as attachment points for BWASP transects.

contours from the coast to the offshore limit of the study area. The spatial lag along the east/west axis associated with a single survey corresponds to the width between the longitudinal bins within which transects are generated. This lag averages  $0.5^\circ$  of longitude, resulting in a range of 17.25 to 19.5km from the northern to southern borders of the study area, respectively.

## DISCUSSION

Two fundamental spatial characteristics are inherent in the BWASP survey design: (1) sampling lags along the east/west axis arising from the spacing between adjacent transects; and (2) heterogeneity in the long-term survey coverage probabilities. The first characteristic should be considered when examining phenomena that are concurrent with a single survey, as stated in Dungan *et al.*'s (2002) fourth guideline for designing a field survey or experiment:

'The sampling lag (or spacing) should be smaller than the average distance between the structures resulting from the hypothesised process. Otherwise one may fail to recognise the structures (e.g. patches) as separate from one another....'

It is not possible to detect patches or variability along the east/west axis of the BWASP study area on scales smaller than the average distance between transect lines for a single survey. In contrast, the scale of investigations into one-dimensional phenomena that can be measured along a north/south axis, such as the median depth at which bowhead whales migrate, are limited only by sample size, temporal distribution of survey effort and the variability in whale distribution. These, in turn, affect the ability of a statistical analysis to separate ecological signal from noise (sampling error or effects of unobserved or unmodeled phenomena)

(Houghton *et al.*, 1984). For certain analyses, such as estimating density, relative density, or habitat use, it might be possible to pool the BWASP data across years (or across time periods within a single year) to achieve higher sample (transect) density and therefore reduce the spatial lag associated with the transect spacing on a single survey. However, such an analysis may be biased if the spatial variability in long-term survey coverage probabilities and the temporal variability in effort across years (discussed below) are not accounted for. One simple method for accounting for the former is to incorporate a measure of survey effort (e.g. transect length) into the analysis.

Scientists and resource managers who are interested in whether the BWASP data can adequately inform their research or decision-making processes should ask the following two questions below.

- (1) What scales of variability in bowhead whale distribution or relative abundance are relevant to the question under investigation?
- (2) What is the range of scales over which the process under examination (for example, eddies, fronts, prey patches, or anthropogenic disturbance) could influence bowhead whale distribution or relative abundance?

If the scales of interest are smaller than the relevant sampling lags identified above for the BWASP data set, and if ecological arguments exist for not pooling survey effort across surveys in order to reduce the sampling lags, then another sampling method or survey design should be used to address the question.

There is a need for a similar examination of the BWASP survey design and field protocol with respect to: (1) time;

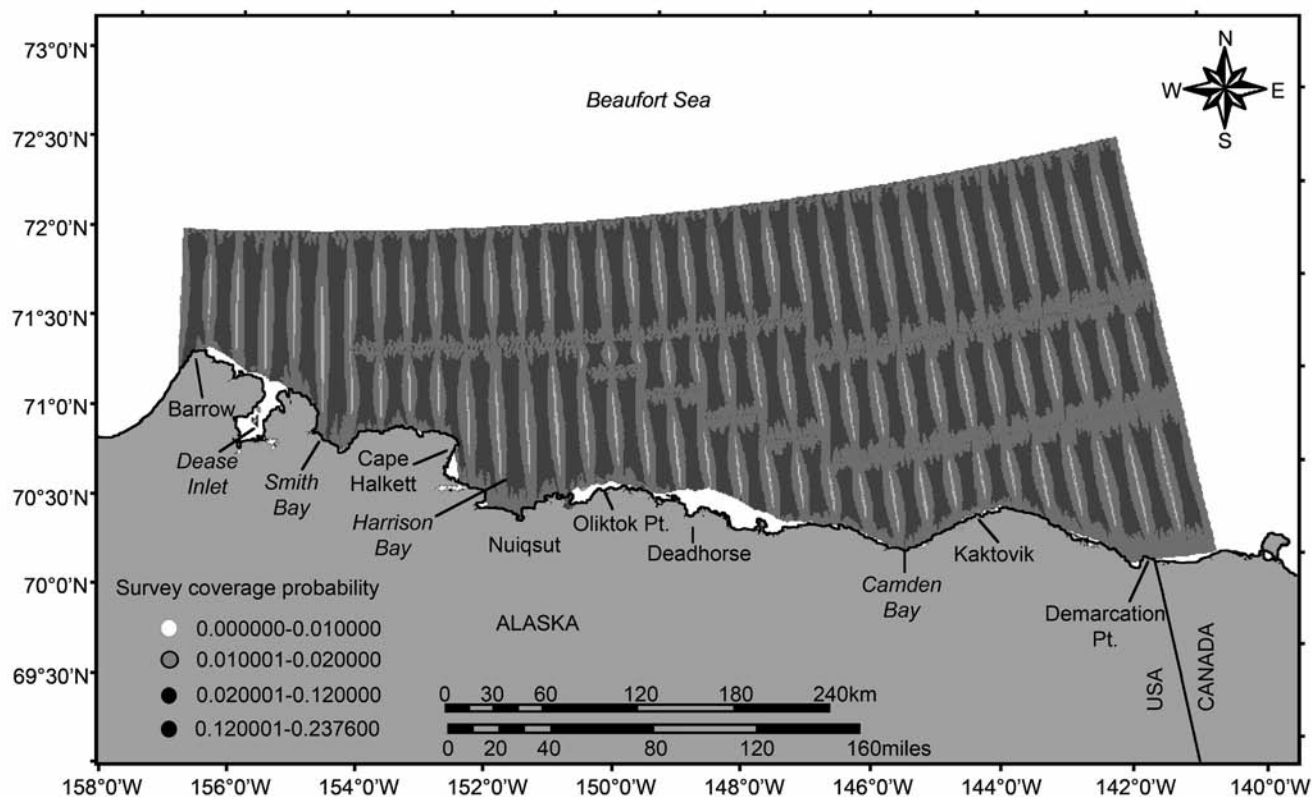


Fig. 3. Spatial distribution of survey coverage probability under the BWASP survey design within fine-scale ( $500\text{m} \times 500\text{m}$ ) grid cells computed by the simulation exercise with 5,000 simulated surveys.

and (2) space and time. The BWASP surveys do not encompass the entire duration of the autumn bowhead whale migration. Although the timing of the surveys has been relatively consistent across the years, the spatiotemporal coverage (the specific times at which certain regions within the study area are surveyed) has been neither consistent nor systematic. Factors that influenced the decision of where to fly included the following: reported or observed weather conditions; distribution of offshore seismic or drilling activity; occurrence of whaling near Cross Island in the central Alaskan Beaufort Sea and Kaktovik in the eastern Alaskan Beaufort Sea (the aerial surveys avoided these areas during the indigenous hunts); and, for the early survey years, an informal weighting of effort allocation by survey block based on the spatial variability in the relative abundance of bowhead whales throughout the study area during previous survey years (Monnett and Treacy, 2005). For the early survey years, examples exist where the decision to fly on a given day was dependent on sighting locations from the previous day, resulting in disproportionate and unplanned survey effort in areas of relatively high bowhead density and temporal autocorrelation in the data. In addition, areas such as the northeastern survey blocks that had low sighting rates in the early years tended to be undersampled in later years. Givens (2009) used sensitivity analyses to determine how the results of his spatiotemporal analysis of relative density of BCB bowheads based on the BWASP data would be affected by three hypothetical scenarios: (1) oversampling in the western region of the BWASP study area; (2) concentration of survey effort in areas where bowhead whales were thought to be present; and (3) oversampling in the western region plus concentration of survey effort in

areas where bowhead whales were thought to be present in the western region. Sensitivity analyses such as Givens' (2009) are helpful in identifying the strengths and weaknesses of specific analyses when interpreting BWASP data, which were sometimes collected using complex spatial and temporal sampling schemes.

In conclusion, the BWASP surveys have increased understanding of the broad-scale patterns of bowhead whale (and other cetacean) distribution, relative abundance and

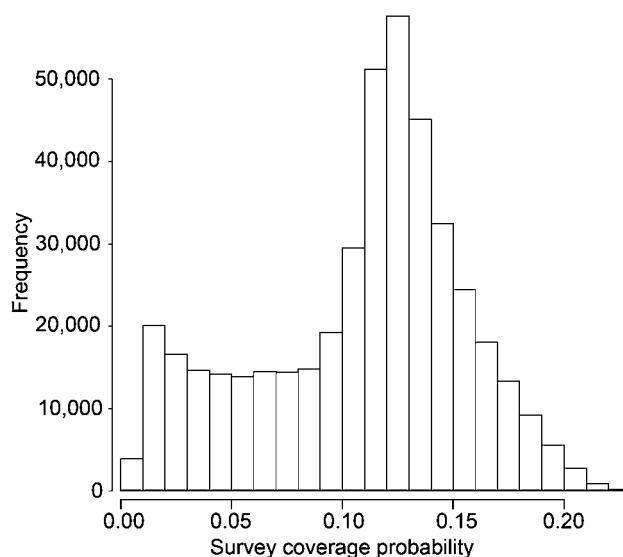


Fig. 4. Frequency histogram of survey coverage probabilities throughout the BWASP study area under the BWASP survey design. The frequencies indicate the number of times a simulated transect crossed through a  $500\text{m} \times 500\text{m}$  cell.

behaviour in the Alaskan Beaufort Sea during the autumn. Quantification of the spatial characteristics of the BWASP survey design has provided greater understanding of the utility and limitations of the BWASP data for other applications. Sampling lags in the BWASP survey design of approximately 20km along the east/west axis limit the spatial scale of phenomena that can be detected using data from a single BWASP survey. Depending upon the research question, it may be possible to pool data across surveys in order to conduct analyses on finer spatial scales, although results from some analyses might be biased if the spatial heterogeneity in the long-term survey coverage probabilities (or survey effort) and the temporal variability in the data are not accounted for. Investigations into smaller scale (less than 20km) phenomena oriented strictly in a north/south (offshore/onshore) direction might be possible using data from a single survey, depending on sample sizes and variability in the data, due to the continuous sampling along this axis (Houghton *et al.*, 1984). To put these numbers into perspective, spatial scales spanning hundreds of meters to hundreds of kilometers are typically relevant to bowhead whale feeding studies (Ashjian *et al.*, 2010); scales of the order of kilometers to hundreds of kilometers are often appropriate for studies into the effects of sea ice distribution on bowhead whale migration (Moore, 2000; Moore *et al.*, 2000; Moore and Laidre, 2006); similarly, examination of scales ranging from kilometers to hundreds of kilometers are often necessary for conducting research into the effects of anthropogenic disturbances on bowhead whale behaviour, distribution, and relative density, depending on the range of action or the extent of the disturbance and the characteristics of the effects that are of concern (Givens, 2009; Manly *et al.*, 2007; Schick and Urban, 2000). Hierarchical or nested sampling designs may provide valuable insight into phenomena relevant to bowhead whale ecology: broad-scale sampling, as implemented by BWASP, provides a regional context within which to interpret fine-scale data and analyses; fine-scale sampling is necessary to identify and understand local changes in small areas over short time periods. Similar investigations into other ecological systems, sampling designs, and data sets should be encouraged prior to undertaking spatial analyses.

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# Cetacean distribution and relative abundance in Colombia's Pacific EEZ from survey cruises and platforms of opportunity

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## ABSTRACT

Cetacean sighting data collected under various programmes in Colombian Pacific waters were collated with the goal of assessing the distribution and abundance patterns of all species occurring in the exclusive economic zone (EEZ). Distribution maps are presented for 19 species and one genus based on 603 sightings collected between 1986 and 2008. Ordered by sighting frequency, these species were: humpback whale (*Megaptera novaeangliae*); striped dolphin (*Stenella coeruleoalba*); common bottlenose dolphin (*Tursiops truncatus*); pantropical spotted dolphin (*Stenella attenuata*); common dolphin (*Delphinus delphis*); Risso's dolphin (*Grampus griseus*); sperm whale (*Physeter macrocephalus*); rough-toothed dolphin (*Steno bredanensis*); short-finned pilot whale (*Globicephala macrorhynchus*); mesoplodont whales (*Mesoplodon* spp.); Cuvier's beaked whale (*Ziphius cavirostris*); melon-headed whale (*Peponocephala electra*); false killer whale (*Pseudorca crassidens*); killer whale (*Orcinus orca*); spinner dolphin (*Stenella longirostris*); dwarf sperm whale (*Kogia sima*); Bryde's whale (*Balaenoptera edeni*); pygmy killer whale (*Feresa attenuata*); minke whale (*Balaenoptera acutorostrata*) and fin whale (*Balaenoptera physalus*). Concentrations of sightings were observed in three geographic areas: (1) the continental shelf (depths <200m) and the contiguous continental slope (200–2,000m); (2) over the Malpelo Ridge, an offshore bathymetric feature and (3) the northeast corner of the EEZ between Golfo de Cupica and the border with Panamá, although we do not rule out that these patterns could be an artefact of non-random effort. In inshore waters, the most frequently seen species were pantropical spotted dolphin, common bottlenose dolphin and humpback whale. For several of the data sets we provide encounter rates as indices of relative abundance, but urge caution in their interpretation because of methodological limitations and because several factors that affect sightability could not be accounted for in these estimates. Our results provide useful information for ongoing regional research and conservation initiatives aimed at determining occurrence, population status and connectivity within adjacent EEZs in the eastern tropical Pacific. Suggested research priorities include conducting dedicated surveys designed for estimating abundance and monitoring trends throughout the EEZ and focused studies in areas of special interest like the continental shelf, the Malpelo Ridge and the vicinity of Cupica and Cabo Marzo. More research is also needed in terms of quantifying the sources and impact of anthropogenic mortality on population size. Studies characterising genetic diversity and stock discreteness in coastal species (pantropical spotted dolphin and common bottlenose dolphin) would help inform local management strategies.

KEYWORDS: SOUTH AMERICA; EASTERN TROPICAL PACIFIC OCEAN; SURVEY-VESSEL; INCIDENTAL SIGHTINGS; ABUNDANCE ESTIMATE; INDEX OF ABUNDANCE; DISTRIBUTION; HABITAT; BREEDING GROUNDS

## INTRODUCTION

On 23 May 2007, Colombia's government, through its Ministries of Environment and Foreign Affairs, announced its intention to adhere to the International Convention for the Regulation of Whaling of 1946, motivated by the country's policies in regard to the non-lethal use of cetacean species<sup>11</sup>. This initiative was passed into law by Congress as Ley 1348 of 31 July 2009 (Anon., 2009) and on 19 May 2010 it received the approval of the Constitutional Court (Anon., 2010). Additionally, through the San José Declaration of 2 April 2004, Colombia, together with the governments of Ecuador, Costa Rica and Panamá, agreed to the establishment of the 'Eastern Tropical Pacific Seascape,' an initiative for the integrated management of the rich biological resources within the marine protected areas around the islands of Cocos (Costa Rica), Coiba (Panamá), Malpelo and Gorgona (Colombia), and Galápagos (Ecuador) (Anon., 2005;

Shillinger, 2005; <http://www.cmarpacifico.org/>). These international instruments reflect the country's commitment to the conservation of its biological diversity in the Pacific Ocean. In this context, scientific information on the distribution and abundance of protected resources in its waters is essential for the development of adequate management plans.

Colombia's coastline along the Pacific Ocean has an extent of 1,300km and its exclusive economic zone (EEZ) covers an area of about 330,000km<sup>2</sup> (DIMAR, 1988) (Fig. 1). The continental shelf (depths <200m) and slope (200–2,000m) are wide south of 4°N but very narrow to the north, especially between Cabo Corrientes and the border with Panamá (Fig. 1). The Malpelo Ridge, a submarine mountain range running on a southwest-northeast axis, rises to the surface from depths greater than 2,000m at Malpelo Island and is the most prominent feature in the offshore region (Fig.

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<sup>11</sup><http://www.minambiente.gov.co/contenido/contenido.aspx?conID=786&catID=433>.



Table 1

List of 23 cetacean species whose presence has been confirmed within Colombian Pacific waters.

Common name	Scientific name	Source
Pantropical spotted dolphin	<i>Stenella attenuata</i>	Vidal (1990); Flórez-González and Capella (1995)
Spinner dolphin	<i>Stenella longirostris</i>	Vidal (1990)
Striped dolphin	<i>Stenella coeruleoalba</i>	Vidal (1990)
Rough-toothed dolphin	<i>Steno bredanensis</i>	Vidal (1990)
Common dolphin	<i>Delphinus delphis</i>	Vidal (1990); Flórez-González and Capella (1995)
Common bottlenose dolphin	<i>Tursiops truncatus</i>	Vidal (1990); Flórez-González and Capella (1995)
Risso's dolphin	<i>Grampus griseus</i>	Vidal (1990); Flórez-González and Capella (1995)
Fraser's dolphin	<i>Lagenodelphis hosei</i>	Vidal (1990)
Melon-headed whale	<i>Peponocephala electra</i>	Vidal (1990)
Pygmy killer whale	<i>Feresa attenuata</i>	Vidal (1990)
False killer whale	<i>Pseudorca crassidens</i>	Vidal (1990); Flórez-González and Capella (1995)
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	Vidal (1990); Flórez-González and Capella (1995)
Killer whale	<i>Orcinus orca</i>	Vidal (1990); Flórez-González and Capella (1995)
Sperm whale	<i>Physeter macrocephalus</i>	Vidal (1990); Flórez-González and Capella (1995)
Dwarf sperm whale	<i>Kogia sima</i>	Vidal (1990); Flórez-González and Capella (1995)
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	Flórez-González and Capella (1995)
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Vidal (1990); Flórez-González and Capella (1995)
Minke whale	<i>Balaenoptera acutorostrata</i>	Vidal (1990)
Bryde's whale	<i>Balaenoptera edeni</i>	Vidal (1990); Flórez-González and Capella (1995)
Sei whale	<i>Balaenoptera borealis</i>	Vidal (1990)
Humpback whale	<i>Megaptera novaeangliae</i>	Vidal (1990); Flórez-González and Capella (1995)
Fin whale	<i>Balaenoptera physalus</i>	Vidal (1990)
Blue whale	<i>Balaenoptera musculus</i>	Mora-Pinto <i>et al.</i> (1995); Van Waerebeek <i>et al.</i> (1997)

1). At least 23 cetacean species are known to occur in these waters (Flórez-González and Capella, 1995; Flórez-González *et al.*, 2004a; Vidal, 1990) (Table 1). Extensive biological information and a comprehensive conservation strategy exist for the humpback whale (*Megaptera novaeangliae*) as a product of more than 20 years of study (Flórez-González *et al.*, 2007). Efforts also have been undertaken to document the cetacean fauna inhabiting the waters around the islands of Gorgona (Flórez-González and Capella, 2001; Flórez-González *et al.*, 2004b) and Malpelo (Herrera *et al.*, 2007). However, much less is known about the occurrence of cetaceans outside these locations, in particular for those species occurring in offshore waters. Abundance estimates for selected species have been presented by Gerrodette and Palacios (1996) based on regional-scale line-transect surveys for the period 1986–1993 (Table 2), but no more recent estimates are available and no comprehensive maps of cetacean distribution have ever been published for Colombia's EEZ. This paper presents, for the first time, distributional maps for 19 species and one genus occurring in Colombian waters, based on a compilation of sightings collected aboard survey cruises and platforms of

opportunity between 1986 and 2008. It also provides, with some important caveats, group encounter rates and typical group sizes to give a more complete picture of the occurrence patterns of these species. Finally, the paper discusses what has been learned from these efforts and identifies gaps in knowledge and research needs.

## DATA SOURCES

Since the purpose was to obtain as complete a picture as possible of the patterns of cetacean occurrence in Colombia's Pacific EEZ, sightings data were compiled from dedicated cetacean surveys as well as from platforms of opportunity operating in these waters between 1986 and 2008. Details of these programmes are as follows.

### SWFSC line-transect cruises

The Southwest Fisheries Science Center (SWFSC), part of the National Marine Fisheries Service (NMFS) of the U.S. National Oceanic and Atmospheric Administration (NOAA), has conducted systematic line-transect surveys for cetaceans throughout the eastern tropical Pacific (in international waters as well in the EEZs of several Central and South American

Table 2

Estimates of cetacean abundance ( $N$ , in number of animals) and density ( $D$ , in number of animals per 1,000km<sup>2</sup>) for Colombia's Pacific EEZ, with lower ( $N_{low}$ ) and upper ( $N_{up}$ ) limits of the 95% confidence intervals, based on SWFSC line-transect surveys conducted between 1986 and 1993 (source: Gerrodette and Palacios, 1996).

Common name	Scientific name	$N$	$N_{low}$	$N_{up}$	$D$
Pantropical spotted dolphin	<i>Stenella attenuata</i>	3,934	1,755	8,820	11.9
Striped dolphin	<i>Stenella coeruleoalba</i>	25,785	17,324	38,379	78.3
Rough-toothed dolphin	<i>Steno bredanensis</i>	4,366	1,869	10,200	13.3
Common dolphin	<i>Delphinus delphis</i>	12,369	4,136	36,989	37.5
Common bottlenose dolphin	<i>Tursiops truncatus</i>	7,171	3,548	14,493	21.8
Risso's dolphin	<i>Grampus griseus</i>	7,266	3,599	14,668	22.1
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	1,140	450	2,892	3.5
Beaked whales	<i>Ziphius cavirostris</i> and <i>Mesoplodon</i> spp.	30,784	10,633	89,119	93.4
Sperm whale	<i>Physeter macrocephalus</i>	1,248	643	2,422	3.8
Bryde's whale	<i>Balaenoptera edeni</i>	109	37	321	0.3

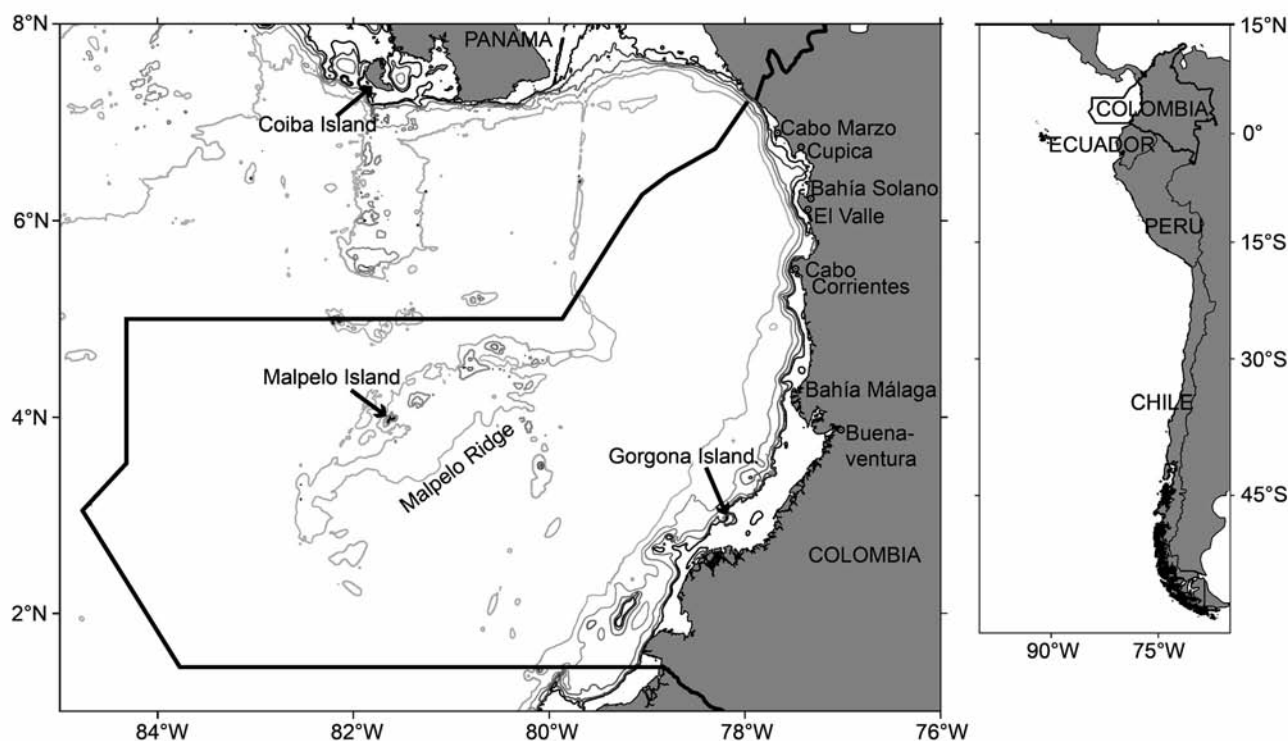


Fig. 1. Left: Colombia's exclusive economic zone (EEZ) in the Pacific Ocean (source: DIMAR, 1988). Localities mentioned in the text are labelled. Bathymetric contours correspond to the 100, 200, 500, 1,000 and 2,000m isobaths (source: SRTM30\_PLUS global topography v.6.0, available from <http://topex.ucsd.edu/>). Right: Political boundaries of Colombia and its location in the Southeast Pacific.

countries) every few years between 1986 and 2006 (1986–1990, 1992, 1998–2000, 2003 and 2006). The purpose of these surveys is to estimate population size and to monitor trends in the abundance of several dolphin stocks that have been affected by incidental mortality in the international purse-seine fishery for tuna (Gerrodette, 2002). The methodology has been documented in detail elsewhere (e.g. Gerrodette and Forcada, 2005; Kinzey *et al.*, 2000; Wade and Gerrodette, 1993), but briefly, the ship-based surveys take place from late July to early December following pre-determined random tracklines at a nominal cruising speed of 10 knots (18.5km/h). A team of three observers conduct visual searching for cetaceans during daylight hours (dawn to dusk) from the ship's flying bridge using 25x150mm pedestal-mounted binoculars in sea state conditions ranging from 0 to 6 in the Beaufort scale. Angle and radial distance to each sighting are recorded upon initial sighting, and the ship is then diverted to approach the animals in order to obtain species identity and group size. Between 1986 and 2000, two 52m research vessels, the *McArthur* and the *David Starr Jordan*, were used, both having an observation height of 11m above the water line. An additional ship, the 57m R/V *Endeavor*, with an observation height of 10m, was used during the 1998 survey. Starting with the 2003 survey, the *McArthur* was replaced with the 68m *McArthur II*, with an observation height of 15m.

#### The *Siben* and *Odyssey* expeditions

Two expeditions to study cetaceans in South American waters were conducted under the joint auspices of the Ocean Alliance (under the former names of Long-term Research Institute and Whale Conservation Institute) and the Interpolar Research Society. The purpose of these expeditions was to

study the biology of the sperm whale (*Physeter macrocephalus*) and the humpback whale while providing training in cetacean research techniques to local scientists (see also Pardo *et al.*, 2009). The first expedition operated in Colombian waters aboard the R/V *Siben*, a 25.9m sailboat, between May and July 1998 (Torres *et al.*, 1988), while the second one took place at various times during 1993 (February, September, October) and 1994 (April) aboard the R/V *Odyssey*, a 28.4m sailboat (Ocean Alliance, unpublished data). On both ships, two observers maintained visual watches during daylight hours (07:00–18:00h, weather permitting), using the naked eye or hand-held binoculars. On the *Siben*, the observation was conducted from the bow and the stern (3–4m above the waterline), while on the *Odyssey* observers were positioned atop the ship's pilothouse (4m above the waterline) and in the crow's nest on the main mast (18m above the waterline). Sightings of other cetacean species were recorded while searching for the target species but the associated search effort data were not available.

#### DIMAR oceanographic cruises

The Dirección General Marítima de Colombia (DIMAR), through its Centro de Control de Contaminación del Pacífico (CCCP), conducts long-term studies of the El Niño phenomenon in Colombia's Pacific EEZ with a series of biannual oceanographic cruises known as 'Pacífico' (normally in February or March) and 'ERFEN' (in September). Each cruise uses one of two ships, either R/V *Providencia* or R/V *Malpelo*, both 50.9m long, and takes about 20 effective sea days to complete. Two national non-profit organisations, *Fundación Yubarta* and *Fundación Malpelo*, have placed marine mammal observers on seven of these cruises between 2004 and 2008. Observation effort takes place during travel

between oceanographic stations at a cruising speed of 10 knots for *Malpelo* (18.5km/h) and 11 knots (20.4km/h) for *Providencia*. An observer searches for cetaceans from the ship's flying bridge 10m above the water line using 7x50mm hand-held binoculars. Unlike the SWFSC surveys, sightings are not closed on, so only cetacean groups that occur near the ship can be identified and counted. For this reason, search effort is only conducted under acceptable viewing conditions (no fog or rain, and in Beaufort sea states of 3 or less).

### Dive and Seascape charter trips

*Fundación Malpelo* and *Fundación Yubarta* have also placed marine mammal observers on 39 chartered trips to the offshore islands of Malpelo and Gorgona between 2004 and 2008. Twenty-four of these were dive trips organised by the company *Embarcaciones Asturias* and 17 were dedicated research trips conducted under the auspices of Conservation International's 'Eastern Tropical Pacific Seascape Program.' One additional dive charter trip in 2008 organised by Fundación Cabo Mar covered the coastal segment from Cabo Marzo-Buenaventura. All trips used M/V *Maria Patricia*, which has a cruising speed of 8 knots (14.8km/h). Observations took place during transit between the originating port (Buenaventura) and the island destinations as well as during transit between destinations. Searching was conducted by one to three observers from the vessel's top deck at a height of 4m above the waterline under acceptable viewing conditions (no fog or rain, and in Beaufort sea states of 3 or less). The vessel was diverted to approach sightings when conditions allowed during the Seascape trips but not during the dive trips. Sightings collected at the dive sites (i.e. at anchor or while circumnavigating the islands) were removed from the data set to avoid introducing bias by island-associated communities at these biologically rich localities.

### Sports-fishing charter trips

Cetacean observations were collected on coastal sports-fishing trips organised by Fundación Cabo Mar between 2000–2001 and 2004–2008. During these periods, 20 daily trips were conducted along one of three coastal routes: Buenaventura-Bahía Solano, Bahía Solano-Cupica and Cupica-Cabo Marzo. An additional route between the locality of El Valle and offshore waters was covered on one occasion. Two fiberglass boats with outboard engines were used: M/V *La Cotizada* (23ft long, two 40hp engines) between 2000 and 2005; and M/V *El Gran Blanco* (32ft, two 115hp engines) between 2006 and 2008. Two observers located near the boat's bow collected sighting data at a height of 2.2m and 2.7m above the water line, respectively for each boat. Travel speed was variable, ranging between 12 and 30km/h depending on navigation conditions.

## DATA ANALYSIS

### Sighting categories

In the field, sightings were classified under 38 different identification categories including subspecies, species and higher taxonomic levels such as genus, family, etc. For analysis purposes, several of these categories were pooled into more manageable or meaningful species groupings as follows. Species having several recognised subspecies or sighting categories (see Dizon *et al.*, 1994) were pooled into

a single species. Thus, a single 'pan-tropical spotted dolphin (*Stenella attenuata*)' category was created from three categories: offshore; coastal and unidentified subspecies. Similarly, a 'spinner dolphin (*Stenella longirostris*)' category was created by pooling four categories: eastern; whitebelly; Central American and unidentified subspecies. Conversely, sightings possibly belonging to several related species were combined into a single category when field identification to species level was not possible due to inconspicuous behaviour and/or lack of easily distinguishable features. This was the case for unidentified sightings in the genus *Mesoplodon*, for which a 'mesoplodont whales (*Mesoplodon* spp.)' category was created by pooling sightings of Blainville's beaked whale (*M. densirostris*) with sightings identified to the genus level only.

A single-species category was created by pooling confirmed sightings of the target species with sightings belonging either to the target species or to a related species when the two are difficult to separate in the field. This was done only in cases where biogeographic evidence indicates that the presence of the related species in the study area is unlikely or extremely rare. Thus, a 'Bryde's whale (*Balaenoptera edeni*)' category was created by pooling sightings positively identified as Bryde's whales (i.e., when the auxiliary ridges on the head of the animal were clearly seen) with those identified as 'either sei (*B. borealis*) or Bryde's whales' (i.e. when a very close examination at the animal's head was not obtained and therefore identification remained uncertain). Positive identification of the sei whale in the field can be very difficult, but no confirmed sightings of this species have been made anywhere in the eastern tropical Pacific during the long-standing surveys by the SWFSC. In a similar manner, a 'dwarf sperm whale (*Kogia sima*)' category was created by pooling sightings positively identified as dwarf sperm whales with those identified as *Kogia* sp. In this case, it is possible that some of the *Kogia* sp. sightings belonged to the pygmy sperm whale (*K. breviceps*), although only one confirmed sighting of this species has been reported south of 24°N by the extensive SWFSC surveys.

Sightings classified under nine 'unidentified' categories: unidentified beaked whale; unidentified rorqual (*Balaenoptera* sp.); unidentified dolphin; unidentified small whale; unidentified large whale; unidentified cetacean; unidentified whale; unidentified small delphinid and unidentified medium delphinid, were not used in this study. In this manner, 20 sighting categories are reported here: 19 individual species and the genus *Mesoplodon*.

### Encounter rates

Species encounter rates were computed for each data source separately (except for the *Siben* and *Odyssey* expeditions, which lacked effort data), based on the sightings recorded while search effort was being conducted. These are reported as group sightings per unit search effort in Appendices 1–5 using the original measurement unit recorded (i.e. kilometers or hours). Since the methodology for group size estimation was variable among the different sources (see section on 'Biases and caveats'), average group size was not used in the calculation of relative abundance to avoid introducing further bias. For ease in presentation and discussion, the estimated encounter rates for all sources are summarised in Table 3 in



the same units (groups per km scaled by 1,000). This was accomplished by multiplying the effort hours collected by the dive/Seascope and the sports-fishing trips by the vessel speed (14.8km/h and an average 21km/h, respectively).

Due to methodological differences, direct comparison of the estimated encounter rates between sources would be problematic (see ‘Biases and caveats’ in the next section). Nevertheless, we attempt to provide interpretation by according each species a qualitative rank based on the average encounter rate from all sources, where ‘low’ corresponds to species with encounter rates of less than 1 group per 1,000km, ‘intermediate’ to species with encounter rates between 1 and 3 groups per 1,000km and ‘high’ to species with encounter rates greater than 3 groups per 1,000km (Table 3).

### Sighting frequency and group size statistics

All identified on-effort sightings were pooled into a single data set containing a total of 488 records. Sighting frequency is reported as the number of sightings for each species in this data set. Group size statistics (range, average, median and standard deviation) for each species were computed from this data set.

### Distribution

Identified sightings from all sources, including those collected during non-effort periods or from sources with no search effort data and in all Beaufort sea state conditions, were combined into a single data set containing a total of 603 records belonging to the 20 sighting categories. Species distribution maps were created based on these data.

## RESULTS AND DISCUSSION

### Effort and associated sightings

#### SWFSC (1986–2006)

A total of 7,784km of visual effort were traversed by NOAA vessels during the SWFSC line-transect surveys in Colombian waters (Fig. 2a). A total of 238 identified

sightings were made while on-effort belonging to 16 species and the genus *Mesoplodon* (see Appendix 1).

#### *Siben and Odyssey expeditions (1988, 1993, 1994)*

The *Siben* Expedition in Colombian waters consisted of three legs during which 11 sightings of six species were collected, while the *Odyssey* Expedition consisted of four legs during which eight sightings of four species were collected (see Appendix 2). The routes followed by both expeditions are shown in Fig. 2b.

#### DIMAR (2004–2008)

A total of 8,587km of effort and 178 sightings belonging to 14 species and the genus *Mesoplodon* were recorded aboard DIMAR vessels during on-effort periods (see Appendix 3). A map of the cruise tracks while on effort is shown in Fig. 2c.

#### Dive and Seascope trips (2004–2008)

A total of 264hr (3,907km) of effort and 46 sightings belonging to 13 species were recorded during the transits between Buenaventura and the diving destinations (see Appendix 4). A map of the effort segments for these trips is shown in Fig. 2d.

#### Sports-fishing trips (2000–2001 and 2004–2008)

A total of 108hr (2,268km) of observation were conducted during which 26 cetacean sightings belonging to four species were recorded (see Appendix 5). A schematic map of the daily routes is presented in Fig. 3.

### Patterns of cetacean occurrence

The compiled sightings data set contained records for 19 cetacean species and one genus within Colombia’s Pacific EEZ. Distribution maps for these taxa are presented in Figs 4–6. Of the 23 species previously reported in these waters (Table 1) only three were absent from our data set: Fraser’s dolphin (*Lagenodelphis hosei*); sei whale and blue whale

Table 3

Estimated encounter rates (in groups per 1,000km) by source for 19 cetacean species and one genus, based on the on-effort sightings. The ranked encounter rate (low < 1, 1 ≤ intermediate < 3, and high ≥ 3 groups per 1,000km) is based on the average from all sources (in parenthesis) and is arbitrary.

Common name	Species name	SWFSC	DIMAR	Dive/seascope	Sports-fishing	Ranked encounter rate
Pantropical spotted dolphin*	<i>Stenella attenuata</i>	1.93	1.86	1.28	4.08	Intermediate (2.29)
Spinner dolphin*	<i>Stenella longirostris</i>	0.39		0.26		Low (0.32)
Striped dolphin	<i>Stenella coeruleoalba</i>	8.99	2.21	1.54		High (4.25)
Rough-toothed dolphin	<i>Steno bredanensis</i>	1.54	0.47	0.26		Low (0.76)
Common dolphin	<i>Delphinus delphis</i>	1.67	0.70	2.82		Intermediate (1.73)
Common bottlenose dolphin	<i>Tursiops truncatus</i>	3.21	2.45	2.82	5.44	High (3.48)
Risso’s dolphin	<i>Grampus griseus</i>	3.21	0.35	0.26		Intermediate (1.27)
Melon-headed whale	<i>Peponocephala electra</i>	0.64		0.26		Low (0.45)
Pygmy killer whale	<i>Feresa attenuata</i>	0.26				Low (0.26)
False killer whale	<i>Pseudorca crassidens</i>		0.23	0.77	0.45	Low (0.48)
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	0.77	0.70	0.51		Low (0.66)
Killer whale	<i>Orcinus orca</i>	0.26	0.12	0.51		Low (0.30)
Sperm whale	<i>Physeter macrocephalus</i>	3.47	0.23			Intermediate (1.85)
Dwarf sperm whale*	<i>Kogia sima</i>	0.51				Low (0.51)
Mesoplodont whales*	<i>Mesoplodon</i> spp.	1.41	0.12			Low (0.77)
Cuvier’s beaked whale	<i>Ziphius cavirostris</i>	0.51	0.23	0.26		Low (0.33)
Minke whale	<i>Balaenoptera acutorostrata</i>		0.12			Low (0.12)
Bryde’s whale*	<i>Balaenoptera edeni</i>	0.51				Low (0.51)
Fin whale	<i>Balaenoptera physalus</i>		0.12			Low (0.12)
Humpback whale	<i>Megaptera novaeangliae</i>	1.28	10.83	0.26	1.81	High (3.55)

\*Pooling of related sighting categories was done for these species as described in the text.



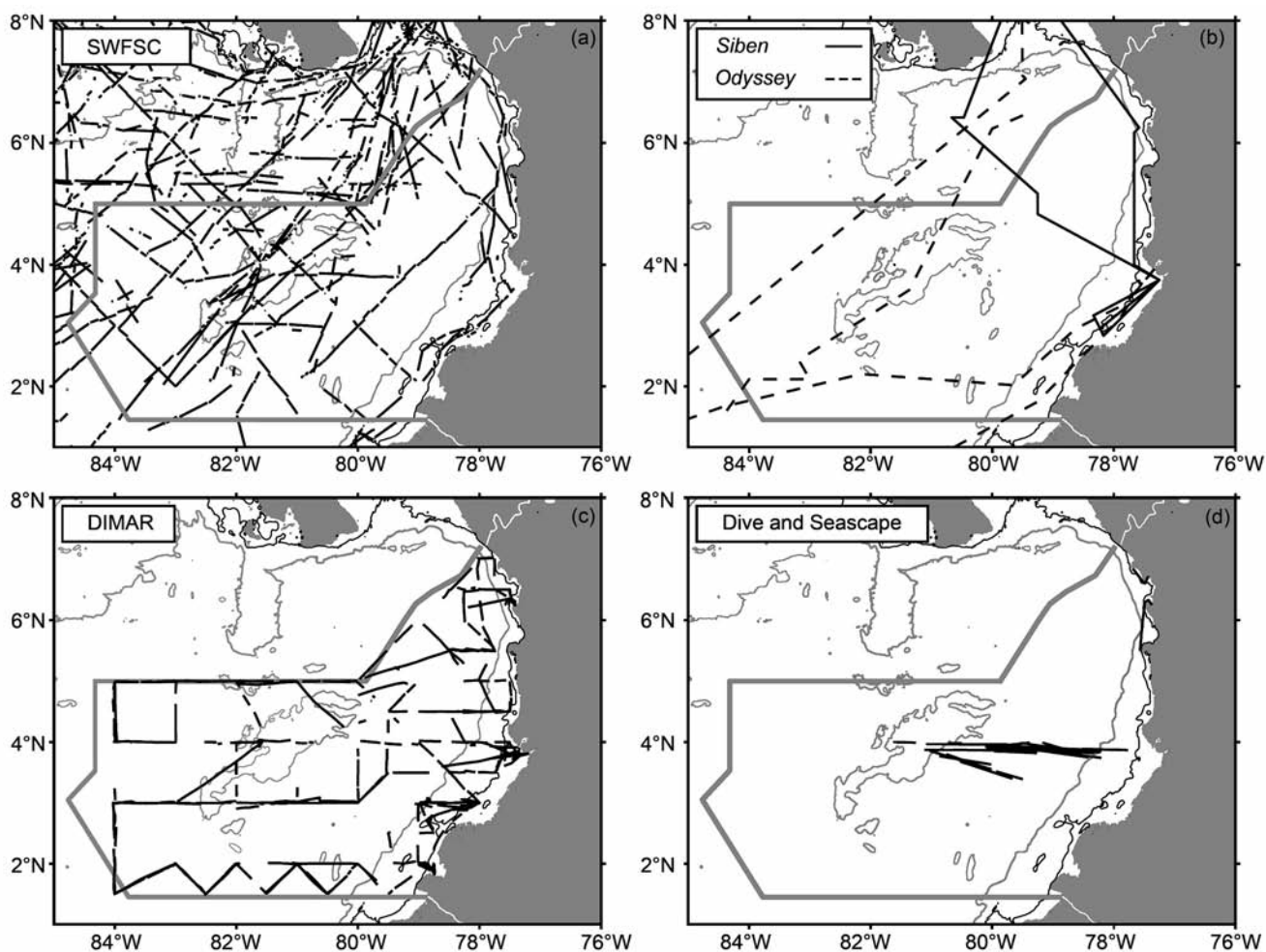


Fig. 2. (a) On-effort segments of trackline followed by NOAA vessels during SWFSC line-transect surveys (1986–2006). (b) Tracks followed by the *Siben* Expedition (May–July 1988) (solid black line) and the *Odyssey* Expedition (February 1993, September–October 1993 and April 1994) (dashed black line). (c) On-effort segments of trackline followed by DIMAR vessels during oceanographic cruises (2004, 2006–2008). (d) On-effort segments of trackline followed by M/V *Maria Patricia* during dive and Seascope charter trips (2004–2008). For clarity, only the bathymetric contours corresponding to the 100m (black) and 2,000m (gray) isobaths are shown (source as in Fig. 1).

(*Balaenoptera musculus*), suggesting they are exceedingly rare in the region. The estimated encounter rates for the 19 species are summarised in Table 3 for all sources for which effort data were available. Although density was not estimated, the following species accounts include a comparison of the density values reported by Gerrodette and Palacios (1996) for selected species in Colombia's EEZ with the corresponding density estimates for the neighbouring waters of Panamá and Ecuador, to give a regional context. The aim is to provide a synthesis of information on cetacean occurrence in Colombia's Pacific EEZ, while warning about its biases and limitations.

#### Pantropical spotted dolphin (*Stenella attenuata*)

This species was well represented in inshore waters, where sightings tended to occur in clusters around Gorgona Island (where it is a year-round resident; Flórez-González and Capella, 2001), outside Bahía de Buenaventura and from Golfo de Cupica to the Panamá border (Fig. 4a). Multiple scattered sightings also occurred throughout the offshore region. This pattern probably corresponds to the coastal and offshore subspecies (Dizon *et al.*, 1994; Escorza-Treviño *et al.*, 2005), as both were reported in the data. Pantropical spotted dolphin had an intermediate ranked encounter rate (Table 3) and it was the fourth most frequently sighted species

(Table 4). Average group size was 94 and the range was 2–400 (Table 4). Based on an earlier data set, Gerrodette and Palacios (1996) reported a density estimate for Colombia's EEZ of 11.9 pantropical spotted dolphins per 1,000km<sup>2</sup> (Table 2). This number is substantially lower than the density estimate for Panamá's EEZ (58.8 animals per 1,000km<sup>2</sup>) to the north, but higher than that for Ecuador's EEZ (8.3 animals per 1,000km<sup>2</sup>) to the south (Gerrodette and Palacios, 1996).

#### Spinner dolphin (*Stenella longirostris*)

The few spinner dolphin sightings in the data set were made on the slope and over the Malpelo Ridge (Fig. 4a). Three subspecies or forms of this species were reported within Colombia's EEZ: eastern (*S. l. orientalis*); whitebelly (a presumed hybrid between *S. l. longirostris* and *S. l. orientalis*) and Central American (*S. l. centroamericana*) (Dizon *et al.*, 1994). The ranked encounter rate was low for this species (Table 3). Average spinner dolphin group size was 96 and the range was 1–226 (Table 4).

#### Striped dolphin (*Stenella coeruleoalba*)

The species was well distributed in offshore waters and absent from inshore waters (Fig. 4b). Striped dolphin had a high ranked encounter rate (Table 3) and it was the second

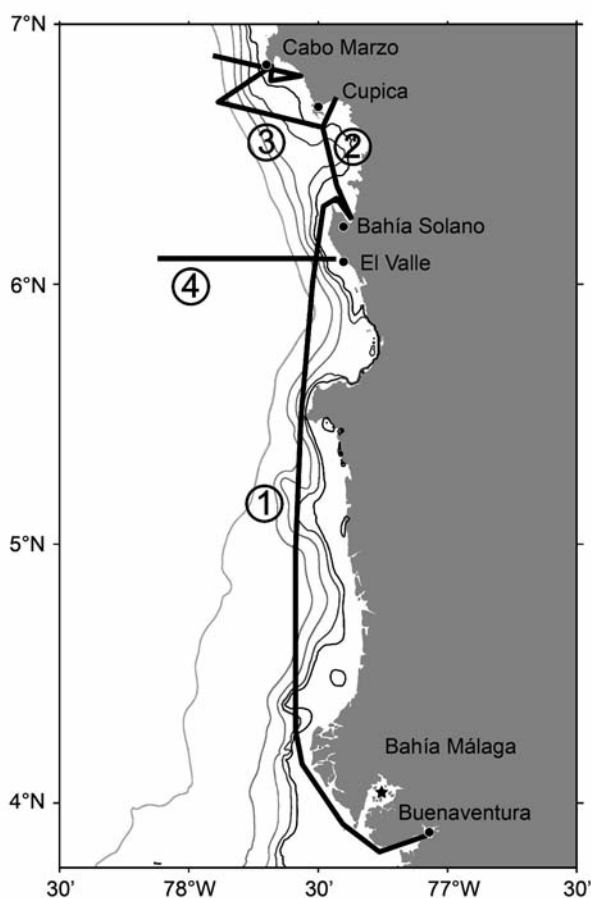


Fig. 3. Typical daily routes followed by the coastal sports-fishing trips (2000–2001, 2004–2008). Encircled numbers correspond to: (1) Buenaventura-Bahía Solano route; (2) Bahía Solano-Cupica route; (3) Cupica-Cabo Marzo route and (4) El Valle-offshore route. Bathymetric contours correspond to the 100, 200, 500, 1,000 and 2,000m isobaths (source as in Fig. 1).

most frequently sighted species in the data set (Table 4). Average group size was 71 and the range was 3–1,500 (Table 4). According to Gerrodette and Palacios (1996), striped dolphin is probably the most abundant dolphin species in Colombia's EEZ (Table 2). The existing density estimate for this species in Colombia's EEZ (78.2 animals per 1,000km<sup>2</sup>; Table 2) is somewhat higher than that reported for Panamá (64.3 animals per 1,000km<sup>2</sup>) or Ecuador (72.6 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### *Rough-toothed dolphin (Steno bredanensis)*

The species occurred in the offshore region, mostly south of 5°N (Fig. 4c). Rough-toothed dolphin had a low ranked encounter rate (Table 3). Average group size was 35 and the range was 5–90 (Table 4). The existing density estimate for the species in Colombia's EEZ (13.3 animals per 1,000km<sup>2</sup>; Table 2) is higher than that reported for Panamá (6.9 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### *Common dolphin (Delphinus delphis)*

Common dolphins were found primarily in offshore waters, especially in the northeastern part of the EEZ (including the vicinity of Cabo Marzo) (Fig. 4c). This species had an intermediate ranked encounter rate (Table 3) and it was the fifth most frequently sighted in the data set (Table 4). Average group size was 155 and the range was 3–800 (Table

4). The existing density estimate for this species in Colombia's EEZ (37.5 animals per 1,000km<sup>2</sup>; Table 2) is substantially lower than that reported for Panamá (129.4 animals per 1,000km<sup>2</sup>) or Ecuador (402.2 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### *Common bottlenose dolphin (Tursiops truncatus)*

Like the pantropical spotted dolphin, this species was well represented in inshore waters, with multiple sightings scattered throughout the offshore region as well (Fig. 4d). This suggests the occurrence of inshore and offshore ecotypes known from around the world (e.g. Natoli *et al.*, 2004). Most of the inshore sightings occurred north of 4°N, especially between Bahía Solano and Cabo Marzo, and in the offshore region several occurred over the Mapelo Ridge (Fig. 4d). Bottlenose dolphin had a high ranked encounter rate (Table 3) and it was the third most frequently sighted species in the combined data set (Table 4). Average group size was 25 and the range was 1–300 (Table 4). The existing density estimate for common bottlenose dolphin in Colombia's EEZ (21.8 animals per 1,000km<sup>2</sup>; Table 2) is substantially lower than that reported for Panamá (53.3 animals per 1,000km<sup>2</sup>), and somewhat lower than that reported for Ecuador (26.5 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### *Risso's dolphin (Grampus griseus)*

This dolphin was found primarily in offshore waters, including over the Mapelo Ridge (Fig. 4d). Ranked encounter rate was intermediate for this species (Table 3). Average group size was 13 and the range was 1–59 (Table 4). The existing density estimate for Risso's dolphin in Colombia's EEZ (22.1 animals per 1,000km<sup>2</sup>; Table 2) is higher than that reported for Panamá (12.7 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### *Melon-headed whale (Peponocephala electra)*

The handful of sightings of melon-headed whale in the database were made south of 5°N just offshore of the continental slope (Fig. 5a). Ranked encounter rate was low for this species (Table 3). Average group size was 206 and the range was 10–434 (Table 4).

#### *Pygmy killer whale (Feresa attenuata)*

Only two sightings were collected for this species, one of which occurred over the Malpelo Ridge (Fig. 5a). Ranked encounter rate was low for this species (Table 3). Average group size was 35 and the range was 25–45 (Table 4).

#### *False killer whale (Pseudorca crassidens)*

Of the eight false killer whale sightings in the combined data set, four were made offshore near the Malpelo Ridge and the remaining four were made near Cabo Marzo, in the northeast corner of the EEZ (Fig. 5a). Ranked encounter rate for this species was low (Table 3). Average group size was 62 and the range was 2–300 (Table 4).

#### *Short-finned pilot whale (Globicephala macrorhynchus)*

This species was well distributed throughout the offshore region, including over the Malpelo Ridge, but one sighting was made in the northeast corner of the EEZ near the border

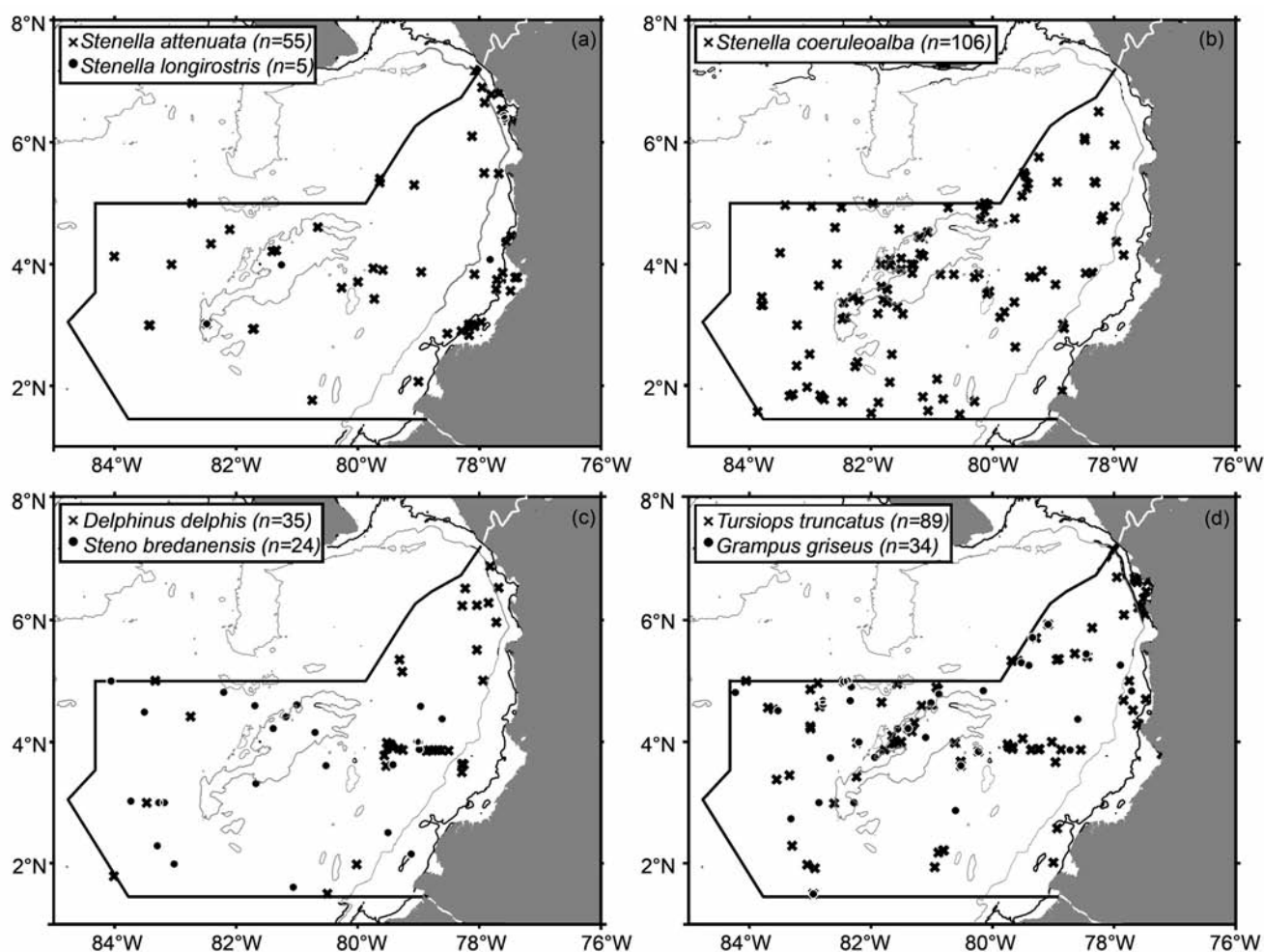


Fig. 4. Distribution maps in Colombia's Pacific EEZ based on sightings from all sources combined (1986–2008) for: (a) pantropical spotted dolphin (*Stenella attenuata*) and spinner dolphin (*Stenella longirostris*); (b) striped dolphin (*Stenella coeruleoalba*); (c) common dolphin (*Delphinus delphis*) and rough-toothed dolphin (*Steno bredanensis*) and (d) common bottlenose dolphin (*Tursiops truncatus*) and Risso's dolphin (*Grampus griseus*). The number of sightings for each species is indicated. For clarity, only the bathymetric contours corresponding to the 100m (black) and 2,000m (gray) isobaths are shown (source as in Fig. 1).

with Panamá (Fig. 5b). Short-finned pilot whale ranked encounter rate was low (Table 3). Average group size was 16 and the range was 1–80 (Table 4). The existing density estimate for this species in Colombia's EEZ (3.5 animals per 1,000km<sup>2</sup>; Table 2) is substantially lower than that reported for Panamá (15.2 animals per 1,000km<sup>2</sup>) or Ecuador (13.1 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### Killer whale (*Orcinus orca*)

The few sightings of this species were scattered in the offshore region south of 4°N (Fig. 5b). Killer whale ranked encounter rate was low (Table 3). Average group size was 5 and the range was 3–8 (Table 4).

#### Sperm whale (*Physeter macrocephalus*)

Sperm whale was distributed primarily in the offshore region, including over the Malpelo Ridge (Fig. 5c). Ranked encounter rate for this species was intermediate (Table 3). Average group size was 10 and the range was 1–34 (Table 4). It is worth noting that despite relatively continuous coverage between 1986 and 2008, all but two sightings were made prior to 1998, suggesting that sperm whale has shifted its distribution in recent years and that it is no longer present in the Colombian EEZ in the same numbers as in the early years

of sampling. The home range of the sperm whale in the eastern tropical Pacific spans ~2,000km (Whitehead *et al.*, 2008), and hence it is possible that the observed trend is, at least in part, a reflection of the species' multi-year displacements throughout the region. The existing sperm whale density estimate in Colombia (3.8 animals per 1,000km<sup>2</sup>; Table 2) is based on data for the period 1986–1993 and is somewhat lower than that reported for Panamá (5.3 animals per 1,000km<sup>2</sup>) or Ecuador (5.4 animals per 1,000km<sup>2</sup>) for the same period (Gerrodette and Palacios, 1996).

#### Dwarf sperm whale (*Kogia sima*)

There were few sightings of dwarf sperm whale, which were scattered over the slope and in the offshore region, although one sighting was made near Cabo Marzo, in the northeast corner of the EEZ (Fig. 5c). This species had a low ranked encounter rate (Table 3) and was only sighted during SWFSC surveys. Average group size was 2 and the range was 1–3 (Table 4).

#### Mesoplodont whales (*Mesoplodon spp.*)

Mesoplodont whales were well distributed in the offshore region south of 5°N, including over the Malpelo Ridge (Fig. 5d). Two sightings also were made near Cabo Marzo, in the



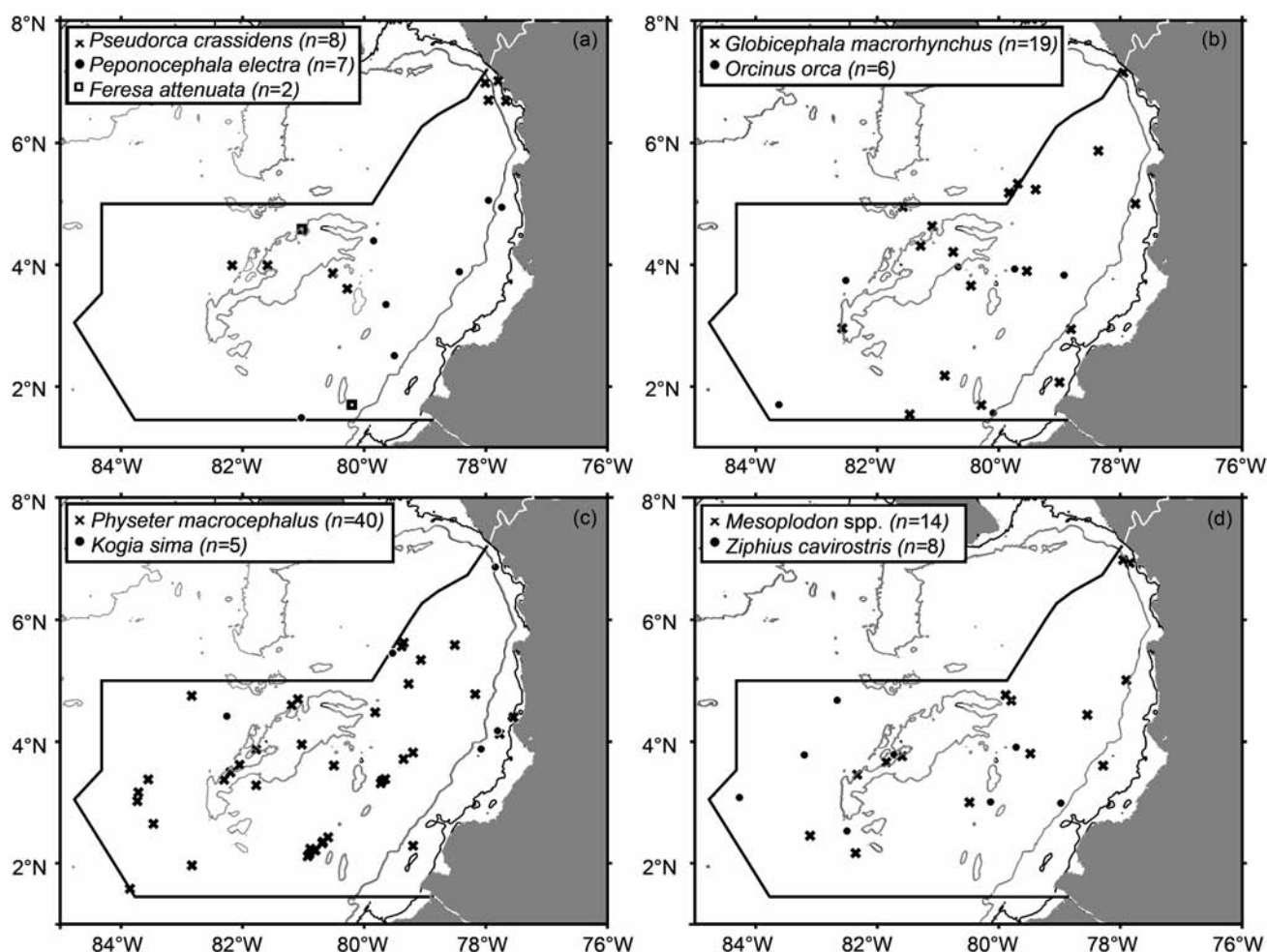


Fig. 5. Distribution maps in Colombia's Pacific EEZ based on sightings from all sources combined (1986–2008) for: (a) false killer whale (*Pseudorca crassidens*), melon-headed whale (*Peponocephala electra*) and pygmy killer whale (*Feresa attenuata*); (b) short-finned pilot whale (*Globicephala macrorhynchus*) and killer whale (*Orcinus orca*); (c) sperm whale (*Physeter macrocephalus*) and dwarf sperm whale (*Kogia sima*); and (d) mesoplodont whales (*Mesoplodon* spp.) and Cuvier's beaked whale (*Ziphius cavirostris*). The number of sightings for each species is indicated. For clarity, only the bathymetric contours corresponding to the 100m (black) and 2,000m (gray) isobaths are shown (source as in Fig. 1).

northeast corner of the EEZ (Fig. 5d). The only mesoplodont species with positive identifications in the data set was Blainville's beaked whale ( $n = 2$ ). Although this genus had a low ranked encounter rate in this study (Table 3), the original combined data set contained 17 sightings of 'unidentified beaked whales,' some of which were probably mesoplodonts. Therefore, when combined with Cuvier's beaked whale (*Ziphius cavirostris*) (as done in Gerrodette and Palacios, 1996), the beaked whales as a group are probably the most abundant medium-sized cetaceans in the Colombian EEZ (Table 2). Average group size was 3 and the range was 1–5 (Table 4). The existing density estimate for all the beaked whales combined (*Z. cavirostris*, *Mesoplodon* spp. and unidentified beaked whales) for Colombia (93.4 animals per 1,000km<sup>2</sup>; Table 2) is higher than that reported for Panamá (69.7 animals per 1,000km<sup>2</sup>), but lower than that for Ecuador (117.6 animals per 1,000km<sup>2</sup>) (Gerrodette and Palacios, 1996).

#### Cuvier's beaked whale (*Ziphius cavirostris*)

The few sightings for this species occurred offshore, mainly in the western part of the EEZ including over the Malpelo Ridge (Fig. 5d). Cuvier's beaked whale had a low ranked encounter rate (Table 3). Average group size was 1 and the range was 1–2 (Table 4).

#### Minke whale (*Balaenoptera acutorostrata*)

This species was only sighted once during the DIMAR cruises in the northeastern part of the EEZ (Fig. 6) and it had a low ranked encounter rate (Table 3). The group size for this sighting was 1 (Table 4).

#### Bryde's whale (*Balaenoptera edeni*)

The few offshore sightings of this species were made in the western part of the EEZ, including over the Malpelo Ridge (Fig. 6). Bryde's whale had a low ranked encounter rate (Table 3). However, the original combined data set contained 16 sightings of 'unidentified rorquals (*Balaenoptera* sp.),' some of which could have belonged to this species. Therefore, it is possible that this rorqual is more common than indicated by the positively identified sightings. Average group size was 2 and the range was 1–2 (Table 4). The existing density estimate for Bryde's whale in Colombia's EEZ (0.3 animals per 1,000km<sup>2</sup>; Table 2) is the same as that reported for Panamá (Gerrodette and Palacios, 1996).

#### Fin whale (*Balaenoptera physalus*)

This species was only sighted once during the DIMAR cruises in the southwestern corner of the EEZ (Fig. 6) and it had a low ranked encounter rate (Table 3). The group size for this sighting was 1 (Table 4).



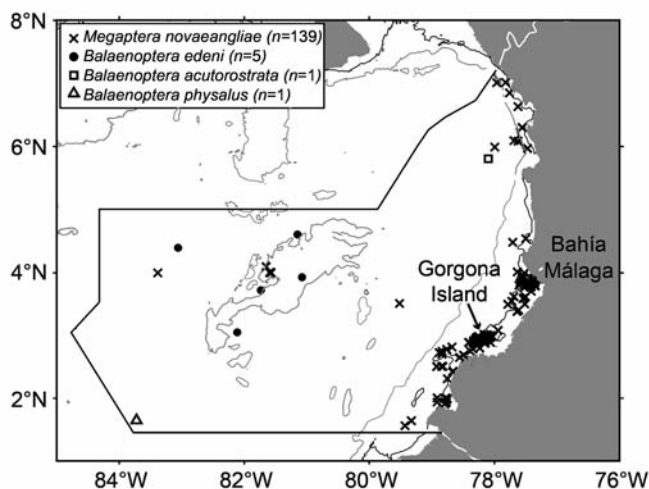


Fig. 6. Distribution map for humpback whale (*Megaptera novaeangliae*), Bryde's whale (*Balaenoptera edeni*), minke whale (*Balaenoptera acutorostrata*) and fin whale (*Balaenoptera physalus*) in Colombia's Pacific EEZ based on sightings from all sources combined (1986–2008). The number of sightings for each species is indicated. For clarity, only the bathymetric contours corresponding to the 100m (black) and 2,000m (gray) isobaths are shown (source as in Fig. 1).

#### Humpback whale (*Megaptera novaeangliae*)

This was primarily an inshore species, common south of 4°N and with fewer sightings to the north (Fig. 6). This distribution pattern has been related to the decreasing width of the continental shelf toward the north (Herrera *et al.*, 2008). Two sites that showed high concentration of humpback whale sightings were the waters surrounding Gorgona Island and the vicinity of Bahía Málaga (Fig. 6). These two sites have been previously identified as important for the species in Colombian waters (e.g. Flórez-González *et al.*, 2007). A few offshore sightings also were recorded, including over the Malpelo Ridge (Fig. 6). Most sightings were made during the second part of the year and probably belong to the Southeast Pacific stock (IWC Breeding Stock G) during their winter migration to low latitudes (Flórez-González *et al.*, 2007).

However, a few sightings north of 4°N from March, April and May suggest that Northeast Pacific animals may also use the Colombian EEZ (cf. Acevedo-Gutiérrez and Smultea, 1995; Calambokidis *et al.*, 2000; Rasmussen *et al.*, 2007).

Humpback whale had a high ranked encounter rate (Table 3) and it was the most frequently sighted species in the combined data set (Table 4). Average group size was 2 and the range was 1–6 (Table 4). Photo-identification based population estimates exist for Gorgona Island (1,366 individuals in 2003, 95% CI = 775–3366; Escobar, 2009) and for Bahía Málaga (575 individuals in 2001, 95% CI = 474–676; Flórez-González *et al.*, 2003). Group composition and behaviour at these two sites is quite different (Escobar, 2009; Flórez-González *et al.*, 2003), however, highlighting the importance of determining the provenance and the segments of the population using the various concentration sites along the breeding range of the Southeast Pacific stock, which extends from northern Peru to western Panama and into Costa Rica (Flórez-González *et al.*, 2007). The most recent population-wide estimates for this stock are ~6,000–7,000 animals (Félix *et al.*, 2011; Johnston *et al.*, 2011), although these estimates are based on photo-identification studies conducted in Ecuador only.

#### Biases and caveats

The depictions of cetacean occurrence in the Colombian EEZ presented above assume implicitly that sampling was random. None of the studies used here were designed for this specific purpose (the SWFSC surveys were randomised at the regional level but coverage within the Colombian EEZ was not necessarily random) and therefore it is possible that these patterns could be an artefact of non-random effort. Further, although the overall trends in species encounter rates were qualitatively similar among data sources covering similar regions (e.g. SWFSC and DIMAR), we urge caution in the use of these encounter rates as quantitative indices of abundance for several reasons arising from methodological differences in data collection. First, the observation height

Table 4

Sighting frequency (#Si) and group size statistics ( $G_{rng}$ : range;  $G_{avg}$ : average;  $G_{med}$ : median;  $G_{sd}$ : standard deviation) for 19 cetacean species and one genus based on all on-effort sightings ( $n=488$ ) recorded in Colombia's Pacific EEZ between 1986 and 2008.

Common name	Scientific name	#Si	$G_{rng}$	$G_{avg}$	$G_{med}$	$G_{sd}$
Humpback whale	<i>Megaptera novaeangliae</i>	108	1–6	1.9	2.0	1.1
Striped dolphin	<i>Stenella coeruleoalba</i>	95	3–1,500	70.5	38.1	157.7
Common bottlenose dolphin	<i>Tursiops truncatus</i>	69	1–300	25.0	7.0	50.9
Pantropical spotted dolphin*	<i>Stenella attenuata</i>	45	2–400	93.7	50.0	104.7
Common dolphin	<i>Delphinus delphis</i>	30	3–800	155.1	66.9	211.6
Risso's dolphin	<i>Grampus griseus</i>	29	1–59	12.9	10.2	12.5
Sperm whale	<i>Physeter macrocephalus</i>	29	1–34	10.0	5.8	9.6
Rough-toothed dolphin	<i>Steno bredanensis</i>	17	5–90	34.9	32.8	24.4
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	14	1–80	15.8	7.8	20.8
Mesoplodont whales*	<i>Mesoplodon spp.</i>	12	1–5	2.6	2.5	1.2
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	7	1–2	1.4	1.2	0.5
Melon-headed whale	<i>Peponocephala electra</i>	6	10–434	206.2	206.6	158.7
False killer whale	<i>Pseudorca crassidens</i>	6	2–300	61.5	20.0	117.1
Killer whale	<i>Orcinus orca</i>	5	3–8	5.3	5.0	2.1
Spinner dolphin*	<i>Stenella longirostris</i>	4	1–226	95.5	77.5	111.2
Dwarf sperm whale*	<i>Kogia sima</i>	4	1–3	1.6	1.2	0.8
Bryde's whale*	<i>Balaenoptera edeni</i>	4	1–2	1.5	1.2	0.6
Pygmy killer whale	<i>Feresa attenuata</i>	2	25–45	35.1	35.1	13.9
Minke whale	<i>Balaenoptera acutorostrata</i>	1	1	1.0	1.0	0.0
Fin whale	<i>Balaenoptera physalus</i>	1	1	1.0	1.0	0.0

\*Pooling of related sighting categories was done for these species as described in the text.

varied widely among platforms (2–15m), as did vessel speeds (14–30km/h). Second, the number of observers onboard these platforms varied between one and three, they used different sighting methods (25x binoculars, 7x binoculars, unaided eye) for scanning the area in front of the vessels and they had different levels of experience in species identification and group size estimation. Third, some of the sources (e.g. DIMAR and dive trips) collected observations in ‘passing mode’ (i.e. when the ship is not diverted from the trackline to approach a distant sighting), which severely limits species identification and accurate group size estimation (Barlow and Forney, 2007; Dawson *et al.*, 2008). Finally, the use of simple encounter rates as indices of relative abundance does not take into account the effects of group size, species behaviour, sea state and swell height on detectability. These variables are known to impact the estimation of perpendicular sighting distances in studies designed to estimate abundance based on line-transect methodologies, and therefore it is recommended that encounter rates be adjusted to the effective half-strip width, which can be estimated for several sighting categories and sea states if radial distances (sighting to ship) are appropriately collected as part of the survey protocol (Barlow *et al.*, 2001; Dawson *et al.*, 2008). It is because of these shortcomings in the data that we did not compute density.

## CONCLUSIONS AND RECOMMENDATIONS

Shortcomings notwithstanding, the general picture of cetacean relative abundance in Colombia’s EEZ suggests that common bottlenose dolphin, humpback whale and striped dolphin are the most regularly encountered species, followed by pantropical spotted dolphin, sperm whale, common dolphin and Risso’s dolphin. In terms of distribution, apparent concentrations of sightings were observed in three geographic areas: (1) the inshore area from the coastline to the continental shelf (depths <200m) and the contiguous continental slope (200–2,000m), where significant stocks of coastal species may be found; (2) the Malpelo Ridge, an offshore bathymetric feature where several oceanic species were observed; and (3) the northeast corner of the EEZ near the border with Panamá, centred around Cupica and Cabo Marzo, where both coastal and oceanic species may occur due to the presence of deep water very close to the coast. These apparent ‘hot spots’ and their underlying environmental drivers should be formally tested in an ecological framework as was done recently for the DIMAR data set by Herrera (2009), who found that the area to the southwest of Malpelo Island had the highest species richness and relative abundance of the entire EEZ, at least during the first part of the year.

With some modifications to the current data collection protocols more accurate estimates of abundance could be obtained. These would involve conducting appropriately randomised and stratified surveys and collecting and incorporating sighting parameters in the estimation of encounter rate. These surveys should also consider the marked oceanographic seasonality of the region (e.g. Rodríguez-Rubio *et al.*, 2003) in order to capture any seasonal differences in species occurrence patterns (cf.

Herrera, 2009). Additionally, long-term monitoring will be useful in detecting population trends and in documenting distributional shifts (as appears to have occurred with sperm whale) in response to climatic variation or otherwise. In this regard, the biannual DIMAR cruises are in a unique position to fill some of these knowledge gaps.

The use of passive acoustics for documenting occurrence could be a complementary approach in some specific areas and for selected species. Although this technology has its own limitations, it has been demonstrated to be effective for the long-term monitoring of the calling behaviour of both mysticete and odontocete species (e.g. Johnston *et al.*, 2008; Mellinger *et al.*, 2007; Rayment *et al.*, 2009; Soldevilla *et al.*, 2010). As an example, a network of sea-floor mounted hydrophone instrument packages could be deployed over the Malpelo Ridge to monitor species like sperm, humpback and beaked whales at this important but remote area.

Finally, localised studies of coastal species, focusing on residence patterns (e.g. Suárez, 1994), genetic structure (e.g. Escorza-Treviño *et al.*, 2005), and population impacts arising from interactions with vessel traffic, fisheries and directed catches (e.g. Avila *et al.*, 2008; Capella *et al.*, 2001; Mora-Pinto *et al.*, 1995; Palacios and Gerrodette, 1996) should yield additional information for management strategies at the local level.

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## Appendix 1

### DETAILS OF SURVEY EFFORT AND SIGHTING STATISTICS FOR SWFSC LINE-TRANSECT SURVEYS (1986–2006).

Table A1.1  
Survey effort by year conducted by the SWFSC within Colombia's Pacific EEZ (1986–2006).

Year (km)	Cruise	Vessel	Effort
1986	MOPS86	R/V <i>David Starr Jordan</i>	252.2
1986	MOPS86	R/V <i>McArthur</i>	376.1
1987	MOPS87	R/V <i>McArthur</i>	782.2
1987	MOPS87	R/V <i>David Starr Jordan</i>	475.0
1988	MOPS88	R/V <i>David Starr Jordan</i>	334.8
1988	MOPS88	R/V <i>McArthur</i>	596.4
1989	MOPS89	R/V <i>David Starr Jordan</i>	373.2
1990	MOPS89	R/V <i>David Starr Jordan</i>	351.6
1992	PODS92	R/V <i>McArthur</i>	1,730.8
1992	PODS92	R/V <i>David Starr Jordan</i>	636.9
1998	SPAM98	R/V <i>McArthur</i>	127.7
1998	SPAM98	R/V <i>Endeavor</i>	480.9
1998	SPAM98	R/V <i>David Starr Jordan</i>	325.5
2000	STAR00	R/V <i>McArthur</i>	544.9
2006	STAR06	R/V <i>David Starr Jordan</i>	396.2

Table A1.2  
Summary of effort, number of sightings (#Si) and encounter rate (ER, in sightings per 1,000km) collected under various sea state conditions (Beaufort scale) and swell height (in feet) during SWFSC line-transect surveys within Colombia's Pacific EEZ (1986–2006).

	Effort (km)	#Si	ER
Total	7,784.4	300	38.54
<b>By sea state</b>			
0	14.2	1	70.55
1	113.7	18	158.31
2	404.6	65	160.65
3	601.3	53	88.15
4	1,315.7	91	69.16
5	1,818.6	69	37.94
6	31.1	3	96.38
<b>By swell height*</b>			
0	7.2	0	0.00
1	138.2	8	57.87
2	357.8	30	83.84
3	1,476.1	76	51.49
4	1,209.7	27	22.32
5	365.7	11	30.08
6	444.8	11	24.73
7	81.2	4	49.24
8	117.6	4	34.01

\*Number of sightings with no swell height recorded = 129.



Table A1.3

Number of on-effort sightings (*#Si*), average group size (*G*) and encounter rate (*ER*, in number of groups per 1,000km) for all identified species within Colombia's Pacific EEZ, from SWFSC line-transect surveys (1986–2006).

Common name	Scientific name	<i>#Si</i>	<i>G</i>	<i>ER</i>
Pantropical spotted dolphin*	<i>Stenella attenuata</i>	15	84.2	1.93
Spinner dolphin*	<i>Stenella longirostris</i>	3	77.4	0.39
Striped dolphin	<i>Stenella coeruleoalba</i>	70	48.4	8.99
Rough-toothed dolphin	<i>Steno bredanensis</i>	12	27.3	1.54
Common dolphin	<i>Delphinus delphis</i>	13	126.9	1.67
Common bottlenose dolphin	<i>Tursiops truncatus</i>	25	15.6	3.21
Risso's dolphin	<i>Grampus griseus</i>	25	12.2	3.21
Melon-headed whale	<i>Peponocephala electra</i>	5	245.5	0.64
Pygmy killer whale	<i>Feresa attenuata</i>	2	35.1	0.26
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	6	9.9	0.77
Killer whale	<i>Orcinus orca</i>	2	5.3	0.26
Sperm whale	<i>Physeter macrocephalus</i>	27	10.4	3.47
Dwarf sperm whale*	<i>Kogia sima</i>	4	1.6	0.51
Mesoplodont whales*	<i>Mesoplodon</i> spp.	11	2.7	1.41
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	4	1.5	0.51
Bryde's whale*	<i>Balaenoptera edeni</i>	4	1.5	0.51
Humpback whale	<i>Megaptera novaeangliae</i>	10	2.6	1.28

\*Pooling of related sighting categories was done for these species as described in the text.

## Appendix 2

### DETAILS OF ROUTES COVERED AND SIGHTINGS COLLECTED DURING THE *SIBEN* AND *ODYSSEY* EXPEDITIONS (1988, 1993, 1994).

Table A2.1

Dates and routes of the *Siben* and *Odyssey* expeditions in Colombian Pacific waters. Effort information was not available for these data sets.

Date	Route	Vessel
23–27/05/88	Panamá-Bahía Solano-Buenaventura-Gorgona	R/V <i>Siben</i>
26/06–12/07/88	Buenaventura-Panamá	R/V <i>Siben</i>
24–27/07/88	Buenaventura-Gorgona-Buenaventura	R/V <i>Siben</i>
09–16/02/93	Panamá-Galápagos	R/V <i>Odyssey</i>
20–21/09/93	Galápagos-Bahía Málaga	R/V <i>Odyssey</i>
05–09/10/93	Bahía Málaga-Galápagos	R/V <i>Odyssey</i>
12–19/04/94	Galápagos-Panamá	R/V <i>Odyssey</i>

Table A2.2

Number of sightings (*#Si*) and average group size (*G*) for all identified species observed during the *Siben* Expedition in Colombian Pacific waters (May–July 1988).

Common name	Scientific name	<i>#Si</i>	<i>G</i>
Pantropical spotted dolphin	<i>Stenella attenuata</i>	2	45.0
Rough-toothed dolphin	<i>Steno bredanensis</i>	1	42.0
Common dolphin	<i>Delphinus delphis</i>	1	95.0
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	1	8.0
Sperm whale	<i>Physeter macrocephalus</i>	1	20.0
Humpback whale	<i>Megaptera novaeangliae</i>	5	2.4

Table A2.3

Number of sightings (*#Si*) and average group size (*G*) for all identified species observed during the *Odyssey* Expedition in Colombian Pacific waters (February 1993, September–October 1993 and April 1994).

Common name	Scientific name	<i>#Si</i>	<i>G</i>
Common bottlenose dolphin	<i>Tursiops truncatus</i>	1	20.0
Risso's dolphin	<i>Grampus griseus</i>	1	7.0
Sperm whale	<i>Physeter macrocephalus</i>	3	22.7
Humpback whale	<i>Megaptera novaeangliae</i>	3	1.7

## Appendix 3

## DETAILS OF SURVEY EFFORT AND SIGHTING STATISTICS FOR OCEANOGRAPHIC CRUISES ABOARD DIMAR VESSELS (2004, 2006–08).

Table A3.1

Visual effort conducted in passing mode, Beaufort sea states of 3 or less and good sighting conditions during oceanographic cruises aboard DIMAR vessels (2004, 2006–08).

Dates	Cruise	Vessel	Effort (km)
24/09–08/10/04	ERFEN-04	R/V <i>Providencia</i>	551.1
03–27/03/06	Pacifico-06	R/V <i>Malpelo</i>	1,703.4
15–26/09/06	ERFEN-06	R/V <i>Providencia</i>	811.3
24/01–18/02/07	Pacifico-07	R/V <i>Malpelo</i>	1,717.9
03–28/09/07	ERFEN-07	R/V <i>Providencia</i>	1,369.0
09–28/03/08	Pacifico-08	R/V <i>Providencia</i>	1,372.3
06–26/09/08	ERFEN-08	R/V <i>Malpelo</i>	1,061.9

Table A3.2

Number of sightings (#*Si*) and average group size (*G*) and encounter rate (*ER*, in number of groups per 1,000km) for all identified species, collected during oceanographic cruises aboard DIMAR vessels (2004, 2006–08).

Common name	Scientific name	# <i>Si</i>	<i>G</i>	<i>ER</i>
Pantropical spotted dolphin	<i>Stenella attenuata</i>	16	80.1	1.86
Striped dolphin	<i>Stenella coeruleoalba</i>	19	142.1	2.21
Rough-toothed dolphin	<i>Steno bredanensis</i>	4	53.8	0.47
Common dolphin	<i>Delphinus delphis</i>	6	185.5	0.70
Common bottlenose dolphin	<i>Tursiops truncatus</i>	21	9.1	2.45
Risso's dolphin	<i>Grampus griseus</i>	3	18.0	0.35
False killer whale	<i>Pseudorca crassidens</i>	2	104.7	0.23
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	6	24.2	0.70
Killer whale	<i>Orcinus orca</i>	1	5.0	0.12
Sperm whale	<i>Physeter macrocephalus</i>	2	4.5	0.23
Mesoplodont whales	<i>Mesoplodon</i> spp.	1	1.0	0.12
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	2	1.0	0.23
Minke whale	<i>Balaenoptera acutorostrata</i>	1	1.0	0.12
Fin whale	<i>Balaenoptera physalus</i>	1	1.0	0.12
Humpback whale	<i>Megaptera novaeangliae</i>	93	1.8	10.83

## Appendix 4

## DETAILS OF SEARCH EFFORT AND SIGHTING STATISTICS FOR DIVE AND SEASCAPE CHARTER TRIPS (2004–08).

Table A4.1

Daily visual effort conducted in passing mode, Beaufort sea states of 3 or less and good sighting conditions aboard M/V *Maria Patricia* during dive and Seascape charter trips (2004–08).

Date	Effort (hr)	Route	Date	Effort (hr)	Route
14 February 2004	9.0	Buenaventura-Malpelo	11 March 2006	10.0	Gorgona-Malpelo
22 February 2004	10.0	Malpelo-Buenaventura	14 March 2006	10.0	Malpelo-Buenaventura
15 March 2004	9.8	Buenaventura-Malpelo	8 April 2006	10.7	Buenaventura-Malpelo
16 March 2004	4.0	Malpelo-Buenaventura	15 April 2006	10.6	Malpelo-Buenaventura
20 June 2004	2.0	Malpelo-Buenaventura	27 August 2006	4.0	Gorgona-Malpelo
18 December 2004	9.0	Malpelo-Buenaventura	18 March 2007	7.8	Buenaventura-Malpelo
24 March 2005	9.0	Gorgona-Malpelo	27 March 2007	4.3	Malpelo-Buenaventura
31 March 2005	11.7	Malpelo-Buenaventura	3 April 2007	6.2	Gorgona-Malpelo
12 April 2005	9.7	Buenaventura-Malpelo	10 April 2007	3.0	Malpelo-Buenaventura
13 April 2005	4.5	Malpelo-Buenaventura	21 March 2008	1.3	Buenaventura-Malpelo
21 April 2005	8.0	Malpelo-Buenaventura	30 March 2008	9.2	Malpelo-Buenaventura
10 August 2005	6.0	Gorgona-Malpelo	26 May 2008	9.0	Cabo Marzo-
14 August 2005	12.5	Malpelo-Buenaventura			Buenaventura

Table A4.2

Number of sightings (*#Si*) and average group size (*G*) and encounter rate (*ER*, in number of groups per 100hr) for all identified species, collected aboard M/V *Maria Patricia* during dive and Seascope charter trips (2004–08).

Common name	Scientific name	<i>#Si</i>	<i>G</i>	<i>ER</i>
Pantropical spotted dolphin	<i>Stenella attenuata</i>	5	54.0	1.90
Spinner dolphin	<i>Stenella longirostris</i>	1	150.0	0.38
Striped dolphin	<i>Stenella coeruleoalba</i>	6	101.6	2.28
Rough-toothed dolphin	<i>Steno bredanensis</i>	1	50.0	0.38
Common dolphin	<i>Delphinus delphis</i>	11	245.7	4.17
Common bottlenose dolphin	<i>Tursiops truncatus</i>	11	28.9	4.17
Risso's dolphin	<i>Grampus griseus</i>	1	15.0	0.38
Melon-headed whale	<i>Peponocephala electra</i>	1	10.0	0.38
False killer whale	<i>Pseudorca crassidens</i>	3	6.0	1.14
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	2	15.0	0.76
Killer whale	<i>Orcinus orca</i>	2	5.5	0.76
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	1	2.0	0.38
Humpback whale	<i>Megaptera novaeangliae</i>	1	2.0	0.38

## Appendix 5

### DETAILS OF ROUTES COVERED AND SIGHTINGS COLLECTED DURING DAILY COASTAL SPORTS-FISHING TRIPS ORGANISED BY FUNDACIÓN CABO MAR (2000–01, 2004–08).

Table A5.1

Visual effort conducted during 21 daily coastal sports-fishing trips organised by Fundación Cabo Mar (2000–01, 2004–08).

Dates	Route	Vessel	Effort (hr)
July 2000*	Buenaventura-Bahía Solano	M/V <i>La Cotizada</i>	7
28 May 2001	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	7
July 2001*	Bahía Solano-Cupica	M/V <i>La Cotizada</i>	2
July 2001*	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	6
July 2001*	Bahía Solano-Cupica	M/V <i>La Cotizada</i>	3
29 December 2004	Buenaventura-Bahía Solano	M/V <i>La Cotizada</i>	9
30 December 2004	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	2
3 January 2005	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	5
4 January 2005	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	2
7 January 2005	Bahía Solano-Cupica	M/V <i>La Cotizada</i>	3
3 May 2005	Cupica-Cabo Marzo	M/V <i>La Cotizada</i>	6
January 2006*	Cupica-Cabo Marzo	M/V <i>El Gran Blanco</i>	8
1 March 2007	Bahía Solano-Cupica	M/V <i>El Gran Blanco</i>	4
6 March 2007	El Valle-offshore	M/V <i>El Gran Blanco</i>	4
10 April 2007	Buenaventura-Bahía Solano	M/V <i>El Gran Blanco</i>	4
15 April 2007	Buenaventura-Bahía Solano	M/V <i>El Gran Blanco</i>	7
11 May 2007	Buenaventura-Bahía Solano	M/V <i>El Gran Blanco</i>	5
11 May 2007	Bahía Solano-Cupica	M/V <i>El Gran Blanco</i>	3
2 January 2008	Cupica-Cabo Marzo	M/V <i>El Gran Blanco</i>	8
3 February 2008	Bahía Solano-Cupica	M/V <i>El Gran Blanco</i>	4
6 February 2008	Buenaventura-Bahía Solano	M/V <i>El Gran Blanco</i>	9

\*The specific date for these trips was not available.

Table A5.2

Number of sightings (*#Si*) and average group size (*G*) and encounter rate (*ER*, in number of groups per 100h) for all identified species, collected during 21 daily coastal sports-fishing trips (2000–01, 2004–08).

Common name	Scientific name	<i>#Si</i>	<i>G</i>	<i>ER</i>
Pantropical spotted dolphin	<i>Stenella attenuata</i>	9	155.8	8.57
Common bottlenose dolphin	<i>Tursiops truncatus</i>	12	72.8	11.43
False killer whale	<i>Pseudorca crassidens</i>	1	2.0	0.95
Humpback whale	<i>Megaptera novaeangliae</i>	4	2.0	3.81

# Observations of killer whales off East Antarctica, 82°–95°E, in 2009

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## ABSTRACT

Observations of killer whales (*Orcinus orca*) during a survey off East Antarctica, 82°–95°E revealed previously undescribed variations in pigmentation and group associations. During the survey 24 killer whale groups were sighted south of 60°S and classified, when possible, to Types A, B, or C based on their external morphology. Sufficient observation was available for nine groups to be classified: 2 groups of Type A; 1 mixed group of Type A and Type B; 3 groups of Type C; and 3 groups with eyepatch pigmentation intermediate in size between Types B and C. These whales may represent an intergrade between Types B and C or a previously unrecognised form. One of the 'intermediate' groups was observed feeding in a multi-species aggregation with other cetaceans in deep water. Clearly distinguishable Type A and Type B whales were observed feeding together in a mixed aggregation, the first time that this has been documented.

KEYWORDS: KILLER WHALE, ANTARCTIC, COLOURATION, TAXONOMY

## INTRODUCTION

During an International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) cruise off East Antarctica, 82°–95°E, in 2008–2009, killer whales (*Orcinus orca*) were sighted frequently. In all, 24 groups totalling 360 individuals were sighted during 25 survey days south of 60°S (Ensor *et al.*, 2009). Given the recent interest in the taxonomy of Antarctic killer whales (LeDuc *et al.*, 2008; Morin *et al.*, 2010; Pitman and Ensor, 2003; Pitman *et al.*, 2007), the observations yield relevant new information on the pigmentation, behaviour and distribution of these whales in a geographic area with little previously reported information.

Pitman and Ensor (2003) described field characteristics and biological observations on three visually recognisable forms of killer whales found in Antarctica. The forms are distinguished by the presence or absence of a dorsal cape and the relative size and orientation of the white eyepatch, resulting in the classification of three types. Type A, similar to killer whales that occur worldwide, does not exhibit a dorsal cape and has a medium-sized eyepatch oriented parallel to the body axis. Type B has a dorsal cape and a large eyepatch (described as at least twice as large as that of Type A) oriented parallel to the body axis. Type C has a dorsal cape and a small, forward-slanted eyepatch at an angle to the body axis. Pitman and Ensor (2003) proposed that the types are different ecotypes and may represent separate species. Subsequent research has investigated this theory, although definitive taxonomic status is yet to be confirmed. Pitman *et al.* (2007) found that total body lengths of Type C killer whales, based on aerial photogrammetry, were substantially shorter than those of Type A. Examining mitochondrial DNA, LeDuc *et al.* (2008) reported a slight level of divergence between Types A, B and C, also finding that Types B and C were closely related. Analysing complete

mitochondrial genomes, Morin *et al.* (2010) obtained similar results, with Type A more divergent from Types B and C, which were more closely related. Krahn *et al.* (2008) used stable isotope analysis to explore the prey preferences of Type C, confirming that it is a fish-eater. All of the Type C killer whales sampled for these investigations were from the Ross Sea region of Antarctica (165°E–165°W longitude), a minimum distance of 2,700km from our study area.

## METHODS AND RESULTS

The 2008–2009 research cruise was a whale sighting survey conducted as part of the IWC-SOWER programme. This long-term research has primarily been aimed at obtaining circumpolar data for estimation of abundance of the Antarctic minke whale (*Balaenoptera bonaerensis*). The main focus of the 2008–2009 cruise was to study temporal changes in the spatial distribution of Antarctic minke whales in relation to pack ice recession. The research area ranged from 82° to 95°E and from the pack ice edge north 111 km (60 n.miles). The area was surveyed multiple times on constructed survey lines from 19 January through 12 February 2009, using the research vessel *Shonan Maru No.2* (length 64m). The research protocol included closing and passing modes, i.e. some cetacean sightings were approached with the ship for data collection, and other sightings were 'passed' and data were collected without turning the ship toward the sighting. (For more information about the cruise see Ensor *et al.*, 2009.)

During the survey, researchers attempted to classify every encountered group of killer whales to type (A, B or C). This was difficult in some cases when the survey was in passing mode and the whales did not come close to the ship, thus most of those groups remain unclassified. Eight sightings were photographed, which aided in the determination of type. Two groups were identified as Type A; 1 mixed group of Type A and Type B; 3 groups of Type C; and 3 groups with

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eyepatch characteristics intermediate between Types B and C. Details of four of the sightings (1 mixed Type A and Type B group and the 3 B/C intermediate groups) are given below.

#### Observation of mixed Type A and Type B group

The mixed type group was sighted at 05:47hr on the morning of 21 January, 28km from the ice edge (sighting no. 001). A total of 20 minutes was spent observing and photographing this group at 63°45'S 92°18'E. There were 18 killer whales feeding in a slick about 40m in diameter, together with feeding seabirds. Blood was apparent in the slick but no carcass or animal remains were seen. The slick was suggestive of a marine mammal kill. Sixteen of the killer whales were clearly Type A (Fig. 1a). Two of the whales in the group were clearly Type B (Fig. 1b). The Type A and B whales intermingled, although the two Type B whales were often swimming together. Different individuals (Type A and Type B) would submerge and then emerge in different places with many changes of direction. No aggressive interactions were observed between the types. The whales appeared focused on feeding and the subsurface activity.

#### Observations of potential Type B/C intermediates

On three occasions groups were encountered that exhibited features of both Type B and C whales. All whales had dorsal capes (common to Types B and C). The eyepatches were forward-slanted (Type C), but the size and shape of the eyepatch varied within the groups, ranging from small to medium-large in size. Type C whales typically have small, narrow eyepatches (Jefferson *et al.*, 2008; Pitman and Ensor, 2003; Pitman *et al.*, 2007); Fig. 2 provides an example. The larger eyepatches observed were relatively longer and wider – intermediate in size between Type C and Type B (Figs 3a and b). Details of the observations follow.

#### 19 January

A group of 15 killer whales (sighting no. 010) was photographed in passing mode on 19 January at 63°33'S 95°06'E, 9km from the ice edge. This group exhibited a variety of moderately-sized eyepatches, all forward-slanted. The eyepatches were larger than that of typical Type C whales from the Ross Sea yet still slanted. The whales had a yellowish diatom film visible on the body. A group of 45 Type C killer whales (sighting no. 011) was subsequently sighted 2km from this group. We photographed a third of this group. Most of the photographed whales had smaller, typical Type C eyepatches, but three whales had eyepatches of a moderate size, so it is possible that this may also have been an 'intermediate' type group.

#### 26 January

On 26 January (sighting no. 033), a group of 30 killer whales was sighted at 64°12'S 83°20'E, 24km from the ice edge, 169km from the continental slope front (1,000m contour) and in >3,000m of water. The whales were travelling in several subgroups; individuals in the larger subgroups were clustered tightly together. Photographs reveal individuals with dorsal capes and with small to moderate size, forward-slanted eyepatches. Two whales had large forward-slanted eyepatches. The group was photographed in passing mode. Interestingly, this group was sighted 2km from another group



Fig. 1a. Type A killer whales seen feeding with Type B's on 21 January 2009.



Fig. 1b. Type B killer whale seen feeding with Type A's on 21 January 2009. Note the large eyepatch, dorsal cape and yellowish cast.



Fig. 2. Type C killer whale from the Ross Sea, 29 January 2004 with a small eyepatch and yellowish cast. (Photo T. Miura, IWC-SOWER 2003–2004.)

of killer whales (sighting no. 036), unclassified to type, group size 17, that was later observed to be joined by a pair of baleen whales classified taxonomically as 'like minke whale'. Sighting no. 036 was viewed in passing mode and no photographs were obtained.

#### 9 February mixed species feeding aggregation

On 9 February, a mixed-species feeding aggregation was encountered (sightings no. 034–038) that included scattered groups of killer whales (totalling 51 individuals), 2 Antarctic minke whales, 2 fin whales (*Balaneoptera physalus*), 1 humpback whale (*Megaptera novaeangliae*) and feeding flocks of seabirds numbering several thousands. Large numbers of shearwaters (*Puffinus* spp.) were among the flocks. The sightings were centred at 64°19'S 88°53'E, near the ice edge among scattered belts of ice floes, and approximately 148km from the slope front in 3,000m of water. About an hour was spent observing the aggregation and several groups of killer whales were approached for



Fig. 3a. Killer whale with a medium-large size, forward-slanted eyepatch, 9 February 2009. The eyepatch is larger than a Type C from the Ross Sea, appearing intermediate in size between Types C and B. This whale is from a different group than the whale in Fig. 3b.



Fig. 3b. Killer whale with a medium-large size, forward-slanted eyepatch, 9 February 2009. The eyepatch is larger than a Type C from the Ross Sea, appearing intermediate in size between Types C and B. This whale is from a different group than the whale in Fig. 3a.

photographs and skin biopsy sampling. One biopsy sample from a killer whale was collected. A sonobuoy was deployed near the aggregation but no sounds attributed to killer whales, Antarctic minke, fin or humpback whales were detected during one hour of recording.

There were 10–12 groups of killer whales, with group sizes ranging from 4–15 whales. While the groups were associated, they remained distinct with no observed exchange of individuals. The groups included mixed sex and age classes; most contained one or more juveniles, and calves were present in at least three groups. (Age classes were based on relative body size and calves swimming in echelon position.) The mature animals appeared smaller in body size than Type A killer whales. The pigmentation varied subtly between groups: all exhibited dorsal capes, but the capes of some were minimally present while others were quite pronounced. Many groups consisted of individuals with a yellowish cast. There was variation in eyepatch size relative to the body, both between and within groups. All eyepatches observed (minimum number = 39) were markedly forward-slanted; many were of a medium-large size, thus appearing to be intermediate between Type B and C eyepatches (Figs 3a and b). The degree of variation in pigmentation between groups, and that no interchange of individuals between groups was observed, suggests these whales represented a temporary aggregation.

All of the species in this aggregation appeared to be feeding. A fin whale rolled on its side at one point and the killer whales were diving and milling. Small groups of killer whales (4–6 whales) were observed following the fin whales,

sometimes diving closely by a fin whale's head or tail. The behaviour did not seem aggressive and the fin whales did not appear to be agitated by the close approaches of the killer whales. Similarly, the behaviour of the Antarctic minke whales and the humpback whale appeared unaffected by the killer whales' presence. Prey items may have included krill and mesopelagic fish.

## DISCUSSION

The whales in three sightings described here off east Antarctica exhibited larger than usual eyepatches for Type C killer whales. Given the variation in eyepatch size between individuals within groups, these whales may represent an intergrade of Types B and C. Previous accounts of the Antarctic killer whale types have not reported intermediates between types (LeDuc *et al.*, 2008; Pitman and Ensor, 2003). Genetically Types B and C are very similar (LeDuc *et al.*, 2008; Morin *et al.*, 2010), although Morin *et al.* (2010) found a shallow divergence between them (three fixed differences among 16,290 mitochondrial base pairs). Given the genetic similarity, LeDuc *et al.* (2008) mentions the possibility of a B/C intermediate although such a form was not known at the time. The Type C samples in the Morin *et al.* (2010) and LeDuc *et al.* (2008) studies were from the Ross Sea, a minimum distance of 2,700km from our study area, and the Type B samples were from the Antarctic Peninsula/South Georgia/South Sandwich Islands/Falkland Islands regions, a minimum distance of 5,500km from our study area. Another explanation for the B/C 'intermediate' that we report is that it may not be an intermediate but a previously undescribed form characteristic of this region of East Antarctica, whether a unique form or a variant Type C. Genetic analysis of killer whales from east Antarctica, as well as additional photographs and field observations, may clarify the distinctiveness of the B and C Types and where the form we observed fits into the taxonomy.

The mixed feeding group of Type A and B killer whales was the first reported encounter of this kind. Prior to our cruise there were no observations of mixed type schools (Berzin and Vladimirov, 1983; Pitman and Ensor, 2003). It seems likely that the killer whales formed a temporary association during a feeding event. Both types are known to prey on marine mammals (Pitman and Ensor, 2003). Given that the Type B whales were yellow with diatoms and the Type A's were not supports a short-term association since it would be unlikely that the whales had been occupying the same water masses over time. Thus it appears that different types do mix, at least occasionally, during feeding events such as the one reported here. This is new information relevant to the sympatry of killer whale populations in the Antarctic.

Currently the taxonomic status of the different morphological forms (body size and pigmentation) of killer whales in Antarctica and their roles within the Antarctic ecosystem are not completely understood. Continued field observations and photographic and biological sampling of all forms are needed to clarify their status.

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# Winter sighting of a known western North Atlantic right whale in the Azores

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## ABSTRACT

A right whale (*Eubalaena glacialis*) from the western North Atlantic population, sighted in the Azores, was subsequently found to have moved back to the northwest Atlantic. The whale was sighted in the Azores on 5 January 2009 travelling in a west-south westerly direction at a constant speed. A photographic match was found to an adult female in the North Atlantic Right Whale Catalogue. The whale's previous last sighting, on 24 September 2008 in the Bay of Fundy, Canada, implies movement to the Azores of at least 3,320 km in 101 days. It was subsequently resighted in the Bay of Fundy on 2 September 2009, 237 days after being seen in the Azores. This appears to be the only documented evidence of a western North Atlantic right whale outside its normal range in winter, and provides additional evidence of the potential for interbreeding between western North Atlantic right whales and the remnant eastern population.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; ATLANTIC OCEAN; EUROPE; MOVEMENTS; DISTRIBUTION; STOCK IDENTITY; MANAGEMENT; NORTHERN HEMISPHERE

## INTRODUCTION

The North Atlantic right whale (*Eubalaena glacialis*) was severely depleted by centuries of exploitation and in the 1950s the species was considered extinct or very nearly so (Kraus and Rolland, 2007). However, right whales used to be common and wide ranging along coastal waters on both sides of the North Atlantic, from Florida and West Africa in the south, to the Labrador Sea and Norway in the north, extending to waters off southern Iceland and Greenland (Kraus and Rolland, 2007). The severe reduction in population size was accompanied by a considerable contraction in the species' range and by its virtual disappearance from what were once important habitat areas. In the northeast Atlantic, records of right whales in former whaling grounds, such as the Bay of Biscay, Cape Farewell, the British Isles and northern Norway, are now rare and scattered. Between 1900 and 1982, fewer than 140 right whales were captured in European waters, the majority of which were taken off the British Isles to 1923 (Brown, 1986). In addition, eight right whales were sighted in various locations in the eastern North Atlantic (Jacobsen *et al.*, 2004). The southernmost records from the 20th century are from the Canary Islands (Vidal Martin, pers. comm.) and a winter survey off West Africa failed to detect any right whales in Cintra Bay (Morocco), thought to be the only historical calving ground in the eastern Atlantic (Notarbartolo di Sciara *et al.*, 1998). Historical whaling records suggest that right whales also occupied a wider range in the northwest Atlantic. The low number of sightings during the 20th century in Newfoundland and in the Labrador Sea suggests right whales are now

infrequent in these former whaling grounds (Knowlton *et al.*, 1992).

Eastern and western North Atlantic right whales have always been considered as two separate management stocks (IWC, 1986). Recently, mitochondrial DNA analysis of archaeological and museum specimens has suggested that the eastern and western populations were not genetically differentiated (Rosenbaum *et al.*, 2000). Nonetheless, the paucity of sightings in the eastern Atlantic and the lack of recovery there have been interpreted as an indication of population subdivision over centuries of exploitation persisting to the present day.

At present, the eastern population is presumed functionally extinct and the remnant population of right whales, consisting of about 400 whales (Pettis, 2009), is mostly restricted to the coastal waters of United States and Canada (Hamilton *et al.*, 2007). Five critical habitats or conservation areas have been identified, including four feeding and one calving ground. In spring and early summer, right whales usually concentrate in the Great South Channel (east of Cape Cod) and Cape Cod Bay, whereas in summer and fall, they are mainly found in the Bay of Fundy and Roseway Basin (south of Nova Scotia) (Fig. 1). The calving ground, located off the coast of Florida and Georgia, is mainly visited in winter by pregnant females and a few calves and non-calving females (Kraus and Rolland, 2007). While a considerable part of the population seems to aggregate seasonally in these habitats, several whales appear, regularly or occasionally, to use areas other than the typical foraging and calving grounds (Jacobsen *et al.*, 2004; Knowlton *et al.*, 1992). To date, these alternative habitats

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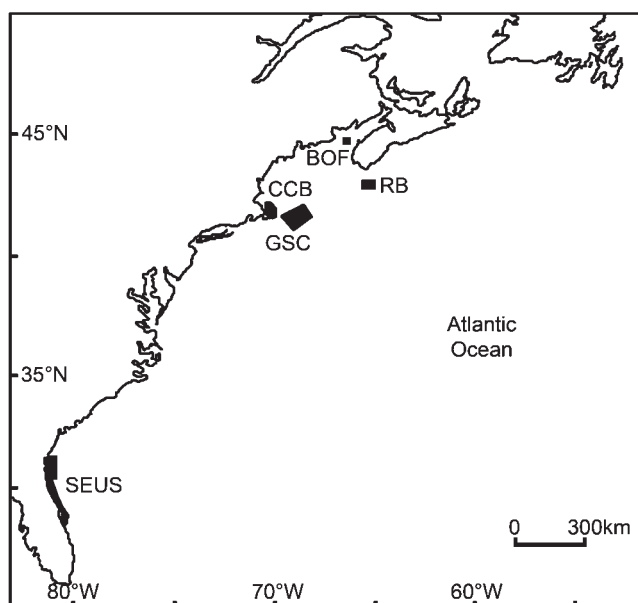


Fig. 1. Critical habitats or conservation areas of western North Atlantic right whales: SEUS = Southeast United States, GSC = Great South Channel, CCB = Cape Cod Bay, BOF = Bay of Fundy, RB = Roseway Basin.

have not been identified and the ranging behaviour of a segment of the population remains poorly understood. A wintering area for non-calving whales has only recently been discovered in the central Gulf of Maine (Tim Cole, pers. comm.) but it is unclear whether other wintering areas exist. The identification of these habitats and knowledge of the movements between them is crucial to ensure the protection of this highly endangered population throughout all its range.

This paper reports the sighting off the Azores of an individually identified right whale from the western North Atlantic population and documents its movement back to the northwest Atlantic. Long range match is examined in light of historic and present knowledge of the distribution and movements of the species and potential implications for population structure and management are discussed.

## MATERIALS AND METHODS

The Archipelago of the Azores (Portugal) is located between 37° and 41°N and 25° and 31°W, extending more than 600km along a northwest–southeast axis and crossing the Mid-Atlantic Ridge. It is the most isolated archipelago in the North Atlantic, situated 1,500km west of mainland Portugal and 3,200km from the eastern coast of the United States (Fig. 2). The archipelago is characterised by an absence of continental slope and the occurrence of deep waters (>2,000m) at short distance from the coast with scattered seamounts. It is situated at the northern edge of the North Atlantic Subtropical Gyre. The Gulf Stream feeds the area, and its southeastern branch generates the eastward-flowing Azores Current. The Gulf Stream, North Atlantic and Azores currents, and the dynamic Azores Front, are responsible for creating a complex pattern of ocean circulation, with strong seasonal and annual variations, resulting in high salinity, high temperature and low-nutrient waters (Santos *et al.*, 1995).

The whale was detected by two experienced land-based observers (cliff lookouts) employed by whalewatching companies. At the time, one lookout was collecting

information for the Department of Oceanography and Fisheries of the University of the Azores (DOP/UAç) on the presence of cetaceans off the southern coast of the islands of Faial and Pico (Fig. 2). The lookout searched for cetaceans in an area of approximately 800km<sup>2</sup>, extending from the coastline up to 22km offshore, using 15×80mm mounted binoculars with a compass. Observations were carried out from 1 February 2008 until 29 September 2009, whenever visibility and weather conditions allowed. Data on sighting effort, environmental and visibility conditions were collected for each period of continuous observation (ranging from 1–3 hours) and whenever weather conditions changed. For each sighting the lookout recorded the initial time and approximate location, the species, estimated number of individuals, behaviour and composition of the school. All information was recorded on standardised data sheets.

The lookout immediately contacted DOP/UAç to report the sighting and directed a research vessel to the site. The whale was followed for approximately one hour, until the sun set at 17:41. Every time the whale surfaced, its position, heading and behaviour were recorded. Photographs of the head, flanks and a partial fluke were taken with a Nikon F-70S digital camera equipped with a 70–300mm lens, and a Canon 30D equipped with a 100–400mm lens. The best photographs were sent to the North Atlantic Right Whale Catalog maintained at the New England Aquarium to see if the whale was known.

## RESULTS AND DISCUSSION

From February 2008 to September 2009, the lookout carried out 2,607 hours of observations in 474 days. During that period, 1,769 cetacean sightings were recorded. The whale was sighted on 5 January 2009 at 15:44, less than one nautical mile south of the island of Pico, heading westwards at a steady pace (Fig. 2). At 16:37 the DOP/UAç research vessel approached the whale and biologists onboard confirmed the identification as a right whale. The individual showed normal swimming behaviour, appeared to be in good physical conditions and had no obvious injuries that would suggest it was in distress. Over one hour, the whale travelled in a west-south westerly direction (mean course = 265°; SD = 21°) at an average speed of 7.1km h<sup>-1</sup> (SD = 3.1km h<sup>-1</sup>). Dives ranged from 4 to 12 min and the time interval between dives varied from 2 to 4 min.

Examination of the lookout's sighting records on the days prior to and after the sighting suggested the right whale did not remain in or return to the area. Although visibility conditions at that time of year are usually poor, the lookout scanned the area every day from 31 December 2008 to 10 January 2009. Thirty-three cetacean schools were recorded in the area during those days but there were no sightings of baleen whales.

Photographs taken were compared to the NARW Catalogue and a match was found to right whale no.3270. The whale was named *Pico* after the island near where it was seen. According to information from the Catalog website<sup>1</sup>, before being observed in the Azores, *Pico's* last sighting was on 24 September 2008, in the Bay of Fundy, Canada. This

<sup>1</sup> Sighting history available from the North Atlantic Right Whale Catalog (<http://www.neaq.org/rwcatalog>)

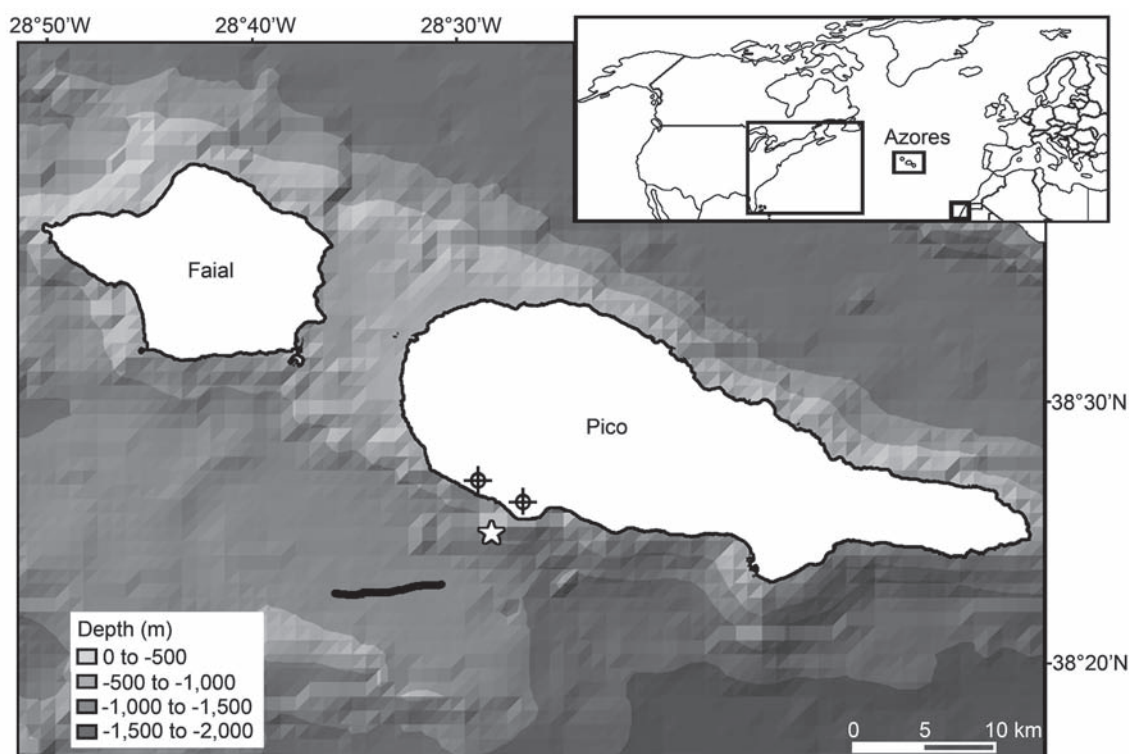


Fig. 2. Sighting of the North Atlantic right whale in the Azores: the star indicates the approximate position of the initial sighting reported by the lookouts and the line shows the reconstructed path of the whale. Inset shows the location of the Azores relative to the habitats of right whales in the western North Atlantic and to the historical wintering ground in Cintra Bay, Morocco.

means that *Pico* travelled at least 3,320km in 101 days. *Pico* was resighted in the Bay of Fundy on 2 September 2009, 237 days after being seen in the Azores. *Pico* appeared to be in good physical condition apart from a healed scarring that wrapped around the entire tail stock, strongly suggesting the whale had been recently entangled in fishing gear.

*Pico* is an adult female, first photographed in June 2002, in the Great South Channel, about 100km east of Cape Cod. *Pico* was then observed every year, except 2004, in the typical northern habitat of the western North Atlantic population. From March through July, *Pico* was frequently encountered in the Great South Channel; she was observed twice in August, in Roseway Basin and on George's Bank. Since 2006, *Pico* has been regularly found in the Bay of Fundy in August through late September. *Pico* has been rarely sighted during autumn and winter and her movements at this time of the year are not well documented. From 2002 to 2008, she was observed three times in November, January and February, always in the Gulf of Maine.

*Pico's* sighting in the Azores is the only record of the species in the area within the last 60 years. Combining all the information available on catches and sightings, we found a total of 11 records of right whales in the area. Clarke (1981) reported that seven right whales were captured between 1873 and 1888 by the Azorean open-boat whaling industry, which targeted sperm whales (*Physeter macrocephalus*). Another right whale was reportedly struck in 1914 but it proved difficult to capture and was cut loose (Brown, 1986). In his checklist of cetaceans from the Azores, Chaves (1924) claims to have seen right whales off the Azores twice but he gives no details on these observations. The last unconfirmed sighting occurred sometime between 1939 and

1949 and was reported by a whaling land-based lookout (Clarke, 1981).

Information summarised from 19<sup>th</sup> century American whaling logbooks has led to the possibility of a right whale summer ground in the central North Atlantic (Reeves, 2001). That area, which included the whole Azores archipelago and extended further west (to 48°W) and north (to 43°N), was depicted on charts representing locations where right whales were sighted, killed or struck by whaling vessels. However, Reeves *et al.* (2004) later reported that nearly all the occurrences of right whales in those charts has been incorrectly identified from the original logbooks and dismissed the idea that the area may have been an alternative offshore foraging ground for right whales. Similarly, there is no evidence that the Azores was an important historic whaling ground for European whalers before the nineteenth century (Aguilar, 1986; Reeves *et al.*, 2007; Smith *et al.*, 2006). Thus, it seems unlikely that right whales were ever abundant in the Azores, although sporadic catches and sightings show they occasionally occurred there.

Most of the whales known from the NARW Catalogue are regularly seen at least in one of the five well studied key habitats. Yet, several catalogued whales show sighting frequencies well below the average of the rest of the population (Hamilton *et al.*, 2007). Some of these 'irregular' whales were photographed in the Gulf of St. Lawrence, off Newfoundland, in the Labrador Basin and off Iceland (Knowlton *et al.*, 1992). *Pico*, on the other hand, was seen consistently in the population's foraging habitats and would probably be classified as a 'regular' whale. *Pico's* documented excursion to the Azores and back supports previous photo-identification and satellite-telemetry studies

showing that even 'regular' whales may range widely, sometimes over relatively short periods of time (Knowlton *et al.*, 1992; Mate *et al.*, 1997). Perhaps the most extreme example comes from *Porter*, an adult male known and frequently photographed in the western North Atlantic since 1981. In 1999, *Porter* travelled over 5,000km from the Great South Channel, where he was last seen in May, to northern Norway, where he spent more than one month, between August and September, foraging in the fjords. Less than five months later, *Porter* was back in the western North Atlantic (Jacobsen *et al.*, 2004).

Distant sightings of right whales from the western population have all occurred in summer and fall (between July and October), in well-known historical whaling grounds. This has led to the suggestion that some of these sites may represent alternative summer foraging (Smith *et al.*, 2006) or nursery areas (Knowlton *et al.*, 1992) for some whales. To the best of our knowledge, the sighting of *Pico* in the Azores during January is the only documented sighting of a western North Atlantic right whale outside the population's normal range in winter. The lack of information on winter movements of this population lends additional interest to this excursion to offshore waters, although we can only speculate on the reason for its occurrence.

The time of *Pico's* sighting in the Azores agrees with previous, albeit scarce, information on the occurrence of right whales in the region. The three dated records of right whales caught in the Azores are from January, March and April (Clarke, 1981), and all recent sightings in the eastern North Atlantic south of or at the latitude of the Azores have been in January and February (4 in Madeira, 3 in the Canary Islands and 1 south of Portugal) (Brown, 1986; Jacobsen *et al.*, 2004; Vidal Martin, pers. comm.). These sightings could not be matched to whales from the western population and were presumed to be of whales from the eastern population. It should be stressed that survey effort in the region during winter is usually low because of poor weather and right whales may occur more frequently than suggested by the sighting data.

As noted by Baumgartner *et al.* (2007), apart from the migration of pregnant females to calving grounds, long-distance movements of right whales are likely motivated by their need to find food. The diving behaviour, constant speed and heading, indicate *Pico* was travelling and not foraging when observed in the Azores. Moreover, the biological productivity of the waters around the Azores is low in winter (Woods and Barkmann, 1995). Inspection of remotely-sensed surface chlorophyll and temperature data in the months and weeks prior to the sighting did not reveal any unusual bloom of primary productivity capable of supporting important aggregations of zooplankton that might have attracted a right whale. Thus, it is unlikely that the presence of the whale in the Azores was caused by food availability. This does not exclude the hypothesis that *Pico's* extensive movement was associated with feeding opportunities elsewhere in offshore waters.

Alternatively, and given the timing of this sighting, *Pico's* excursion could have been triggered by reproductive events. *Pico's* date of birth is unknown but the shape of her head suggests she was at least two years old in 2002 when first sighted and photographed, meaning she would have been

over nine years old when seen in the Azores. Female North Atlantic Right whales reach sexual maturity at an average age of nine years (Hamilton *et al.*, 1998). Therefore, although *Pico* has never been photographed in the calving ground, nor has she ever been seen with a calf in 2009, she could have been sexually mature or be close to reaching sexual maturity. A recent study has shown that adult, reproductively available (i.e. not already calving or resting) females do not travel to the calving grounds in winter unless pregnant (Browning *et al.*, 2010). If *Pico* was pregnant we would have to assume that she had lost her calf before being observed in the Azores. On the other hand, Kraus *et al.* (2007) suggested that, as females approach sexual maturity, they are more likely to be found on the mating grounds than on the calving grounds. The location of the mating grounds is unknown but given that calves are born in December – March and gestation is assumed to last approximately one year (Best, 1994), mating must occur where whales winter.

The Azores are located in a straight trajectory between the western North Atlantic foraging areas, where *Pico* was last seen, and the only wintering and possibly calving ground known in the northeast Atlantic, situated off northwest Africa, in the region of Cintra Bay. During the nineteenth century, American whaling vessels captured or sighted at least 13 right whales in Cintra Bay in November, February and March (Schevill and Moore, 1983). The three most recent sightings of cow and calf pairs in Madeira (February 1967), south of Portugal (February 1995) (Jacobsen *et al.*, 2004), and in the Canary Islands (1976 and January 1999) (Vidal Martin, pers. comm.) support the notion of a winter calving ground to the south of these areas and suggest the area may still be visited by a few whales. Although a 25 day winter survey in 1996 in the region did not find any right whales, the visibility was poor and the survey effort may have been insufficient to detect whales that certainly are rare and scattered (Notarbartolo di Sciarra *et al.*, 1998).

Recently, paternity analyses have shown that the majority of calves from the western population were not fathered from males that have been genetically sampled and that the remaining unsampled males that are catalogued cannot account for all the unidentified paternities (Frasier *et al.*, 2007). These findings and results from other analyses suggest the population size must be higher than the current estimate from photo-identification data (Frasier *et al.*, 2007). Considering the intensive sampling carried out throughout the typical range of the population, it is likely that these unidentified whales use habitats that have not yet been discovered.

Whether *Pico's* long excursion was motivated by feeding needs or reproduction, there is no reason to believe that the Azores was the destination. It is possible that the Azores and their location on the Mid-Atlantic Ridge served as a navigation landmark to *Pico* in this offshore area. It is also plausible that the whale used the proximity of the Azores Front that originates from the Gulf Stream as a navigational cue. Though a link between western right whales and the remnant eastern population has yet to be established, the sighting of *Pico* in the Azores provides additional evidence of the potential for interbreeding between whales from each side of the Atlantic.



Despite nearly 75 years of protection, the North Atlantic right whale remains one of the most endangered baleen whales in the world. Although in recent years the population appears to have been increasing (Waring *et al.*, 2009), the recovery has been slow, mainly due to low reproductive rates and high mortality from entanglements in fishing gear and vessel collisions (Kraus *et al.*, 2007). The death of only a few females per year can endanger the survival of this species (Fujiwara and Caswell, 2001). Throughout the years, distinct management measures have been enforced to protect right whales in their western North Atlantic habitats. However, the recent sighting in the Azores and others made elsewhere (Jacobsen *et al.*, 2004; Knowlton *et al.*, 1992) suggest that at least some whales may have ranges that extend beyond the coastal waters of North America, to areas where they may be subject to various threats. Given the current status of this population, increased attention should be paid to these apparently exceptional long range movements.

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# Genetic diversity and population structure of humpback whales (*Megaptera novaeangliae*) from Ecuador based on mitochondrial DNA analyses

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## ABSTRACT

Information on the genetic characterisation of humpback whales (*Megaptera novaeangliae*) wintering off Ecuador (Breeding Stock G) is presented. Mitochondrial DNA was extracted and sequenced from 230 skin samples collected between 2002 and 2008 to establish the genetic diversity of this population. From 182 usable samples, 41 different haplotypes were found, eight of which were new and unique. Haplotype diversity ( $h \pm SD$ ) was estimated to be  $0.922 \pm 0.012$  and the nucleotide diversity ( $\pi \pm SD$ )  $0.019 \pm 0.009$ . A comparison with other areas within the Southeast Pacific (Colombia and Magellan Strait) and the Antarctic Peninsula suggested panmixia within Breeding Stock G, even though significant differentiation was found with Magellan Strait ( $p < 0.0001$  in both  $F_{ST}$  and  $\Phi_{ST}$ ). An additional analysis with the exact test of population differentiation showed significant differences in haplotype frequencies between breeding areas in Ecuador and southern Colombia ( $p < 0.01$ ), suggesting some level of stratification at breeding grounds as supported by photo-identification studies. The Ecuadorian dataset included haplotypes reported in all three Southern Hemisphere ocean basins indicating recent gene flow within the Southern Hemisphere. The population showed a male-biased sex ratio in adult animals of 2.16:1. Further research and a larger number of samples from breeding areas in the north (Panama and Costa Rica) are required to appropriately assess the extent of structure in this population.

KEYWORDS: HUMPBACK WHALE; GENETICS; BREEDING GROUNDS; SOUTH AMERICA; BREEDING STOCK G

## INTRODUCTION

Many baleen whale populations carry out extensive migrations between summer feeding grounds in polar waters and wintering breeding grounds located in temperate and tropical waters (e.g. Mackintosh, 1942). The humpback whale (*Megaptera novaeangliae*) is one of the species in which such a migrating pattern is most evident because of their coastal distribution around continental coasts and oceanic archipelagos where they concentrate for breeding (Dawbin, 1966). For management purposes, whaling areas were traditionally divided by pragmatic boundaries based on whaling records and biological data; thus in the Southern Hemisphere baleen whale populations were assigned by the International Whaling Commission (IWC) to six management areas, I–VI (Donovan, 1991). The Eastern and Southeastern Pacific waters were included in Area I (120°W–60°W). As part of an in-depth assessment of Southern Hemisphere humpback whales, the IWC Scientific Committee has recently designated the Southeast Pacific as Breeding Stock G (IWC, 1998).

The discreteness of the Southeast Pacific humpback whale population was assumed for a long time (Kellogg, 1929; Mackintosh, 1942; Omura, 1953), despite a lack of evidence to support this. Only recently, based on photo-identification (Garrigue *et al.*, 2002; Stevick *et al.*, 2004) and genetic analyses (Caballero *et al.*, 2001; Olavarría *et al.*, 2007), this has been confirmed by comparisons with neighbouring Southern Hemisphere breeding stocks.

Within the Southeast Pacific, humpback whales are distributed during the austral winter along the Northwestern coast of South America, mainly off Colombia and Ecuador, but also further north, off Panama and Costa Rica (Acevedo-Gutiérrez and Smultea, 1995; Kellogg, 1929; Mackintosh, 1942; Townsend, 1935). Photo-identification studies have been used to investigate movements of whales among these wintering areas (e.g. Castro *et al.*, 2008; Félix *et al.*, 2009; Flórez-González *et al.*, 1998). These studies reported photo-identification matches between Ecuador and Colombia, Colombia and Panama, Ecuador and Peru, Colombia and Peru, and Ecuador and Costa Rica, indicating that exchange of individuals among these regions occur, and expanding the range of the wintering grounds of this population within the Southeast Pacific to an overall 3,000km of coastal environment (Félix *et al.*, 2009).

Breeding areas in the Southeast Pacific have been also linked to the feeding areas on the west side of the Antarctic Peninsula and the Magellan Strait in southern Chile (Acevedo *et al.*, 2007; Capella *et al.*, 2008; Castro *et al.*, 2008; Garrigue *et al.*, 2002; Rasmussen *et al.*, 2007; Stevick *et al.*, 2004; Stone *et al.*, 1990) and in a few cases to further east of the Antarctic Peninsula into the Southwestern Atlantic Ocean (Dalla Rosa *et al.*, 2008). Sightings of humpback whales almost all year round off Peru (Ramírez, 1988) and south of Ecuador suggest that not all whales from this stock complete an annual migration. Some animals may remain in between the breeding grounds or the feeding areas in the

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highly productive waters of the Humboldt Current off Peru and Chile, where there are predictable concentrations of food (Papastavrou and Van Waerebeek, 1997). This behaviour is not exclusive to this stock (e.g. Best *et al.*, 1995; Craig and Herman, 2003).

Genetic studies have been conducted in recent years in different locations in the Southeast Pacific, including breeding grounds off mainland Ecuador and the Galapagos Islands (Félix *et al.*, 2007; 2011), Gorgona Island and Málaga Bay in Colombia (Caballero *et al.*, 2000; 2001; Olavarria *et al.*, 2007) and feeding areas in the Magellan Strait in southern Chile (Capella *et al.*, 2008; Olavarria *et al.*, 2006) and along the west coast of the Antarctic Peninsula (Olavarria *et al.*, 2000). Such studies based on mitochondrial DNA (mtDNA) sequence analyses have provided an overview of genetic diversity that appears to be the lowest among humpback whale stocks in the Southern Hemisphere (Olavarria *et al.*, 2007). These studies have also shown a lack of genetic differentiation between the Antarctic Peninsula feeding area and the Colombian breeding ground (Caballero *et al.*, 2001; Olavarria *et al.*, 2007; 2000) confirming the links between feeding and breeding areas as revealed previously from photo-identification data (Acevedo *et al.*, 2007; Stevick *et al.*, 2004). Interestingly, the whales inhabiting the Magellan Strait, represent a separate feeding aggregation (Acevedo *et al.*, 2007) which is genetically distinct from the Antarctic feeding area (Olavarria *et al.*, 2006). Despite this information, some knowledge gaps remain, particularly regarding population structure and migration.

This report presents new mtDNA control region analysis on the genetic diversity of humpback whales sampled off Ecuador. It expands previous analyses conducted in this region to include comparisons between neighbouring wintering areas as well as between individuals sampled in Ecuador and feeding areas in Southern Chile and the Antarctic Peninsula. Information from the other Southern Hemisphere areas has enabled a first insight regarding gene flow at a hemispheric scale in this species.

## MATERIALS AND METHODS

### Sampling

Humpback whale skin samples were obtained between 2002 and 2008 off Ecuador. Four samples were collected from beached animals and 225 from sloughed skin (Amos *et al.*, 1992). One sample was obtained from biopsying with a Barnett crossbow equipped with a 60cm long arrow and modified tip (Lambertson, 1987). This sample was collected in Galapagos Islands, about 1,000km off Ecuador. Sloughed skin samples were obtained during the breeding seasons 2006–2008 (July–October) from onboard whalewatching vessels departing from Salinas, Ecuador (2°10'S, 81°00'W; Fig. 1). Sampling was conducted by a research team as part of a long-term research programme (see Felix and Haase, 2005, for additional references on this study).

When sampling for sloughed skin, boat skippers were asked to approach the site where a whale entered the water after an energetic surface display. Small pieces of skin were scooped from the upper water column with a net with fine mesh (1–2mm). Pieces of skin were stored in 2mL containers

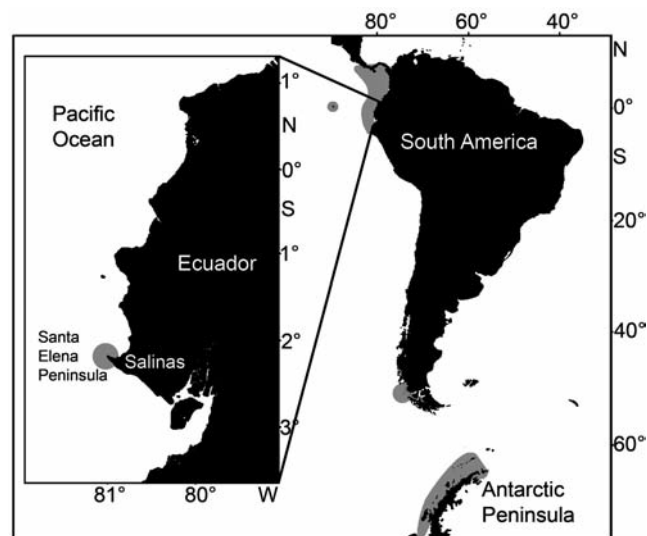


Fig. 1. The study area at Salinas off the Santa Elena Peninsula, Ecuador (left). Distribution range of the Breeding Stock G: feeding grounds at the Antarctic Peninsula and Magellan Strait and breeding grounds in the northwestern coast of South America and Central America (right).

with either a solution of DMSO saturated NaCl or 50–95% ethanol. The net was thoroughly washed with sea water until no pieces of skin were visible on its surface, and then the device was considered ready for the next sampling attempt. Once on shore, samples were stored at 4°C for up to six months prior to laboratory analysis.

Usually only one animal was sampled per group in order to minimise resampling, however, occasionally it was possible to collect two or three samples, presumably from different individuals. When more than one sample was taken from the same group, resampling was assumed if the sex and mtDNA of the samples matched and only one sample was included in the statistical analyses. This criterion was not applied when cow-calf pairs were sampled. Some 'false' duplicated samples could have been left out of the analysis when no genetic fingerprinting was undertaken.

Sampled whales were photographed for individual identification, using the pigmentation pattern on the ventral side of the flukes (Katona *et al.*, 1979). It was possible to photo-identify half of the sampled whales ( $n = 83$ , 47%). The bias introduced by resampling (between groups) was assumed to be comparable to the within-year resighting rate obtained by photo-identification. This rate was 3.1% in the period 2006–2008, thus we assumed a low rate of resampling. Moreover, when photo-identified individual sampled whales were compared, it was found that only one whale was sampled twice.

### Molecular analyses

A fragment of approximate length 500bp of the mitochondrial DNA control region (CR) was amplified via the Polymerase Chain Reaction (PCR; Saiki *et al.*, 1988) using standard reaction conditions (Palumbi, 1996). For the PCR, we used the primer combination t-Pro-whale Dlp1.5 (5'-TCACCCAAAGCTGRARTTCTA-3') and Dlp8 (5'-CCATCGWGATGTCTTATTTAAGRGGAA-3') (Baker *et al.*, 1998; Olavarria *et al.*, 2007). The PCR profile was as follows: an initial denaturation at 95°C for 2 minutes, 36



cycles of 94°C for 30 seconds, 55°C for 1 minute and 72°C for 1 minute and 30 seconds, and a final extension at 72°C for 5 minutes. Free nucleotides and primers were removed from the PCR products using the PCR Cleaning kit (Invitrogen). PCR products were sequenced in both directions using the standard protocols of Big Dye™ terminator sequencing chemistry on an ABI 3100 automated capillary sequencer (Perkin Elmer), using the same PCR primers.

All sequences were manually edited and aligned using Sequencher 4.1 software (Gene Codes Corporation). Sequences were trimmed to 469bp to match a consensus region analysed previously (Olavarria *et al.*, 2006; 2007). Control region sequences were aligned and compared using MacClade (Maddison and Maddison, 2000) to identify haplotypes. Ecuador haplotypes were compared with haplotypes previously identified in other five humpback whale populations in the South Pacific (Colombia-Antarctic Peninsula, New Caledonia, Tonga, Cook Is. and French Polynesia) and Western Australia (Olavarria *et al.*, 2006; 2007). A search of Genbank was made with those new haplotypes that did not match the South Pacific to define whether they were unique or reported in other populations.

Sex specific markers for gender determination followed the methodology of Gilson *et al.* (1998), which amplify a 224bp fragment of the *SRY* gene located on the Y chromosome. As internal positive control against PCR amplification failure, the homologous ZFY/ZFX region (445bp) was amplified. Thus, in the electrophoresis analysis two bands of 224 and 445bp were present in males and only one of 445bp in females.

### Data analyses

Genetic diversity at haplotype ( $h$ ) and nucleotide ( $\pi$ ) levels were computed using the software Arlequin Ver 3.1 (Schneider *et al.*, 2006). Haplotype frequencies ( $F_{ST}$ ) and nucleotide ( $\Phi_{ST}$ ) composition were compared between Ecuador and Colombia, Antarctic Peninsula and Magellan Strait (Olavarria *et al.*, 2007) using an Analysis of Molecular Variance (AMOVA) (Excoffier, 1995). A comparison based on haplotype frequencies of stratified data from 2006–2008 by sex and year, as well as between sites in the Southeast Pacific, were additionally tested with an exact test of population differentiation which test the non-random distribution of haplotypes into population samples under the hypothesis of panmixia (Raymond and Rousset, 1995). Both AMOVA and exact test were implemented using the Arlequin software.

## RESULTS

### Genetic diversity

From the 230 samples obtained off Ecuador, 42 were eliminated because they were considered to be duplicates or because they failed sequencing and sexing, leaving 188 samples for subsequent analyses (sequencing, sexing or both). From the successful sequenced samples ( $n = 182$ ) 41 haplotypes were identified, of which eight were new and unique (GenBank accession numbers HQ241479–86) and one was recorded previously in the Magellan Strait (haplotype Mno03Ma02; C. Olavarria, unpublished data) (Table 1). The remaining 32 haplotypes were previously

found either in the Southeast Pacific or in other Southern Hemisphere stocks (see below). The variable sites nucleotides included two insertion/deletions, 42 transitions and 3 transversions. Haplotype diversity ( $h \pm SD$ ) was estimated to be  $0.922 \pm 0.012$  and the nucleotide diversity ( $\pi \pm SD$ )  $0.019 \pm 0.009$ . The mean of pair-wise differences was  $8.99 \pm 4.16$  SD.

### Sex composition

The sex identification analyses revealed a significant sex bias towards males of 2.16:1 in adult animals (104 males and 48 females;  $\chi^2 = 20.63$ ,  $p < 0.01$ ). In the case of calves, the sex ratio was also skewed toward males (1.78:1) but the difference was not statistically significantly (16 males and 9 females;  $\chi^2 = 2$ ,  $p > 0.05$ ).

### Population structure by sex

A comparison of haplotype composition by sex was made to examine possible variability within the population. For this purpose information from 171 individuals with known haplotype and sex (53 females and 118 males) was used. Through AMOVA tests, haplotype composition of females and males separately (two groups) was compared. Less than half of the total haplotypes in the sampled population were shared by both sexes ( $n = 20$ , 48.8%), but the two most common haplotypes (SP32 and SP90) were found in similar proportion in both sexes (Table 1). There were 15 haplotypes found only in males and six identified only in females. Still, no significant differences in haplotype frequency and nucleotide composition between sexes were found ( $F_{ST} = -0.001$ ,  $p = 0.33$  and  $\Phi_{ST} = 0.0075$ ,  $p = 0.347$ ).

When comparison included sex and year (six groups) significant differences in haplotype frequency and nucleotide composition were found between females in 2006 and females in 2007 ( $p < 0.01$  in both cases), as well as between females in 2006 and males in the three years in haplotype frequency ( $p < 0.05$  in all cases) and between females in 2006 with males in 2007 and 2008 at nucleotide composition ( $p < 0.05$  in both cases) (Table 2). Similar results were obtained with the exact test of population differentiation (using 100,000 Markov chain steps); a highly significant difference in haplotype frequency between females in 2006 and females in 2007 ( $p = 0.004$ ) and a significant difference between females in 2006 and males in all years ( $p < 0.05$  in all cases) was found.

### Comparisons with other areas of Breeding Stock G

Ecuadorian haplotype frequencies were compared with other locations in the Southeast Pacific including breeding (Colombia) and feeding areas (Magellan Strait and the Antarctic Peninsula), as reported by Olavarria *et al.* (2006; 2007). The frequency of the two most common haplotypes reported in Ecuador (SP90 and SP32) was similar in Colombia and the Antarctic Peninsula. The former haplotype occurred also in the Magellan Strait with much higher incidence (80.77%) but the second was absent, as were most of the haplotypes found in the Southeast Pacific and Antarctic whales. The haplotype found in Galapagos (SP61) was recorded six times off mainland Ecuador, once in Colombia and twice in the Antarctic Peninsula. Overall,

Table 1

Ecuador humpback whale haplotype diversity and frequency of mtDNA control region sequences and proportion of haplotypes by sex and year (period 2006–08,  $n = 171$ ). Haplotype nomenclature follows Olavarria *et al.* (2006, 2007), Engel *et al.* (2008) and Rosenbaum *et al.* (2009).

Haplotype (466 pb)	Females					Males					Overall	
	2006	2007	2008	Total	%	2006	2007	2008	Total	%	<i>n</i>	%
SP1	–	1	1	2	3.8	4	1	5	10	8.5	12	7.0
SP8	–	–	–	–	–	–	–	3	3	2.5	3	1.8
SP10	–	–	–	–	–	–	1	3	4	3.4	4	2.3
SP14	–	–	1	1	1.9	1	–	–	1	0.8	2	1.2
SP16	1	–	–	1	1.9	–	–	–	–	–	1	0.6
SP19	–	–	–	–	–	–	3	–	3	2.5	3	1.8
SP25	1	–	1	2	3.8	2	2	3	7	5.9	9	5.3
SP26	1	–	2	3	5.7	–	–	–	–	–	3	1.8
SP32	–	2	3	5	9.4	3	3	4	10	8.5	15	8.8
SP33	1	–	1	2	3.8	2	–	1	3	2.5	5	2.9
SP35	–	–	–	–	–	–	–	1	1	0.8	1	0.6
SP41	–	1	–	1	1.9	–	–	–	–	–	1	0.6
SP42	1	–	–	1	1.9	1	–	–	1	0.8	2	1.2
SP43	–	–	–	–	–	–	–	1	1	0.8	1	0.6
SP50	–	1	1	2	3.8	2	–	–	2	1.7	4	2.3
SP52	–	–	–	–	–	1	–	1	2	1.7	2	1.2
SP54	–	–	1	1	1.9	–	–	1	1	0.8	2	1.2
SP60	1	–	1	2	3.8	3	1	2	6	5.1	8	4.7
SP61	1	–	2	3	5.7	1	–	1	2	1.7	5	2.9
SP62	–	–	2	2	3.8	2	1	3	6	5.1	8	4.7
SP63	–	–	1	1	1.9	–	–	2	2	1.7	3	1.8
SP68	–	2	–	2	3.8	–	1	–	1	0.8	3	1.8
SP70	–	–	–	–	–	–	–	2	2	1.7	2	1.2
SP72	–	–	–	–	–	–	1	–	1	0.8	1	0.6
SP73	1	–	–	1	1.9	–	1	2	3	2.5	4	2.3
SP90	–	4	5	9	17.0	9	8	10	27	22.9	36	21.1
SP98	–	3	1	4	7.5	1	3	2	6	5.1	10	5.8
SP100	–	–	1	1	1.9	–	1	–	1	0.8	2	1.2
SP101	–	–	–	–	–	–	1	–	1	0.8	1	0.6
Mno03Ma02	–	–	2	2	3.8	–	2	–	2	1.7	4	2.3
EC001	–	–	–	–	–	1	–	–	1	0.8	1	0.6
EC002	–	–	–	–	–	1	–	–	1	0.8	1	0.6
EC003	1	–	–	1	1.9	–	–	–	–	–	1	0.6
EC004	1	–	–	1	1.9	–	–	–	–	–	1	0.6
EC005	–	1	–	1	1.9	–	–	2	2	1.7	3	1.8
EC006	–	–	–	–	–	–	–	1	1	0.8	1	0.6
EC007	–	–	–	–	–	–	–	1	1	0.8	1	0.6
EC008	–	–	1	1	1.9	–	–	1	1	0.8	2	1.2
HBA040	–	–	1	1	1.9	–	–	–	–	–	1	0.6
HBA112/BRA15–97	–	–	–	–	–	–	–	1	1	0.8	1	0.6
HBR002/BRA03–98	–	–	–	–	–	–	–	1	1	0.8	1	0.6
<b>Total</b>	<b>10</b>	<b>15</b>	<b>28</b>	<b>53</b>	<b>100</b>	<b>34</b>	<b>30</b>	<b>54</b>	<b>118</b>	<b>100</b>	<b>171</b>	<b>100</b>

Ecuador humpback whales shared 21 haplotypes of 27 previously reported from Colombia (78%), 17 of 25 from Antarctic Peninsula (68%) and four from Magellan Strait (100%). There were six haplotypes shared within the breeding Stock G that have not been found in other Southern Hemisphere stocks (SP32, SP60, SP61, SP90, SP98 and SP101).

A pair-wise AMOVA between Ecuador and the other Stock G locations calculated a between variance of 5.45% and a within variance of 94.55%. The high proportion of the within variance indicates a high genetic similarity between the compared sites, as expected for a panmictic population. A significant difference was found between Ecuadorian and Magellan Strait whales in both haplotype frequency and nucleotide composition ( $p < 0.0001$  in both cases) (Table 3). The exact test of population differentiation (using 30,000 Markov chainsteps) confirmed a highly significant difference between Ecuador and Magellan Strait, but also revealed a highly significant difference in haplotype frequency between the two breeding areas, Ecuador and Colombia

( $p = 0.00171 \pm 0.0016$ ), indicating some level of structure at these breeding grounds.

### Comparisons with other Southern Hemisphere stocks

When the Ecuador haplotype dataset was compared with other Southern Hemisphere humpback whale stocks, 26 haplotypes matched. There were 20 haplotypes shared with South/Southwest Pacific stocks, three with the Southeast Indian Ocean stock (SP16, SP35 and SP70) (Olavarria *et al.*, 2007) and three with Southwest Indian/Southeast Atlantic stocks (HBA040, HBA112/BRA15/97 and HBR002/BRA03-98), two of the later had been first recorded also in the Southwest Atlantic (Engel *et al.*, 2008; Rosenbaum *et al.*, 2009), indicating some level of genetic interchange across the entire Southern Hemisphere.

### DISCUSSION

From our analyses of humpback whales sampled in Ecuador some interesting aspects on population structure of Breeding Stock G were revealed. In terms of genetic variability,

Table 2

Pair-wise test of differentiation for mtDNA control region sequence by sex and year based on the  $F_{ST}$  and  $\Phi_{ST}$  indices (values are below and above the diagonal, respectively). F = females, M = males, period 2006–08. The significance was analysed using 5,000 non-parametric permutations of the data matrix. Significant  $p$ -values are highlighted in bold.

	F2006		F2007		F2008		M2006		M2007		M2008	
	Value	$p$ -value	Value	$p$ -value	Value	$p$ -value	Value	$p$ -value	Value	$p$ -value	Value	$p$ -value
F2006	—	—	1.622	<b>0.009</b>	0.175	0.238	0.675	0.054	0.862	<b>0.034</b>	0.603	<b>0.049</b>
F2007	0.17	<b>0.008</b>	—	—	0.22	0.157	−0.033	0.45	0.017	0.356	0.164	0.174
F2008	0.016	0.245	0.02	0.187	—	—	−0.095	0.677	−0.074	0.581	−0.16	0.953
M2006	0.076	<b>0.045</b>	−0.007	0.502	−0.010	0.662	—	—	−0.099	0.698	−0.051	0.607
M2007	0.09	<b>0.03</b>	−0.001	0.397	−0.007	0.577	−0.012	0.697	—	—	0.003	0.376
M2008	0.061	<b>0.043</b>	0.012	0.227	−0.016	0.943	0.006	0.629	−0.0001	0.392	—	—

Ecuadorian whales showed a slightly higher diversity than whales sampled in other known breeding and feeding areas in the Southeast Pacific and the Antarctic Peninsula (see Olavarria *et al.*, 2006; 2007). Although high, the diversity of this stock is one of the lowest in the Southern Hemisphere, perhaps as a result of whaling activities during the 19th and 20th centuries and/or a low gene flow with other Southern Hemisphere stocks.

The general results at regional level, as revealed by the AMOVA analysis, suggest panmixia in the Breeding Stock G. Most of the haplotypes in Ecuadorian whales were also found in other sites of the Southeast Pacific and the east of Antarctic Peninsula, the main feeding area of this stock. The proportion of the two most common shared haplotypes (SP32 and SP90) was similar between Ecuador, Colombia and the Antarctic Peninsula. However, the exact test of population differentiation revealed a significant difference in haplotype frequency between two adjacent breeding areas, Ecuador and Colombia, despite the fact that they share 78% of haplotypes. This unexpected result contradicts the  $F_{ST}$  analysis in favour of stratification at the breeding grounds. Nevertheless, our sample contains many haplotypes with low frequencies which may have reduced the degree of certainty of the exact test as it does not take into account genetic distances between haplotypes but frequencies.

A plausible explanation for the heterogeneity between adjacent breeding grounds off western South America could be related to variability in whales' migrating behaviour. When the Ecuadorian population was modelled using photo-identification data with open population models with a large sample ( $n = 1,511$ ) similar inconsistencies were found, probably because sampling in the study area favoured less transient individuals (Félix *et al.*, 2011). It has been demonstrated that females tend to have a higher level of fidelity than males in both breeding and feeding grounds

(Rizzo and Schulte, 2009; Rosenbaum *et al.*, 2009; Weinrich *et al.*, 2006). Therefore, if heterogeneity was introduced in our sampling process due to differences in site fidelity by sex, most probably it occurred with females, as males clearly showed absence of stratification in our dataset. In addition, differences in migratory patterns of both sexes were found in Hawaii, with males undertaking the winter migration more often than females (Craig and Herman, 2003). This may introduce another source of heterogeneity, particularly in studies with few years of data like ours. Our analysis when the dataset was broken down by sex and year, despite showing a higher level of stratification in females than in males, is not very useful at elucidating the topic because some female strata had small sample sizes and therefore results are difficult to consider as conclusive. However, genetic differentiation by sex in migrating western South Pacific whales suggest a more complex migratory pattern than previously considered in this species and highlight the necessity to conduct comparisons disaggregating data by sex (Valsecchi *et al.*, 2010).

Despite the significant differences at haplotype and nucleotide levels between Ecuador and Magellan Strait whales, all four haplotypes found in this small feeding area were also present in Ecuadorian samples. It is not clear whether those whales breed off Ecuador or just passed through our study area in their way to breeding areas located further north. But photo-identification studies on Magellan Strait whales showed a correspondence 10 times higher (but not significantly different) with breeding areas in Panama/Costa Rica than with Ecuador (Acevedo *et al.*, 2007), suggesting, again, some level of stratification at breeding grounds. In another study with a larger sample from Colombia, Capella *et al.* (2008) found a similar level of interchange between Magellan Strait and Colombia (0.093,  $n = 1,042$ ) as the one reported by Acevedo *et al.* (2007) between Magellan Strait and Ecuador (0.09,  $n = 927$ ). Even though the distinctiveness of the Magellan Strait from the Antarctic Peninsula as two different feeding areas of the Breeding Stock G had been demonstrated previously (Acevedo *et al.*, 2007; Olavarria *et al.*, 2006) regular gene flow between whales belonging to both feeding areas is expected to occur during the breeding season.

Shared haplotypes with distant populations such as the Indian and South Atlantic Oceans in the Ecuadorian sample included both sexes, demonstrating possible recent gene flow through the three southern ocean basins. While those matches could also be the result of common ancestral lineages, additional information is available on extensive

Table 3

Pair-wise test of differentiation for mtDNA control region sequence between whales sampled in Ecuador and in other sites of distribution of the Breeding Stock G based on the  $F_{ST}$  and  $\Phi_{ST}$  indices. The significance was analysed using 5,040 non-parametric permutations of the data matrix.

	Colombia ( $n = 148$ )	Magellan Strait ( $n = 52$ )	Antarctic Peninsula ( $n = 89$ )
$F_{ST}$	−0.0006	0.1761	0.00263
$p$ -value	0.475	<b>&lt;0.0001</b>	0.2221
$\Phi_{ST}$	−0.0055	1.7400	0.0251
$p$ -value	0.468	<b>&lt;0.0001</b>	0.2240



movement across humpback whale stocks in the Southern Hemisphere (Chittleborough, 1965; Pomilla and Rosenbaum, 2005; Robbins *et al.*, 2008; Rosenbaum *et al.*, 2009; SPWRC *et al.*, 2006; Steel *et al.*, 2008). Further collaboration between research groups working on this species in the Southern Hemisphere will provide a better understanding of the level of present days gene flow in this species at a hemispheric scale.

The sex bias found in this study with males outnumbering females (2.16:1) is similar to that reported in other studies carried out at breeding areas (2.4:1 in Eastern Australia, Brown *et al.*, 1995; 1.86:1 in Hawaii, Craig and Herman, 2003; 1.95:1 in the South Pacific, Olavarria *et al.*, 2007; 1.7:1 in the North Atlantic, Palsbøll *et al.*, 1997; 1.9:1 in Gabon and 2.4:1 in Madagascar, Pomilla and Rosenbaum, 2006). This difference is therefore unlikely to have been due to a variation in surfacing behaviour between the sexes. It has been postulated that the sex bias observed at breeding grounds could be related to migration behaviour (see Craig and Herman, 2003; Dawbin, 1966) given that such a difference does not occur at feeding grounds (Clapham *et al.*, 1995), neither in the unique non-migrant population of the Arabian Sea (Mikhalev, 1997). The results of our analysis by sex and haplotype composition and the absence of significant differences regarding sex proportions in calves, support the belief of differences in the migrating behaviour of adult animals in this species as a valid explanation for the skewed proportion toward males found at breeding grounds.

In summary, genetics studies confirm connections of whales belonging to the Breeding Stock G among Ecuador, Colombia, Magellan Strait and the Antarctic Peninsula, but also suggest some heterogeneity in the breeding assemblage. The current available information suggests that differences in migrating behaviour between sexes with females showing higher level of site fidelity than males would be the cause of heterogeneity in breeding individuals. If stratification at breeding grounds occurs in this population it seems to be weak, at least in the case of better sampled areas in south of Ecuador and south of Colombia (some 700km apart); still a large part of the breeding area remains poorly under surveyed. Molecular studies are required to be conducted in the northernmost part of the wintering distribution of the Breeding Stock G (Panama and Costa Rica) to appropriately assess the level of population structure.

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# A new classification method to simplify blue whale photo-identification technique

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## ABSTRACT

Individual identification of blue whales is based on unique pigmentation patterns. Historically photo-identification has been based on the pigmentation patterns observed on a large portion of the animal's flanks. The new classification method presented here is based primarily on seven dorsal fin shapes and secondarily on five pigmentation patterns selected from a minor portion of the flank adjacent to the dorsal fin. This classification is then applied to a blue whale catalogue that comprises 621 individuals photo-identified in the waters adjacent to the Baja California Peninsula in Mexico. The classification system adequately divides the number of individuals per dorsal fin category and pigmentation patterns. It has been useful not only for reducing time and for matching photographs more efficiently but also has facilitated the finding of intra-catalogue photographic recaptures or photo-recaptures and has enhanced the efficiency of the field work. This new classification method should be considered by other blue whale researchers and for future inter-catalogue comparisons.

KEYWORDS: TECHNIQUE; PHOTO-ID; BLUE WHALE

## INTRODUCTION

Since the cessation of whaling, knowledge of the biology of free-ranging species through identification photographs of individuals has been substantial. The photo-identification technique, applied to the blue whale, *Balaenoptera musculus* (Sears *et al.*, 1990) has proven to be useful to investigate movement patterns (Calambokidis *et al.*, 2009; Calambokidis *et al.*, 1990; Gendron, 2002), and in the estimation of population abundance and survival rates through mark-recapture models (Calambokidis and Barlow, 2004; Ramp *et al.*, 2006; Ugalde de la Cruz, 2008).

Blue whales are currently considered endangered under the IUCN Red List of threatened species and three subspecies are recognised worldwide although the intra-specific taxonomy of the Northeastern Pacific blue whales is ambiguous (Reilly *et al.*, 2008). The abundance estimates based on capture-recapture method for the northeastern Pacific range are around 2,000 blue whales (Calambokidis and Barlow, 2004). Evidence from photographic recaptures shows some of these whales move to the Gulf of California (Calambokidis *et al.*, 1990). This region serves as a nursing and feeding area for approximately 300 blue whales during winter-spring season (Gendron, 2002). At the Laboratory of Cetacean and Chelonian Ecology based in CICIMAR-IPN, an identification catalogue of blue whale photographs has been built which encompasses a data series of 25 years. The main objective is to monitor the blue whales that visit this area for long term conservation purposes. Identification photographs and biological samples are collected to develop a comprehensive individual sighting history to serve as the basis of several current research projects.

Standard photo-identification technique consists in taking photographs at a perpendicular angle to a large portion of the left and right flanks of the animal including the dorsal fin and comparing them with individual photographs that have been classified into several pigmentation patterns (Sears *et*

*al.*, 1990). The photos are usually taken during the last respiration when the whale is preparing for a deep dive. Depending on whale behaviour and maritime conditions when photographic attempts are made, it may not always be possible to obtain a photo of a large portion of the flank in one frame. In Sears' classification, photographs of whales that showed only small portions of the flank are problematic to classify.

Since no computer-assisted matching program has yet been developed for blue whales, comparing identification photographs by hand can become a laborious task, especially when the number of individuals is large. This paper proposes a new classification method for blue whale photo-identification that simplifies the photograph comparison by hand.

## METHOD

The Baja California blue whale catalogue (Baja CA Catalogue) maintained at CICIMAR includes photographs obtained in coastal and offshore waters adjacent to the Baja California Peninsula. Most of the effort has been conducted in the southwestern region of the Gulf of California (Fig. 1). The photographs were taken between 1985 and 2009 and comprise 621 individuals (unpublished data). This work has been accomplished with the collaboration of the Mingan Island Cetacean Study (2003; 2004; 2006; 2009), Cascadia Research Collective (2001; 2004; 2006), Universidad Autónoma de Baja California Sur, as well as with the help of other researchers and naturalist-guides with opportunistic photographs taken in the study area.

Initially, a 35mm reflex EOS Canon camera coupled with a 70–300 telephoto lens, with black and white film was used. Since 2005, photographs have been taken using colour digital EOS (10D, 20D and 30D) Canon cameras with a 100–300 telephoto lens. The quality of each photograph in the catalogue has been rated from one (excellent) to 4 (bad)



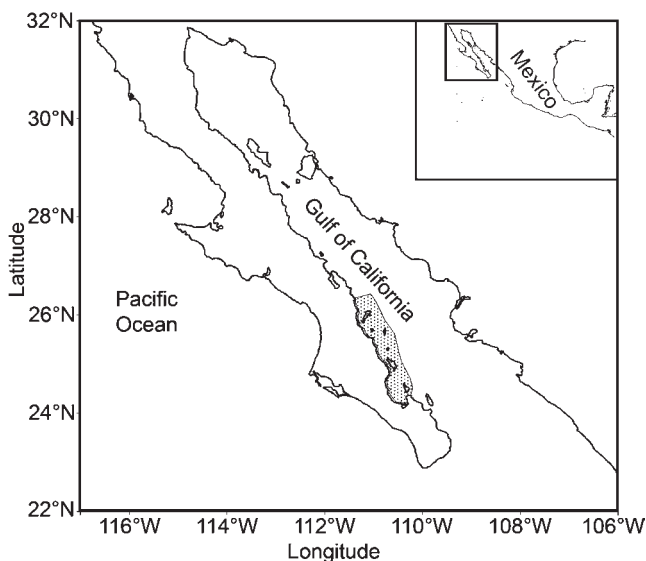


Fig. 1. Study area around the Baja California Peninsula where blue whales were photographed. Shaded area denotes the southwestern region of the Gulf of California where most of the effort has been conducted.

according to the focus, camera angle, and exposure. Quality 4 photographs contain features that are useful to identify the individual; however, for population parameter estimations they are not taken into account (Hammond, 1986; Hammond *et al.*, 1990).

Distinct pigmentation patterns observed on blue whales do not change with time therefore all individuals can be photo-identified (Sears *et al.*, 1990), including calves born during the winter season (Gendron, 2002). Of the 621 individuals contained in the Baja CA Catalogue, 57.2% of them possess photographs of both flanks, while 23.8% and 19.0% have only one flank, the right and left, respectively. Until 2009, 92 calves have been photo-identified and 40% of them have been re-sighted from 1 to 15 years later. This catalogue was initially classified by following the method of Sears *et al.* (1990). Over the years, changes were made to simplify the comparison of whale photographs which led to this new classification method.

### Description of the classification

The only criterion needed is that photographs of the flank must contain the dorsal fin with, preferably, a sufficient area of adjacent pigmentation (see Fig. 2). The method is centred primarily on seven categories based on dorsal fin shapes (Fig. 3). A further category includes undefined dorsal fins for photographs in which the angle may bias the dorsal fin classification. In these cases, the photographs are temporally classified as undefined, until a better photograph of this

particular individual is obtained. Furthermore, photographs included in each dorsal fin category are secondarily classified into five pigmentation patterns that progressively change from light to dark (Fig. 4). Photographs showing insufficient areas of pigmentation around the dorsal fin or taken with poor light exposure may not be categorised and are classified temporally under undefined pigmentation patterns.

New photographs are assigned to dorsal fin and pigmentation categories in accordance with the opinions of two persons that keep the catalogue up to date. In order to test how subjective this new photograph classification is, a set of 70 photographs (10 of each dorsal fin category including all pigmentation categories) of qualities 1 to 3 were chosen from the Baja CA Catalogue and then classified independently by four observers with little to extensive experience in blue whale photo-identification. The results were then compared with the category previously assigned in the Baja CA Catalogue. Furthermore, to test how consistent the categorisation is over time, duplicates of five individuals, first photographed as calves and then years later, were included and mixed in the set of photographs selected. A chi-squared test ( $p < 0.05$ ) was used to verify if all dorsal and pigmentation categories were assigned in concordance with the Baja CA Catalogue. As significant differences were found, a subdivision of the test was made to verify which category failed to distinguish from the others by removing the category that contributes with a relatively larger amount to the previous calculated chi-square (Zar, 1996).

### RESULTS

The classification applied to the Baja CA Catalogue of blue whale photographs showed that the seven dorsal fin types were not equally represented but they formed a suitable division of it (Table 1). The falcate dorsal fin was the most abundant type comprising 33.5% of the individuals compared to the mutilated dorsal fin that corresponds to 4.3%. Only 2.9% of the individuals were classified in the undefined dorsal fin category.

As for the pigmentation patterns, the most commonly observed was the light mottled with a frequency of 36.5% while the least common was the dark pattern (12.6%; Table 1). Only 6% of all individuals were included in the undefined category, mostly due to the poor light exposure.

There were significant differences in the selection of categories made by the observers and the ones assigned in the Baja CA Catalogue ( $\chi^2 = 18.6$ , degrees of freedom (df) = 6,  $p = 0.0049$ ). Notably, the most ambiguous category was the falcate-triangular dorsal fin with only 45% of matches with the Baja CA Catalogue (Table 2). This ambiguity was associated with the contiguous categories of triangular and

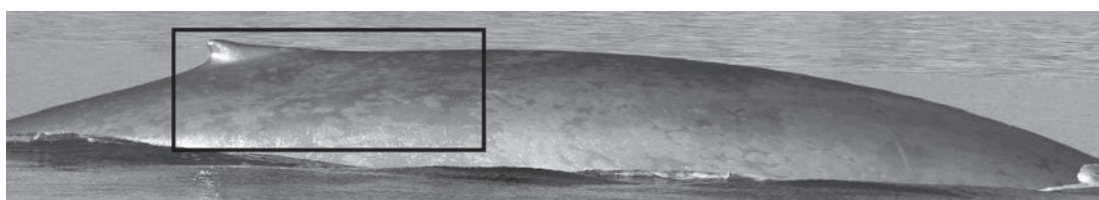


Fig. 2. Example of a blue whale identification photograph included in the Baja California blue whale catalogue. The area delimited by the box indicates the minimum body area needed for photograph comparisons.

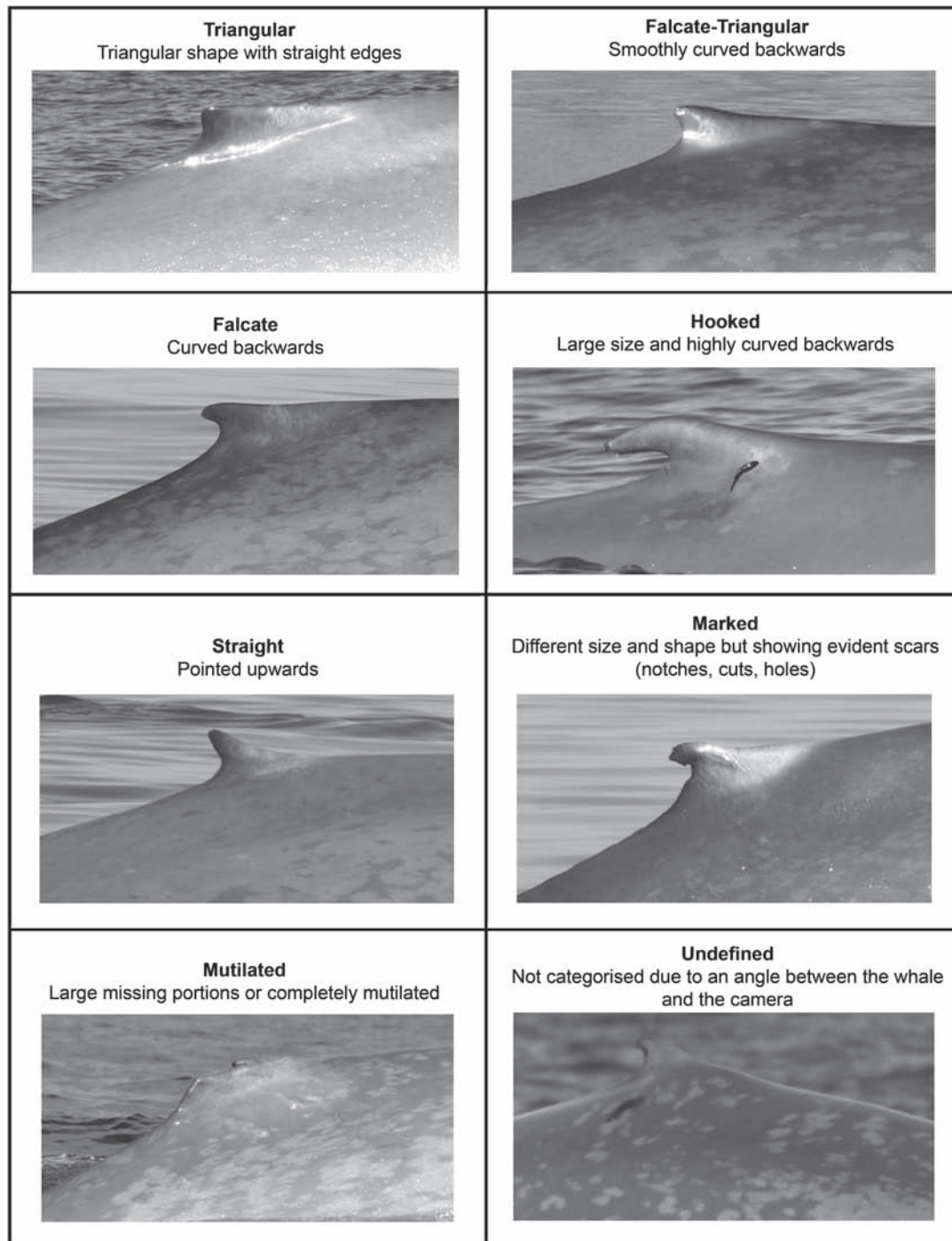


Fig. 3. Description and photographs of eight dorsal fin categories used as the first classification step in the blue whale photo-identification method.

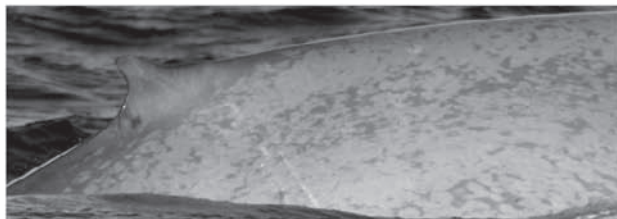
Table 1

Number of individual blue whales classified per dorsal fin and pigmentation categories included in the Baja California blue whale catalogue.

Pigmentation patterns	Dorsal fin categories								Total (%)
	Triangular	Falcate-triangular	Falcate	Hooked	Straight	Marked	Mutilated	Undefined	
Light	6	14	25	21	8	4	2	3	13.4
Light-mottled	15	34	80	36	25	19	10	8	36.5
Striped	8	11	26	14	10	6	3	2	12.9
Balanced	8	22	34	17	12	15	6	2	18.7
Dark	5	11	33	11	8	8	1	1	12.5
Undefined	5	6	10	7	1	1	5	2	6.0
Total (%)	7.6	15.8	33.5	17.1	10.3	8.5	4.3	2.9	100



**Light:** prevailing light grey colour without or with few dark grey spots



**Light-mottled:** prevailing light grey colour with several dark grey spots



**Striped:** variable colour but with an evident band or line located on or near the spinal cord



**Balanced:** no prevailing colour due to a uniform distribution of light and dark grey spots



**Dark:** prevailing dark grey colour with several light grey spots

Fig. 4. Description and photographs of the five pigmentation patterns used as a second classification step in the blue whale photo-identification method.

falcate dorsal fins. The falcate-triangular category contributed largely to the chi-square calculated. After removing this category no significant difference between the other six categories was found ( $\chi^2 = 6.5$ ,  $df = 5$ ,  $p = 0.26$ ). These categories ranged between 70 and 100% of matches with those assigned in the Baja CA Catalogue. As expected, the mutilated dorsal fin was the least ambiguous category. Ambiguities observed for the other categories were also associated with the contiguous dorsal fin shapes.

For the pigmentation patterns the range of matches between observers and the catalogue assignments was over 75% for all categories (Table 3), however a small but significant difference was observed ( $\chi^2 = 10.1$ ,  $df = 4$ ,  $p = 0.038$ ). The most ambiguous categories were the light mottled and the balanced pigmentation patterns. They contributed similarly to the chi-square calculated. The subdivision of the test revealed that only the combined effect of these two categories leads to significant differences, contrasting the results when only one of those categories was removed ( $\chi^2 = 5.6$  and  $6.1$ ,  $df = 3$ ,  $p = 0.133$  and  $p = 0.107$ , respectively). Likewise, the ambiguity was mostly related to the adjacent pigmentation patterns (Table 3).

Consistency in dorsal fin and pigmentation categorisation over time showed a similar trend, with 65% matches in dorsal fin assignment between observers and the catalogue. Ambiguities were observed between falcate-triangular and falcate dorsal fin shapes (20%) and between falcate and hooked shapes (15%). For the pigmentation pattern there were 85% of matches and ambiguousness was mostly found between light and light-mottled categories.

## DISCUSSION

The potential of this new classification method is founded in the combination of the dorsal fin shape and pigmentation patterns categories. By separating the photographs in 48 combinations (including the undefined categories), the number of photographs to compare is greatly reduced.

Similar to other classification systems, the proposed dorsal fin shape and pigmentation categories are not exclusively distinct, as for the mutilated or marked dorsal fins, but are centred on shapes and pigmentation that change progressively. This characteristic has led to a degree of uncertainty in the categorisation, which was particularly noted for the falcate-triangular dorsal fin and the light mottled and balance pigmentation patterns.

These results were obtained by comparing the category selections made by observers with different experience in blue whale photo-id work. Including observers with less experience reflected a situation for new research groups starting to work on blue whales, in order to test this classification method from a broad perspective. Our experience with this method has found that, with time, classification becomes less ambiguous.

In the process of photo-identification, the categories that most represent the dorsal fin and the pigmentation observed in the photograph are first compared. To assure that a match has not been omitted, the comparison is extended first with the adjacent pigmentation categories and then with the adjacent dorsal fin category in addition to the undefined categories. This process avoids comparing photographs that share combinations that have a very low probability of a photographic match (i.e. light with dark, or triangular with hooked).

Categorisation of individual dorsal fin and pigmentation over time, such as those that were first photo-identified as calf and recaptured at later age, also showed the same ambiguities with contiguous categories as found for the other whales photographs. There was no modification of dorsal fins or change noted in the pigmentation pattern over time.



Table 2

Percentage of matches between dorsal fin categories elections made by the observers compared to the Baja California Catalogue (Baja CA Catalogue) classification of 70 blue whales photographs and the second elections for the photographs unmatched.

Dorsal fin category (Baja CA Catalogue)	Matches (%)	Second elections unmatched photographs (%)	
Triangle	72.0	Straight (20.0)	Falcate-triangular (8.0)
Falcate-triangular	45.0	Falcate (35.0)	Triangular (20.0)
Falcate	77.5	Hooked (15.0)	Falcate-triangular (7.5)
Hooked	82.5	Falcate (15.0)	Straight (2.5)
Straight	95.0	Falcate (2.5)	Falcate-triangular (2.5)
Marked	87.5	Mutilated (12.5)	
Mutilated	100.0		

Table 3

Percent of matches between pigmentation categories elections made by the observers compared to the Baja California Catalogue (Baja CA Catalogue) classification of 70 blue whales photographs and the second elections for the photographs unmatched.

Pigmentation category (Baja CA Catalogue)	Matches (%)	Second elections unmatched photographs (%)		
Light	93.0	Light-mottled (7.0)		
Light-mottled	77.0	Light (18.0)	Striped (2.5)	Balanced (2.5)
Striped	85.0	Light-mottled (7.5)	Balanced (5.0)	Dark (2.5)
Balanced	76.5	Dark (11.0)	Striped (8.5)	Light-mottled (4.0)
Dark	89.0	Balanced (8.0)	Striped (3.0)	

Here the different category selections may also have been caused by the quality of the photograph that served as recaptures.

Since the exact age of these individuals at their first sighting as calves is known, the blue whale photo-identification technique constitutes a powerful tool in the long term sighting history data set. This contrasts with most other species of whales in which not all individuals can be photo-identified due to a lack of colour pattern or scars (Agler *et al.*, 1990; Rugh, 1990) or due to the fact that the calves show changes in the pigmentation patterns over the years (Carlson *et al.*, 1990) or their behaviour prevents photographing the body part used in the photo-identification technique (Arnbom, 1987).

There are, however, two factors in the blue whale photo-identification technique that can cause misidentification or negatively influence the photo-identification process. The first is the acquisition of marks on the dorsal fin or in the worse cases its mutilation. Therefore, during the comparison of marked or mutilated dorsal fin photographs, if no photo-recapture is found, the comparison with the other dorsal fin categories will be required to assure that the mark or mutilation has not been recently acquired. During the study period, only four whales presented conspicuous changes in their dorsal fin; one was mutilated and the three others showed new marks.

The other factor that might interfere with the certainty of the uniqueness of individual pigmentation patterns is the effect of skin desquamation (Sears *et al.*, 1990). This is a natural phenomenon in cetaceans (Geraci *et al.*, 1986) and sloughed skin is observed and may be sampled from most individual blue whales (Gendron and Mesnick, 2001). However, it is observed more frequently on the flanks of lactating females than non-lactating females or males ( $\chi^2 = 59.84$ ;  $p < 0.05$ ; Ugalde de la Cruz, 2005). This characteristic may be related to physiological factors that take place during

pregnancy and lactation (Perryman and Lynn, 2002; Randall *et al.*, 2002). It is probable that some lactating females may be misidentified during the photo-identification process due to large areas of desquamation on their flanks obstructing the pigmentation patterns normally visible. Although this problem is not observed in all lactating females, a special emphasis is recommended in those cases, since the estimation of population reproductive parameters relies on females (Barlow and Clapham, 1997). Likewise, this new classification method based on dorsal fin identification may improve the matching comparison of these females.

Although 68% of the blue whale individuals in the catalogue are now represented in digital images, the difference in the image quality of black and white and colour digital photographs has not been evaluated in the identification process. While good black and white pictures are normally easy to match, the coloured digital images may be improved with software. The efficiency in matching digital photographs may be biased upwards especially since 2005 when digital cameras began to be used. Still only a low percent of the individuals in black and white photographs (4.2%) and digital images (1.6%) are contained in the undefined pigmentation category.

Overall, this method has been useful not only for reducing comparison time and thus allowing more efficient matching, but also in facilitating the finding of intra-catalogue photographic recaptures or photo-recaptures, a major bias when abundance estimations are performed (Hammond *et al.*, 1990). At sea, it has improved survey efficiency by allowing rapid identification of individuals. Depending on the type of photo-identification survey, recognition of individuals may be required to avoid spending unnecessary time photographing the same individual or duplicating skin-blubber biopsy samples within and between seasons. To achieve this objective, a catalogue of previously biopsied individuals classified into these dorsal and pigmentation



categories allow us to accomplish rapid comparison of a newly photographed whale (digital camera viewing) with those included in the field catalogue.

The results of the classification experiment appear to suggest that it may be convenient to remove the falcate-triangular dorsal fin category in order to group all falcate shapes together. However, grouping them in one category would increase the number of photographs considerably. On the other hand, leaving these two categories separate, there are still 77.5% and 45% probability of finding a match within the falcate and triangular falcate categories respectively (see Table 2) with less time consumed for the comparison. As for the light mottled or balanced pigmentation categories, we believe grouping them with the contiguous pigmentation categories will not change substantially the process of photographic comparison, since these are secondary classifications adjacent to each other in every dorsal fin category.

Finally, we encourage other blue whale researchers to test this classification method based on dorsal fin shapes and pigmentation patterns. If it proves as useful as it has been for us, this method will improve large comparison photographs between catalogues.

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# An investigation of acoustic deterrent devices to reduce cetacean bycatch in an inshore set net fishery

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## ABSTRACT

In Europe, problems with the use of pingers on larger fishing vessels have raised the question as to whether pingers would be practical on smaller vessels, which are a large proportion of the European static net fishing fleet. In this study, four netting vessels less than 10m long used AQUAmark pingers on part of their nets off the southwest coast of Britain over a 12 month period. Boat skippers recorded ease of use. Acoustic click detectors were deployed on test and control nets to assess the response of cetaceans to the pingers. No significant practical problems, apart from premature failure of pingers, were encountered. During the study, only one harbour porpoise was bycaught, in an unpingered net. In 650 days of acoustic data from pingered and non-pingered nets, matched by location, date and boat, there was a highly significant reduction in the number of porpoise clicks recorded at nets with pingers to 48% of the number predicted from the number recorded at control nets (range 35–51%). To assess habituation, single, modified pingers that were active for alternate seven hour periods were moored below a click detector at two sites, one of which has strong tides and high levels of associated ambient noise. This study showed a stronger pinger effect at the quiet site and a much reduced effect at the noisy site. There was evidence of a period of exclusion of porpoises following pinger use that could exceed seven hours, and no evidence of habituation. Results suggest that pingers are practical on small vessels, that they reduce harbour porpoise activity around nets and are therefore likely to reduce bycatch. Easier means of detecting pinger failure are needed. Pingers should be considered as a bycatch mitigation method in small vessel fisheries using bottom set nets.

KEYWORDS: BYCATCH; EUROPE; HARBOUR PORPOISE; COMMON DOLPHIN; ACOUSTICS; GILLNET FISHERY

## INTRODUCTION

The incidental catch of marine mammals in fishing gear, especially static nets, is one of the greatest immediate threats to marine mammals throughout the world; the death toll from fishing nets far exceeds the deliberate take of marine mammals (Hodgson *et al.*, 2007; Reeves *et al.*, 1996). Field studies with acoustic pingers on set gillnets have shown reductions in bycatch of harbour porpoise (*Phocoena phocoena*) in a sink gillnet fishery (Kraus *et al.*, 1997; Trippel *et al.*, 1999) and of common dolphins (*Delphinus delphis*) in a drift net fishery (Barlow and Cameron, 2003). There have also been a number of studies of the effectiveness of acoustic alarms using simulations at sea (Carlström *et al.*, 2009; Cox *et al.*, 2003; Culik *et al.*, 2001) and studies of their effects on captive animals (e.g. Kastelein *et al.*, 2000) and in the wild (Culik *et al.*, 2001). These successful trials of acoustic alarms contributed to the introduction of European Union Council Regulation No 812/2004 that made the use of acoustic deterrents (pingers) mandatory in certain areas on vessels larger than 15m in length using static bottom set fishing nets. Since this legislation was passed, practical problems in using pingers on these vessels have emerged (Caslake and Lart, 2006) and few vessels are currently using them. EUC Regulation 812/2004 imposes no direct action to reduce cetacean bycatch on vessels of less than 15m, but does require appropriate monitoring of their bycatch.

Globally, there is extensive evidence that cetacean bycatch occurs in many areas where gill or tangle net fisheries occur within cetacean habitats (Perrin *et al.*, 1994). In

Cornwall there is also evidence of a major decline in small cetaceans during the second half of the 20th century (Tregenza, 1992).

This study was undertaken in Cornwall, in the southwest of the UK mainland. The adjacent Celtic Sea region has a documented porpoise bycatch in gillnets estimated in 1992 at around 2,200 animals per annum (Tregenza *et al.*, 1997). The Cornwall Wildlife Trust Marine Strandings Network (CWT MSN) annual report for 2007 identifies 75% of harbour porpoises (*Phocoena phocoena*) examined as showing signs of having been bycaught in gillnets/tangle nets (Loveridge and Loveridge, 2007).

Cornwall has a small, but well recognised, resident group of inshore bottlenose dolphins (*Tursiops truncatus*), which has shown a decline in the average observed group size over the last 17 years to levels at which the loss of any individual will have a significant impact on the survival potential of this group (Wood, 1998). The UK Stranding Investigation Programme Report for 2009 documents the cause of death of one of the two bottlenose dolphin strandings, in Cornwall, during this year as due to net entanglement.

The southwest of the UK has over 500 registered inshore vessels with licenses (data from Marine Management Organisation) allowing them to deploy bottom set gillnets.

## METHOD

### The fishery

The nets used most by small vessels in Cornwall are tangle nets, commonly termed 'monk nets'. Tangle nets generally consist of 267mm mesh monofilament netting with a leaded

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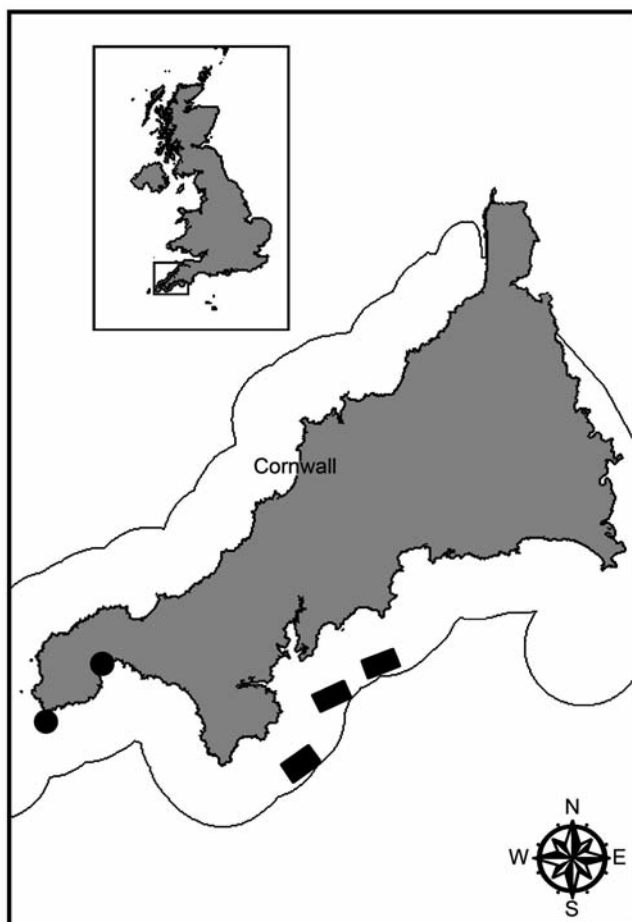


Fig. 1. Approximate areas (squares) of fishing effort in relation to the six nautical mile limit and points showing cycling pinger deployment.

footrope and a headline with no, or minimal, buoyancy, usually with a hanging ratio of 0.3<sup>1</sup> to target benthic species such as monk fish (*Lophius americanus*). These nets are pushed flat onto the seabed in tidal currents. They are set for approximately five days 'soak time' depending on weather conditions at depths ranging from 20 to 100m. The fishery operates throughout the year.

Four commercial fishing vessels less than 10m in length setting monk nets volunteered to take part in this trial. All nets were deployed within a day's steam of the home port and within the six nautical mile limit (Fig. 1).

Test nets were equipped with pingers spaced at 200m intervals. Fishermen were asked to keep the control nets at least one nautical mile away from test nets. Each skipper was entirely responsible for deploying and recovering the equipment with their fishing gear while continuing with normal fishing activity in order to test the practical aspects of using pingers during normal working conditions. Where possible, skippers were requested to deploy test and control nets on the same days. Skippers recorded any cetacean bycatch with the date, time, position and possible species.

### Pingers

The pinger used in this study was the AQUAmark 100, which is an acoustic pinger designed and produced by AQUATEC

<sup>1</sup> i.e. The length of the fishery net when made up divided by the length of the original sheet of netting.



Fig. 2. Pinger attached to foot rope of static netting.

(<http://www.aquatecgroup.com>). The AQUAmark 100 has a wideband, frequency modulated, ping within the range of porpoise hearing (pings: 20–140 kHz). The pings last 0.4 seconds, and are repeated at random intervals between 4 and 15 seconds. They are in accordance with Set 1 of EUC Regulation 812/2004.

### Click detectors

Acoustic click detectors, (C-PODs, Chelonia Limited UK) were used to assess the response of cetaceans to the pingers. C-PODs are fully automated, static, passive acoustic monitoring systems that detect echolocating odontocetes by recognising their ultrasonic sonar click trains and distinguishing these from the sounds made by boat echo-sounders and other sources. The system achieves sufficiently low false positive rates to allow its use in areas of very low cetacean density (Verfuss *et al.*, 2007). Each vessel in the trial was equipped with two C-PODs, which were deployed at the end of 1km tiers of monk net, one of which was equipped with active pingers. The approximate detection distance for harbour porpoises by a C-POD is c.500m.

Visual validation, using a method based on Verfuss *et al.* (2004), of automated identification of porpoise sonar in the data showed few false positives. The analysis here is solely of porpoise detections as only 170 minutes of encounters with dolphins (probably common or bottlenose dolphins) were recorded throughout the trial.

As the daily detection rates are influenced by the seasonal pattern of porpoise activity (which is not naturally symmetrically distributed around the mean or median) the pinger effect was assessed using a sign test of the fraction of days in which the number of clicks detected on pinged nets exceeded the number of clicks detected on control nets. The test was performed as a two-tailed test.

To investigate changes in behaviour caused by the pingers, the ratio of loud clicks to weak clicks was considered. The presumption was made that loud clicks indicated animals close to the C-POD. The estimated extreme maximum range of detection for the C-POD is probably 300–400m for harbour porpoises. The C-POD has a sound pressure scale limited to 25 Pascals peak-to-peak. Many received clicks exceed this upper limit but their amplitude is recorded as the scale maximum, which is nominally 255. 'Weak clicks' were defined as having scale amplitudes of less than 127, while 'loud clicks' were defined as having amplitudes greater than 127.



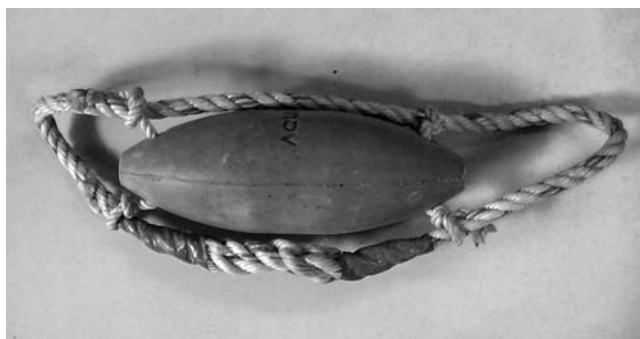


Fig. 3. Pinger tied into rope loop ready to be attached to netting.

### Static mooring trials

A small number of pingers were modified to have a seven hour cycle of normal pinging alternating with seven hours with no pings. The seven hour cycle was chosen to ensure that tidal and diurnal effects could not remain synchronised with the cycle of pinger activity. This experimental method was first used by Carlstrom *et al.* (2009). These ‘cycling’ pingers were deployed on longer term fixed moorings, with a C-POD but with no associated net. One was deployed in Mounts Bay on the south coast of Cornwall (50°06′44.69N, 05°28′45.23W) a site with low tidal flows, and one on the Runnelstone reef, a location further west with fast currents and moving sand creating high levels of ambient noise.

## RESULTS

### Practicality of pinger deployment

The pingers were placed on the footrope of the net, at the junction between panels of net that are typically around 100m long. Initially there were concerns with tangling of the nets from the addition of pingers. However a successful method of rigging the pinger was developed quickly by the skippers and worked well (Figs 3 and 4).

The majority of problems reported with tangling were at the beginning of the trial and were relatively small. Only one major tangling incident occurred which was due to buttonholing (where the pinger drops through the mesh of lower layers of net on deck and then tangles the net on re-deployment). This incident resulted in fishing effort being stopped for approximately 30 minutes.

All data were collected over a 12 month period. One of the four boats did not produce any paired data (where acoustic data is available for both the test and control nets on the same day).

The four boats acoustically monitored 1,150 days of soak time (i.e. time during which nets are in the water) between April 2009 and April 2010, of which 640 days had data from C-PODs on both pingered and non-pingered nets set by the same vessel on the same day.

### Cetacean bycatch

Four porpoise and no dolphin bycatches were recorded during the trial. Only one bycaught animal was from an acoustically monitored experimental net, and this was a non-pingered net.

### Acoustic data: pingers on nets

Acoustic data were analysed as clicks per day, identified by the C-POD software, and validated by visual inspection of the raw data. The data showed that the rate of recording harbour porpoise clicks at nets with pingers was between 35–51% of the rate at control nets (Table 1). Reduction in detections when pingers are active was highly significant (two tailed sign test  $p < 0.001$ ). No significant difference was found in the proportion of weak or loud clicks logged when the pinger was active. At the end of the working trial, 7 of the 23 pingers were found to be inactive. The time of failure is not known as the pings are ultrasonic (i.e. not audible) and the pingers were not otherwise tested during the trial.

### Static mooring trial

Cycling pingers were deployed at two sites, one in Mounts Bay and one off on the Runnelstone Reef (see Fig. 1). These sites differed considerably, with the Runnelstone Reef area being subject to strong tidal currents and prevailing swell, whereas the Mounts Bay site is a relatively quiet site with weaker tidal flows. Data collected from the respective sites varied considerably (Table 2) The pinger at the quiet site failed after 48 days and provided a single unplanned test of the ‘recovery time’ before the return of animals after the end of pinger activity.

The Mounts Bay pinger worked for 53 days during which

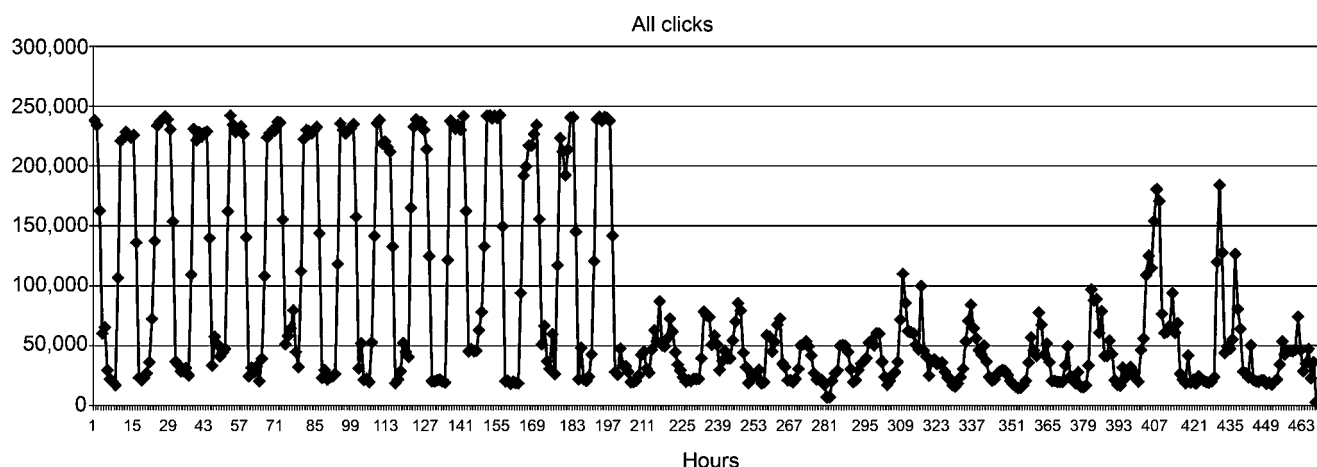


Fig. 4. Number of clicks per hour for one week before and after pinger failure, showing the clear seven hour cycle of the pinger before failure.

Table 1  
Number of clicks recorded on test and control nets per vessel.

Vessel	Clicks logged: non-pingered nets	Clicks logged: pingered nets	Pingered net clicks as % of non-pingered nets
1	7,856	2,727	35%
2	39,960	20,371	51%
3	1,946	802	41%
<b>All vessels</b>	<b>49,762</b>	<b>23,900</b>	<b>48%</b>

time six OFF periods had harbour porpoise detections but there were none during ON periods (Table 3). In Mounts Bay data pinger pings are clearly recorded by the C-POD, and ended abruptly on 12 July 2010 at 06:32. The hourly acoustic record for the week before and after the end of pinger activity is shown in Figs 4 and 5. The large peaks in the click counts in the lower panel show the periods when the pinger was active. Following the pinger failure a weaker tidal/diurnal cycle in ambient noise is seen, and there are more porpoise detections. We cannot, on the basis of this single unscheduled test, exclude the possibility that this change was coincidental.

Most acoustic encounters consist of several trains of clicks detected as the sonar beam of the cetacean sweeps across the logger during the period that the animal is within detection range. An autocorrelation of the detection times of clicks at each site showed a fall to below the 5% level of significance ( $2/\sqrt{N}$ ) at five minutes. This is an indication of the duration of a porpoise visit to the pinger locality. The seven hour ON or OFF half-cycles in the Mounts Bay data were analysed using simple probabilities on the basis that half-cycles of either phase were independent samples. The mean rate of detection was 6 in 98 half-cycles. The probability of no detection in seven hours was 0.9388 giving, for the 49 successive seven hour periods with no detection, a significant one-tailed probability of 0.045.

The Runnelstone reef data showed that the pinger was deployed and was still working at 81 days when the C-POD memory filled to capacity and logging was ended. The results were surprising when compared to the Mounts Bay site. Where the Mounts Bay data showed nearly complete exclusion (or non-vocalisation) even during the OFF periods of harbour porpoises within a C-POD detection range of the

pinger, the Runnelstone data showed more porpoise activity and a strikingly smaller difference between the two phases of the pinger cycle.

At the Runnelstone site ON periods with porpoise activity were 49% of the fraction of OFF periods that were porpoise-positive giving a significant two-tailed  $p$  value of  $< 0.001$  using the sign test.

#### Acoustic data: habituation

Habituation could not be tested on the net data as the location of the nets was not controlled. Too few detections were made during the active life of the Mount's Bay cycling pinger to assess any trend. At the Runnelstone site a linear regression on the number of clicks detected per day showed a fall of 57% during the 81 day period monitored. This may be a seasonal pattern. The rate of fall, assessed by linear regression, was higher in ON periods than in OFF periods, giving no evidence of a reducing pinger effect which would be expected to appear as a reduced rate of fall during ON periods.

## DISCUSSION

#### Practical issues of pinger use in the fishery

Hauling and shooting of nets differs on these small vessels from the larger offshore vessels studied in a Seafish pinger trial (Caslake and Lart, 2006) in that the nets are shot from the stern directly from net bins or from the deck, without going through a tube, and are recovered using smaller haulers than on the larger vessels. Once the net has been hauled and the fish picked out, the nets are put through the flaking machine, which helps lay the nets in a bin with the headline and footrope separated and ready for a clean deployment (Caslake and Lart, 2006).

The method of rigging the pingers as developed during the trial worked well and there were few concerns about using the pingers by the end of the trial. Caslake and Lart (2006) reported that on larger offshore vessels pingers were caught up and shot out at high speed in the direction of the crew member working the flaking machine. This problem was not apparent on the smaller vessels in this trial due to different placements of the equipment and crew. The problems of tangling encountered on larger vessels were also greatly

Table 2  
Loud clicks recorded on test and control nets.

Vessel	Loud clicks non-pingered nets	Loud clicks pingered nets	Pingered net loud clicks as a % of non-pingered net	Weak clicks non-pingered nets	Weak clicks pingered nets	Pingered net weak clicks as a % of non-pingered net
1	1,678	359	21%	6,178	2,368	38%
2	8,133	4,600	57%	31,827	15,771	50%
3	282	116	41%	1,664	686	41%
<b>All</b>	<b>10,093</b>	<b>5,075</b>	<b>50%</b>	<b>39,669</b>	<b>18,825</b>	<b>47%</b>

Table 3  
Percent of clicks during the on cycle of modified pingers.

Static mooring site	Number of ON/OFF cycles	A = ON cycles with porpoise detections	B = OFF cycles with porpoise detections	A as % of B
Runnelstone reef	281	124	251	49%
Mounts Bay	49	0	6	0%

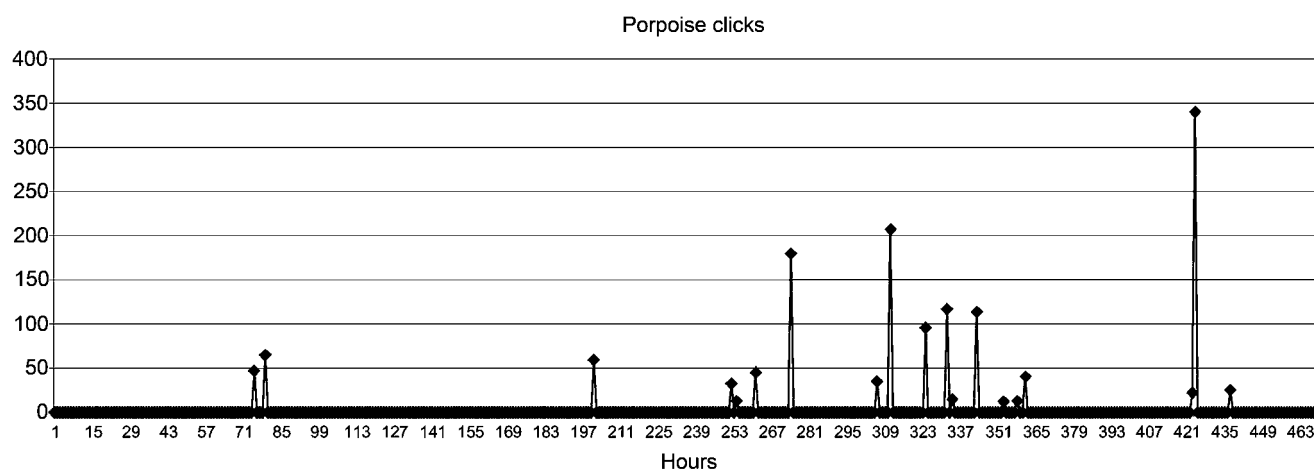


Fig. 5. Porpoise click detections per hour for one week before and after the pinger failure.

reduced in this trial, due to the smaller lengths of nets and the use of net bins.

The placement of pingers on the footrope rather than the head rope of the set nets used in this trial has the following advantages: the head rope is not pulled down by the weight of the pinger; the pinger contributes usefully to the weight of the footrope; it may reduce the risk of ‘button-holing’ during deployment; and there is usually less tension on the footrope during hauling, putting less stress on the pinger. There has been concern that pingers on the bottom will be less audible to porpoises, but as these nets are deployed on a predominantly even sea bed a major effect is unlikely.

Concerns raised by the skippers taking part in the trial were mainly about the battery life of the pinger and the cost of putting them on all their fishing gear, rather than any other practical problems. These concerns were confirmed when pingers were recovered at the end of the trial and 7 out of 23 were found to be inactive, most likely due to flat batteries as no external damage was observed.

Skippers found some difficulties in deploying the C-PODs on working nets because of their large size (90×800mm), but despite these difficulties they did obtain a substantial volume of useful data.

### Pinger effectiveness

The data presented show a marked decrease of acoustic activity around those nets equipped with pingers. This was mirrored by the static cycling pinger deployments, but these showed a marked difference in the size of the effect. The most plausible explanation of the difference between the two cycling pinger deployments is a reduced response to pingers where background noise is louder. This may have implications elsewhere and merits further investigation.

The difference between static cycling pingers and those deployed on nets may also in part be due to pingers losing power or failing during the net trial so that some ‘pingered’ data may have come from nets where the pinger is silent. There may also have been some deployments in which the C-POD was more distant from the nearest active pinger than expected (there was some evidence for this in acoustic data files in which pinger activity could not be identified where it was expected).

Analysis of the loudness of clicks recorded showed no significant indication that porpoise echolocation varied with the presence of pingers. It is possible that porpoises echolocate more loudly in response to the pinger, as they can vary the sound pressure level of their clicks over a wide range (Villadsgaard *et al.*, 2007). It was not possible to make any inference from the acoustic data on the extent of displacement of the porpoises by the pinger.

The failure of several pingers may have been due in part to the immersion switch on the AQUAmak 100 being ON during net storage in bins in which they do not fully dry out, however the manufacturer’s specification states a lifetime of one to two years with continuous immersion, dependent on temperature, or up to four years in a typical fishery with seasonal or discontinuous deployment. The specified lifetime should have covered the whole of this trial.

Palka (2008) reports evidence that porpoise bycatch in the US Northeast gillnet fishery in New England, where pingers are mandatory, is not as low as earlier trials suggested it would be, and concluded that inactive or absent pingers were a major part of the explanation plus a possibility that gaps in a line of active pingers may actually increase bycatch. The present study, and those findings, indicate that pinger monitoring needs to be simpler.

### Habituation and recovery times

It has been a source of quite widespread concern that pingers might impede the movement of porpoises or exclude them from critical habitat (e.g. Cox *et al.*, 2001). No evidence was seen of habituation to the pinger which is consistent with the findings of Palka (2008). Further studies with cycling pingers could be made at low cost using the same study design and would be valuable in establishing the recovery time more accurately. The seven hour cycle used here was probably too short to allow ‘recolonisation’ of the exclusion zone in the quiet site, but was not too short in the noisy site.

### CONCLUSIONS

This study has shown that functioning pingers are likely to reduce harbour porpoise bycatch rate in this inshore tangle net fishery. It seems unlikely that habituation will become a problem for harbour porpoises although further work is needed to demonstrate this.



Further work is urgently needed to investigate the life-time of available pingers in real time fisheries. Cycling pinger trials, with a longer activity cycle, could identify recovery time, the possible effects of ambient noise, habituation and the response of dolphins more accurately. The cycling pinger trial design used here proved to be an efficient and very low cost method of assessing responses to man-made sounds.

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# Detecting changes in the distribution of calling bowhead whales exposed to fluctuating anthropogenic sounds

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## ABSTRACT

This paper describes an analysis approach designed to detect the effects of fluctuating anthropogenic underwater sound on the distribution of calling bowhead whales (*Balaena mysticetus*) during migration. The anthropogenic sounds in this case were associated with an offshore oil production island (Northstar Island) in the Beaufort Sea northwest of Prudhoe Bay, Alaska, but the method has wider applicability. In autumn, bowhead whales migrate westward at varying distances offshore where some are exposed to Northstar sounds. Anthropogenic effects, if present, were hypothesised to be most pronounced in the southern (proximal) part of the migration corridor. Underwater sound levels were measured continuously *ca.* 500m from Northstar, and locations of calling whales were determined by a seafloor array of directional acoustical recorders. Weighted quantile regression related the 5th quantile of offshore call distance to anthropogenic sounds and other covariates. Case weights were inversely proportional to both probability of detection and location uncertainty. Due to potential dependencies in call locations, block permutation of uncorrelated whale call clusters was used to assign significance levels to coefficients in the quantile regression model. Statistical model selection was used to determine the anthropogenic sound measures most correlated with the 5th quantile of offshore call distances, after allowing for natural within-season variation quantified by day–night changes, distance of the call east or west of Northstar, and date. Data used to illustrate the method were collected over 29 days in September 2003 and included 25,176 bowhead calls. The estimated offshore distance of the 5th quantile call was 0.67km (95% confidence interval 0.31 to 1.05km) farther offshore when tones associated with Northstar were recorded in the 10–450Hz band during the 15 minutes just prior to each call. The method has been applied successfully to similar data collected near Northstar in other years, and may be useful in other studies that simultaneously collect data on animal locations and fluctuating stimuli.

KEYWORDS: ACOUSTICS; ARCTIC; BOWHEAD WHALE; MIGRATION; MODELLING; MONITORING; MOVEMENTS; NOISE; SURVEY-ACOUSTIC

## INTRODUCTION

In autumn each year, bowhead whales (*Balaena mysticetus*) migrate west-northwest along the north coast of Alaska enroute to their over-wintering habitat in the Bering Sea (Moore, 2000; Moore and Reeves, 1993; Treacy *et al.*, 2006). In early 2000, an oil production island named Northstar was constructed in 12m of water *ca.* 10km offshore and 20km west of Prudhoe Bay, Alaska, in the Beaufort Sea (Fig. 1). In a typical year, most bowheads travel westward more than 10km seaward of Northstar (Moore, 2000; Moore and Reeves, 1993; Treacy *et al.*, 2006), but occasionally bowheads have been observed <1km from Northstar. A whale within several kilometres of the island could be exposed to underwater industrial sounds, especially during periods of high island sound production or low ambient noise conditions (Blackwell and Greene, 2006). This raises concerns because underwater sound emanating from various other industrial activities (such as ship operations, marine seismic surveys, and offshore drilling) is known to displace some migrating whales (Richardson *et al.*, 1995).

Given both the bowhead's protected status under various environmental regulations, including the US Marine Mammal Protection Act and a local ordinance designed to address concerns of subsistence whale hunters in the Inupiat community, a monitoring study at Northstar was required. The overall objective of this monitoring study was to assess

bowhead whale responses to sounds associated with Northstar activities. Previous measurements of underwater sounds near oil industry activities have shown that sound levels associated with activities on gravel islands are lower than those associated with drillships, dredges and seismic surveys to which bowhead whales sometimes react (Richardson *et al.*, 1995). The monitoring study at Northstar was designed to detect responses that heretofore would have been considered subtle.

Previous studies of whale deflection around anthropogenic sound sources have often focused on detecting deflection of individuals (Croll *et al.*, 2001; Malme and Miles, 1985; Richardson *et al.*, 1985; 1995). Some of these studies tracked individual whales, usually by visual means, as they passed a sound source, or as a sound source passed the whales. By comparing tracks with and without exposure to anthropogenic sounds, or by considering received sound levels, these studies sought to assess deflection. Other studies have used aerial surveys to look for locally-reduced animal densities near a sound source (e.g. Mobley, 2005; Richardson *et al.*, 1999). In fact, aerial surveys of waters surrounding the future Northstar site were conducted prior to 2000. However, in both types of studies sample sizes near the sound source were usually limited to (at most) tens of individuals due to difficulties sighting or following individual whales, inability to observe visually at night, weather limitations, etc. A power

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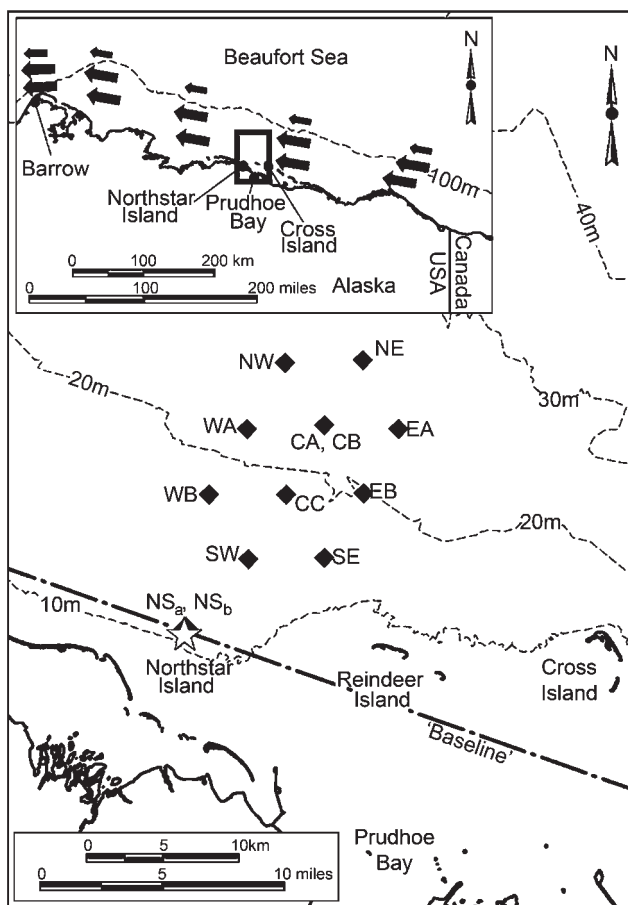


Fig. 1. Study area location in northern Alaska (box within inset), showing the main autumn migration corridor of bowhead whales (thick arrows); 100m depth contour is near the shelf-break. Detail shows DASAR locations (diamonds) within the study area northeast of the Northstar oil development. Two DASARs were located at the CA-CB location. Dashed WNW-ESE line through Northstar is the baseline from which perpendicular 'offshore distances' were measured.

analysis of prior aerial survey data from the Northstar area (T. McDonald, WEST, unpublished) indicated that sighting rates of >15 individuals per 1,000km of flight would be required to detect a 50% reduction in whale groups within a circle of radius 10 miles surrounding Northstar with 50% probability in 3 years. Because historical sighting rates in the general vicinity were lower than 15 individuals per 1,000km unless the migration corridor was unusually close to shore (Miller *et al.*, 1996) and 50% power to detect a 50% reduction was insufficient, it was apparent that the typical sample sizes in these types of studies would not yield the required level of sensitivity at Northstar.

The alternative approach used here focuses on call locations. This approach takes advantage of the fact that bowheads call frequently during both spring and autumn migration (Clark *et al.*, 1986; Moore *et al.*, 1989), and that these calls can be localised using directional hydrophones (Greene *et al.*, 2004). By associating changes in the location or shape of a spatial distribution of calls with changes in anthropogenic sound, certain types of disturbance effects can be investigated. Such an approach can take advantage of continuous acoustic monitoring, account for natural variation in the call distribution, and yield large sample sizes.

There are, however, three challenges associated with an approach based on call locations. The first applies to all

studies that utilise call locations, while the other two apply to disturbance studies whose objectives are similar to those of this study. The first challenge is that call locations close in space and time are potentially dependent on one another when single whales call more than once or react to other whales, so individual calls are not the appropriate sampling units. Here, this dependency was addressed by applying a block permutation method (Lahiri, 2003). The second challenge is that anthropogenic noise could affect calling rate as well as whale location, which introduces an interpretational challenge that can be difficult to address if estimates of deflection *per se* are sought. This is not a problem if the study's objective is to detect and quantify disturbance-related changes in the distribution of calls, notwithstanding whether such changes arise from changes in whale location or calling rate or some combination of these and other causes. In other words, if anthropogenic noise causes the calling rate (or proportion of whales that call) to vary, changes in the spatial distribution of calls would be evident, but it would be impossible to determine from calls alone whether those changes are due to changes in calling behaviour or to physical displacement of whales or some other cause. In such cases, as here, results should be clearly understood to apply to calling whales rather than to all whales. The third challenge is, disturbance effects are expected to be most pronounced in animals nearest the sound source, and usually to diminish with increasing distance. Depending on industrial sound level at various positions across the width of the migration corridor, whales near the middle of the corridor may not be disturbed while those at the proximal edge may be affected. In other words, the proximal edge of a call distribution may shift but the centre may not. This challenge can be overcome by focusing on one or more quantiles in the call distribution. Recall that the  $x$ th quantile of a univariate distribution (here, offshore distance) is a value below which  $x\%$  of the observations occur, and above which  $(100-x)\%$  occur ('quantile' is synonymous with 'percentile', e.g. the median is the 50th quantile).

The specific objective of this paper is to develop a statistical approach suitable for the situation where effects of underwater sounds on call locations are of concern. The study at Northstar was the motivation for this approach. At Northstar, call locations were determined at times with varying levels of anthropogenic sounds measured near the island (~450m away). The approach then quantified the relationship between emitted anthropogenic sound (predictor variable) and the 5th quantile of offshore distances for local calls (dependent variable), after adjustment for other factors (covariates).

## METHODS

In this study, there were two key types of data: whale call locations offshore of Northstar and underwater sound levels near the island. Call locations were estimated using data from 11 Directional Autonomous Seafloor Acoustic Recorders (DASARs) placed on the seafloor. Underwater sound levels from Northstar were monitored via hydrophones near the island. Previous publications have detailed the field methods, data collection, and data analysis through the call localisation stage (Blackwell and Greene, 2006; Blackwell *et al.*, 2007;

Greene *et al.*, 2004). Those papers describe DASAR design, construction, deployment, field calibration and retrieval, analysis of near-island sound recordings, call extraction and localisation, and general characteristics of the bowhead calls and migration corridor. The parts of those papers describing methods used to localise calls and measure Northstar sound levels are summarised in the next two subsections. The third subsection below describes the statistical approach used to relate the 5th quantile of offshore whale call distances to anthropogenic sounds and covariates. This paper focuses on methodology, and the methods are illustrated using data from one year (2003) of a longer study (Richardson *et al.*, In prep).

### Whale call localisation

In 2003, whale calls were recorded continuously from 19:15 local time on 29 August to 04:39 on 28 September using an array of 11 DASARs deployed 6–21km offshore of Northstar Island (Fig. 1). The area where the DASARs were deployed was within the southern part of the bowhead migration corridor, although historically there has been substantial annual variation in that corridor (Moore, 2000; Treacy *et al.*, 2006). The main bowhead migration season typically extends from around 1 September into mid-October (Moore and Reeves, 1993). Because of deteriorating weather and concerns that they might become irretrievable under pack ice, the DASARs are retrieved as soon as possible after 25 September each year. Retrieval occurred on 28 September in 2003.

Each DASAR receiving a call provided a directional bearing to the call, with some uncertainty (Greene *et al.*, 2004). Calls were localisable when two or (preferably) more DASARs provided intersecting bearings for the same call. Precise DASAR orientations were determined by projecting calibration sounds from known (via GPS) locations around each DASAR. Calibration sounds were played at precisely known times on five dates (approx. weekly) during the 2003 field season. These data were used not only to calibrate each DASAR's orientation but also to correct for slight drift in each DASAR's internal clock. After correcting for clock drift, times of calls were determined to an accuracy of 1–2 sec, which was adequate to assess whether a call received at several DASARs represented a single call or multiple calls. DASARs provided reliable acoustic data up to 450Hz. Most of the energy in the great majority of bowhead calls is below 450Hz. The one exceptional call type ('high' calls) is rare and associated with complex calls, which contain energy below 450Hz (Würsig and Clark, 1993). Therefore, data up to 450Hz were deemed adequate for localisations.

The Huber robust location estimator was applied to triangulate call locations based on the intersection(s) of bearings from multiple DASARs (Greene *et al.*, 2004; Lenth, 1981). The Huber estimator down-weighted the occasional outlying bearing and yielded a location solution more often than alternative techniques. Calls could have been detected by only one DASAR, or missed completely, if the call was weak, occurred far from the DASAR array, or occurred during times when background levels of underwater sound (mainly due to wind and wave action) were high. Even when calls were received by  $\geq 2$  DASARs they occasionally did not produce a location estimate because estimated bearings either did not cross or were too disparate to allow the Huber estimator to converge.

For each estimated call location, a 90% confidence ellipse was calculated using methods in Lenth (1981). These methods were based on the number of DASARs that received the call, the geometry of all pair-wise bearing intersections, disparity of intersections, and inherent variation estimated from calibration data for each DASAR (Greene *et al.*, 2004).

Offshore distances were computed as perpendicular distances from the call's estimated location to a 'baseline' oriented 108° to 288° True (dashed WNW-ESE line in Fig. 1), through Northstar Island and parallel to the general trend of the coast. The Discussion section provides justification for using this measure of offshore distance and information about the lack of sensitivity of results to changes in orientation of the baseline.

Calibration sounds projected near the DASAR array, along with boat noise from the associated vessel, may have temporarily affected whale positions or calling behaviour. Because primary interest was in the effects of operations associated with Northstar itself, periods when the calibration boat was >2km north of Northstar Island, and periods within 2hr after the boat returned to waters <2km north of Northstar, were excluded from analysis. Two hours was chosen based on typical durations of avoidance reactions to boats (usually ½–1hr, Richardson *et al.*, 1985; Richardson and Malme, 1993), plus a 1–1½hr allowance for displacement and behavioural effects to subside. This provision resulted in exclusion of 8% (57.3hr of 705.4hr) of the 2003 field season and 1,506 localised calls.

### Near-island sounds

Underwater sounds produced on the island and by associated vessels were measured 460m or 550m seaward (north) of the northern edge of the island either by a cabled hydrophone prior to its destruction by storm surge (31 August to 16 September 2003) or by a spare DASAR (18–28 September 2003). Both sensors were positioned just above the sea floor in water 12–13m deep (Blackwell and Greene, 2006). From the near-island recordings, sound spectral densities were determined for 1min periods every 4.37min, or ~330 times per day. These spectral densities were used to determine broadband (10–450Hz) and one-third octave band levels for each 1min sampling period. Totals of 5,262 and 3,232 1min samples were obtained from the cabled hydrophone and near-island DASAR, respectively. Because anthropogenic sound was not measured on 16–18 September 2003, *ca.* 2,827 calls recorded during this period were excluded from the analysis.

Near-island sounds received 460m and 550m north of the island were partly from industrial activities on the island, partly from vessels supporting Northstar activities, partly from wind and wave action (Blackwell and Greene, 2006), and partly from other sources. In 2003, broadband (10–450Hz) levels of underwater sound at this location ranged from 90.4 to 136.8 dB re 1  $\mu$ Pa and averaged 103.4dB. To measure sounds associated with industrial activities at Northstar, near-island sounds were quantified via the following five 'Industrial Sound Indices' (ISIs). These measures were later summarised and combined over varying time periods preceding each call (see Table 1) for inclusion as anthropogenic covariates in the analysis, as listed below.



- (1) Sounds in five contiguous  $\frac{1}{3}$  octave frequency bands, centred at 31.5, 40, 50, 63 and 80Hz and spanning the 28–90Hz range, were predominantly associated with industrial activities at Northstar (Blackwell and Greene, 2006). However, some natural (e.g. wind and wave action) and non-Northstar (e.g. non-Northstar boats) sound did occur in these bands. The *isi5* variable was defined to be the sum of the mean-square sound pressures in these five  $\frac{1}{3}$ -octave bands, expressed in dB re 1  $\mu$ Pa. In 2003, this five-band ISI (28–90Hz) ranged from 84.5 to 128.8 dB re 1  $\mu$ Pa and averaged 97.6 dB (on average, 5.7dB less than the broadband (10–450Hz) sound pressure level).
- (2) The near-island recording included prominent and recurrent tonal sounds in the 10–450Hz range at specific frequencies associated with industry activities (Blackwell and Greene, 2006). Tones occurred, for example, when engines generated sounds at constant frequencies. The 0–1 indicator variable *isi.tone.pres* was defined to be true if, during a 1min sample, sound spectral density in any 1Hz band was >5dB above the average spectral density in the four adjacent 1Hz bands (two below, two above, excluding the band being tested). In 2003, tones were present during 57% of the recorded 1min periods.
- (3) The *isi.tone* variable quantified the strength of tones identified by the *isi.tone.pres* measure. When tones were not present in a 1min sample, *isi.tone* was 0. When tones were present, the strength of individual tones was mean-square sound pressure in the 1.7Hz wide Fourier analysis bin (centred on integer Hz) containing the tone minus the average mean-square sound pressure in the four adjacent bins (background noise). The strength of all tones in the 1min sample was the sum of tone strength (on mean-squared sound pressure scale) over all bands defined to have tones (see (2) above). When they occurred, tone strength ranged from 64.5 to 130 dB re 1  $\mu$ Pa and averaged 86.95 dB.
- (4) Vessels routinely visited the island throughout the season, producing both tonal and non-tonal underwater sound. Vessel sounds tended to occur as transients lasting minutes to tens of minutes (Blackwell and Greene, 2006). The 0–1 indicator variable *isi.trans.pres* was true if, for a 1min sample, sound pressure (dB) in the 28–90Hz range was >5dB above sound pressures in these same bands averaged over the previous and subsequent 2h (i.e. a 4h moving average, excluding the 1min sample in question). In 2003, transients occurred during 10% of the recorded 1min periods.
- (5) The *isi.trans* variable quantified the strength of transients identified by *isi.trans.pres*. Strength of transients in a 1min sample was 0 if no transients were present. When a transient was present, *isi.trans* was the difference between sound pressure (dB) in the 28–90Hz range for the 1min sample containing the transient minus that in the 4h moving average in these frequencies that was used to identify the transient. By construction, the minimum strength of transients was 5dB. When they occurred, transient strength averaged 10.2 dB re 1  $\mu$ Pa above the

4h moving average, and ranged to a maximum of 28.9 dB re 1  $\mu$ Pa above the moving average.

### Analysis methods

This section describes estimation of a quantile regression relationship (Koenker, 2004; 2005; Koenker and Bassett, 1978; Koenker and Machoda, 1999; Koenker and Xiao, 2002) between the 5th quantile of offshore distances and anthropogenic sound after adjusting for certain environmental covariates. Conceptually, the quantile regression estimated a semi-linear model with functional form.

$$Q_5(y|x) = \beta_0 + f(\text{non-industry variables}) + g(\text{industry variables})$$

where  $Q_5(y|x)$  was the 5th quantile of offshore distance given the values of all explanatory variables,  $f(\text{non-industry variables})$  was a smooth function of naturally occurring exogenous variables that might be expected to influence offshore distance to calls, and  $g(\text{industry variables})$  was a linear function of anthropogenic sound levels measured ~500m from Northstar (i.e. the ISIs). The remainder of this section describes exclusion criteria for calls, call weighting factors, model selection, computation of significance levels via block permutation, and estimation of anthropogenic effect size under various anthropogenic sound scenarios.

### Call exclusion

Calls that occurred during times of high ambient (background) noise, e.g. during times of high wind and wave action, were more difficult to detect than calls occurring at other times. In particular, this caused calls originating outside the array and at large distances offshore to be underrepresented in the data during times of high background noise (Greene *et al.*, 2004). This bias in sampling, if not addressed, could have caused an apparent positive offshore displacement during low ambient noise periods, and conversely could have hidden a positive offshore displacement during high ambient noise times.

To eliminate this bias, an approach analogous to multiple observer distance sampling (Alpizar-Jara and Pollock, 1996; Buckland *et al.*, 2004, chapter 6; Good *et al.*, 2007) was adopted to estimate the probability of detecting and localising calls. Based on logistic regression models (see Appendix 1), calls were excluded if (for the circumstances of the particular call) the estimated probability of detecting and localising a call was below an arbitrary cutpoint, which was set at <10% (see next paragraph). The net effect was that calls within or close to the DASAR array (generally <10km from its centre) were included unless background sound levels exceeded ~108 dB re 1  $\mu$ Pa, as occurred during large storm events. Calls that occurred far from the array (e.g. >60km from array centre) were generally excluded regardless of background sound levels due to attenuation of the call's strength. In between, calls were included or excluded based on distance from the array, background sound at the time, and whether the call was east or west of the array (Appendix 1). The logistic regressions estimated that a call's probability of detection and localisation decreased as the call's distance from the array increased, or as background sound level increased, or both. Also, calls occurring east of the array were detected and localised with

slightly higher probability than calls west of the array (Appendix 1). The average location where probability of detection and localisation dropped below 50% was ~30km east, west and north of the centre of the DASAR array.

The call exclusion cutpoint was set at 10% for three reasons. First, a 10% cutpoint retained the vast majority of the detected calls (*ca* 90% were retained). Second, it was reasoned that most bias in the sample was represented by calls with small (<10%) probability of detection and localisation because, for every such call detected, the theorem of Horvitz and Thompson (1952) would indicate that >10 similar calls were missed. This contrasts with the fact that over 50% of the calls detected and localised were obtained in situations when detection and localisation probability was estimated to be >95%. Statistical theory implies that  $\leq 0.053$  similar calls were missed for every call detected with probability >95%. Third, during line transect studies that exclude distant sightings for similar reasons, a common criterion for exclusion is probability of detection less than 10% to 15% (Buckland *et al.*, 2001).

To assess whether exclusion of calls with <10% probability of detection affected the results, a sensitivity analysis was run. Following the full quantile regression analysis, the requirement that probability of detection and localisation be >10% was dropped and the entire analysis was re-run using all localised calls. For 2003 (and 2002), effects in the top ('best-fitting') quantile regression models were exactly the same whether or not the '<10% probability' calls were included. In those years, the direction, general magnitude and significance levels of coefficients in the two models were also the same. However, for 2001 and 2004, inclusion of low probability calls, primarily those with estimated locations >100km from the array, destabilised the estimation methods to the point that the quantile regression routine would not converge. The main analyses reported here exclude calls from situations with probability of detection and localisation <10%, which should reduce biases and allows the same procedure to be applied to all years.

#### *Localisation uncertainty weights*

Uncertainty in offshore distance measurements differed by several orders of magnitude among calls. To account for this, a weighting factor derived from the size of the 90% confidence ellipse for the call location was used in all quantile regressions. These weights were calculated as the reciprocal of error ellipse diameter along the 18°–198° axis, which was perpendicular to the 'baseline' that ran through Northstar roughly parallel to shore.

A small number of calls (~2%) were localised via 3 or more DASAR bearings that intersected at nearly a single point. When this happened, the estimated error ellipse was unrealistically small (e.g. <10m<sup>2</sup>) given the uncertainties in individual bearings (Greene *et al.*, 2004). To keep these few calls from dominating the results, we replaced all confidence ellipse diameters less than the 2nd percentile of confidence ellipse diameters with the value of the 2nd percentile.

#### *Detection probability weights*

After excluding '<10% probability' calls, the remaining calls were in situations where detection and localisation probability was 10–99%. Detection and localisation

probability was >95% for the vast majority of calls within 1–2km of the DASAR array perimeter, and was lower for most of those farther away. To account for differential probabilities of inclusion for calls remaining in the analysis, the quantile regression analysis included a weighting factor that was inversely proportional to the probability of detection and localisation under the circumstances of that call. This weighting factor was the Horvitz-Thompson (HT) weight for each call (see Buckland *et al.*, 2004, p. 9; Horvitz and Thompson, 1952; Särndal *et al.*, 1992, p. 43). HT weights have been used in similar situations (e.g. distance sampling) for the same purpose.

Because HT weights were estimated with statistical error, the overall quantile regression analysis was again re-run after the primary analysis was complete, this time without HT weights, to assess whether use of HT weights affected the results. Results were very similar with and without HT weights (see Results). The lack of sensitivity of results to HT weights was not surprising because location uncertainty weights were also included in the analyses. Location uncertainty weights dominated because they decreased faster than HT weights as distance from the array centre increased.

#### *Model selection*

Selection of variables for inclusion in the quantile regression model occurred in two stages. First, a reasonable model for *f(non-industry variables)* containing natural exogenous variables was determined. This 'natural variation' model explained as much variation in offshore distance as possible, given the available predictor variables. Then, models for *g(industry variables)* were added to the natural variation model and the additional predictive strength of the industrial sound variables was assessed. The remainder of this section is a description of these steps.

To start, quantile regression was used to identify the combination of four available non-industry variables (Table 2) that best predicts the 5th quantile of offshore distances. Backward stepwise elimination was used to select variables in the natural variation model. Starting with all four terms in the model, terms were successively removed if their *P*-values were greater than alpha-to-exit = 0.20. Between eliminations, previously deleted terms were restored if their *P*-values diminished below alpha-to-enter = 0.20. Elimination stopped when *P*-values for all terms in the model were below alpha-to-exit = 0.20. *P*-values were computed via block permutation, as described below.

Among the non-industry variables considered in step one, day of the year (0 = 31 August, 1 = 1 September, 2 = 2 September, etc.) and uprange distance (east–west distance of call along axis parallel to baseline) were fitted as nine degree-of-freedom smoothing splines (i.e. variables *dayofyear.smu* and *uprange.smu* in Table 2). This allowed estimation of non-linear and high order polynomial relationships between these variables and the 5th quantile of offshore distance. The degree of smoothness (number of 'anchors' or df) in both splines was chosen by generalised cross validation (Gu and Wahba, 1991; Gu and Xiang, 2001; Wood, 2004) in generalised additive models (Hastie and Tibshirani, 1990) relating mean offshore distance to day of year or uprange distance only.

Step two of model estimation started with the best fitting ‘non-industry’ model from step one, and successively evaluated 49 candidate models containing industrial sound indices arising from seven forms of anthropogenic sound (Table 1) crossed with seven possible averaging times for each ISI. Multiple ISI averaging times were considered because there was no *a priori* basis upon which to predict the most appropriate interval, from a bowhead whale’s perspective, over which to average the sound measurements. In picking the range of averaging times to consider, it was reasoned that the 1min sound measurement closest in time to the call was unlikely to be adequate because disturbance effects, if present, would likely last longer than the 4.37min interval between successive sound measurements. In addition, if changes in the distribution of calling whales arise mostly from changes in location (displacement), responses of whales to Northstar sound would take considerably longer to develop than 4.37min. Typical swimming speed for a bowhead during autumn migration is 4–5km/h (Koski *et al.*, 2002), so whales take a few hours to travel through the area where the DASAR array could reliably detect and locate their calls. Likewise, averaging times greater than 2–3h were not likely to be adequate because a whale could receive and respond to multiple auditory events in such a long time interval. During pilot analyses after each year’s data became available, averaging times of 5–160min were considered. From these analyses, it appeared that a Northstar effect, if present, would be strongest for averaging times between 15 and 120min. For the analyses reported here, the following seven averaging times were used: 15, 30, 45, 60, 70, 90 and 120min. ISI variables averaged over different time periods were not

considered in the same model due to high correlation amongst them.

At the end of step two, the resulting set of 49 fitted models was ranked based on amount of variation explained. The model explaining the highest proportion of residual variation was selected as the best fitting model among those tested for the year in question. Akaike’s Information Criterion (AIC) (Burnham and Anderson, 2004) was not used to rank competing models because AIC is a function of the maximised value of a statistical likelihood, and quantile regression is non-parametric so no statistical likelihood is defined. Following model selection, the significance of terms in the best model was determined by block permutation (described next).

#### Significance levels

Two difficulties prevent straightforward computation of significance for terms in the quantile regression models used here. First, the statistical properties of quantile regression parameters are not mathematically tractable (Bilias *et al.*, 2000; Hahn, 1995; Horowitz, 1998). This prevents use of a tabulated statistical distribution (such as the *t* or *F* distribution). Second, offshore distances were not independent of one another. For example, a particularly vocal whale could yield tens of calls but only one distinct measurement of offshore distance. Or, whales at multiple offshore distances could be calling in response to one another. This lack of independence prevented use of individual calls as the basis for statistical replication.

Given these complications, block permutation (Lahiri, 2003) was used to establish statistical significance levels. Block permutation is closely related to block bootstrap

Table 1

Industrial sound variables and models considered for inclusion in the quantile regression of offshore distances. In total, 49 models reflecting *a priori* notions of anthropogenic sound were considered: seven models  $\times$  seven sound averaging times (XX = 15, 30, 45, 60, 70, 90 and 120min).

Model	Description
<i>isi5.XX</i>	Variable <i>isi5.XX</i> = sound level (in dB re 1 $\mu$ Pa) within the five 1/3rd octaves spanning 28–90Hz, averaged over the 1min samples within XX min immediately prior to the call. This model fit a linear relationship between <i>isi5.XX</i> and the 5th quantile of offshore distance.
<i>isi.tone.pres.XX</i>	Variable <i>isi.tone.pres.XX</i> = 1 when at least one tone (>5dB above levels at neighbouring frequencies) was present at 10–450Hz in the nearshore sound record during XX min immediately prior to the call. <i>isi.tone.pres.XX</i> = 0 when no tone was present during any 1min sampling times in the XX min period. This model estimated the average amount by which the 5th quantile of offshore distance increased or decreased when industrial tones were present prior to the call.
<i>isi.trans.pres.XX</i>	Variable <i>isi.trans.pres.XX</i> = 1 when at least one transient (>5dB above 4h running average background level) was present in the 28–90Hz band nearshore sound record during XX min immediately prior to the call. <i>isi.trans.pres.XX</i> = 0 when no transient was present. This model estimated the average amount by which the 5th quantile of offshore distance increased or decreased when transient sounds of an industrial nature were present prior to the call.
<i>isi.tone.pres.XX</i> + <i>isi.tone.XX</i>	Variable <i>isi.tone.XX</i> = average strength of tones (on mean-square sound pressure scale) over the 1min samples defined to have tones within sample XX min immediately prior to the call. <i>isi.tone.XX</i> = 0 when no tones were present during any 1min sample within XX min prior to a call. Strength of tone in a 1min sample was mean-square sound pressure in a 1.7Hz wide Fourier analysis bin (centred on integer Hz) minus average mean-square sound pressure in 4 adjacent bins (background noise). This interaction model fitted no relationship between <i>isi.tone.XX</i> and offshore distance when no tones were present, and a linear relationship when tones were present.
<i>isi.trans.pres.XX</i> + <i>isi.trans.XX</i>	Variable <i>isi.trans.XX</i> = sum of mean-square sound pressures of transient strength in all 1min samples defined to contain transients within XX min immediately prior to a call, converted to dB re 1 $\mu$ Pa. Transient strength was difference between sound pressure (dB) in the 28–90Hz band of a 1min sample containing the transient and a centred 4h moving average of sound pressure in the 28–90Hz band. <i>isi.trans.XX</i> = 0 when no transients were present during XX min prior to a call. This interaction model fitted no relationship between <i>isi.trans.XX</i> when no transients were present, and a linear relationship when transients were present.
<i>isi.tone.pres.XX</i> + <i>isi.tone.pres.XX</i> * <i>uprange.smu</i>	This model fitted separate smoothed curves relating uprange distance and 5th quantile of offshore distance for times when tones were present in the previous XX min vs. not present.
<i>isi.trans.pres.XX</i> + <i>isi.trans.pres.XX</i> * <i>uprange.smu</i>	This model fitted separate smoothed curves relating uprange distance and 5th quantile of offshore distance for times when transients were present in the previous XX min vs. not present.



Table 2

Natural, or non-sound, variables considered for inclusion in the *f(non-industry variables)* portion of the quantile regression models.

Variable	Degrees of freedom	Description
<i>sunlight</i>	1	Day/night indicator: <i>Sunlight</i> = 1 if sun was above the horizon; <i>sunlight</i> = 0 if sun was below the horizon. Local sunrise and sunset times for Prudhoe Bay, AK, obtained from <a href="http://www.sunrisesunset.com">http://www.sunrisesunset.com</a> .
<i>upstream</i>	1	East/west indicator: <i>Upstream</i> = 1 if location was on or east of a line extending through DASAR CB (Fig. 1) and Northstar (i.e. uprange distance >0). <i>Upstream</i> = 0 if location was west of this line (i.e. uprange distance <0).
<i>uprange.smu</i>	9	Smoothed (via B-spline) function of east-west distance along baseline, in meters. Computed based on distance from Northstar to the point on the baseline closest to the call, with call locations east and west of Northstar coded as positive and negative values, respectively. B-splines allowed estimation of piecewise cubic polynomials between nine ‘anchors’ (or ‘knots’, seven internal, two at extremes) spaced evenly from the lowest to the highest observed values of uprange distance. Number of ‘anchors’ was chosen by generalised cross validation (Wood, 2004) in a generalised additive model relating offshore distance to this variable.
<i>dayofyear.smu</i>	9	Smoothed (via B-spline) function of day of the year, coded as 1 September = 1, 2 September = 2, etc. Otherwise calculated as for <i>uprange.smu</i> .

methods (Fitzenberger, 1997; Lahiri, 2003), which have an established history of application in quantile regression for confidence interval construction. In this case, block permutation was used to establish the null distribution of the drop-in-dispersion *F* statistics (Cade and Richards, 2006) and confidence limits for coefficients in both the ‘natural’ and ‘industrial’ quantile regression models. Details of the drop-in-dispersion *F* test and derivation of confidence limits via block permutation appear in Appendix 2.

To apply block permutation, ‘blocks’ composed of calls belonging to independent groups of whales must be identified. Here, however, neither individuals nor pods could be identified, let alone pods that might be in communication with one another. Instead, uncorrelated ‘blocks’ of calls were sought and serve equally well in the method. Uncorrelated blocks of calls were constructed by the hierarchical clustering procedure described in Appendix 3. This procedure grouped calls close in space and time until the centroid locations and average arrival times of calls within groups were uncorrelated, as measured by Mantel’s test.

All estimation and significance testing was performed using the R programming language (R Development Core Team, 2005) augmented with packages *quantreg*, *mgcv*, and *splines* (<http://cran.r-project.org/web/packages/>). *Quantreg* (version 3.85) performs quantile regression using a linear programming approach (Koenker and D’Orey, 1987). The *splines* package was used to compute B-spline orthogonal base transformations of the date and uprange distance variables. The *mgcv* package computed a generalised cross validation estimate for the number of knots (or df) in the B-spline transformations, which in turn determined their smoothness.

## RESULTS

A total of 45,622 calls were received by the DASAR array during the 29.4-day recording period in 2003. Of these, 8,778 were received by only one DASAR (preventing triangulation) and 3,907 others could not be localised because the bearings involved were too disparate, leaving 32,937 localised calls. Of these, 1,506 were excluded because they were localised during times when this project’s research boat was servicing the array, 3,428 were excluded because probability of detection in the prevailing circumstances was <10%, and 2,827 were excluded because corresponding measurements of industrial sounds (ISI) were missing (i.e. between the time

when the cabled hydrophone was lost and installation of a DASAR near Northstar). This left 25,176 call locations in the quantile regression analysis. Fig. 2 shows estimated locations of most localised whale calls, excluding those estimated to be beyond the mapped area.

Calls were detected in ‘pulses’, both in time and in space, during each year of this study (Blackwell *et al.*, 2007). This was evident in plots of offshore distances as a function of date (Fig. 3). For example, most calls were detected 10km and farther offshore on 7 September 2003, but six days later, on 13 September, numerous calls were detected very close to shore (Fig. 3). Clustering of calls in time and space is consistent with numerous observations by both Inupiat whalers and researchers (Blackwell *et al.*, 2007, pp.260, 264). For purposes of statistical analysis, the 25,176 calls were grouped into 3,000 clusters (Appendix 3).

Considering non-anthropogenic variables only, the best-fitting quantile regression model contained *upstream* ( $\beta = -415\text{m}$ , 95% CI  $-740\text{m}$  to  $-96\text{m}$ ,  $P = 0.023$ ), *dayofyear.smu* ( $P = 0.001$ ) and *uprange.smu* ( $P = 0.001$ ). None of the coefficients in this model changed substantially when anthropogenic sound variables were added. For consistency and brevity, we focus on the models containing both natural variables and anthropogenic sound variables, and do not report the 18 coefficients for *dayofyear.smu* and *uprange.smu* in the natural variation model.

Anthropogenic sound quantified in 49 ways was added to the best natural model and the resulting models were ranked according to the amount of variation they explained. The top 25 of these 49 models are summarised in Table 3. For 2003, no single anthropogenic sound model stood out from others among the top 21 models in explaining variation in the 5th quantile of offshore distance. The proportion of variation explained by the 21st-ranked model was only 3.8% less than that for the top ranked model (Table 3). These top 21 models included all three single-variable measures of sound averaged over all seven averaging times that were considered. All these single-variable measures of sound were similarly effective in predicting the southern portion of the call distribution, and similar conclusions might be expected from any of these models. The sound measure coefficient in each of the top 21 models was positive, indicating that, regardless of the sound measure or assumed averaging time, the southernmost calling whales tended to be farther offshore when industrial sounds increased.



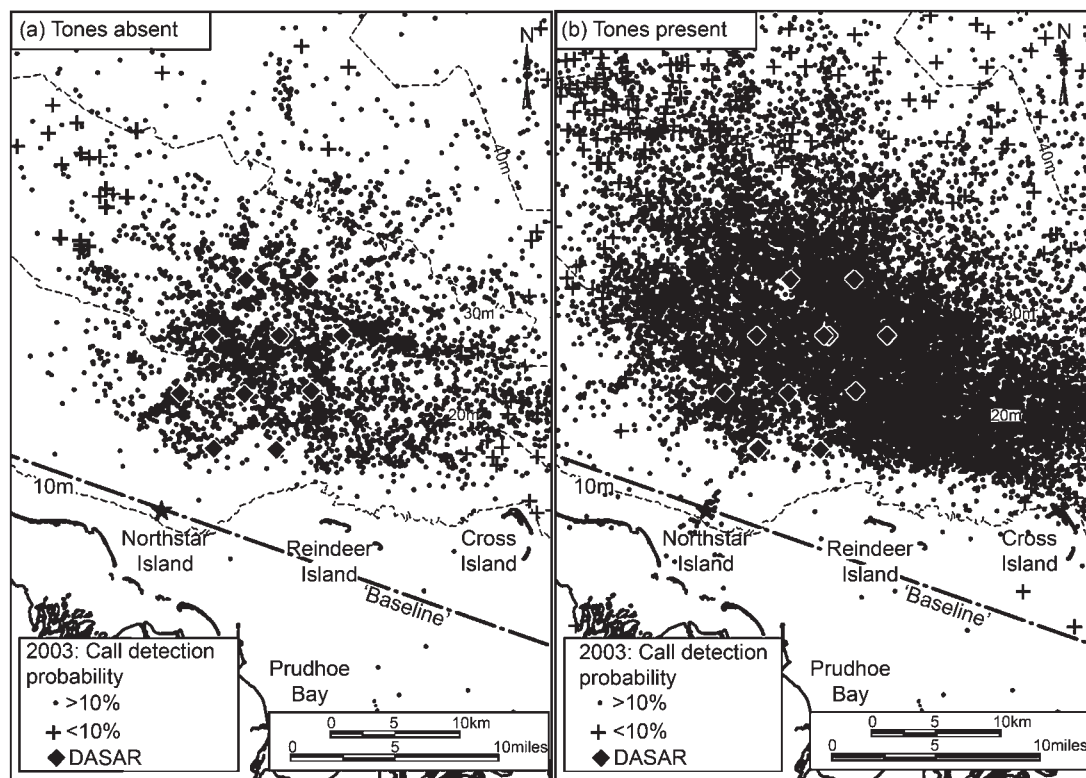


Fig. 2. Maps of estimated whale-call locations in 2003. Whale calls are distinguished according to the absence (a) or presence (b) of prominent tones near Northstar in the 15min period preceding each call [see Table 1 for definition of *tones present*]. Calls detected in situations where the probability of detection and localisation was <10% are also distinguished.

Although the top 21 models all had similar predictive abilities, the remainder of this section focuses on the ‘best’ predictor model because model averaging (Burnham and Anderson, 2004) is not possible without a likelihood-based criterion of model fit. The best-fitting (top) model allowed for *upstream*, *dayofyear.smu*, *uprange.smu* and *isi.tone.pres.15*. Coefficient estimates and confidence intervals for this model appear in Table 4. Each of these effects is described below.

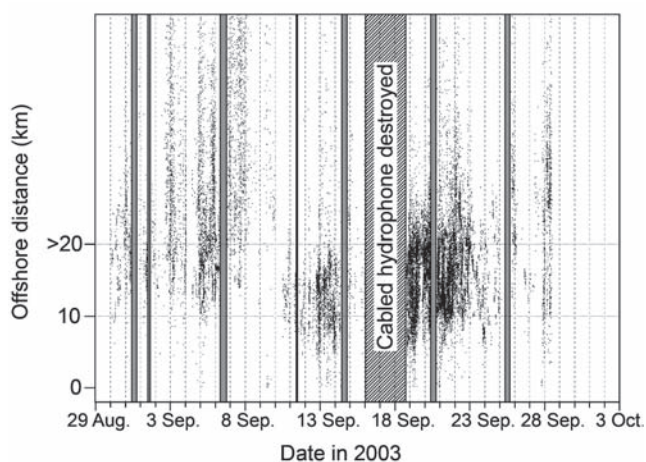


Fig. 3. Offshore distance for every detected whale call estimated to be within 50km of shore vs. date during the 2003 study period. All localised calls are included, regardless of probability of detection. Distances >20km offshore have large uncertainties and should only be used as an index of the frequency of whale calls far from Northstar. Shaded vertical segments delimit time slots when our vessel was in the DASAR array; whale calls during those periods were not analysed and were excluded from the graph. Calls arriving on 16, 17 and most of 18 September could not be used because storm surge destroyed the near-island recording equipment. Date labels appear at the start of each day (00:00 AkDT).

The seasonal variable *dayofyear.smu* included in the best model indicated that the normal (in the absence of prominent tones) southern edge of the distribution of whale calls varied substantially throughout the season. The 5th quantile of the offshore distances of calling whales ranged over time from 3.9 to 10.3km offshore of Northstar (Fig. 4a) when underwater sound near Northstar did not include any prominent industrial tones. The dates in 2003 when (in the absence of prominent tones) the 5th quantile achieved those minimum and maximum offshore distances were 16 and 4 September, respectively. These 5th-quantile offshore distances were determined at the study’s centreline – a straight line through Northstar and DASAR CB.

The effects quantified by *uprange.smu* and *upstream* were both significant ( $P \leq 0.001$ ) in the best fitting model. In general, the southern edge of the distribution of bowhead calls, as estimated by these two effects, was approximately parallel to the baseline and to the broad-scale trend of the coast within ~25km east and ~10km west of Northstar (Fig. 4). However, the overall trend of the 5th quantile deviated farther offshore ~10km downstream (west) of Northstar when compared to upstream of Northstar. The *upstream* effect estimated the 5th quantile to be 0.75km farther offshore west of Northstar than east (95% CI = 0.44 to 1.1km, Table 4). Relatively few call locations with high location accuracy were obtained >10–15km west of Northstar, so the 5th quantile estimates in this region were necessarily estimated with less precision than those within and nearer to the DASAR array.

Presence of a tone within 15min preceding the call (i.e. *isi.tone.pres.15*) was statistically significant at  $P = 0.006$  in the best fitting model for bowhead call locations in 2003.

Table 3

Industrial effects in the top twenty-five 5th quantile regression models as ranked by proportion of variation explained. All models also included natural factors *upstream*, *dayofyear.smu*, and *uprange.smu* (see Table 2). Here,  $F_{\text{effect}}$  is the drop in dispersion statistic of Cade and Richards (2006) measuring the proportion of residual variation explained by adding the industrial sound term to the model.  $\% \Delta F_{\text{effect}} = 100(\max(F_{\text{effect}}) - F_{\text{effect}}) / \max(F_{\text{effect}})$ .  $df$  = number of coefficients estimated in the anthropogenic portion of the model.

Model	$df$	$F_{\text{effect}}$	$\% \Delta F_{\text{effect}}$
<i>isi.tone.pres.15</i>	1	3,875.1	0.0
<i>isi.tone.pres.30</i>	1	3,842.6	0.8
<i>isi5.90</i>	1	3,790.0	2.2
<i>isi5.15</i>	1	3,786.1	2.3
<i>isi5.45</i>	1	3,783.8	2.4
<i>isi5.30</i>	1	3,782.7	2.4
<i>isi5.70</i>	1	3,782.0	2.4
<i>isi5.60</i>	1	3,779.9	2.5
<i>isi.tone.pres.45</i>	1	3,778.7	2.5
<i>isi.trans.pres.90</i>	1	3,775.1	2.6
<i>isi5.120</i>	1	3,770.6	2.7
<i>isi.tone.pres.70</i>	1	3,761.9	2.9
<i>isi.tone.pres.90</i>	1	3,758.6	3.0
<i>isi.tone.pres.60</i>	1	3,758.1	3.0
<i>isi.trans.pres.70</i>	1	3,753.2	3.1
<i>isi.trans.pres.15</i>	1	3,750.2	3.2
<i>isi.trans.pres.30</i>	1	3,749.3	3.2
<i>isi.trans.pres.60</i>	1	3,746.8	3.3
<i>isi.trans.pres.45</i>	1	3,746.5	3.3
<i>isi.tone.pres.120</i>	1	3,737.7	3.5
<i>isi.trans.pres.120</i>	1	3,726.1	3.8
<i>isi.tone.pres.30 + isi.tone.30</i>	2	1,943.5	49.8
<i>isi.tone.pres.15 + isi.tone.15</i>	2	1,939.6	49.9
<i>isi.tone.pres.90 + isi.tone.90</i>	2	1,938.9	50.0
<i>isi.tone.pres.70 + isi.tone.70</i>	2	1,927.0	50.3

Table 4

Coefficients and 95% confidence intervals for effects in the best fitting 5th quantile regression model for data collected in 2003 relating offshore distance to natural and anthropogenic sound variables. Units of *upstream* and *isi.tone.pres.15* coefficients are metres. Coefficients for *dayofyear.smu* and *uprange.smu* are unitless due to B-spline transformation of these variables.

Term	2003		
	Coefficient	Low 95%	Upper 95%
<b>Background Model</b>			
(Intercept)	16,529.4	16,529.4	16,529.4
<i>upstream</i>	-749.7	-1,064.0	-439.7
<i>dayofyear.smu.1</i>	2,519.4	-2,119.6	7,317.2
<i>dayofyear.smu.2</i>	4,778.3	875.6	8,797.4
<i>dayofyear.smu.3</i>	-5,016.3	-9,066.4	-1,011.8
<i>dayofyear.smu.4</i>	-2,986.8	-6,212.7	86.9
<i>dayofyear.smu.5</i>	-179.2	-3,650.6	3,122.4
<i>dayofyear.smu.6</i>	-191.9	-3,244.8	2,872.8
<i>dayofyear.smu.7</i>	-592.2	-4,883.5	3,446.4
<i>dayofyear.smu.8</i>	-3,682.5	-9,033.1	2,472.1
<i>dayofyear.smu.9</i>	-1,052.1	-4,934.6	3,856.6
<i>uprange.smu.1</i>	689.3	-7,284.1	6,851.1
<i>uprange.smu.2</i>	-9,550.9	-14,446.6	-6,615.2
<i>uprange.smu.3</i>	-7,599.1	-13,093.0	-3,867.8
<i>uprange.smu.4</i>	-8,996.9	-14,277.9	-5,719.4
<i>uprange.smu.5</i>	-5,270.8	-10,565.2	-1,767.6
<i>uprange.smu.6</i>	-7,193.2	-12,578.6	-3,853.2
<i>uprange.smu.7</i>	-2,894.5	-8,425.8	900.0
<i>uprange.smu.8</i>	-10,020.6	-16,088.2	-4,778.5
<i>uprange.smu.9</i>	-14,029.2	-21,189.7	-7,179.4
<b>Anthropogenic Model</b>			
<i>isi.tone.pres.15</i>	666.9	309.9	1,053.9

The positive coefficient for *isi.tone.pres.15* indicated that the 5th quantile of offshore distance tended to be 0.67km (95% CI 0.31 to 1.05km) farther offshore when tones were present (Table 4). Fig. 4b plots the estimated 5th quantile of offshore distance for times with and without tones on a typical day of the season (21 September 2003). For comparison, with *isi.tone.pres.15* removed from the model, the predicted intersection of the 5th quantile and the centreline changed an average of 0.55km each day. Thus, the estimated anthropogenic effect (0.67km) was approximately equal to natural average daily changes, and was small when compared to the natural range of the 5th quantile (6.45km) observed during the entire season (Fig. 4b vs. 4a, Table 4). A similarly small but statistically significant anthropogenic effect was found in the autumns of 2001, 2002 and 2004 at times when levels of underwater sound near Northstar were elevated (Richardson *et al.*, In prep).

## DISCUSSION

The primary goal of this analysis was to demonstrate a statistical method appropriate for detecting and quantifying effects of a specific source of anthropogenic sound on a distribution of calling whales measured via acoustic localisation. Data from a single year (2003) of a 4-year study focusing on Northstar Island in the Beaufort Sea are used to demonstrate the method. Results from all four years of the project, and a discussion of the biological implications of those results will appear elsewhere (Richardson *et al.*, In prep). Statistical issues surrounding the analysis are discussed here, while biological interpretation, importance,

and management implications are addressed in the other paper. The statistical issues here centre on assumptions made during analysis and whether the analysis incorrectly detected an effect that was not actually present.

Throughout this discussion, it should be kept in mind that this was an observational study. An important assumption of observational studies is that all major sources of variation or disturbance are known, adequately measured, and correctly included in the appropriate models. This assumption becomes increasingly difficult to justify as the number of potential anthropogenic or natural effects increases. If nuisance variation is not adequately modelled, establishing the validity of primary effects can be difficult or impossible. Likewise, if multiple anthropogenic effects act cumulatively or interactively, quantifying the combination of factors that influence the primary response (here, the call distribution) may be difficult and never fully satisfactory. If either nuisance variation or an anthropogenic effect is not adequately modelled, the specific methods used here may not be adequate or may break down entirely. In this study, there is reason to believe that nuisance variation and anthropogenic effects were adequately modelled, as outlined below.

## Overall design

In many studies designed to detect impacts of human activities, data from a reference or control area are compared to those from an impacted area both before and after the supposed impact (McDonald *et al.*, 2000). Such designs are efficient for detecting anthropogenic effects, but are difficult

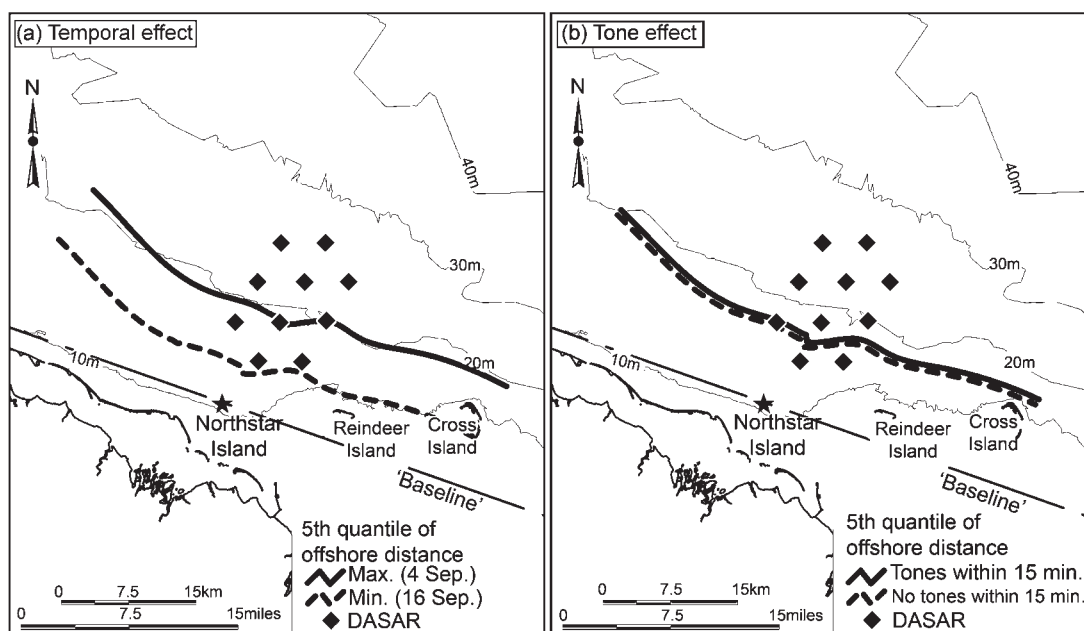


Fig. 4. Estimated 5th quantiles of offshore distance to whale calls at times in 2003 when (a) those quantiles were at their minimum and maximum distances offshore and (b) prominent anthropogenic tones were present vs. absent near Northstar. For (a), 5th quantiles were predicted by the final quantile regression model (Table 4) assuming no industrial sound effect (i.e. *isi.tone.pres.15* = 0). For (b), 5th quantiles were predicted by the final quantile regression model for a typical day (21 September 2003; *dayofyear* = 21) with and without prominent underwater tones during the 15min interval immediately preceding the call. In (b), estimated displacement with tones = 0.67km (95% CI = 0.31 to 1.10km).

to apply in an observational setting such as this. In Northstar's case, no nearby location was entirely appropriate as a reference area due to varying physical conditions and varying amounts of human activity along the coast. These human activities included boat traffic, oil exploration, oil production and subsistence hunting. In addition, no comparable 'before Northstar' data were available. Consequently, the 'reference' condition used here consisted of times when less anthropogenic sound was being emitted from Northstar, rather than reference areas.

The overall design assumed that a dose-response relationship existed between whale behaviour and anthropogenic sound. In particular, the analysis assumed that a whale receiving enough anthropogenic sound would change its calling behaviour or offshore distance in a way that would affect the distribution of calls. The design also assumed that at least some whales in the southern (proximal) part of the migration corridor would detect Northstar sound at times when elevated levels of Northstar sound were measurable ~500m from Northstar. This was an appropriate assumption because, at times, Northstar-related vessel sound is detectable above background sound levels at distances as far as 27km offshore (Blackwell and Greene, 2006).

### Interpretation of the response

Whether or not there is much physical displacement, it was recognised *a priori* that exposure of bowhead whales to Northstar sound might affect some aspect(s) of bowhead calling behaviour such as calling rate or source level of calls. Call types, frequencies, durations and received levels were logged during this study, and possible noise-induced changes in calling are being investigated (Blackwell *et al.*, unpublished data). In the meantime, the present analysis does not attempt to differentiate actual displacement from effects

on calling behaviour. A noise-related change in the distribution of bowhead calls represents a disturbance effect on some aspect(s) of bowhead whale behaviour regardless of the mechanism. Here, the two most likely mechanisms causing change in the call distribution are shifts in the physical distribution and changes in calling behaviour. However, Blackwell *et al.* (2012) found that bowhead calls were directional, thereby admitting the possibility that orientation of the individual could play a role in affecting the distribution of detectable calls. Regardless of the mechanism, identifying the presence and general magnitude of an anthropogenic effect is a useful step. Subsequent research should seek to identify the specific aspect(s) of behaviour that are subject to noise-induced effects.

### Offshore distances

The responses analysed here were offshore distances, defined as the perpendicular distances of calling whales from a 'baseline' oriented parallel to the broad-scale alignment of the coast and of bowhead migration in autumn (Figs 1–4). However, bowhead headings in autumn are quite variable (e.g. Würsig *et al.*, 2002), leaving open the possibility that the average direction of travel could differ from the baseline orientation by as much as  $\pm 10^\circ$ . To test whether choice of baseline orientation might have affected results, the baseline's orientation was changed by  $-10^\circ$ ,  $-5^\circ$ ,  $+5^\circ$  and  $+10^\circ$  (positive = counter-clockwise) and the significance of all terms in the best fitting model was re-computed. Under all four rotations of the baseline, all terms in the best fitting model remained significant at  $P \leq 0.011$ . Relative to its location when tones were absent, the 5th quantile of offshore distance with tones present was estimated to be displaced by 0.69, 0.68, 0.63 and 0.62km for rotations of  $-10^\circ$ ,  $-5^\circ$ ,  $+5^\circ$  and  $+10^\circ$ , respectively, as compared with 0.67km for  $0^\circ$



rotation. The 95% CIs were 0.26 to 1.07km for  $-10^\circ$ , 0.28 to 1.04km for  $-5^\circ$ , 0.28 to 1.00km for  $+5^\circ$ , and 0.26 to 0.97km for  $+10^\circ$ , vs. 0.31 to 1.05km for  $0^\circ$ . Thus, the results are robust in relation to plausible changes in baseline orientation.

### Radial distances

An obvious alternative to offshore distance as a response was the radial distance of calls from Northstar. Offshore distances were analysed because undisturbed bowheads are generally thought to migrate parallel to the coast, and offshore distances were thought to provide a more powerful and sensitive measure of displacement in this case. However, the predominant whale activity (i.e. migrating or feeding or milling, etc.) and the nature of the sound source (e.g. stationary or mobile) may affect which measure is most sensitive in other studies. Here, the question of sensitivity was largely moot because offshore distances were quite similar to radial distances in the relatively narrow east-west region where calls were located with sufficient precision to receive substantial weight in the analysis. Indeed, when the final quantile regression model was applied to radial distances, change in the 5th quantile of radial distance was 0.51km (95% CI = 0.22 to 0.81) when tones were present. These results are essentially identical to those for offshore distances (i.e. 0.67km, 95% CI = 0.31 to 1.05).

### Linearity of effects

The relationship between offshore distance and certain natural covariates could not be assumed linear, and was estimated (within the quantile regression) via trend-following techniques, i.e. B-splines. However, for simplicity the relationship between offshore distance and anthropogenic sound levels was assumed to be either linear or discontinuous (i.e. on-off). This assumption was made because the goal was detection of any anthropogenic effects, not detailed characterisation of its functional form. Fitting a linear relationship between offshore distance and anthropogenic sound levels will detect changes under a wide variety of potential non-linear relationships. For example, a linear model should detect change if whales displace a fixed distance or stop calling altogether in response to levels of anthropogenic sound above some threshold (i.e. a step or threshold effect).

It is possible that both linear and discontinuous terms might fail to detect certain complex non-linear relationships. For example, there might be attraction or increased calling rate as sound level increased from low to moderate, but avoidance or reduced calling rate at the highest sound levels. Thus, in other studies it might be desirable to consider non-linear functions of sound level. In this study, it is conceivable that a complex effect could be missed by fitting a linear or on-off relationship. However, we detected an apparent relationship, and it is inconceivable how that could occur fallaciously by assuming a linear or on-off relationship.

### Permutation blocks

Many passing whales were expected to emit a number of calls in succession, and this would cause statistical dependency in the locations (and resulting offshore distances) of individual calls. Because independent whales or independent whale pods could not be distinguished by

their calls, it was necessary to find a proxy for dependent groups that would neither over- nor under-estimate the strength and statistical significance of anthropogenic sound effects. Hierarchical cluster analysis was used to group call locations in time and space until there was no measurable autocorrelation between cluster centroids (Appendix 3). These clusters were then used to assess significance during all quantile regressions. This technique allowed for interdependence of offshore distances within the identified clusters, but treated separate clusters as uncorrelated.

The clusters no doubt incorporated calls from single whales calling repeatedly, calls from different whales within pods, and calls from whales within different pods that sometimes were in acoustic contact with one another. In other words, the cluster analysis could have identified either more or fewer uncorrelated groups of whales than actually existed. If too few clusters were identified, i.e. if two or more independent groups of whales were sometimes unnecessarily combined into one cluster, the power of the study to detect anthropogenic sound effects would be reduced. If too many clusters were identified, i.e. if an interdependent group of calls was sometimes split into two or more clusters, the risk of incorrectly rejecting the null hypothesis could be larger than the nominal significance level (here 5%). Given that the current analysis provided evidence of an effect of anthropogenic sound on the offshore distribution of calls, the concern here is that too many clusters might have been identified. If so, sample size was overrepresented and the apparent effect of Northstar sound on offshore distances might have been false (spurious).

In actuality, the structure of some clusters suggests that the number of groups was lower than necessary. A small number of clusters spanned extremely long time periods (on the order of a week), and most of these clusters were small and centred far from the DASAR array. It is implausible that all whales within such 'groups' were somehow interdependent. Such clusters probably included multiple uncorrelated groups and should have been split into two or more clusters.

Nonetheless, it was of interest whether the apparent Northstar effect would disappear if fewer clusters were used in the block permutation procedure. To investigate this, clusters were sorted based on average arrival time of all calls in the cluster, and pairs of temporally adjacent clusters were amalgamated to reduce the number of clusters by 50%. The best-fitting model was then re-estimated and significance levels were re-computed. The significance level of all non-industrial terms in the best model remained  $<0.001$  when half the number of clusters were used, and the significance of *isi.tone.pres.15* changed from  $P = 0.006$  under the original clustering to  $P = 0.009$  with  $\frac{1}{2}$  the number of clusters – within the error range of the permutation method. The estimate of displacement when anthropogenic tones were present within 15min preceding a call was unchanged, with slight variation in its confidence interval due to the stochastic nature of the permutation test (estimate = 0.67km with 95% CI 0.26 to 1.04km). Thus, even though the long time spans in some call clusters indicate that too few clusters may have been used in the main analysis, the results are robust in relation to uncertainty about the most appropriate number of clusters to use for block permutation.

### Sound averaging time

Prior to data collection, there was no specific basis on which to predict the averaging time most relevant to bowhead whales (see Analysis Methods/Model Selection, much earlier). Based partly on a pilot analysis, the current analysis considered averaging times of 15, 30, 45, 60, 70, 90 and 120min preceding the call in question. A broader exploratory analysis seeking alternative acoustic measures and averaging times most strongly related to changes in the distribution of calls might be interesting, but further exploratory analysis was not undertaken here. The present analysis identified a measure of sound that was significantly correlated with offshore distances (*isi.tone.pres.15*; Table 4), along with other acoustic measures that were (for 2003) almost as closely related (Table 3). Further exploration and testing of the data would have exacerbated concerns about multiple testing issues and the possibility of a spurious result (see 'Overfitting and data mining?', below).

### Model selection

The approach taken here allows, insofar as the data permit, for effects of natural environmental factors on the southern edge (5th quantile) of the distribution of calls offshore of Northstar. The method for selecting the best-fitting quantile regression model first incorporated a combination of non-industrial variables, and then assessed the ability of anthropogenic sound variables to explain remaining variation. This approach agrees with the usual ANOVA testing philosophy wherein the significance of the factor of primary concern (here anthropogenic sound) is assessed after accounting for variation explained by other factors. Allowance for the effects of natural covariates is expected to increase the power to detect and characterise the factor of main interest. However, with natural variables being fitted first, anthropogenic effects might appear insignificant if they were correlated with natural variables. For example, if industrial sound levels were higher during daylight than during night, and whales actually responded to industrial noise, adding *sunlight* to the model first could have masked the industrial effect. In this case, industrial sound levels and *sunlight* would be confounded. When a variable of interest is confounded with one or more other variables in an observational (uncontrolled) study, it is impossible to separate their effects by any analysis technique. Fortunately, in this study, anthropogenic sound measures showed no large correlations with natural variables that would indicate significant confounding or deleterious effects on interpretation. All model coefficients remained stable regardless of which other effects were included in the model.

Alternative model selection procedures might perform step-wise selection over all variables, not just natural ones, or might include more interactions among variables. This study incorporated a logical, constrained (non-open-ended) and repeatable model selection procedure that arrived at a useful model for detecting and characterising anthropogenic sound effects on the distribution of whale calls. An alternative model selection procedure utilising the same set of covariates might give a slightly different or refined picture of anthropogenic sound effects in 2003. However, given the similarities in goodness-of-fit for the 21

best-fitting models (Table 3), defensible alternative models utilising these measures of sound would almost certainly confirm the presence of a response to anthropogenic sound.

### Overfitting and data mining?

As this analysis procedure was developed and refined, there was discussion of multiple comparison issues, possible overfitting, and the increased likelihood of spurious effects when data are 'mined' for significant effects. This issue is directly related to the 'experiment-wise' alpha level of the study and to the idea that, with  $\alpha = 0.05$ , we might expect 2–3 seemingly-significant tests among 49 (the number of anthropogenic sound models considered) by chance alone. Historically, these topics have been a source of much discussion in the statistics literature (see Hochberg and Tamhane, 1987; Saville, 1990; Tukey, 1994). One point of view is represented by Saville (1990) who argued that all testing procedures designed to protect experiment-wise significance levels are inconsistent except the unrestricted least significant difference (LSD) procedure (or multiple *t* test). Other researchers control multiple comparison problems by testing only a constrained set of hypotheses defined *a priori* (Burnham and Anderson, 2002; 2004). Others argue that a correction similar to Bonferroni's (Miller, 1981; Steel *et al.*, 1996) should be done whether or not hypotheses were defined *a priori*. Many would argue that all results, however derived, are unconfirmed until replicated by independent studies. Here, multiple testing problems were controlled by testing a constrained set of hypotheses, in large part defined *a priori*, about anthropogenic sound effects. However, the sound hypotheses tested were not strictly *a priori* because analysis procedures evolved over an extended period of data collection, preliminary analysis and peer review. In addition, pilot analyses were used to confirm that sound averaging times in the 15 to 120min range were reasonable.

The key question is whether the identified effects and model are real and likely to be replicated in subsequent studies. The authors offer the following five arguments that results of this study are robust and will be substantiated in future.

- (1) It made sense *a priori* that some combination of the sound averaging times and anthropogenic sound measures would be related to displacement or changes in whale calling behaviour in the southern part of the migration corridor, if either were occurring.
- (2) Previous disturbance studies, corroborated by pilot analyses of Northstar data, indicated that sound averaging times within the range considered here were reasonable.
- (3) Several similar combinations of averaging time and sound measure were strongly related to offshore distances (Table 3); the chances that all these relationships were spurious are low.
- (4) Results are robust to revision of several key analysis decisions (i.e. inclusion probability weights, baseline orientation, identified clusters, and radial distances).

(5) Separate applications of this method to data from 3 additional autumn migration seasons (2001, 2002, 2004) has found anthropogenic sound effects each year, although the specific measure of sound most closely associated with the effect was different each year (Richardson *et al.*, In prep.).

Ultimately, verification (or otherwise) of a disturbance effect on the distribution of calling bowhead whales that receive relatively low levels of anthropogenic sound will come through additional data collection and replication. To help ensure future studies have similar or better power to detect the same sized effects, we recommend that (1) future studies focus on the most sensitive (proximal) portion of the spatial distribution (the southern edge of the migration corridor in this study), (2) additional covariates be considered where relevant, (3) whale identities be distinguished if possible, and (4) average calling rates for the population or (ideally) for individual whales be estimated if possible. If a future study has similar or higher power and is not confounded by the effects of additional factors (e.g. additional disturbance sources), it is reasonable to believe that the results described here will stand. If so, further work would be needed to determine whether the change in distribution of calling whales reflects a change in location of the whales, a change in calling behaviour, or both.

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## Appendix 1

### DETERMINING PROBABILITY OF DETECTION AND LOCALISATION

#### Methods

Probability of detecting and localising a whale call was estimated using two logistic regression analyses. First, a logistic regression function was estimated to model probability of detection by two or more DASARs as a declining function of distance from the centre of the DASAR array, measured background sound level at the time, and whether the source was east or west of the array. Other variables considered for inclusion were distance uprange parallel to the baseline, distance offshore perpendicular to the baseline, and non-linear (quadratic and log) transformations of these two distances. Calibration sounds projected from known locations and received (or not received) at various DASARs (Greene *et al.*, 2004) were used to estimate coefficients of this regression. Second, another logistic regression estimated probability of localising a call given that it was detected by 2+ DASARs. (Detection by multiple DASARs did not guarantee a location estimate; inability to localise occurred primarily when bearings were highly disparate and non-crossing.) Variables considered for inclusion in the second regression were measured background sound level at the time, call type, number of DASARs detecting the call, time of day, average low frequency of the call, average high

frequency, average duration (log transformed), average signal level, average signal-to-noise ratio, mean direction of bearings, dispersion among bearings, and the proportion of bearing intersections (out of  $n(n - 1) / 2$  possible intersections, arcsin transformed). All calls received by 2+ DASARs, and whether or not each yielded a location estimate, were used to estimate coefficients of the second regression.

Background sound levels used in both logistic models were measured at the DASAR farthest from Northstar (NE; Fig. 1). Northstar sounds were on occasion received at DASAR NE, but were less likely to propagate to that location than to closer DASARs, and were weaker at NE. A measure of total underwater sound at NE, both natural and anthropogenic, was acceptable as a proxy for background sound in these analyses because anthropogenic sounds recorded at NE were intermittent and (when detected) weak. Calls were in fact often recorded and localised during times of strong industrial sound.

Variable selection for both logistic regressions was conducted by forward selection using the AIC criterion (Burnham and Anderson, 2004), i.e. terms were added to the model one-at-a-time until the AIC statistic increased. Following variable selection via stepwise AIC, a generalised

linear mixed model identical to the first regression was estimated to check for and account for potential dependencies in the detection of calibration sounds (the independence of localisations given detection, an assumption of the second regression, was clearly reasonable). Dependencies in detections at different DASARs could have been introduced by un-modelled environmental conditions or by the human operators processing the calls. The generalised linear mixed models were estimated using the SAS GLIMMIX macro. Error structures examined were compound symmetric, spatial power, spatial Gaussian, and spatial exponential errors, along with the uncorrelated (independent) structure. Fit of all the generalised mixed linear models was assessed using AIC, and the one with lowest AIC was deemed best.

Given probability of detection by a single DASAR, modelled via the first logistic regression, probability of detection by 2 or more DASARs was computed as  $1 - \text{Pr}(\text{detection by 1 DASAR}) - \text{Pr}(\text{detection by 0 DASARs})$ . Probability of detection by 0 DASARs was computed as

$$P(\text{detection by 0 DASARs}) = (1 - p_{i1}) \times (1 - p_{i2}) \times \dots \times (1 - p_{in}),$$

where  $p_{ij}$  was the modelled probability of detecting call  $i$  on DASAR  $j$ . Probability of detection by exactly 1 DASAR was computed as

$$\begin{aligned} P(\text{detection by 1 DASAR}) &= p_{i1} \times (1 - p_{i2}) \times (1 - p_{i3}) \times \dots \times (1 - p_{in}) + \\ &\quad (1 - p_{i1}) \times p_{i2} \times (1 - p_{i3}) \times \dots \times (1 - p_{in}) + \\ &\quad \vdots \\ &\quad (1 - p_{i1}) \times (1 - p_{i2}) \times (1 - p_{i3}) \times \dots \times p_{in}. \end{aligned}$$

Given probability of detection by 2 or more DASARs and probability of obtaining a localisation given detection by 2+ DASARs, modelled via the second logistic regression, the joint probability of detecting and localising a call was computed as the product:  $\text{Pr}(\text{detection and localisation}) = P(\text{detection at 2+ DASARs}) P[(\text{obtain a location}) | (\text{detection at 2+ DASARs})]$ .

## Results

The final forward step-wise logistic regression for probability of detection by a single DASAR was

$$\ln \left( \frac{\pi_{ij}}{1 - \pi_{ij}} \right) = 63.947 - 5.395ddl - 0.373ambsound - 5.950upstream + 0.798ddl \times upstream + 0.023ddl \times ambsound - 0.013ambsound \times upstream.$$

where  $ddl$  was the natural logarithm of distance to DASAR,  $ambsound$  was ambient noise level, and  $upstream$  was the indicator variable for whether the call originated to the east or west of the DASAR array. When non-independent error structures were allowed in this model (using GLIMMIX), the model assuming independence had lowest AIC. Even under high ambient-noise conditions, this model predicted high overall probabilities of detection by 2+ DASARs ( $> 70\%$ ) inside the DASAR array. When ambient sound levels were lower, predicted probability of detection by 2+ DASARs was higher in all areas. Although  $upstream$  was involved in two interaction terms, the coefficients of these interaction terms were small relative to other coefficients. Given this, the relatively large negative coefficient of  $upstream$  itself caused the estimated probability of detecting a call to the southeast of the centreline to be lower than that to the northwest.

Locations were not obtained for ~4.4% of calls detected by 2+ DASARs. Among calls detected by exactly 2 DASARs, the non-location rate was slightly higher at 7.5% of calls. The final forward step-wise logistic regression model for the probability of obtaining a location given detection by 2+ DASARs was

$$\ln \left( \frac{\pi_{ld}}{1 - \pi_{ld}} \right) = -2.817 - 0.001xbar + 0.380ybar + 5.903intp - 0.535dur + 0.014s2n$$

where  $\pi_{ld}$  was the conditional probability of obtaining a location, the pair  $(xbar, ybar)$  was mean bearing direction,  $intp$  was proportion of bearing intersections (arcsin transformed),  $dur$  was call duration (logarithmic transformed), and  $s2n$  was average signal-to-noise ratio among the DASARs detecting the call. Most of the model's explanatory power was achieved through  $intp$ . AIC of the univariate model containing  $intp$  alone was very similar to AIC with all included variables (AIC = 7,217 with  $intp$  alone vs. 7,178 with all variables). All other univariate models were very poor predictors (AIC  $> 17,000$  for all).

## Appendix 2

### DROP IN DISPERSION TEST VIA BLOCK PERMUTATION

The drop in dispersion test proceeded as follows. The quantile regression residual for the  $i$ -th call in a model containing all effects under consideration was defined as

$$r_i^f = y_i - \sum_{j=0}^p \hat{\beta}_j^f x_{ij}$$

where  $y_i$  was offshore distance of the  $i$ -th call,  $x_{ij}$  was the value of the  $j$ -th covariate for the  $i$ -th call,  $\hat{\beta}_j^f$  was the estimated  $j$ -th covariate's quantile regression coefficient in the full model, and  $p$  was the total number of (non-intercept) covariates in the full model. Dispersion of the full model was

$$D_f = \sum_{i=1}^n w_i r_i^f (\tau - I(r_i^f < 0))$$

(Cade and Richards, 2006, Eqn. 2.1) where  $\tau$  was the quantile of interest (i.e. 0.05),  $n$  was the total number of calls in the data base,  $w_i$  was the weighting factor inversely proportional to the  $i$ -th call's error ellipse width and probability of inclusion, and  $I(r_i^f < 0)$  was an indicator function equalling one if  $r_i^f < 0$  and 0 if  $r_i^f \geq 0$ . Estimates of the coefficients  $\hat{\beta}_j^f$  were obtained by minimising  $D_f$ , so dispersion of the full model was simply the obtained minimum. The drop in dispersion test statistic was computed by dropping the covariate being tested from

the full model, recomputing coefficients and residuals of the now reduced quantile regression model (labelled  $\hat{\beta}_j^r$  and  $r_i^r$ ), and then recomputing the reduced value of dispersion  $D_r$ . The drop in dispersion test statistic was then

$$F_{\text{effect}} = \frac{D_r - D_f}{D_f}$$

(Cade and Richards, 2006, Eqn. 2.1).

To compute significance levels, the distribution of  $F_{\text{effect}}$  under the null hypothesis of no effect (i.e. when  $H_0: \hat{\beta}_j^f = 0$  was true) was required. Following standard permutation testing methods (Manly, 2007), the null distribution of  $F_{\text{effect}}$  was constructed using random block permutations of the original data as follows. A large number (999) of null data sets with  $\hat{\beta}_j^f$  exactly zero were obtained by randomly permuting blocks of partial residuals  $r_i^r$ , where blocks were defined by the hierarchical cluster analysis (Appendix 3), and associating them with un-permuted values of the explanatory variables. This permutation broke any association between responses and explanatory variables and assured that  $\hat{\beta}_j^f = 0$  in every permuted data set, yet preserved any correlation of residuals that existed within the clusters. The full and reduced models were re-fitted to the randomly permuted residuals and  $F_{\text{effect}}$  for the term being considered was recomputed. The distribution of these 999  $F_{\text{effect}}$  values plus the original  $F_{\text{effect}}$  represented the distribution of  $F_{\text{effect}}$  under the null hypothesis of no relationship. Significance of the term being considered was the number of  $F_{\text{effect}}$  greater or equal to the original  $F_{\text{effect}}$  out of 1,000, divided by 1,000.

Ninety-five percent confidence intervals for coefficients of *g(industry variables)* in the best fitting model were computed using Hall's percentile method (Hall, 1992, p.36; Manly, 2007, p.48). This method approximated the distribution of true errors in  $\beta_j$ , i.e.,  $\varepsilon = \hat{\beta}_j - \beta_j$ , by the distribution of coefficients,  $\hat{\beta}_j^*$ , obtained by fitting the best model to randomly permuted blocks of residuals. Both the distribution of  $\hat{\beta}_j^*$  and  $\varepsilon$  had zero means, and by construction, variation in the distribution of  $\hat{\beta}_j^*$  approximated the variation in  $\varepsilon$ . To compute the confidence interval for  $\beta_j$ , the percentiles  $\varepsilon_L$  and  $\varepsilon_H$  were computed from the distribution of 999 coefficients obtained by block permutation such that

$$\Pr(\varepsilon_L < \hat{\beta}_j^*) = \alpha / 2$$

and

$$\Pr(\hat{\beta}_j^* < \varepsilon_H) = 1 - \alpha / 2,$$

where  $\alpha = 0.05$ . Assuming the distribution  $\hat{\beta}_j^*$  of is a good approximation to the distribution of  $\varepsilon$ ,

$$\Pr(\varepsilon_L < \hat{\beta}_j - \beta_j < \varepsilon_H) \approx 1 - \alpha$$

so the  $100(1 - \alpha)\%$  confidence interval for  $\beta_j$  was

$$\hat{\beta}_j - \varepsilon_H < \beta_j < \hat{\beta}_j - \varepsilon_L.$$

Similarly, the  $100(1 - \alpha)\%$  CI for displacement of quantiles when sound was above ambient was

$$\hat{D} - d_H < D < \hat{D} - d_L$$

where  $d_L$  and  $d_H$  were computed as the  $(\alpha/2)$ -th and  $(1 - \alpha/2)$ -th percentiles of displacements computed from the 999 sets of coefficients obtained via block permutation.

## Appendix 3

### HIERARCHICAL CLUSTER ANALYSIS TO DETERMINE BLOCKS

Hierarchical, agglomerative clustering (Manly, 2005) was performed to group whale call localisations within a given autumn until cluster centroids were uncorrelated in time and space. Clustering started with  $N$  clusters, where each localisation was its own cluster, and cycled through a total of  $N-1$  iterations during which 2 clusters were merged to form a new cluster. During each iteration, Ward's algorithm (Ward, 1963) was used to determine which clusters were merged. At each iteration, space-time correlation among cluster centroids was calculated using Mantel's procedure (Legendre and Legendre, 1998), and agglomeration stopped when the Mantel Statistic was small and negative. The largest number of clusters with a negative correlation in space and time was chosen as the final clustering.

Mantel's procedure calculated the Spearman rank correlation coefficient (Conover, 1999) between corresponding elements of a  $N \times N$  spatial difference matrix and an  $N \times N$  temporal difference matrix. Unfortunately, it was not feasible to compute Mantel's statistics on more than ~6,400 clusters due to the large size of these matrices. When the number of calls was >6,400, a contiguous (in time) block of 5,000 clusters was randomly selected, Mantel's statistic was computed, and the average Mantel Statistic from 100 such randomly chosen (with replacement) blocks was used as the measure of correlation that stopped cluster agglomeration. All space-time coordinates were standardised prior to clustering by subtracting their mean and dividing by standard deviation (Manly, 2005).

Despite sub-sampling to compute Mantel's statistics, Ward's method could not be applied to data sets larger than ~6,400 observations (i.e. 2002–2004). Clustering was therefore performed separately on subsets of locations, where the subsets were chosen based on 90% error polygon size. To choose subsets, all localisations in a year were sorted based on 90% error polygon size, and contiguous blocks of 6,400 locations were taken as the subsets. As a check that sub-setting was not introducing correlation among calls in different subsets, the between-cluster and average within-cluster space-time correlations among all clusters in all subsets were calculated and observed to be a small negative number.

Clustering was accomplished using the contributed package CLUSTER (<http://cran.r-project.org/src/contrib/Descriptions/cluster.html>) and the R statistical software package (R Development Core Team, 2005). Computation of Mantel's statistic was accomplished in R using the contributed package VEGAN (Oksanen *et al.*, 2005).

In 2003, average space-time correlation prior to clustering was  $\bar{r} = 0.163$ . The 25,176 whale call localisations considered in 2003 were grouped into 3,000 clusters. The final between-cluster space-time correlation was  $-0.025$ , with average within-cluster space-time correlation of 0.089 (standard deviation = 0.48). The median distance in time between two localisations within a cluster was 13.9h.



# Genetic structure of common bottlenose dolphins (*Tursiops truncatus*) inhabiting adjacent South Florida estuaries – Biscayne Bay and Florida Bay

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## ABSTRACT

Coastal common bottlenose dolphins show a variety of migration and residency patterns adding to the difficulty of defining stocks for management purposes. Genetic structure plays an important role in identifying population stocks of dolphins. This study examines genetic differentiation in common bottlenose dolphins both between two social groups occurring in Biscayne Bay, Florida and between Biscayne Bay and an adjacent group of dolphins in Florida Bay. Skin biopsy samples were sequenced at the mitochondrial DNA (mtDNA) control region and genotyped at microsatellite loci. Significant genetic differentiation was found between bottlenose dolphins in Biscayne Bay and Florida Bay (mtDNA  $F_{ST} = 0.139$ ,  $p \leq 0.001$ ; microsatellite  $F_{ST} = 0.042$ ,  $p \leq 0.001$ ) supporting independent management stock status for these two populations. Within Biscayne Bay, evidence of weak but significant population differentiation was found between the two social groups using microsatellite markers ( $F_{ST} = 0.0149$ ,  $p \leq 0.009$ ); however, differentiation was not evident from the mtDNA-based estimates of  $F_{ST}$  and  $\phi_{ST}$ . The lack of differentiation at mtDNA coupled with field observations indicating overlapping home ranges for these two groups suggests ongoing, though perhaps low, levels of interbreeding. These data are insufficient to warrant splitting the Biscayne Bay management stock at this time.

KEYWORDS: GENETICS; BIOPSY SAMPLING; SITE FIDELITY; NORTH AMERICA; ATLANTIC OCEAN; COMMON BOTTLENOSE DOLPHIN

## INTRODUCTION

The common bottlenose dolphin (*Tursiops truncatus*) is found throughout temperate and tropical waters worldwide (Reynolds *et al.*, 2000). Two morphologically and genetically distinct bottlenose dolphin ecotypes exist in the western North Atlantic, a deep water ecotype (offshore) and a shallow water ecotype (coastal) (Hersh and Duffield, 1990; Hoelzel *et al.*, 1998; Mead and Potter, 1995; Rosel *et al.*, 2009). Coastal bottlenose dolphin populations vary extensively in residency patterns, migration and site fidelity (Hohn, 1997; Wells and Scott, 1999). For example, a seasonally migrating population of bottlenose dolphins spends winter months in the coastal waters of central North Carolina and migrates as far north as Long Island, New York during the summer (Rosel *et al.*, 2009; Waring *et al.*, 2008), while other bottlenose dolphins are year-round residents of embayments and estuaries along the southeast US Atlantic and Gulf of Mexico coasts (Rosel *et al.*, 2009).

Identifying population structure and distinguishing resident estuarine stocks is important for effective management and conservation of bottlenose dolphins. In the USA, the Marine Mammal Protection Act (MMPA) mandates that human-caused mortality and serious injury of a specific management stock should not exceed a level that would cause the stock to decline and/or prevent recovery of a depleted stock. The accurate identification and delineation of stocks for management purposes is critical to both determining population abundance status and in assigning human-caused mortalities to the correct stock. Within

estuarine systems, resident populations may be particularly susceptible to chronic impacts on survival and productivity associated with factors such as environmental toxins, disease and harmful algal blooms (Reeves and Ragen, 2003; Schwacke *et al.*, 2004). Hence, understanding the population boundaries and residence patterns is critical for understanding the exposure of stocks to these environmental stressors.

Photo-identification studies have been useful in determining residence patterns of dolphins; however, there is no consistent definition used to distinguish resident from non-resident groups. Residency has been described as a group of dolphins having stable home ranges or repeated occurrences in a given area over a period of years (Wells and Scott, 1999). Some estuarine populations have been studied long term (> 10 years) using photo-identification techniques and have animals that meet the above definition of residency; these include Charleston, South Carolina (Speakman *et al.*, 2006; Zolman, 2002), the Indian River Lagoon system on the Florida east coast (Mazzoil *et al.*, 2005) and Sarasota Bay on the Florida west coast (Wells, 1991; 2003). The variability of residency and migratory patterns observed for bottlenose dolphins, combined with a continuous distribution throughout the species' range, make it difficult to clearly define and distinguish resident populations.

In addition to other methods, genetic markers are commonly used to investigate population structure in dolphins (e.g. Curry and Smith, 1997; Rosel *et al.*, 1999; Wade and Angliss, 1997). Sellas *et al.* (2005) found

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significant genetic differentiation between resident bottlenose dolphins in Sarasota Bay, Florida and those found in nearshore coastal Gulf of Mexico waters just outside of Sarasota Bay. Their results indicate that little interbreeding is occurring, despite sightings of mixed groups of resident dolphins from Sarasota Bay with those primarily sighted in the nearshore Gulf of Mexico (Sellas *et al.*, 2005). Several other studies also have found genetic structure on a remarkably small geographic scale in bottlenose dolphins inhabiting unobstructed inshore habitats such as Little Bahama Bank, Bahamas (Parsons *et al.*, 2006). Rosel *et al.* (2009) found significant genetic differentiation among five populations of dolphins in the western North Atlantic spanning from Jacksonville, Florida north to New Jersey. Two of these populations were separated by as little as 80km (Georgia and Jacksonville) while others were thought to seasonally migrate and potentially overlap in space and time.

This study examines genetic differentiation both within bottlenose dolphins occurring in Biscayne Bay and between these and an adjacent group of dolphins in Florida Bay, Florida. Biscayne Bay is a shallow subtropical estuary located along the east coast of Miami-Dade County, Florida (Fig. 1). Northern Biscayne Bay is extensively developed and separates the cities of Miami and Miami Beach. The Bay opens to the Atlantic Ocean in the centre through a series of tidal channels and then extends south where it is less developed and connects to Florida Bay through Barnes and Blackwater Sounds. The National Marine Fisheries Service, Southeast Fisheries Science Center (NMFS/SEFSC) has been conducting a photo-identification (photo-ID) project of bottlenose dolphins in Biscayne Bay since 1990 (Litz, 2007). To date, over 200 individual dolphins have been catalogued and many of these appear to be long-term residents with sightings across multiple years and seasons (NOAA Fisheries, unpublished data). Analyses of the sighting histories and association patterns of known individuals from the Biscayne Bay photo-ID data demonstrated that there are at least two overlapping social groups of animals in the Bay; those that are sighted primarily in northern Biscayne Bay and those that are sighted primarily in southern Biscayne Bay (Litz, 2007).

Florida Bay is bounded by the mainland of Florida to the north, the Florida Keys to the east and south, and is open to the Gulf of Mexico to the west (Fig. 2). It is divided into a series of semi-isolated shallow basins by mudbanks and mangrove islands that restrict circulation (Torres and Urban, 2005). Studies suggest that bottlenose dolphins are present throughout Florida Bay year-round (Engleby *et al.*, 2002; McClellan *et al.*, 2000). In May of 2003, a targeted mark-recapture study was conducted and estimated the abundance of bottlenose dolphins using Florida Bay during that month as 514 (Read *et al.*, pers. comm.).

Biscayne and Florida Bays have no geographic barriers preventing bottlenose dolphins from travelling throughout or beyond the Bays; therefore, resident dolphins from either Bay could mix and possibly interbreed with neighbouring dolphin communities. However, if mating between social groups or embayments is rare, genetic divergence could develop over time. This study used both maternally inherited mitochondrial DNA and biparentally inherited microsatellite markers to investigate genetic differentiation of dolphins

within Biscayne Bay, particularly between the identified northern and southern social groups. In addition, samples from dolphins inhabiting Biscayne Bay were compared to those from Florida Bay to investigate the genetic differentiation between dolphins inhabiting these adjacent embayments.

## METHODS

### Biopsy sample collection and sighting histories

Skin samples were obtained from common bottlenose dolphins in Biscayne Bay using remote biopsy techniques with a dart fired from a modified .22 caliber rifle (Hansen *et al.*, 2004). Samples were primarily collected between May 2002 and April 2003 ( $n = 63$ ) with 19 additional samples collected during November 2003 and March 2004. Field days were rotated throughout the Bay and survey effort was varied by time of day and location to minimise the chance of encountering the same dolphins. This sampling regime was designed to ensure the samples collected reflected the true diversity of the Biscayne Bay community. Biopsy darts were quickly retrieved and the samples were removed and processed immediately. Skin was separated from the blubber and stored at room temperature in 20% dimethyl sulfoxide (DMSO) saturated with sodium chloride. The blubber was placed in cryogenic Teflon vials in and stored in a  $-80^{\circ}\text{C}$  freezer for storage for organohalogen pollutant analyses (Litz *et al.*, 2007). Darts, forceps and scalpel handles were cleaned using a method similar to that described by Hansen *et al.* (2004).

During biopsy collection, the dorsal fin of each sampled animal was photographed using digital video and/or still photography. These dorsal fin photos were compared to the NOAA Fisheries, SEFSC Biscayne Bay bottlenose dolphin photo-ID catalogue (Litz, 2007). For each sampled animal that was matched to the catalogue, the mean latitude and mean longitude of the animal's sighting history was calculated and used as the geographic reference for the sample. If an animal was sighted more than once during a survey day, only the first sighting of that day was used for that individual. The mean was chosen because it is weighted towards the majority of the animal's sightings and can be used as a continuous variable. For any tests that required an *a priori* geographic division of the data, animals with mean latitudes north of  $25.61^{\circ}\text{N}$  were considered northern and animals with mean latitudes south of  $25.61^{\circ}\text{N}$  were considered southern. If a sample could not be matched to the catalogue, the sample collection site was used for its geographic reference. Sample sizes are listed in Table 1.

Skin biopsy samples were collected from bottlenose dolphins in Florida Bay using similar methods in 1998 and 2002 during a collaborative study among the National Ocean Service, the Dolphin Ecology Project and NOAA Fisheries (Fair *et al.*, 2003). All skin samples were stored at room temperature in 20% DMSO saturated with sodium chloride.

### DNA extraction and sexing

Skin (15–25mg) was minced and digested in 250 $\mu\text{l}$  of extraction buffer [10mM Tris HCl (pH 8), 2mM EDTA (pH 8), 10mM NaCl, 1% SDS, 8mg/ml DTT, and 0.2mg/ml proteinase K] overnight at  $50^{\circ}\text{C}$  (Rosel and Block, 1996). The DNA was extracted from the homogenised tissue using two

phenol-chloroform (v/v 1:1) extractions and one chloroform extraction in Phase Lock gel® tubes (Eppendorf). The DNA was ethanol-precipitated and re-suspended in 10mM Tris HCl (pH 7.6), 1mM EDTA (pH 8), and stored at –20°C.

Molecular sexing of the Biscayne Bay samples was completed using a multiplex PCR reaction that targets both the ZFX genes from the X chromosome and the SRY gene from the Y chromosome (Rosel, 2003). The primers, PCR reaction and cycling profile used were the same as those described by Rosel (2003) with the exception that the concentration of DNA in the samples was unknown. Therefore, 2.0µl of DNA template was added to each 25µl reaction. Florida Bay biopsies were sexed in one of three ways: as in Rosel (2003) directly from skin or from DNA, or under identical conditions of Rosel (2003) but using only three primers: ZFX0923R, ZFY00767R, ZFYX0582F (Bérubé and Palsbøll, 1996).

### Mitochondrial DNA sequencing

Biscayne Bay samples were sequenced at a laboratory within the University of Miami. A 356 base pair segment of the control region of the mitochondrial DNA was amplified using the primers L15824 and H16265 (Rosel *et al.*, 1999). Samples collected in Biscayne Bay were amplified in 25µl PCR reactions containing 20mM Tris HCl pH 8.0, 50mM KCl, 0.1% Tween 20, 1.5mM MgCl<sub>2</sub>, 0.25µM of each primer, 200µM dNTPs, 1 unit of Taq DNA polymerase, and 2µl of DNA template. The thermal cycler profile consisted of initial denaturation at 94°C for 2 minutes, 30 cycles of 94°C for 10 seconds, 50°C for 10 seconds, and 72°C for 20 seconds, followed by a final extension of 5 minutes at 72°C. PCR products were purified by ExoSAP-IT® (USB Corporation) by adding 2µl of ExoSAP-IT® to 5µl of PCR product and incubating at 37°C for 15 minutes followed by 80°C for 15 minutes. PCR products were cycle-sequenced using the same forward primer and 2µl of purified product following protocols supplied by the manufacturer of the Big Dye® terminator v1.1 cycle sequencing kit (Applied Biosystems, Inc.). Approximately one-third of the DNA samples were also cycle-sequenced using the reverse primer to verify sequence accuracy. Products were cleaned with Sephadex columns (Princeton Separations) according to manufacturer's directions and resolved using an ABI Prism® 310 Genetic Analyzer (Applied Biosystems, Inc.). Sequences were edited and aligned using Bioedit v5.0.9 (Hall, 2001).

Florida Bay samples were amplified and sequenced at the NOAA Fisheries SEFSC Marine Mammal Molecular Genetics Laboratory using the same primers as the Biscayne Bay samples. Concentrations of the DNA extractions from Florida Bay were measured using a fluorometer (Amersham Biosciences). Samples were amplified in 25µl PCR reactions containing 20mM Tris HCl pH 8.4, 50mM KCl, 1.5mM MgCl<sub>2</sub>, 0.3µM of each primer, 150µM dNTPs, 1.25 unit of Taq DNA polymerase, and 25ng of DNA template. The thermal cycler profile consisted of initial denaturation at 94°C for 30 seconds, 35 cycles of 95°C for 30 seconds, 55°C for 30 seconds, and 72°C for 30 seconds, followed by a final extension of 7 minutes at 72°C. PCR products were purified by gel purification (1% SeaPlaque® GTG® Agarose in 1×TAE) followed by agarase treatment. PCR products were cycle-sequenced in both the forward and reverse directions

using 1µl of purified product following protocols supplied by the manufacturer of the Big Dye® terminator v1.1 cycle sequencing kit (Applied Biosystems, Inc.). Cycle sequencing products were cleaned by ethanol precipitation and resolved using an ABI Prism® 3130 Genetic Analyzer (Applied Biosystems, Inc.). Sequences were edited in Sequence Navigator (Applied Biosystems, Inc.), and aligned in SeqPup v0.6 (Gilbert, 1995).

### Microsatellites

Biscayne Bay samples were genotyped at 14 loci and Florida Bay samples were genotyped at 10 of the same loci. For logistical reasons, the genotyping occurred in two different laboratories. Three loci were analysed from different samples in both laboratories. Raw data from these loci were analysed in allelogram (available at: <http://code.google.com/p/allelogram/>) with binning normalised by a control sample. The Allelogram analysis confirmed that there were no scoring differences between the two laboratories. At the University of Miami, Biscayne Bay samples were PCR amplified at seven microsatellite loci (Appendix 1) developed by Caldwell *et al.* (2002). Each PCR reaction contained 20mM Tris-HCl, pH 8.0, 50mM KCl, 0.1% Tween 20, 1.5mM MgCl<sub>2</sub>, 0.25µM of each primer, 200µM dNTPs and 1 unit of Taq DNA polymerase. 2µl of DNA template was added to each 25µl reaction. The thermal cycler profile consisted of initial denaturation at 94°C for 2 minutes, followed by 30 cycles of 94°C for 10 seconds, annealing temperature (Appendix 1) for 10 seconds, and 72°C for 20 seconds, followed by a final extension of 5 minutes at 72°C. Each locus was amplified alone and then TtruGT6, TtruGT48, TtruGT39, TtruAAT40, TtruAAT44, and TtruGT162 were diluted at a v/v 1:20 ratio with water and co-loaded for genotyping. TtruGT51 was loaded independently. All samples were genotyped on an ABI Prism® 310 Genetic analyzer at the University of Miami using the Genescan-500 Tamara size standard (Applied Biosystems, Inc.). Genotyping used the Genotyper 2.1 and Genescan Analysis 3.1 software (Applied Biosystems, Inc.).

The Biscayne Bay samples were genotyped at seven additional loci (Ttr04, Ttr11, Ttr19, Ttr34, Ttr48, Ttr58, Ttr63) (Rosel *et al.*, 2005) at the NOAA Fisheries Laboratory. Twenty-five microliter amplification reactions consisted of 20mM Tris-HCl, pH 8.4, 50mM KCl, 1.5mM MgCl<sub>2</sub>, 200µM dNTPs, 1 unit of Taq DNA polymerase, 25ng of DNA template, and primer concentrations varied from 0.16µM to 0.4µM as listed in Appendix 1. Thermal cycler profiles are listed in Appendix 1. Three pairs of loci were multiplexed (Ttr04 and Ttr11; Ttr34 and Ttr48; Ttr58 and Ttr63) and each pair was loaded separately for genotyping. Ttr19 was PCR amplified and loaded independently.

These seven loci were also used to genotype the Florida Bay samples along with TtruGT39, TtruGT48 and TtruGT51 (Caldwell *et al.*, 2002) (Appendix 1). DNA from one sample was used as a positive control and a negative control with no DNA was run with each set of amplifications. All Florida Bay samples and these seven loci for Biscayne Bay samples were genotyped on an ABI Prism® 310 Genetic analyzer using the Genescan 500 Tamara size standard (Applied Biosystems, Inc.). Genotyping used the Genotyper 2.1 and Genescan Analysis 3.1 software (Applied Biosystems, Inc.).



### Statistical analyses

Genetic structure within Biscayne Bay was investigated by comparing northern Biscayne Bay dolphins (NBB, mean latitudes north of 25.61°N) to southern Biscayne Bay dolphins (SBB, mean latitudes south of 25.61°N). Florida Bay data were compared to Biscayne Bay as a whole and to each of the Biscayne Bay subgroups, NBB and SBB. There were seven pairs of animals sampled in Biscayne Bay that were known from the photo-ID study to be mother/calf pairs. Data from the known mother/calf pairs were compared to ensure they had shared at least one allele at each locus. Calves were excluded from all other analyses.

For the mtDNA data, haplotype ( $h$ ) and nucleotide ( $\pi$ ) diversity (Nei, 1987) were calculated using the program Arlequin (Nei, 1987; Schneider *et al.*, 2000). Pairwise  $F_{ST}$  and  $\phi_{ST}$  values between Florida Bay and Biscayne Bay and within Biscayne Bay were estimated using an analysis of molecular variance (AMOVA) in Arlequin (Excoffier *et al.*, 1992; Schneider *et al.*, 2000; Weir and Cockerham, 1984). Evolutionary distances between the sequences were estimated using the Tamura-Nei model (Tamura and Nei, 1993) with no gamma correction. The significance values for both  $F_{ST}$  and  $\phi_{ST}$  were obtained by 10,000 permutations; sequential Bonferroni corrections were applied to the  $p$  values (Rice, 1989). To represent the differences among haplotypes, a phylogenetic network was constructed using the software Network and the median-joining algorithm. The recommended default settings were used (weights 10, epsilon 0). The network was re-calculated with increasing epsilon values (by increments of 10 up to 60) to confirm the full median network had been calculated with the default parameters (Bandelt *et al.*, 1999).

For the microsatellite data, Hardy-Weinberg Equilibrium and linkage disequilibrium tests were conducted on Biscayne Bay data (14 loci) and Florida Bay data (10 loci) using GENEPOP (Raymond and Rousset, 1996). A Markov chain method was used to estimate  $p$  values using the following parameters: dememorisation of 1,000, 1,000 batches and 1,000 iterations per batch with the exception of the linkage disequilibrium test where 2,000 batches were run (Guo and Thompson, 1992). Sequential Bonferroni corrections were applied to all  $p$  values (Rice, 1989). Tests for duplicate samples were carried out using the program Identity (Amos, 2000). Probabilities of identity ( $P_{ID}$ ) were estimated using the software Gimlet (Valière, 2003). Gimlet provides both an unbiased estimate of  $P_{ID}$  and  $P_{IDsibs}$ , which is a more conservative measure of the power of the microsatellite data to resolve siblings. Expected and observed heterozygosities were calculated in GENALEX 6 (Peakall and Smouse, 2006). GENALEX 6 was also used to estimate  $F_{ST}$  (Wright, 1965) by AMOVA (Excoffier *et al.*, 1992; Weir and Cockerham, 1984).  $F_{ST}$  was calculated between Florida Bay and Biscayne Bay using 10 loci.  $F_{ST}$  was also calculated within Biscayne Bay using all 14 loci genotyped and results were very similar. Therefore, the results from the tests using the 10 loci in common between Biscayne Bay and Florida Bay are presented. The significance values were obtained by 10,000 permutations and sequential Bonferroni corrections were applied to the  $p$  values (Rice, 1989).

Pairwise relatedness values were estimated among all individuals within each sampling location (Biscayne Bay and

Florida Bay) using the web based software RERAT (Lynch and Ritland, 1999; Schwacke and Rosel, 2005). The average  $r$  value for the known mother/calf pairs was 0.507. As a result one member of each pair with an  $r > 0.5$  was removed in addition to the seven known calves. Pairwise  $F_{ST}$  and  $\phi_{ST}$  were re-estimated from the mtDNA data and pairwise estimates of  $F_{ST}$  were recalculated from the microsatellite data using the same methods described above.

The software 'STRUCTURE' (Pritchard *et al.*, 2000) was used to investigate population structure using the microsatellite data without requiring *a priori* divisions of the data. STRUCTURE uses a Bayesian clustering technique to probabilistically assign individuals with multilocus genotypes to one or more populations based on Hardy-Weinberg expectations and linkage equilibrium (Pritchard, 2004; 2000). Models were run under the admixture ancestry model and the no admixture model. Results from the two ancestry models were similar and results from the admixture model are presented. The correlated allele frequency model was applied, which assumes that the frequencies in the different populations are likely to be similar, probably due to migration or shared ancestry (Falush *et al.*, 2003; Pritchard, 2004). The results presented were obtained with a burn-in length of 100,000 followed by a run length of 100,000. The models were run for several values of  $K$  (1, 2, 3, 4 and 5 populations) using the microsatellite data from 10 loci with both Biscayne Bay and Florida Bay samples combined. The model for each  $K$  was run independently five times to verify stability in results. The model gives the log likelihood of the data conditional on the specified  $K$  and the posterior probability of each  $K$  was calculated assuming a uniform prior of  $K$  (Pritchard, 2004). A larger posterior probability indicates the best fit model.

## RESULTS

### Sample collection and sex determination

Sixty-five survey days were completed in Biscayne Bay during which 135 biopsy attempts were made. A total of 82 skin samples were collected; 17 of which were duplicates as determined by photo analysis. An additional nine skin samples were obtained during preliminary sampling in 2000 and four samples were obtained from animals that stranded in Biscayne Bay, for a total of 78 samples (Fig. 1). Seventy-four percent of samples collected were matched to the NOAA, SEFSC Biscayne Bay photo-ID catalogue. The remaining 26% of sampled animals could not be matched to the catalogue because they either had a distinct fin not recognised in the catalogue, a non-distinct fin, or poor photos and/or video of the biopsy attempt prevented identification. A total of 53 samples were available from Florida Bay (Fig. 2).

Mitochondrial DNA sequencing identified a total of 10 samples (2 from Biscayne Bay and 8 from Florida Bay) with offshore haplotypes (details discussed below). These animals are not likely to be residents of the embayments and were therefore removed from all statistical analyses. In addition, the Identity (Amos, 2000) program indicated eight pairs of identical samples from the microsatellite data. The agreement of sequence and sex information for these pairs was verified. In each case, at least one member of the pair had not been identified or matched to the photo-ID catalogue,

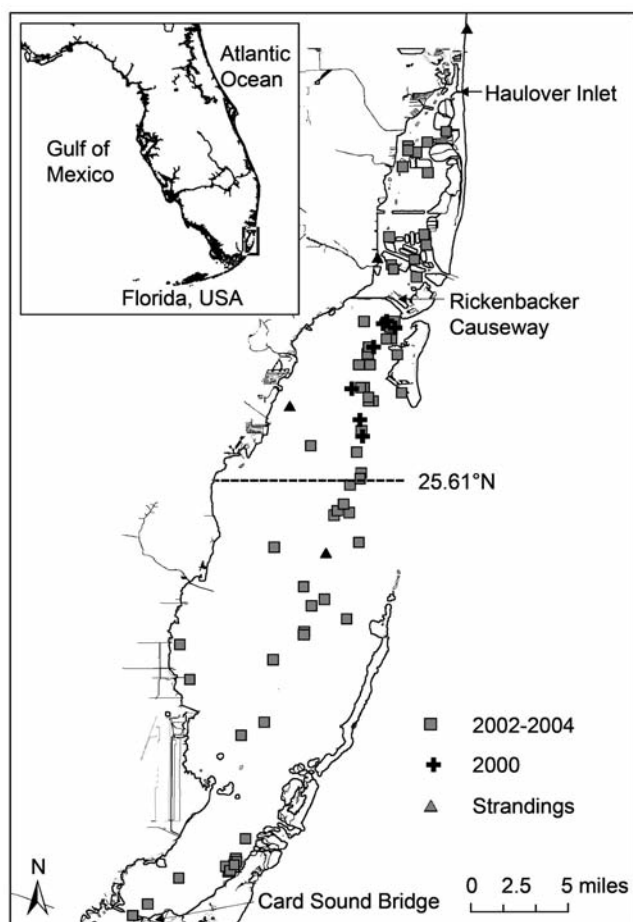


Fig. 1. Location of skin biopsy samples and four samples from stranded dolphins collected from Biscayne Bay, FL.

such that it was possible that the same animal was sampled twice. One member from each of these pairs (6 from Biscayne Bay and 2 from Florida Bay) was removed from all data analyses. Of the remaining 70 samples from Biscayne Bay, 26 were females, 42 were males and two samples could not be sexed due to poor DNA quality. Thirty-six of the samples were from dolphins from northern Biscayne Bay and 34 were from southern Biscayne Bay. Of the remaining 43 samples from Florida Bay, 31 were males and 12 were females. The probability of two individuals having identical genotypes ( $P_{ID}$ ) in Biscayne Bay (14 loci) is  $7.86 \times 10^{-12}$  and  $P_{ID\text{sib}}$  is  $4.34 \times 10^{-5}$ . In Florida Bay (10 loci) the  $P_{ID}$  is  $1.57 \times 10^{-8}$  and  $P_{ID\text{sib}}$  is  $8.86 \times 10^{-4}$ .

### Mitochondrial DNA sequences

The mitochondrial control region was sequenced and aligned from all Biscayne Bay and Florida Bay samples. Offshore haplotypes were identified based on fixed site differences in the sequences and phylogenetic analysis. Four offshore haplotypes were found with eight variable sites, two insertion/deletions and six transitions (Appendix 3, Genbank accession numbers GQ504085, GQ504087, HQ383684 and HQ383685). Three of the offshore haplotypes were found in eight Florida Bay samples and one was found in two samples from dolphins stranded in Biscayne Bay. Seven coastal haplotypes were found with 11 variable sites consisting of one insertion/deletion and 10 transitions (Appendix 3, Genbank accession numbers AY997307 – AY997309,

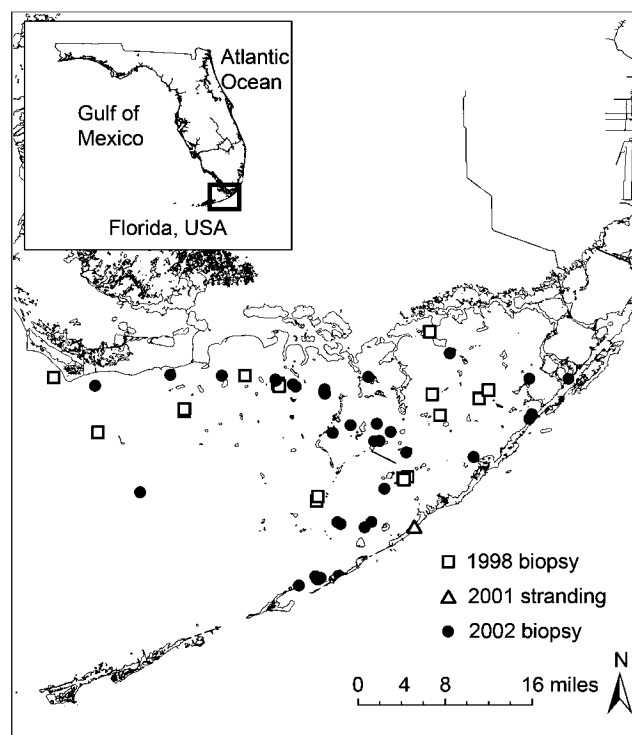


Fig. 2. Location of skin biopsy samples and one sample from a stranded dolphin collected from Florida Bay, FL.

GQ504101, GQ504103, GQ504049 and HQ383686). Three of the coastal haplotypes were found in both Bays, two were unique to Biscayne Bay, and two were unique to Florida Bay (Table 1). The two most common haplotypes in Florida Bay were not found in Biscayne Bay and the two most common haplotypes in Biscayne Bay were found in Florida Bay at the lowest frequencies. The median-joining network of the seven coastal haplotypes is shown in Fig. 3.

Both haplotype and nucleotide diversity based on coastal haplotypes were higher in Florida Bay than Biscayne Bay (Table 1). While samples from each Bay consisted of five coastal haplotypes, more than 70% of the Biscayne Bay samples consisted of two haplotypes (Ttr32 or Ttr15), whereas the haplotypes were more evenly distributed in Florida Bay. The mtDNA sequence data indicate significant differentiation between Florida Bay and Biscayne Bay as a

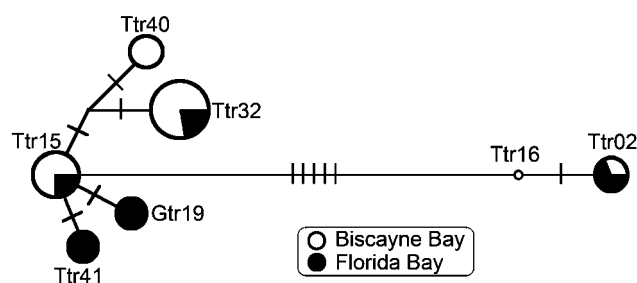


Fig. 3. Median-joining network of coastal haplotypes generated by the median-joining algorithm (Bandelt *et al.*, 1999). The size of the circle representing each haplotype is proportional to the frequency of that haplotype in the total sample. The colours represent the proportion of the haplotypes found in each population (Florida Bay in black and Biscayne Bay in white). The branch lengths are proportional to the number of changes between the haplotypes and each hash mark represents one change. One intermediate ancestral node is indicated between Ttr15, Ttr40, and Ttr32.

Table 1

mtDNA coastal haplotypes; number of samples per haplotype ( $n$ ) and frequency (Freq.) per population. Numbers in parentheses indicate the number of calves from known mother/calf pairs removed from the analyses. The frequencies were calculated from the data excluding these seven calves.

mtDNA coastal haplotypes	All Biscayne Bay ( $n = 70$ )		North Biscayne Bay ( $n = 36$ )		South Biscayne Bay ( $n = 34$ )		Florida Bay ( $n = 43$ )	
	$n$	Freq.	$n$	Freq.	$n$	Freq.	$n$	Freq.
Ttr02	4	0.064	4	0.133	0	0	9	0.209
Ttr15	17(1)	0.270	6(1)	0.200	11	0.333	6	0.140
Ttr16	1	0.016	0	0	1	0.031	0	0
GTtr19	0	0	0	0	0	0	11	0.256
Ttr32	29(4)	0.460	17(3)	0.567	12(1)	0.364	8	0.186
Ttr40	12(2)	0.190	3(2)	0.100	9	0.273	0	0
Ttr41	0	0	0	0	0	0	9	0.209
Haplotype diversity	$0.6856 \pm 0.0357$		$0.6322 \pm 0.0772$		$0.7027 \pm 0.0295$		$0.8117 \pm 0.0174$	
Nucleotide diversity	$0.0061 \pm 0.0038$		$0.0073 \pm 0.0045$		$0.0047 \pm 0.0032$		$0.0096 \pm 0.0056$	

whole ( $F_{ST} = 0.1388, p \leq 0.0001$ ;  $\phi_{ST} = 0.1677, p \leq 0.0001$ ) and also between Florida Bay and each of the Biscayne Bay subgroups (Table 2). No significant difference was found between the two geographic subgroups of Biscayne Bay ( $F_{ST} = 0.0463, p = 0.0684$ ;  $\phi_{ST} = 0.0344, p = 0.1034$ ). Results did not change after estimating relatedness and removing 10 individuals from Biscayne Bay and 5 individuals from Florida Bay (Biscayne Bay vs. Florida Bay:  $F_{ST} = 0.1305, p \leq 0.0001$ ;  $\phi_{ST} = 0.1810, p \leq 0.0001$ ; Within Biscayne Bay:  $F_{ST} = 0.0159, p = 0.2226$ ;  $\phi_{ST} = 0.0350, p = 0.1200$ ).

### Microsatellite loci

The Biscayne Bay samples were genotyped at 14 loci and the Florida Bay samples were genotyped at 10 loci. Sixteen private alleles were found across the 10 loci in common, 13 of which were found only in Biscayne Bay and three only in Florida Bay. All loci were in Hardy-Weinberg Equilibrium (HWE) after sequential Bonferroni correction, and pair-wise tests for linkage showed no significant linkage disequilibrium. The number of alleles per locus, observed vs. expected heterozygosity and HWE  $p$ -values are listed in Table 3. Analyses reveal significant differentiation between Florida Bay and Biscayne Bay as a whole ( $F_{ST} = 0.0416, p \leq 0.001$ ), and also between Florida Bay and each of the Biscayne Bay subgroups (Table 2). A significant  $F_{ST}$  was also found between the northern and southern Biscayne Bay subgroups ( $F_{ST} = 0.015, p = 0.009$ ). Results did not change after estimating relatedness and removing one animal from each pair where  $r > 0.5$  (Biscayne Bay vs. Florida Bay:  $F_{ST} = 0.0380, p \leq 0.001$ ; within Biscayne Bay:  $F_{ST} = 0.0138, p = 0.024$ ).

Table 2

mtDNA  $F_{ST}$  and  $\phi_{ST}$  statistics and microsatellite  $F_{ST}$  statistics for pairwise comparisons between Florida Bay (FB), Biscayne Bay as a whole (BB), northern Biscayne Bay dolphins (NBB), and southern Biscayne Bay dolphins (SBB).

	mtDNA		Microsatellite
	$F_{ST}$	$\phi_{ST}$	$F_{ST}$
BB vs. FB	0.1353, $p \leq 0.0001$	0.1658, $p \leq 0.0001$	0.0407, $p \leq 0.0001$
NBB vs. FB	0.1357, $p \leq 0.0001$	0.1396, $p = 0.0011$	0.0509, $p \leq 0.0001$
SBB vs. FB	0.1437, $p \leq 0.0001$	0.1788, $p \leq 0.0001$	0.0380, $p \leq 0.0001$
NBB vs. SBB	0.0463, $p = 0.0638$	0.0344, $p = 0.1034$	0.0149, $p = 0.0074$

The results from the STRUCTURE model runs indicate the best fit model for the Biscayne Bay and Florida Bay samples combined is the two population model ( $K = 2$ ; Table 4). The two population model ( $K = 2$ ; Fig. 4), shows a split that corresponds exactly to the division of Florida Bay and Biscayne Bay samples in the data. The three population model ( $K = 3$ ; Fig. 4) was unable to differentiate a third population division. The results from testing four and five populations ( $K = 4$  and  $K = 5$ , respectively) were similar to that of three populations and are not shown.

### DISCUSSION

Haplotype diversity found in the Biscayne Bay mtDNA sequences was similar to that found in other inshore resident dolphin populations in Sarasota Bay, FL, Charlotte Harbor, FL, Matagorda Bay, TX and Abaco Island, Bahamas (Parsons *et al.*, 2006; Sellas *et al.*, 2005) and was higher than that found in three communities of dolphins in Jacksonville, FL (Caldwell, 2001). In a study of five bottlenose dolphin populations in the northwest Atlantic, Rosel *et al.* (2009) found inshore resident populations had lower diversity than nearshore coastal dolphin populations. The haplotype diversity of Biscayne Bay was higher than those found in the inshore populations in Rosel *et al.* (2009) but still lower than the nearshore coastal animals. Florida Bay's haplotype diversity was slightly higher than Biscayne Bay and very similar to that found in a nearshore coastal Gulf of Mexico dolphin population off Sarasota, Florida (Sellas *et al.*, 2005). The haplotype diversity was also higher than the nearshore coastal bottlenose dolphins along the US Atlantic Coast (Rosel *et al.*, 2009). The higher diversity in Florida Bay compared to Biscayne Bay may be explained by the distribution of haplotypes. Florida Bay haplotypes were more evenly distributed across samples, whereas the majority of Biscayne Bay samples (73%) had one of two haplotypes. The greater haplotype diversity found in Florida Bay and the higher presence of offshore haplotypes implies that there may be a greater degree of mixing, and possibly a larger population size, in Florida Bay than Biscayne Bay. Future studies of residency patterns in Florida Bay dolphins may help verify this.

Significant genetic differentiation was found between Biscayne Bay and Florida Bay in both the mtDNA control region ( $F_{ST}$  and  $\phi_{ST}$ ) and the microsatellite loci ( $F_{ST}$ ).



Table 3

Number of microsatellite alleles (Na), observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), and Hardy-Weinberg Equilibrium p-value (p) per locus and population.

Locus	All	Biscayne Bay				Florida Bay			
	Na	Na	$H_o$	$H_e$	p	Na	$H_o$	$H_e$	p
Ttr04	7	7	0.705	0.743	0.095	6	0.744	0.720	0.350
Ttr11	6	6	0.787	0.794	0.900	6	0.744	0.768	0.284
Ttr19	4	4	0.246	0.237	0.208	3	0.535	0.501	1.000
Ttr34	5	5	0.667	0.607	0.825	4	0.465	0.513	0.413
Ttr48	5	5	0.300	0.323	0.409	3	0.163	0.226	0.115
Ttr58	4	3	0.459	0.493	0.250	4	0.535	0.574	0.012
Ttr63	14	13	0.869	0.850	0.280	10	0.907	0.852	0.810
TtruGT39	4	4	0.656	0.591	0.450	4	0.535	0.526	0.800
TtruGT48	6	6	0.610	0.594	0.543	3	0.571	0.544	0.641
TtruGT51	9	8	0.787	0.725	0.576	8	0.791	0.771	0.635
TtruAAT40	–	5	0.656	0.614	0.629	–	–	–	–
TtruAAT44	–	4	0.567	0.518	0.565	–	–	–	–
TtruGT142	–	6	0.869	0.788	0.235	–	–	–	–
TtruGT6	–	7	0.733	0.677	0.260	–	–	–	–

STRUCTURE also differentiated the two populations without requiring *a priori* assignments. The estimates of  $F_{ST}$  from the microsatellite data and the mtDNA data were similar to  $F_{ST}$  values found between bottlenose dolphins in other regions (including between Sarasota Bay, FL and the nearshore coastal Gulf of Mexico and between populations around Abaco Island Bahamas; Table 5) (Parsons *et al.*, 2006; Sellas *et al.*, 2005). The microsatellite  $F_{ST}$  was also similar to that found between bottlenose dolphins in other parts of the world including between those in the Western and Eastern Mediterranean Sea (Natoli *et al.*, 2005) and between the United Kingdom and Northeast Scotland (Nichols *et al.*, 2007). The genetic differentiation found between Florida Bay and Biscayne Bay in both maternally inherited mtDNA and biparentally inherited nuclear markers suggests both male and female philopatry to their respective Bays.

It has been suggested that complex social structure, differential habitat utilisation and foraging specialisation may all contribute to natal site fidelity and thus reduced dispersal in both sexes (Natoli *et al.*, 2005; 2004; Parsons *et al.*, 2006; Rosel *et al.*, 2009; Sellas *et al.*, 2005). For example, significant genetic differentiation among five populations of bottlenose dolphins along the US east coast was attributed to habitat differences and social facilitation of foraging strategies (Rosel *et al.*, 2009). It is possible that both social structure and differential habitat utilisation play a role in the site fidelity observed in both Biscayne Bay and Florida Bay. Social structure analysis of Biscayne Bay dolphins

showed strong evidence of long term social bonds (Litz, 2007). Female bottlenose dolphins have been shown to strongly associate with other females in groups called bands (Connor *et al.*, 2000). Analysis confirmed the presence of female bands in Biscayne Bay and identified at least one female calf who rejoined her natal group (Litz, 2007). Several long-term male pair bonds were also identified in Biscayne Bay, supporting the idea that lack of dispersal of both sexes could be linked to complex social bonds. While Biscayne Bay and Florida Bay do not have vastly different habitat types, there are subtle differences. Northern Biscayne Bay has poor water circulation within largely manmade shorelines (mostly seawalls). Southern Biscayne Bay is much more open with natural mangrove shorelines and Florida Bay is divided into semi-isolated basins divided by mangrove islands and mud banks. While bottlenose dolphins in general show a wide range of foraging behaviours, some specialised behaviours have been observed in these areas. For example, dolphins in northern Biscayne Bay have been observed using the seawall to help catch fish (NOAA, unpublished data). Individual dolphins in Florida Bay have been shown to specialise in one of several foraging tactics, including a very specific mud-ring feeding behaviour rarely seen elsewhere (Torres and Read, 2009). These authors found strong evidence that dolphins in Florida Bay limited their spatial distribution to habitats that are most suitable for that foraging type leading to strong site fidelity. The strong genetic differentiation found between Biscayne Bay and Florida Bay indicates restricted genetic exchange between them. This result, coupled with distinct foraging strategies in both locations further supports the growing body of evidence that bay and estuarine populations of bottlenose dolphins exhibit strong site fidelity and limited genetic exchange with nearby populations despite a lack of barriers to movement and genetic exchange.

At least two social groups of bottlenose dolphins are present in Biscayne Bay, a northern (NBB) and southern (SBB) group (Litz, 2007). Analysis of organic pollutants in the dolphins' blubber provides evidence that these social groups are foraging in different areas of Biscayne Bay (Litz *et al.*, 2007). Despite these differences, many of the animals have overlapping sighting histories in the centre of the Bay

Table 4

Estimated posterior probabilities of K [Pr (K/X)] calculated from the estimated prior distributions of K [ln Pr(X/K)] from the outputs of the STRUCTURE model runs. The K with the greatest probability represents the best fit model and is indicated in bold font.

Number of populations	Florida Bay and Biscayne Bay (10 microsatellite loci)	
	ln Pr (X/K)	Pr (K/X)
K = 1	–2,707	~0
K = 2	–2,604	<b>1</b>
K = 3	–2,658	~0
K = 4	–2,673	~0
K = 5	–2,811	~0

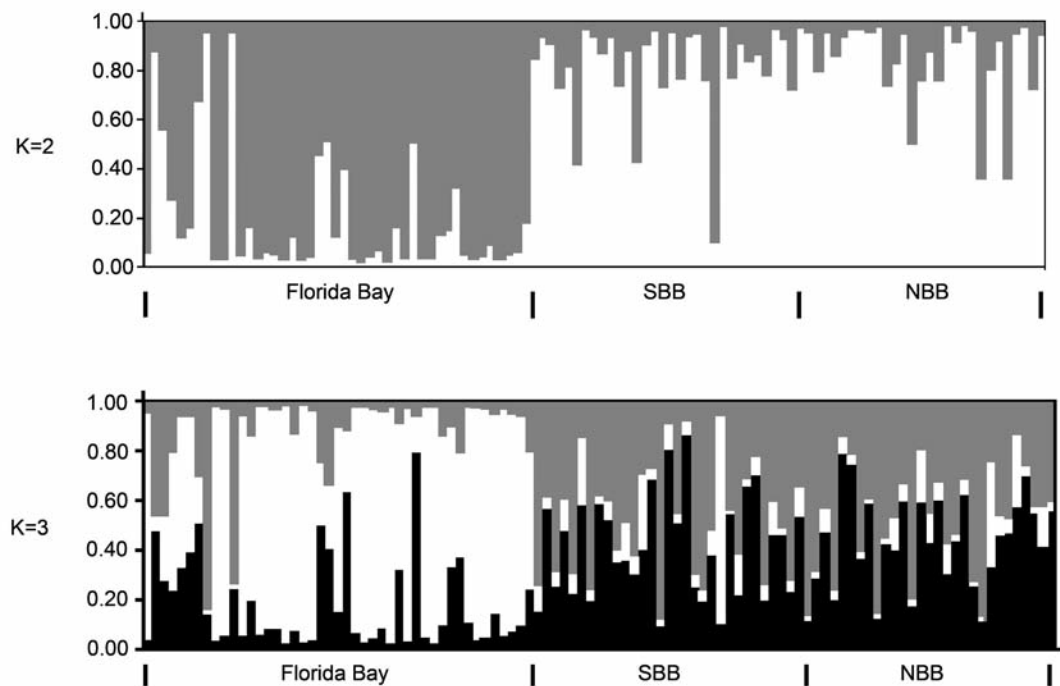


Fig. 4. Output from STRUCTURE runs for two and three populations ( $K = 2$  and  $K = 3$ , respectively) using microsatellite data from 10 loci with Biscayne Bay and Florida Bay samples combined. Each bar represents an individual and the shading represents the proportion ( $y$ -axis) of the individual's genome drawn from each putative population. The regional affiliations of the samples [Florida Bay, southern Biscayne Bay (SBB), and northern Biscayne Bay (NBB)] are labelled below the  $x$ -axis.

and about a third of the photo-ID sightings contain animals from both social groups providing opportunity for interbreeding (Litz, 2007). The social groups are weakly, but significantly differentiated at the microsatellite markers ( $F_{ST} = 0.0149$ ,  $p \leq 0.009$ ), however the mtDNA based estimates of  $F_{ST}$  and  $\phi_{ST}$  within Biscayne Bay were not significant. The lack of significant population structure at the maternally inherited mitochondrial locus within Biscayne Bay is possibly a result of low statistical power. The mtDNA is a single locus, and in this case, seven haplotypes were found but only two were common in Biscayne Bay samples. On the other hand, microsatellite data are highly polymorphic and each locus acts as an independent marker. Therefore, they have the power to describe small genetic differences between populations (Kalinowski, 2002). While no strong evidence of significant population structure within Biscayne Bay was found, the possibility that structure exists but there was insufficient power to detect it cannot be excluded. Additional studies should be conducted to increase the sample size.

Population differentiation runs on a continuum from complete isolation to complete panmixia (Waples and Gaggiotti, 2006). Determining at what point on the continuum two groups should be managed as separate stocks is difficult. The differences in haplotype and genotype frequencies found between Biscayne Bay and Florida Bay and the stable residency patterns observed in Biscayne Bay dolphins (Litz, 2007) provide strong evidence that Biscayne Bay and Florida Bay should be managed as separate biologically-relevant stocks. Within Biscayne Bay, the significant but low level of genetic differentiation at microsatellite markers indicates limited levels of genetic exchange between the two social groups. However, given that the two groups share a single embayment and have overlapping sighting histories, the low value of the  $F_{ST}$  (0.01) and the lack of a significant  $F_{ST}$  value from the mtDNA marker does not provide enough evidence to warrant managing the two social groups as separate biologically-relevant stocks at this time.

Table 5

Comparisons of mtDNA and microsatellite  $F_{ST}$  values for Biscayne and Florida Bays compared to published studies on other bottlenose dolphin populations.

Study areas	mtDNA $F_{ST}$	Microsat. $F_{ST}$	Reference
Biscayne Bay vs. Florida Bay	0.139	0.042	This study
Sarasota Bay vs. Gulf of Mexico	0.113	0.042	Sellas <i>et al.</i> (2005)
3 locations in Abaco, Bahamas	0.192	0.040	Parsons <i>et al.</i> (2006)
Sarasota Bay vs. Tampa Bay	0.137	0.027	Sellas <i>et al.</i> (2005)
Sarasota Bay vs. Matagorda Bay	0.284	0.043	Sellas <i>et al.</i> (2005)
Northern vs. southern Jacksonville	0.698	0.044	Caldwell <i>et al.</i> (2001)
Northern vs. coastal Jacksonville	0.456	0.042	Caldwell <i>et al.</i> (2001)
Eastern vs. western Mediterranean	0.032	0.045	Natoli <i>et al.</i> (2005)
Western United Kingdom vs. NE Scotland	0.049		Nichols <i>et al.</i> (2007)

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## Appendix 1

### GENBANK ACCESSION NUMBERS, FLUORESCENT DYE LABELS, ANNEALING TEMPERATURES, PRIMER CONCENTRATIONS AND ALLELE SIZE RANGES FOR MICROSATELLITE PRIMER PAIRS

Locus	GenBank Accession no.	Dye label	Biscayne Bay			Florida Bay		
			Anneal Temp.	Primer Conc. (μM)	Allele size range	Anneal Temp.	Primer Conc. (μM)	Allele size range
Ttr04*	DQ018982	6-FAM	62	0.20	109–123	62	0.16	109–119
Ttr11*	DQ018981	TET	62	0.20	203–215	62	0.20	203–215
Ttr19*	DQ018980	6-FAM	60	0.15	183–197	60	0.24	183–197
Ttr34*	DQ018984	TET	58	0.15	183–193	58	0.30	183–193
Ttr48*	DQ018983	TET	58	0.20	130–140	58	0.20	130–138
Ttr58*	DQ018985	HEX	63	0.16	179–187	60	0.16	179–197
Ttr63*	DQ018986	6-FAM	63	0.40	102–136	60	0.40	102–134
TtruGT39 <sup>#</sup>	AF416504	6-FAM	55	0.50	154–160	55	0.20	154–160
TtruGT48 <sup>#</sup>	AF416505	HEX	55	0.50	185–223	55	0.24	193–199
TtruGT51 <sup>#</sup>	AF416506	6-FAM	60	0.50	201–217	61	0.28	203–221
TtruAAT40 <sup>#</sup>	AF416500	TET	60	0.50	155–164	–	–	–
TtruAAT44 <sup>#</sup>	AF416501	HEX	60	0.50	82–94	–	–	–
TtruGT142 <sup>#</sup>	AF416507	6-FAM	60	0.50	195–205	–	–	–
TtruGT6 <sup>#</sup>	AF416503	TET	55	0.50	193–214	–	–	–

\*Rosel *et al.* (2005); <sup>#</sup>Caldwell *et al.* (2002).

## Appendix 2

### PCR THERMAL CYCLER PROFILES RUN FOR FLORIDA BAY SAMPLES (10 LOCI) AND BISCAYNE BAY SAMPLES (7 Ttr LOCI ONLY)

	94°C initial denaturation	No. of cycles	94°C	Annealing temp, time	72°C	72°C final extension
Ttr04 and Ttr11	30 sec	30	20 sec	62°C, 20 sec	40 sec	10 min
Ttr19	30 sec	30	20 sec	60°C, 20 sec	40 sec	10 min
Ttr34 and Ttr48	30 sec	28	20 sec	58°C, 20 sec	20 sec	10 min
Ttr58 and Ttr63	30 sec	28	30 sec	60°C, 40 sec	40 sec	15 min
TtruGT39 and TtruGT48	30 sec	30	20 sec	55°C, 20 sec	1 min	15 min
TtruGT51	30 sec	30	20 sec	61°C, 20 sec	40 sec	15 min

## Appendix 3

**POLYMORPHIC SITES IN mtDNA SEQUENCE FOR COASTAL AND OFFSHORE HAPLOTYPES WITH THE SITE NUMBER LISTED AT THE TOP OF EACH COLUMN**

Site number 1 is equivalent to site #62 in the published sequence for GTtr19, Genbank accession number AY997307 (Sellas *et al.*, 2005). A dash indicates a gap and a dot represents identity with the first sequence.

Genbank accession no.		27	74	98	121	152	196	285	286	296	327	328
<b>Coastal haplotypes:</b>												
Ttr32	GQ504101	T	–	T	A	C	G	T	C	T	G	A
Ttr02	AY997308	C	C	.	G	T	A	C	T	.	A	.
Ttr15	GQ504049	.	–	.	.	.	A	.	.	.	A	.
Ttr16	AY997309	C	C	.	G	T	A	C	.	.	A	.
GTtr19	AY997307	.	–	C	.	.	A	.	.	.	A	.
Ttr40	GQ504103	.	–	.	.	.	A	.	.	C	.	.
Ttr41	HQ383686	.	–	.	.	.	A	.	.	.	A	G
		47	105	111	276	277	286	306	332			
<b>Offshore haplotypes</b>												
OTtr21	GQ504085	A	A	G	T	C	C	G	C			
OTtr23	GQ504087	.	G	.	.	–	T	.	T			
OTtr69	HQ383684	.	G	A	–	.	.	A	.			
OTtr49	HQ383685	G	.	.	.	.	.	.	.			





# Collisions of sailing vessels with cetaceans worldwide: First insights into a seemingly growing problem

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## ABSTRACT

Vessel-whale collisions are of growing concern worldwide, but information about collisions involving sailing vessels is especially scarce. This study represents the first global quantification of this kind. A total of 111 collisions and 57 near misses were identified, spanning from 1966 until 2010; 75% of cases was reported for the period from 2002–2010, suggesting an increasing trend. Reported collisions and near misses occurred on all oceans, often during ocean races and regattas, and were most frequent in the North Atlantic. Vessel type and speed as well as circumstances of the incident varied widely, but most often monohulls were involved, predominantly sailing at speeds between 5 and 10 knots. Most reports referred to ‘large whales’ as opposed to ‘small whales’ or ‘dolphins’. The species could be identified in 54 cases. Most recognised animals were humpback or sperm whales. Injuries to the whales varied strongly from ‘not visible’ to ‘dead after collision’, but mostly could not be determined. Sailing crew members were hurt in several cases, including collisions occurring at low speeds, and collisions often damaged vessels, including major impairment and seven cases of vessel loss. The findings presented here suggest that elevated vessel speed contributes to a higher risk of collisions. Conversely, the outcome of a collision (e.g. injury to whale or crew, damage to vessel) appears not to be a direct function of vessel speed. Several measures are discussed which potentially can contribute to mitigating the problem, including placing watchposts, an open dialogue with regatta organisers, changes in the design of regattas and ocean races and public outreach initiatives.

KEYWORDS: CETACEANS; MORTALITY; SAILING VESSELS; SURVEY-ONLINE; SHIP STRIKES

## INTRODUCTION

Collisions between vessels and cetaceans are of growing concern on a global scale. Historical records of collisions date back to the early 17th century, and the worldwide number of collisions appears to have increased steadily during recent decades (IWC, 2008; Laist *et al.*, 2001). Today, collisions may significantly affect the status of cetacean populations in certain areas of the world, namely where both cetaceans and shipping traffic are concentrated (ACCOBAMS, 2005; Carrillo and Ritter, 2010; Panigada, 2006; Pesante *et al.*, 2002). While the issue meanwhile has entered discussions at international levels, with the International Whaling Commission (IWC) playing a major role in raising knowledge and awareness, it is still not known how many whales and/or dolphins are hit each year, although it is widely accepted that collision numbers are mostly underestimated and generally increasing (IWC, 2008).

The types of vessels involved in collisions with whales include tankers, cargo or cruise ships, but also whalewatching vessels, navy ships, hydrofoils, high speed ferries and sailing vessels (Carrillo and Ritter, 2010; Jensen and Silber, 2004; Laist *et al.*, 2001; Van Waerebeek *et al.*, 2007). Information about collisions involving sailing vessels is especially scarce. Despite anecdotal accounts of collisions between sailing boats and cetaceans, no systematic investigation has been conducted. The present study is focused on instances where sailing vessels had a collision or near miss with a cetacean, the reports on which were obtained from a variety of sources.

Most cases where whales were known to be severely hurt or killed occurred at vessel speeds of 14 knots or more and were caused by large ships of 80m or more in length (Laist *et al.*, 2001). While sailing vessels usually are of smaller size, modern racing yachts including multihull vessels frequently reach speeds of more than 20 knots, thereby likely increasing

both collision risk and probability of injuries for humans and cetaceans.

The aim of this study was to examine the issue with a focus on the circumstances under which collisions occur, the types of sailing vessels involved, the prevalence of collisions, possible trends in collisions and risks posed to animals, vessels and sailing crew.

## METHODS

A variety of sources were used to collect collision cases. Initially, the internet was searched for vessel-whale strikes. Additionally, the Google Alert<sup>1</sup> function was used from June 2006 to 31 March 2010; this automatically delivers search results, i.e. links to websites, where defined search words ‘collision whale’ and ‘Kollision Wal’ were detected. This search resulted in regular references to websites (here termed ‘internet reports’) which subsequently were inspected for collision reports involving sailing vessels. Additionally, 16 international internet websites related to world sailing activities and five sailing magazines were contacted. Furthermore, through co-operation with one of the major worldwide sailing websites (*noonsite.com*), an online survey was established.

For this survey, a questionnaire was elaborated including questions about the most important features (based on the IWC ship strike database<sup>2</sup>) of a collision or near miss event. The questions included time, day and location of collisions or near miss events and factors like vessel size, hull type and speed. Enquiries were also made about species type (‘large whale’, ‘small whale’ or ‘dolphin’) and species identification. It was also asked if whales were seen before a collision (or, in the case of a near miss, before a potential

<sup>1</sup> Google Alert is a search engine based internet crawler obtaining keyword related search results from news, web, blogs, and groups.

<sup>2</sup> [http://iwcoffice.org/sci\\_com/shipstrikes.htm](http://iwcoffice.org/sci_com/shipstrikes.htm).

impact), if any avoiding manoeuvres were taken, or if any injuries were observed on the animals after the collision. Other questions dealt with possible injuries to vessel crew, vessel damage, etc. The survey asked 19 questions about the actual incidents and additional information about the identity of the reporter. The questionnaire can be downloaded at [m-e-e-r.de/442.1.html](http://m-e-e-r.de/442.1.html).

The survey was put online in June 2006 and simultaneously announced on *noonsite.com* and *m-e-e-r.org* and via a press release. Additionally, the MARMAM discussion group and the e-mail discussion group of the European Cetacean Society (ECS) were used to announce the online survey and to find out if members of the marine mammal researcher community were aware of any collision or near miss events. A near miss was defined as a close encounter of a vessel with a cetacean (i.e. animal within 30 metres or less) bearing a collisions risk but not leading to an impact.

Survey entries and internet reports were collected until 31 March 2010. Survey entries that did not yield useful information were discarded. Only those cases were considered when a whale had been seen. Where assumptions were made on whether it could have been some other object, records were not taken into account for analyses. Where necessary, the following steps were taken to make data quantifiable: for vessel speed, to receive a more conservative value, the lower value of a given range was set as the travel speed of the vessel. Concerning species identification, the species status was categorised into: (1) *definite*, when there appeared to be no doubt about the species, sometimes with records of distinctive morphological features or behaviours of the animals observed; (2) *probable*, when there was little doubt about the species identity, sometimes with records of distinctive morphological features or behaviours observed; and (3) *possible*, when there was considerable doubt about the identity of the species. For analysis by species, only categories (1) and (2) were considered. The question regarding vessels being 'under sail' or 'motoring' sometimes was answered as 'motorsailing'. These cases were classified as 'motoring', because the crucial aspect here is the vessel engine running (as the potential predominant acoustic cue to the animals). Evidence of vessel damage was further classified into: (1) *minor*, when sailing could be continued without restrictions; (2) *major*, when sailing was only possible in a limited manner; and (3) *vessel loss*, when the vessel finally had to be abandoned or turned out to be irreparable.

## RESULTS

The internet search resulted in 45 reports on collisions and two reports of near miss events. The online survey yielded a total of 66 reports on collisions and 55 reports of near miss events. Thus, a total of 111 collisions and 57 near misses were identified. The majority of internet reports delivered answers to only a fraction of the questions asked because they usually were relatively broad in scope. Likewise, many contributors to the online survey did not answer all questions.

The temporal distribution of incidents spanned from 1966 until 2010 for collisions and from 1979 until 2010 for near miss events. The annual number of reports ranged from 0 to 21 collisions and from 0 to 11 near miss events. 72 (75%) occurred in the period from 2002 until 2010 (see Fig. 1).

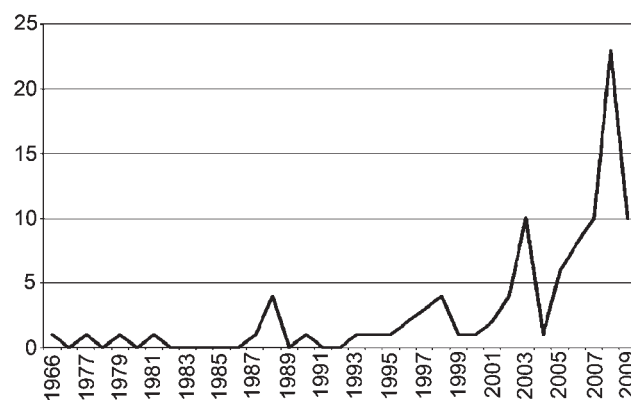


Fig. 1. Number of reported collisions ( $n = 98$ ) between sailing vessels and cetaceans per year worldwide (1966–2009)

Due to the generic difference of collision and near miss events, especially in light of the dissimilarity of their outcomes, results will be presented separately here. Percentage numbers mostly refer to the numbers of cases for which information was available. Accordingly, missing percentages represent the fraction of survey entries without answers or where the answer was 'Not known', and absent information in internet reports, respectively.

### Near miss events

Out of the total of 57, 55 incidents (96.5%) were reported by sailors directly involved and two were found on the internet. The majority of near miss events occurred in the Atlantic Ocean ( $n = 32$ ; 56.2%), 29 in the North Atlantic including the Caribbean Sea and three in the South Atlantic. Eighteen incidents were reported for the Pacific Ocean (12 in the North and 6 in the South Pacific). The Mediterranean Sea accounted for two cases, the Indian Ocean for three, and two were reported from other areas (see Table 1).

A total of 75.4% vessels were monohulls ( $n = 43$ ), and two catamarans. The majority of vessels were made of fibreglass ( $n = 39$ ), followed by aluminium ( $n = 12$ ) with a few vessels being made of wood ( $n = 2$ ) or steel ( $n = 1$ ). The size of the vessels ranged from less than 10m ( $n = 6$ ) to more than 20m ( $n = 1$ ). Most vessels were 10–15m ( $n = 36$ , 62.2%) and three were 15–20m long (see Table 2).

Forty-five near misses (78.9%) occurred during day time, 9 (15.8%) at partial light (dawn/dusk) and two at night time (darkness). 30 times, the animal were seen before the near miss (see Table 2).

During the incident, most vessels were under sail ( $n = 38$ , 66.7%), while 9 (15.8%) were either motoring or motorsailing. The speed of the vessels varied from 2 to 9 knots ( $n = 42$ ). Most vessels travelled at 5–10 knots ( $n = 30$ ), and 12 less than 5 knots (see Fig. 2).

Sixteen sailors reported that they took manoeuvres to avoid the collision (which otherwise they believed would have been very likely), and four reported that they saw the animals only when it was too late to take any action. In 36 cases, the animal was reported to be missed by only a few metres (<15m, most often much less). Four times it was apparently inquisitive behaviour, e.g. approaches by the animals that led to a near miss.

On 35 occasions (61.4%) the animal was categorised as a 'large whale' and 11 times (19.3%) as a 'small whale' (see

Table 1

Locations of collisions and near miss events between sailing vessels and cetaceans (1966–2010).

Location	Collision ( <i>n</i> = 106)	Near miss ( <i>n</i> = 57)	Total ( <i>n</i> = 165)	Total (%)
North Atlantic Ocean	43	26	69	41.8
Caribbean Ocean	5	3	8	4.8
South Atlantic Ocean	12	3	15	9.1
North Pacific Ocean	14	12	26	15.8
South Pacific Ocean	21	6	27	16.4
Northern Indian Ocean	1	2	3	1.8
Southern Indian Ocean	4	1	5	3.0
Mediterranean Sea	3	2	5	3.0
Baltic Sea	1	0	1	0.6
Other	4	2	6	3.6

Table 2

Collisions and near miss events between sailing vessels and cetaceans worldwide (1966–2010): vessel size, vessel type, light conditions and detection of whales.

		Collision	Near miss	Total	Total %
Vessel size	<10m	7	6	13	12.0
	>10m	43	36	79	73.1
	>15m	6	3	9	8.3
	>20m	6	1	7	6.5
	<i>n</i>	62	46	108	
Vessel type	Monohull	64	43	107	88.4
	Catamaran	8	2	10	8.3
	Trimaran	4	0	4	3.3
	<i>n</i>	76	45	121	
Light	Day time	53	45	98	71.5
	Dawn/dusk	9	9	18	13.1
	Night time	19	2	21	15.3
	<i>n</i>	81	56	137	
Whale seen before?	Yes	22	30	52	43.0
	No	54	15	69	57.0
	<i>n</i>	76	45	121	

Table 3a). In 22 instances, the cetacean species was identified. These included sperm whales (*n* = 9), right whales (*n* = 3), gray whales (*n* = 2), humpback whales (*n* = 3) and fin whales (*n* = 2). One case each was reported for blue whales and pilot whales (see Table 3b). However, in 35 cases no species identification was provided. There were no reports about injuries to crew or vessel.

### Collisions

Of a total of 111, 54 incidents (48.6%) were reported by the sailors directly involved and 52 (46.8%) were found on the internet. The majority of collisions occurred in the Atlantic Ocean (*n* = 60, 54.1%), 48 in the North Atlantic including the Caribbean Sea and 12 in the South Atlantic. 35 (31.5%) incidents were reported for the Pacific Ocean (14 in the North and 21 in the South Pacific). The Mediterranean Sea accounted for three cases, the Indian Ocean for five (one in the Northern Indian Ocean and four in the Southern Indian Ocean, see Table 1). Two collisions were caught on film<sup>3</sup>.

Some 82.1% of vessels were monohulls (*n* = 64), 10.3% were catamarans (*n* = 8) and 5.1% were trimarans (*n* = 4). The size of the vessels ranged from less than 10m (*n* = 7) to more than 20m (*n* = 6). Most vessels were 10–15m (*n* = 43)

Table 3

Collisions and near miss events between sailing vessels and cetaceans worldwide (1966–2010). (a) ID category and (b) species identification.

	Collision ( <i>n</i> = 67)	Near miss ( <i>n</i> = 46)	Total ( <i>n</i> = 113)	Total (%)
<b>(a) ID category</b>				
Large whale	51	35	86	76.1
Small whale	12	11	23	20.4
Dolphin	4	0	4	3.5
	Collision ( <i>n</i> = 32)	Near miss ( <i>n</i> = 22)	Total ( <i>n</i> = 54)	Total (%)
<b>(b) Species</b>				
Humpback whale	15	3	18	34.6
Sperm whale	9	9	18	34.6
Gray whale	3	3	6	11.5
Right whale	1	3	4	7.7
Fin whale	1	2	3	5.8
Blue whale	0	1	1	1.9
Pilot whale	1	1	2	3.8
Orca	1	0	1	1.9
Common dolphin	1	0	1	1.9

and six were 15–20m long (see Table 2). The majority (*n* = 55, 76.3%) of vessels were made of fibreglass, with smaller numbers made of wood (*n* = 7), steel (*n* = 5) or aluminium (*n* = 2).

A total of 53 collisions (47.7%) occurred during day time, 9 (8.1%) at partial light (dawn/dusk) and 19 (17.1%) at night time (darkness). In 54 cases (48.6%), the animals were not seen before the collision (see Table 2). This was only the case for 22 incidents (see Table 2). However, in 63 cases (56.8%) the animals were seen after the collision.

Most vessels were under sail (*n* = 86, 90.5%) while 9 (9.5%) were either motoring or motorsailing. 38 (34.2%). Collisions were reported occurring during sailing regattas, most of these being ocean races.

Vessel speed at the time of the collisions varied from 2 to 25 knots (*n* = 65). Most vessels travelled at 5–10 knots (*n* = 39, 60.9%, see Fig. 2), 14 between 10–15 knots (21.9%) and four faster than 15 knots (see Fig. 2). Yet, for 46 incidents

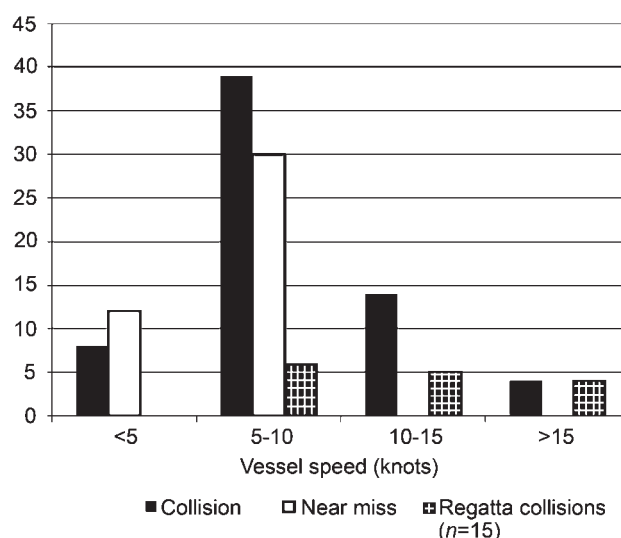


Fig. 2. Collisions (*n* = 65) and near miss events (*n* = 42) between sailing vessels and cetaceans in relation to vessel speed (1966–2010, numbers of chequered bars are also included in black bars).

<sup>3</sup> The video sequences can be watched on the internet at: <http://www.sailvalis.com/Pac%20Cup%2008/Images/Whale.mpg> and [http://www.youtube.com/watch?v=D21iF3N\\_cBY](http://www.youtube.com/watch?v=D21iF3N_cBY), respectively.

(41.4% of the total), vessel speed remained unknown or was not provided. Four sailors reported that they took manoeuvres to try to avoid the collision. Collisions during regattas involved vessel speeds ranging from 7 to 25 knots with a mean of 12.7 (SD = 5.73;  $n = 15$ ), including nine cases where speed was 10 knots or more (see Fig. 2).

On 51 occasions (45.9%) the animals were categorised as a 'large whale' and 12 times (10.8%) as a 'small whale' while four (3.6%) were dolphins (see Table 3a). For 44 accounts (39.6%), no categorisation was made or the answer was 'not known'. In 32 cases, the cetacean species was identified, these included: humpback whales ( $n = 15$ ), sperm whales ( $n = 9$ ), grey whales ( $n = 3$ ), and one each of the following species: right whale, fin whale, pilot whale and orcas/killer whales, as well as one common dolphin (see Table 3b). Again, for the majority of descriptions ( $n = 77$ , 70.6%) no species identification was provided. For five situations, it was reported that juveniles or calves (= 'small animals') were seen, and in one of these cases it was reported that the young animal was hit.

The behaviour of the animals prior to the collision was described for 22 instances. Six times, the animals appeared to be sleeping/logging on the surface, one whale was seen travelling, and two showed inquisitive behaviour, e.g. by approaching the vessel and/or riding its bow wave (two bowriding cases both involved dolphins). Seven times, whales appeared to emerge from below and thus apparently hit the vessel while trying to surface. Three cases involved animals being described as 'attacking' the vessel and in two instances whales leapt onto a vessel. Where sailors described attacks (these involved one group of sperm whales, and one pod each of pilot whales and orcas), the animals' behaviour appeared to be intentional, with the animals actively ramming the vessel in all three cases. Finally, one whale was described as intentionally approaching the vessel and 'rubbing up and down the port side', thereby causing considerable damage. The two cases where large whales leapt onto vessels involved a humpback and a right whale. One of these cases was caught on film as well as on photographs. Finally, one whale was reported to be floating dead on the surface when it was hit.

Cetaceans reportedly were hit by different parts of the vessels, typically by the bow and parts of the keel. Some cases involved damage caused to the daggerboard, a movable keel which is potentially more vulnerable to damage than a fixed keel. Sometimes the collision was described as being relatively soft, felt as a bump or light shudder, but during 18 collisions the vessel came to an abrupt halt. Consequently, there were several reports of crew members being hurt ( $n = 9$ ) including one instance of a crew member going overboard (and 7 out of 17 crew members being injured in that same incident). Crew members were hurt during collisions at vessel speeds ranging from 4–10 knots ( $n = 7$ ), while 'no injury' was reported for collisions happening at speeds from 3–25 knots ( $n = 58$ , Mean 7.84, SD = 4.09).

There were 26 reports indicative of some kind of visible reaction of the whale after the strike. Nine whales were said to 'dive away', and six to 'swim away', both apparent evasive behaviours. Seven whales struck the water surface with either their flukes or flippers and two were observed defecating. One injured whale 'spied' at the vessel just after

the strike. One dolphin hit by a vessel's rudder was described rolling on its side in the wake as if 'stunned or the breath knocked out of it'. Three times it was explicitly stated that there was no apparent reaction by the whale.

Injuries inflicted on the animals varied from 'no visible injury' to 'possibly dead'. In 20 cases (18.3%) blood was seen in the water after the collision, and four whales carried severe visible injuries. One animal supposedly was dead just after a strike with a monohull vessel travelling at 15 knots, a second one was suspected to have 'surely died shortly after the collision'. Six animals were seen to have minor visible injuries, described as e.g. 'minor scratches to the whale's skin', and in 10 cases an apparent injury could not be determined as being minor or severe (five of these cases involved blood seen in the water). On 24 occasions (22.0%), there was 'no visible injury', while for 19 times (17.4%) the answer was 'Not known'.

No relation was identified between the gravity of the injury and the size nor the speed of the vessel. There were severe injuries and/or blood seen in water at speeds ranging from 4 to 25 knots (Mean 9.0, SD = 5.7,  $n = 15$ ) involving 14 vessel sizes ranging from 10 to more than 20 m length, including 11 cases with monohulls and two cases with catamarans.

Vessel damage also varied widely from superficial effects (e.g. paint or antifouling ripped off the hull, scratches or small cracks, broken or bent steel poles, dents) to severe rudder, keel or daggerboard damage and major hull cracks or leaks. Five times, the collision caused the vessel to sink. In another incident, crew and vessel were rescued, but the vessel turned out to be not functional anymore. During the 2010 case when a right whale leapt onto a vessel, the vessel suffered total loss, too. Additionally, several whales performed abrupt body movements at the time of the strike, thus forcefully hitting the vessel and causing damage.

Of the 63 collision events where damage was reported, 29 (46.0%) were classified as minor damage while 27 (42.9%) were considered to have resulted in major damage, where sailing could only be continued with some restriction. As described above, seven strikes (11.1%) resulted in vessel loss.

## DISCUSSION

This study constitutes the first attempt to quantitatively assess collisions involving sailing vessels on a global scale. The internet was found to be an effective means to collect collision reports. However, the number of collision events reported on the world wide web, particularly near misses, is (and probably will remain) restricted. It is clear that only the more spectacular cases will enter news coverage and internet reports in general. Moreover, the information given in internet reports usually is not extensive and generally covers only the most basic aspects of an incident.

Conversely, a large number of collision and near miss reports were collected via the dedicated online survey, which thus was the more efficient way to collect data for this study, especially because survey entries by their nature yielded more detailed information. A considerable interest in the issue on behalf of the 'sailing scene' was noticed, as expressed through a number of e-mails by sailors and sailing website administrations and, of course, through the



establishment of the online questionnaire initiated by a major sailing website. Nevertheless, in numerous cases not all questions of the survey were answered, and thus information repeatedly was limited, too. Moreover, many sailors around the world may have no access to the internet and therefore were not aware of the online survey. Although the online questionnaire could be answered anonymously, there might generally be a certain reluctance to report a collision at all, as in addition to the fact that it may have been an unpleasant experience, sailors may also be unsure if there will be (legal or other) consequences when they report an incident (IWC, 2003; Lammers *et al.*, 2007).

The temporal distribution of collisions and near miss events showed that this is not a new phenomenon. The earliest cases reported occurred in 1966 (collision) and 1974 (near miss), respectively. However, most of the incidents were reported to have happened during the past few years (see Fig. 1). Although this may be a reflection of a true increase in collisions with sailing vessels in recent years, it may also reflect reporting rate. Several factors may potentially lead to an underestimation of collision rates in earlier years. In particular, cases that date back years or decades may not be reported because the details are not clearly remembered. The internet was used as a primary source of data, thus reports in newspaper archives and other written media referring to more historical accounts would have been missed. For example, collision accounts involving sailing vessels are a rarity in the scientific literature (see Table 4), while this study showed that the phenomenon is quite widespread.

Ocean sailing has become a diversion or profession for an increasing number of people around the world. Hence there are many more vessels sailing on the oceans today, which inevitably increases the likelihood of collisions with marine mammals. Although it is assumed that collisions with sailing vessels are less frequent than with motorised vessels (see Lammers *et al.*, 2007), they may not be as rare as previously thought. Yet, this study has to be considered as a first glimpse at how widespread sailing vessel-whale collisions are and how often they occur. While the increase in collision and near miss events during recent years reported here may be interpreted as a representative reflection of a growing number of sailing vessel-cetacean collisions, it is too early to make any assumption about ‘true’ numbers; this is in fact a feature of research on all vessel-whale collisions. It is also likely that no near misses were reported by vessels travelling at high speeds (10 knots or more) because they would typically have been in rougher seas and so less likely to see a whale or been aware of having almost hit it. Quantifying

sailing traffic clearly requires further research but is essential to enable solid estimation or quantification of collision risk.

Although collisions between sailing vessels and cetaceans may occur in any ocean, reports are most common for the Atlantic. This is in line with the geographical distribution of current entries in the IWC ship strike data base (Russell Leaper, pers. comm.) and the fact that there is generally more sailing traffic in the Atlantic with the largest proportion of sailing yachts crossing the North Atlantic (Jeremy Wyatt, Noonsite, pers. comm.). It is worth noting that sailing yachts tend to sail in ‘trade wind zones’ at particular times of year – i.e. when wind speed and direction are favourable; future investigations may highlight such geographical areas.

The large proportion of reports from monohull sailors, generally with fibreglass vessels, reflects the fact that this is by far the most abundant vessel type worldwide. Most large scale ocean races and regattas are conducted with monohull vessels.

### Species affected

Laist *et al.* (2001) and Van Waerebeek *et al.* (2007) name a variety of cetacean species affected by vessel collisions, including large whales and small cetaceans. Carrillo and Ritter (2010) note that certain large whale species are especially vulnerable, namely those ones staying at the surface for longer periods of time, for example right whales (*Eubalaena* spp., see also Knowlton and Kraus, 2001) and sperm whales during resting periods (*Physeter macrocephalus*, see also Ritter, 2010). In 2011, the database contained a total of 452 cases where the species was positively identified and the judgement at the time was that it was a definite ship strike (see summary data from IWC database at [http://www.iwcoffice.org/sci\\_com/shipstrikes.htm](http://www.iwcoffice.org/sci_com/shipstrikes.htm)). The majority were fin, humpback and right whales. In the Mediterranean Sea, fin whales are at highest risk to be hit by vessels (Panigada, 2006). Fin and humpback whales were also the most common species in the US Large Whale Ship Strike Database (Jensen and Silber, 2004). While the high proportion of humpback whales (and large whales in general) corresponds to the findings presented here, there are otherwise considerable differences in the frequency of different species being struck. It is unclear why sailing vessels apparently tend to collide less often with fin whales than with sperm and humpback whales, but one explanation may be the degree of familiarity of sailors with these latter species due to their more obvious morphological and/or behavioural features. However, it may also reflect the behaviour of the species. For example, the relatively high proportion of near miss events involving sperm may be

Table 4

Collisions between sailing vessels and cetaceans: cases identified in the scientific literature ( $n = 8$ ).

Date	Location	Vessel type	Species	Source
Jan. 1897	Mediterranean Sea, France	Yacht	Not known	Panigada <i>et al.</i> (2006)
Jun. 1972	Pacific Ocean	Schooner	Orca	Notarbartolo di Sciara (1977)
Apr. 1973	Mediterranean Sea, Italy	Yacht	16m whale	Panigada <i>et al.</i> (2006)
Feb. 1981	North Pacific Ocean, Hawaii	Trimaran	‘Whale’	Lammers <i>et al.</i> (2007)
Feb. 1995	North Pacific Ocean, Hawaii	65ft sailing vessel	‘Whale’	Lammers <i>et al.</i> (2007)
Oct. 1996	Pacific Ocean, Ecuador	Not known	Possibly sperm whale	Félix and Van Waerebeek (2005)
Dec. 1997	Caribbean	Yacht	‘Whale’	Koschinski (2003)
Jul. 2005	North Atlantic Ocean	Not known	North Atlantic right whale	WDCS (2006)

attributed to their distinctive behaviour of frequently logging on the surface. In addition, sperm and humpback whales were also more approachable by open boat whalers. Whale behaviour clearly warrants further investigation. Given the high prevalence of a lack of species identification, it would be valuable if sailors were encouraged to collect skin or other samples after a collision, where feasible, to facilitate later species identification.

The minority of cases reported in this study relates to animals classified 'small whales' or 'dolphins'. This corresponds to the general knowledge about ship strikes (see Van Waerebeek and Leaper, 2008). The apparent low risk of dolphins colliding with vessels requires further investigation, however, since Van Waerebeek (2007), reported 31% of worldwide collision reports related to small cetaceans. Personal observations of the author in the Canary Islands (unpublished data) provides a similar picture.

### Causes of collisions

The reports revealed that animals were hit by different parts of the vessels, most as expected however were hit by the bow and the keel. Some stated that the daggerboard was also damaged. In ultra-light, high speed boats sailing faster than hull speed, there is minimal hull in the water and the main contact is likely to be the keel or daggerboard. This part of the vessel strongly protrudes from the hull downwards, sometimes by several metres.

Little is known about the sound generated by sailing vessels, but it seems possible that cetaceans may hear an approaching sailing vessel, at least under 'ideal' conditions. Sailing vessels produce faint sounds by the flow of the water along the hull (Richardson *et al.*, 1995 cited in Koschinski, 2003), and daggerboards may contribute their own frequencies. However, under less than ideal circumstances it may be difficult for whales to detect the faint sound of sailing vessels ship noise, due to a variety of biological and physical factors (ACCOBAMS, 2005) or masking through ambient sounds generated by wind, rain and shipping noise (WDCS, 2006). Nonetheless, some collisions occurred while the vessel was motoring or motorsailing. Koschinski (2003) reported that many sailors put on diesel generators when whales are seen to make the vessel more audible. Hence, there is some belief among sailors that cetaceans can be surprised by 'silent' vessels. Of course, running a propeller creates much more noise than either the boat's engine or generator.

The seven reported cases of whales colliding with a vessel from below, assumingly while trying to surface, suggests that these whales were not aware of the vessel. Whales also may be unaware of ships because they are distracted or asleep (WDCS, 2006). This may be especially true for sperm whales which recently were found to perform apparent deep rest close to the surface, not reacting to approaching vessels at all (Miller *et al.*, 2008).

### Vessel speed

For motorised vessels, speed is generally thought to be a major factor concerning the number of collisions (see Laist *et al.*, 2001; Vanderlaan and Taggart, 2007). The reports presented here suggest the same for sailing vessels: Although the majority of collisions occurred at speeds of 5–10 knots

(see Fig. 2), the vast majority of sailing vessels cannot go faster than 8–9 knots which is the displacement hull speed for boats up to about 20m overall length. The fact that 28% of collisions happened at faster speeds despite very few boats sailing at these speeds suggest that speed probably has an effect; collisions during regattas on average occurred at faster speeds than in other contexts.

The number of regattas and ocean races has steadily grown during the past decades, both with monohull and multihull vessels, and there have been significant increases in speed of the vessels in long distance sailing races. There are also increasing numbers of transocean speed record attempts and round the world record attempts in monohulls and multihulls (Oliver Dewar, Global Ocean Race, pers. comm.). Many of these events seem to have at least one account of a collision. Given the scarcity of multihulls, it appears that this vessel type has at least a higher rate of collision reporting, if not a higher rate of strikes. This could be due to their generally higher speed, their involvement in high profile races with good media coverage, their greater vulnerability to damage due to lightweight construction, or a combination of these. It is not clear what percentage multihull vessels represent globally compared to monohulls. Such data are practically non-existent, although the percentage surely is believed to be small (Oliver Dewar, Global Ocean Race, pers. comm.).

Although in half of the collisions (49.5%,  $n = 76$ ), the animals were not seen prior to the impact, a number of sailors who had seen the whale reported that they took steps to circumvent a collision. In 12 cases, this actually helped to avoid a strike, although in four it did not. This underlines that collisions might be prevented if a whale is seen early enough to take action. Obviously, this is dependant on someone being on the helm, which for solo sailors will not always be feasible. A high degree of effectiveness to avoid collisions has been attributed to dedicated look-outs on larger vessels (Weinrich and Pecarcik, 2007) and thus where there are larger sailing crews it might be beneficial to establish a permanent watch-post, at least while sailing in areas where cetacean abundance is known or expected.

### Behaviour of the animals

Some whales hit were recorded as logging on the surface which may be resting or slow travelling behaviours. While floating behaviours might be expected to be particularly risky, the relatively high number of whales being described as surfacing from a dive (i.e. colliding with the bottom/keel of the vessel) is perhaps surprising. It appeared common for animals to surface without noticing an approaching vessel, perhaps due to an unfavourable combination of the ship's speed and the low sound level it produces. In some cases, animals may also actually have been attracted to the vessel before colliding (four near miss events were preceded by apparent 'inquisitive' behaviours on behalf of the animals, two times bowriding behaviours resulted in a collision).

There were reports of collisions being initiated by the cetaceans through apparent aggressive behaviour. Cetaceans attacking vessels have been described before, albeit rarely (but famously), e.g. Philbrick (2000). Van Waerebeek *et al.* (2007) also noted that some cetaceans may violently hit or push vessels. An interesting case involving orcas/killer

whales was described by Notarbartolo di Sciara (1977). Some have speculated whether the right whale which leapt onto a sailing vessel in 2010 did so deliberately. However, such events are beyond the scope of this study, which is focussed on accidental and unintentional strikes.

### **Injuries to sailing crew or cetaceans; vessel damage**

Collisions with whales can pose a serious threat to vessels (IWC, 2008; Jensen and Silber, 2004; Laist *et al.*, 2001), and sailors and ferry passengers (de Stephanis and Urquiola, 2006; Jensen and Silber, 2004). This study also received reports of crew members being hurt during collisions even at rather low speeds (the minimum found was 3 knots). On the other hand, high speed may not automatically lead to injured crew. In fact, no sailors were reported hurt in any of the collisions that occurred at speeds of 15 knots or more. This contrasts with findings by Jensen and Silber (2004) and Vanderlaan and Taggart (2007), although their investigations mainly involved motor vessels. This suggests that factors other than vessel speed have a greater influence, e.g. the whereabouts of crew members and the nature of the collision ('softly' or with an abrupt halt). In particular, sailing vessels are only likely to be travelling fast in sufficient wind. Thus unlike powered vessels which travel fastest on flat water, the motion of the vessel is likely to force the crew into positions where they are braced against the motion of the boat.

Similar considerations may apply for vessel damage. While Jensen and Silber (2004) found that all collisions where the speed was known and resulting in vessel damage took place at speeds of 10 knots or more, this study produced different results. The question is how can collisions at low speed lead to substantial damage. In some cases, whales were observed hitting the surface with their flukes or other body parts when the collision occurred. Startle reactions such as bending the body or slamming the tail fluke may be natural responses to a strike, and in at least some instances this had a greater influence on the degree of vessel damage than vessel size or speed. Factors including the size of the animal, its swimming speed as a function of its behaviour, the angle at which it is hit, its immediate (startle) reaction all can play a major role for the outcome of a collision.

Finally, the seven reports of vessels sinking after a collision are alarming. They underline the potential great threat to the life of a sailor when hitting a whale. A similar scenario was described in IWC (2006, p.13). Again, speed was not a major factor for the vessel loss: one of the instances occurred when a 10–15m monohull hit a sperm whale at a speed of 7 knots. The crew were uninjured in all instances and were rescued safely, but there may have been similar cases without such a happy end.

Similar aspects as described for injured crew may be true for the injuries inflicted to the animals. These varied strongly from 'no visible injury' to 'possibly dead'. One of the cases for which the animal probably died involved a monohull vessel travelling at 15 knots (in the other case vessel speed is unknown). While this case corresponds to the general finding that most collisions causing severe injuries or death occur at greater speeds than 14 knots (Laist *et al.*, 2001), there were several cases where blood was seen in the water involving small vessels (<10m) hitting whales at slow speeds (4–5 knots). This is contrary to the assumption that collisions

with sailing vessels only cause minor injuries (Laist *et al.*, 2001).

Overall, this review suggests that the number of whales that appeared uninjured after the collisions may be overestimated while the severity of an injury may be underestimated (see also IWC, 2003; Lammers *et al.*, 2007; WDCS, 2006). The fact that many sailors had no chance to have a closer look at the animal after the collision (if at all) because the animal is out of sight within seconds, makes it unlikely to detect injuries or to classify them correctly (see e.g. IWC, 2005).

### **CONCLUSIONS**

A variety of measures has been discussed to mitigate the risk of vessel-whale collisions, including speed limitations, on board observers, re-routing and technical modifications or tools (ACCOBAMS, 2005; IWC, 2008; 2011; Pesante *et al.*, 2002). Technical measures up to now mostly have failed to prove their efficacy (ACCOBAMS, 2005; IWC, 2011). Only a fraction of these options will be applicable on sailing vessels. However, there are a number of potential solutions that might contribute to a higher awareness of the issue and the prevention of collisions, respectively.

The most obvious is to keep a sharp lookout during daylight hours. Some collisions reported could probably have been prevented after a whale was seen if avoiding action had been taken. Dedicated observers on board have proven to be an effective means to detect whales in the path of a ship (ACCOBAMS, 2005; Weinrich and Pecarcik, 2007), and combined with a general knowledge about where and when to expect cetaceans, this measure may also be helpful for participants of ocean races and regattas. However, permanent lookouts will only be practical with larger crews and reasonable sighting conditions. Reducing speed as a voluntary measure should be considered anywhere sailors enter important cetacean habitats. Protected areas or regions where cetaceans are known to be abundant should be avoided whenever possible.

Speed limitations by their nature will not be easy to implement for regattas and ocean races (although they are recommended for prime cetacean habitats) but other measures can usefully be considered. Gill (1997) has proposed to shift regatta routes away from the continental shelf, as these are known to commonly be inhabited by cetaceans. A development of this idea would be for other types of habitats and marine protected areas to be avoided by regattas and races (see Tejedor *et al.*, 2007). Important areas for many humpback, right and sperm whale populations are reasonably well known which would make it possible to identify overlaps of regatta routes with high risk areas e.g. migration corridors, areas of seasonal aggregation and prime habitats.

Gill (1997) also suggested conducting acoustic or aerial surveys just prior to a sailing event. This may help determine whether there are cetaceans present or to be expected and if so, to modify routes around as was the case for the Volvo Ocean Race in April 2009<sup>4</sup>.

A final idea might be to start the engine/propeller while under sail in areas of known high cetacean abundance in an

<sup>4</sup> See [http://www.nytimes.com/2009/04/25/sports/othersports/25sailing.html?\\_r=1&ref=sports](http://www.nytimes.com/2009/04/25/sports/othersports/25sailing.html?_r=1&ref=sports).



attempt to make vessels more likely to be detected by cetaceans. The effectiveness of this is unknown but in any case, manoeuvrability will be improved. Experimental investigations are essential to evaluate this or other measures. So far, there are few scientific accounts of cetaceans reacting to acoustic stimuli; and one study showed that right whales returned to the surface after exposure to artificial sounds, making them more vulnerable to ship strikes than before (Nowacek *et al.*, 2004). Future research also should relate species distribution to certain vessel types and contexts (e.g. sailing regattas, etc.).

Education is clearly a major component of minimising collision risk. Sailors must be aware of (a) the risk of colliding with cetaceans; (b) where they are likely to encounter cetaceans; and (c) what can be done to avoid a collision. Without such knowledge, little change will be achieved. This study has shown that there is considerable interest in the issue on behalf of the sailors. Thus it seems realistic to raise further interest and to develop dedicated websites or website sections highlighting the issue. Existing websites thereby should explicitly mention sailing vessels as a potential cause of concern. An intensified dialogue between managers, scientists, NGOs and sailing event organisers is both necessary and feasible. Information campaigns run by regatta organisers' prior to regatta events, or during sailing fairs, could also include training of cetacean identification, mapping areas of high cetacean abundance and producing information materials to provide sailors with simple measures such as 'if you see one whale, the likelihood to encounter more will usually increase' and 'notify other sailors about the presence of whales'. Encouraging sailors to participate in sighting schemes (and even collect skin or other samples for scientific purposes) could further increase co-operations between sailors, scientists and conservationists. In fact, such a co-operation between an NGO and regatta organisers<sup>5</sup> was started during the 2011 Global Ocean Race (Jennifer Lonsdale, pers. comm.).

Given that the IMO is dealing with the issue of vessel-whale collisions, and the International Sailing Federation has consultative status at the IMO, it is recommended that the IMO also address the issue of sailing vessels-whale strikes (see also IWC, 2011).

In addition, if a collision has happened, sailors and regatta administrations must be encouraged to report it, and be informed where to direct such information to, especially the IWC ship strikes database (<http://www.iwcoffice.org>)<sup>2</sup>. The permanent establishment of an online survey such as that developed for this study could play an important role. This review suggests that a precautionary approach is warranted on this issue with the final goal to make sailing safer, both for animals and humans.

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# Whale catches from 19<sup>th</sup> century shore stations in Western Australia

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## ABSTRACT

This paper presents historical data from 19th century shore whaling stations along the Western Australian coast, complementing data already presented in an earlier 1985 analysis. In particular, catch records of the Castle Rock whaling station, Geographe Bay, Western Australia, for the period 1846–53 together with other contemporary records indicate that humpback whales (*Megaptera novaeangliae*) comprised the majority of the colonial shore whalers' catch. It is suggested that this could have been a result of a significant presence of American whale ships in the region in the early 1840s, which had presumably already reduced southern right whale (*Eubalaena australis*) numbers by the time these detailed colonial records were kept.

KEYWORDS: WHALING – HISTORICAL; INDIAN OCEAN; SOUTHERN OCEAN; STATISTICS

## INTRODUCTION

Bannister *et al.* (1981) and Bannister (1986) presented data on 19th century whale catches along the Western Australian coast by American pelagic vessels and colonial shore whaling parties. This paper presents further historical data on 19th century colonial shore-based whaling operations on the west and south Western Australian coasts, providing a synthesis of whale catch and oil production records for the period 1836–1879. It also attempts to establish the extent to which particular species were caught by these small-scale open-boat fisheries, as well as the seasonality of whale migrations and whaling operations and the catch efficiency and speed of decline of whale stocks, especially during the peak impact period of the 1840s. The focus is an analysis of the detailed daily records from the Castle Rock whaling station (Geographe Bay) for the period 1846–53, with broader patterns extracted from official government records, colonial newspapers and other documentary sources.

## HISTORICAL BACKGROUND

Western Australia was colonised by the British in 1829, with shore-based whaling by the settlers commencing on the south coast in 1836 and the west coast in 1837. Despite initial expectations, by the early 1840s hopes that whaling would be a major contributor to the colonial coffers had already faded. High establishment costs with only modest returns resulting in part from a lack of skill drove many early operators out of business. However, several years later, the increasing numbers of pelagic whale ships operating in the region and willing to sell surplus equipment, as well as half a dozen shipwrecks where salvaged gear was auctioned to settlers, made it possible for the colonists to set up small stations quite cheaply (Gibbs, 1998). Similarly, deserting sailors from the pelagic vessels increased the available skill pool, even though these men were equally inclined to desert the shore parties if made an offer by a passing whale ship (e.g. Whitecar, 1860, p.219). However, whatever benefits were provided by the pelagic whalers was balanced against the direct and indirect competition as the American and

French vessels wintered on the coast and took whatever whale species were present (Bannister *et al.*, 1981; Gibbs, 2000).

The shore-based whaling operations on the west and south coasts were carried out independently, although production for western Australian fisheries was often reported for the colony as a whole (Gibbs, 1996). The technologies, techniques and strategies employed by these parties were consistent with other Australasian and international shore-based whaling enterprises of the era (Dakin, 1938; Lawrence and Staniforth, 1998; Pearson, 1983). In some instances, a whaling party might have a small schooner or other vessel assisting with transportation of crews or the flensing of whale carcasses, although most were low-key operations of limited means. Relatively few stations, generally fewer than eight in total, were established in any one year and the whaling parties themselves tended to be quite small in size, employing between two and four whaleboats with 15 to 30 men (Gibbs, 1996). Many of the parties remained based at a single station, waiting for the appearance of right or humpback whales and closing the season once it was decided that the main body of the migration, particularly of humpback whales, had passed. However, after the 1850s, parties on both coasts developed an alternative strategy where they shifted camp two or more times, tracing the migration (presumably of humpback whales) north to south on the west coast and west to east on the south coast. By the close of the industry in the late 1870s, stations operated as far north as the Dampier Archipelago and as far east as Cape Arid. The traditional open-boat shore whaling continued in western Australia until ca.1879 when limited returns finally made the industry non-viable (Gibbs, 1996).

## METHODS

### Historical sources for colonial Western Australian whaling data

Official record-keeping of the production from the small 19th century Western Australian whaling stations was negligible, with the annual statistical record for the colony



(the 'Blue Books'), being the only regular record. Even then, the level of detail varies enormously between years from a single value for whale oil and whalebone, to regional or station-by-station reports on the numbers of men and boats and the number, species and oil yield of individual whales. The two major Western Australian newspapers published between 1836 and 1880, the *Perth Gazette* and the *Inquirer* were also reviewed for any reports of whale catches. Although erratic, these often provide a better idea of the successes of individual stations but by no measure are complete accounts. Colonists and commentators sometimes reported on whaling in other documents but generally only present broad detail on whale sightings and the operation of the industry.

The daily diary of William Seymour<sup>1</sup>, manager of the Castle Rock whaling station established in a small cove in Geographe Bay east of Cape Naturaliste, appears to be the only surviving detailed catch record for a 19th century Western Australian whaling station. Castle Rock was occupied by various parties between 1846 and 1872, and used between two and three whaleboats each season, which was typical of the small Western Australian shore whaling stations (Heppingstone, 1993). Regrettably the diary covers only the period 1846–53, excluding 1851, with most of the entries consisting of a single sentence statement of what whales were chased, struck, and killed each day. The diary was analysed with regard to species sighted and the operational success of the station.

## RESULTS

### The 19th century whaling season

As noted, the small-scale Western Australian whaling operations were restricted to near-shore areas and usually within one or several adjacent bays. This in turn limited the available whale species to those which came in close proximity to the coast, primarily humpback and southern right whales.

The modern humpback whale population in this area (IWC Breeding Stock D) arrives on the southern and western Australian coasts as early as April, although the majority of the northbound group appears in June, moving to the sub-tropical waters of the northwest coast to calve and mate (Bannister, 2008; Chittleborough, 1965). Around mid-August they begin the southward journey, passing closer to shore and sometimes lingering in a bay or area with their calves for up to a week (Collier, 1993; Jenner *et al.*, 2001). Although there are a few stragglers until late November, the migration through Western Australian waters has largely ended by late October. The humpback whale population does not pass along the south coast on their southward run (Chittleborough, 1965). The modern southern right whale population arrives on the southern and lower western Australian coast from about July to calve and mate, returning to subpolar or more southerly regions by mid-November (Bannister, 2008; Bannister, 1985).

The operational period (season) of the 19th century shore whalers was dependent upon the appearance of one or both of these key species. Unfortunately, species identification in

contemporary accounts is often lacking. Writing from the Fremantle region on the west coast, Ogle (1839, p.158) reported that whales frequented the west coast from late May to October. Landor (1847) stated that from about June the whales (presumably humpbacks) proceeded northwards, generally returning southwards around six weeks later. Another correspondent noted humpbacks could arrive off the Fremantle (lower west) coast as early as April (*Perth Gazette*<sup>2</sup>, 22/4/1837), although a decade later there are statements that the Fremantle stations did not normally catch anything before August (e.g. *Inquirer*<sup>3</sup>, 2/8/1848). The shore whaling season for this region appears to have closed by mid to late October (*Perth Gazette*, 6/11/1847; 23/10/1859). Although the dates when whales appeared on the less populated south coast are even less certain, the station at Cheyne Beach east of Albany reported making catches from late June or early July onwards (*Inquirer*, 7/7/1847; 27/6/1850; 15/7/1857; 21/6/1865). The close of the southern season appears to have been in late October or early to mid-November (*Inquirer*, 3/11/1847; 21/11/1849).

The Castle Rock diary of William Seymour shows a nearly two month variation in the commencement date of the whaling season in Geographe Bay, as early as 1 June and as late as 3 August, with the end date within a range of just over one month (30 October to 3 December). There are indications that the opening and closing dates may well have been arbitrary points within the general time frame of the whale migration, with the station manager probably hoping to catch the peak without keeping the station open longer than necessary.

### Catch efficiency

The Castle Rock station records were analysed to determine the efficiency of the operation over an eight year period from 1846 to 1853. Tables 1 and 2 present summaries of the Castle Rock operation by month and year. Seymour's diary suggests that the only reasons why the crews would not pursue a whale were extremely heavy weather, or because the men were already occupied in processing a whale. However, Table 3 shows only about a quarter of chases resulted in a whale being 'struck' with a harpoon, with the later years (1850–53) showing even lower rates of success. Once the whale was struck a variety of things could occur, including the harpoon drawing from the blubber, or the whale (especially humpbacks) turning and destroying the boat. The whale might also run so far out to sea that the men would be forced to cut the line so as not to risk not being able to make their way back to shore (Castle Rock diary, 23/10/46). Despite this, as shown in Table 3 a high proportion (averaging 60%) of struck whales was killed.

As indicated in Table 3, returning a whale carcass to shore by towing behind the whaleboat(s) without the assistance of a larger vessel must have had its own hazards. The mean success rate was only 69%, with carcasses being lost through various factors such as heavy seas, distance to shore or nightfall forcing the boats to cut the line, although it appears

<sup>1</sup> Seymour, F.W. [no date]. Castle Rock diary of Frederick William Seymour. Unpublished manuscript, Battye Library, Accession number 2838A/2.

<sup>2</sup> *Perth Gazette and Western Australian Journal* newspaper (1833–1864), later *Perth Gazette and W.A. Times* newspaper (1864–1874), Perth, Western Australia.

<sup>3</sup> *The Inquirer* newspaper (1840–1855), later *The Inquirer and Commercial News* (1855–1890), Perth, Western Australia.

Table 1

Castle Rock whaling station summary of operations by month (1846–50, 1850–53).

Month	No. of days whales sighted	No. of days whales chased	Chase 'events' per month	Whales struck	Whales killed	Whales brought to shore
June	2	2	2	0	0	0
July	10	6	10	0	0	0
August	45	38	46	16	11	14
September	112	106	161	38	21	16
October	167	155	293	64	39	30
November	64	65	120	30	25	18
December	2	2	5	2	2	0
<b>Total</b>	<b>402</b>	<b>374</b>	<b>637</b>	<b>150</b>	<b>98</b>	<b>78</b>

Table 2

Castle Rock whaling station summary of operations by year (1846–50, 1850–53).

	1846	1847	1848	1849	1850	1852	1853	Total
Days sighted	72	59	80	43	36	65	47	402
Days chased	69	56	71	43	33	58	41	371
Chase events	117	108	121	83	46	95	68	638
Struck	31	28	31	25	7	6	14	142
Killed	20	24	21	17	4	3	4	93
Brought to shore	20	16	17	12	3	2	1	71

that if necessary the crews would row through the night. Although right whales floated when dead, other species including humpbacks could sink, with an effort being made to retrieve them several days later when the decomposition gasses had eventually returned them to the surface. While some of these bodies were re-located and successfully brought back to shore, some or all of the blubber may well have already been stripped by sharks and killer whales (*Orcinus orca*). Seymour's diary suggests that once ashore, the process of flensing a whale and trying-out and barrelling the oil took an average of three days. This could take longer if interrupted by whale chases, although in some instances Seymour (Castle Rock diary, 16/10/1846) mentions the look-out not being kept while trying-out was being completed. Cleaning the whalebone (baleen) seems to have been the least pressing task, done after the trying out was completed or at some later date (Castle Rock diary, 21/8/1852). The oil retrieved was used for lubricants and lighting, especially the fine oil recovered from sperm whales if caught, as well as for other processes such as scouring and bleaching cloth and softening leather. The flexible baleen (whalebone) was used for various purposes including as corset stays and umbrella ribs and even carriage springs, with right whale baleen superior to that from humpbacks (Bannister, 2008, p.22).

It is interesting to note that over the eight years of records, the efficiency of the Castle Rock station actually appears to decline. Even though the decrease in whale sightings may partially account for a drop in performance, in general the

rate of success at striking, killing and returning the whales to shore also fell. This cannot be easily explained by reference to Seymour's journal, although contemporary reports suggest poor management of whale carcasses being towed by the boat crews (*Inquirer*, 19/10/1853).

### Species of catch

The species of whale involved in each chase by the Castle Rock whalers is summarised in Table 4, while the number killed (but not necessarily brought to shore) is presented in Table 5. Humpback whales dominate the sample, forming 79% of the species chased, and 77% of the total killed. Right whales form the next and considerably smaller group at 15% of the species chased and 15% of the total kill. Overall, the catch of humpback versus right whales was in the order of a 5:1 ratio. However, for both species there was a 14% success rate between chasing and killing the animals, suggesting an equal degree of ease (or difficulty) in the pursuit of each type.

The next most commonly-pursued species at Castle Rock was the blue whale (*Balaenoptera musculus*), referred to in Seymour's journal as 'sulphur bottoms'. These animals also migrate north from the Antarctic and along the Western Australian coast as they head towards Indonesian waters (Cousteau and Paccalet, 1988). Up to half a dozen sightings of blue whales were made from Castle Rock each year between August and November. In August of 1853, Seymour (Castle Rock diary, 19/8/1853) also recorded sighting a cow and calf sulphur bottom passing by the station.

Despite chasing blue whales whenever they were within range of the station, the Castle Rock crews were usually unable to strike these animals with their harpoons. This was possibly owing to the 'famed swiftness' of the species (*Inquirer*, 24/9/1851) which was able to flee at up to 15 knots (28km per hour) or faster (Bannister, 2008, p.51). Most whaleboats could only be rowed at about 8km per hour (Ansel, 1978). There is only one report of the Castle Rock party fastening to a blue whale, although on that occasion they were forced to cut the line for unspecified reasons (*Inquirer*, 24/9/1851). There are in fact only two records of

Table 3

Castle Rock: success and efficiency of operations (1846–50, 1850–53).

	1846	1847	1848	1849	1850	1852	1853	Mean
% chases where whales struck	24	26	26	30	15	6	20	21
% struck whales killed	64	86	68	68	57	50	29	60
% killed whales successfully brought to shore	100	67	81	71	75	67	25	69
% chases resulting in whales killed and brought to shore	17	15	14	14	7	2	2	10

Table 4

Species of whales chased at Castle Rock whaling station (1846–50, 1850–53).

	1846	1847	1848	1849	1850	1852	1853	Total
Humpback	87	91	103	69	41	70	45	506
Right	23	14	12	11	4	21	13	98
Other	3	3	6	2	0	4	3	21
Unidentified	4	0	0	1	1	0	7	13
Total	117	108	121	83	46	95	68	638

Table 5

Species of whales killed by the Castle Rock whaling station (1846–50, 1850–53).

	1846	1847	1848	1849	1850	1852	1853	Total
Humpback	11	20	19	16	3	1	2	72
Right	2	4	2	1	1	2	2	14
Other	7	0	0	0	0	0	0	7
Unidentified	0	0	0	0	0	0	0	0
Total	20	24	21	17	4	3	4	93

Western Australian shore-whalers being able to kill blue whales, at the lower west coast station of Bunbury in November 1858 (*Inquirer*, 1/12/1858), and Fremantle in March 1859 (*Perth Gazette*, 1/4/1859). Although the Fremantle whale was lost in transit, the carcass brought in at Bunbury was reported as not yielding as much oil as an ordinary right whale, while its bone was also inferior, if better than that taken from humpback whales (*Inquirer*, 1/12/1858).

Seymour records several sightings of ‘finbacks’, possibly referring to fin whales (*Balaenoptera physalus*) or Bryde’s whales (*Balaenoptera edeni*) (cf. Baker, 1990; Bannister, 2008). The Castle Rock crews are recorded as unsuccessfully chasing finbacks during the 1840s, so that by the 1850s there are sightings of ‘lots of finbacks’ without any indication of pursuit (Castle Rock diary, 16/9/1853). The fleeing speeds of these species, the former at up to 20 knots, or 37km per hour (Bannister, 2008, p.56) was also well beyond the capabilities of the whaleboats. There are no historical references to other Western Australian shore stations sighting or chasing finbacks, although this may be because of limited recording.

There is a single account of the Castle Rock whalers hunting sperm whales (*Physeter macrocephalus*), a species which normally does not approach the shore. In mid August of 1846, Seymour (Castle Rock diary, 14/8/1846) recorded that ‘a score’ of sperm whales (i.e. 20) was raised in Geographe Bay, despite a contemporary report stating that over 200 were seen (*Perth Gazette*, 22/8/1846). Although Seymour’s diary suggests that only seven were taken by the Castle Rock crews, it is possible that as many as 25 were eventually killed by them and another nearby station (*Inquirer*, 2/9/1846). A cow sperm whale with its calf was also taken by the Castle Rock boats just over a decade later (*Inquirer*, 30/9/1857). The only other report of a Western Australian shore station capturing a sperm whale was in 1846, when the Torbay (south coast) crews with assistance from a small vessel, captured a single animal (*Perth Gazette*, 3/10/1846).

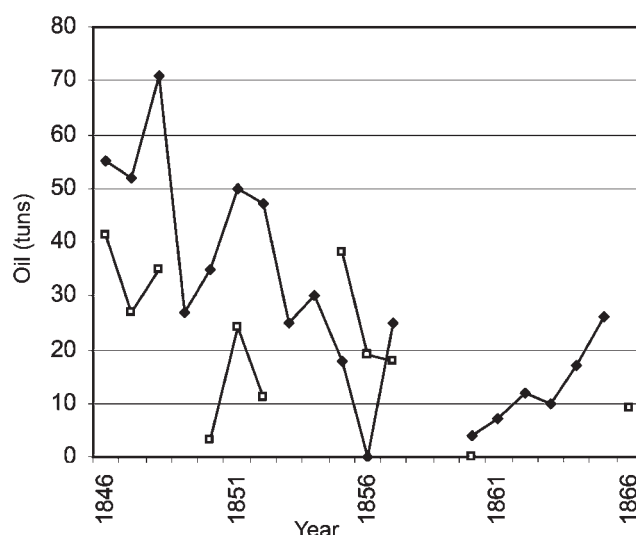


Fig. 1. Reported yield of whale oil (tuns) from Cheyne Beach and Castle Rock stations 1846–1866 (Source: Gibbs, 1996).

Although no other detailed whaling station catch records survive, comparison of the oil yield from Castle Rock against Cheyne Beach, a contemporary south coast station, provides some correlation of major trends. It should be noted that Castle Rock was usually a three-boat west coast fishery, while Cheyne Beach was usually a two-boat south coast fishery (Gibbs, 1996). Even though it might be expected that increasing skill and experience would result in increased production, Fig. 1 shows that the returns of oil at both stations declined over time. From peak yields of 41 tuns<sup>4</sup> and 71 tuns respectively in the late 1840s, by the early 1860s both parties appear to have been reduced to annual returns of consistently less than 15 tuns. As both exhibit almost identical declines in production, this could be indicative of declining whale stocks in the region.

### Catch strategy

Although there are no explicit references in Seymour’s journals to catch strategies, an American whaler who observed the Castle Rock and Bunbury fisheries in the mid-1850s noted:

‘If a whale is attended by a calf, they always fasten to the latter first, knowing that the mother, in her solicitude for her offspring, is very careful not to use her tremendous flukes; or if a humpback, her sweeping fins: but woe betide the boat, unless an experienced boat-header directs it, that is in the vicinity when she discovers that her calf is dead’ (Whitecar, 1860, p.91).

The consistent capture of cow and calf pairs is certainly borne out by Seymour’s records. Over the seven years covered by the diary, 18 cow and calf pairs of humpbacks (36 individuals) were killed, representing 50% of the total humpback catch, or 39% of all whales taken by the station in that period. A high proportion of the remaining catch also represents cows or calves which were taken while the other half of the pair escaped. No cow and calf pairs of right whales are recorded as being taken at Castle Rock.

<sup>4</sup> The standard unit for measuring oil was the tun, equal to 252 gallons (954 litres), or seven barrels of 36 gallons (136 litres) each.

Table 6

Comparison of species specific reports of right and humpback catches 1845–65 (Sources: *Perth Gazette*; *Inquirer*; Bannister, 1986).

Year	<i>Perth Gazette</i>		<i>Inquirer</i>		Bannister (1986)	
	Right	Humpback	Right	Humpback	Right	Humpback
1845	—	—	—	—	20	0
1846	2	1	—	—	32	7
1847	1	—	—	—	10	44
1848	2	3	—	—	14	9
1849	2	2	—	—	0	27
1850	3	5	—	—	2	27
1851	—	—	—	—	8	10
1852	—	—	—	—	4	16
1853	—	—	5	1	5	12
1854	2	—	4	1	8	11
1855	—	—	—	—	19	11
1856	1	4	—	—	6	25
1857	—	16	—	—	14	18
1858	1	8	—	—	18	19
1859	—	4	—	—	0	29
1860	—	—	—	7	0	10
1861	—	—	1	4	1	11
1862	—	—	—	7	2	16
1863	1	—	—	—	0	29
1864	—	—	—	—	0	26
1865	—	—	—	—	1	39
Total	15	43	10	20	164	396

#### Total catch for Western Australian shore whaling

As noted, Seymour's diary provides the only detailed record of catches for a single station, so an attempt was made to determine if the general trends in his records were applicable to the rest of the Western Australian shore whalers of the period. Reports from the *Inquirer*, *Perth Gazette* and the Blue Books (annual colonial statistical return) were collated to extract any specific mention of the species of catches (Table 6). The newspaper sources are irregular and variable in quality, particularly with regard to the south coast, while the Blue Books depended on the information collected by regional government officials, which was most frequently

Table 7

Distribution of whale species caught 1845–65.

	<i>Inquirer</i>		<i>Perth Gazette</i>	
	Humpback	Right	Humpback	Right
<b>West coast</b>				
Port Gregory	11	2	13	0
Fremantle	10	9	5	12
Bunbury	8	5	5	4
Castle Rock	17	11	19	9
<b>South coast</b>				
Torbay	5	0	—	—
Barker Bay	2	0	—	—
Cheyne Beach	20	1	0	1
Total	73	28	42	26

presented as only a gross oil and bone return for each station, or simply for the whole colony. Pre-1845 newspapers rarely noted species, while after the mid-1860s they appear to have lost interest in reporting on local shore whaling except as a filler item. These can be compared to Bannister's (1986) attempt to determine the total humpback and right whale catches by Western Australian shore stations through applying formulae to the annual oil and bone returns reported to the Blue Books.

Bannister's (1985) methodology can be divided into two parts, the first being the use of a ratio of whalebone to oil to ascertain which species was being taken at each station (when this was not stated in the original report). By taking several instances where the bone and oil returns for a known number of individuals of a particular species were provided, Bannister determined that if the reported ratio of oil to bone is greater than 25:1, the animals which had been taken were most likely humpbacks, while a ratio of equal to or less than 25:1 indicates right whales. This is consistent with Morton's (1982, p.53) research which suggests right whales taken in New Zealand waters provided approximately 100 tons of oil

Table 8

Reported oil yields (tuns) from individual whales [8(2) represents a report of 8 tuns from 2 whales].

Years	Humpback (tuns)	Mean (tuns)	Right (tuns)	Mean (tuns)
<i>Perth Gazette</i>				
1836–40	—	—	—	—
1841–45	—	—	—	—
1846–50	2, 3	2.5	8, 8(2), 6	5.5
1851–55	—	—	12	12
1856–60	3, 8(2), 10(3), 17.5(4)	3.2	3	3
1861–65	—	—	—	—
1866–70	—	—	—	—
<b>Mean</b>		<b>2.85</b>		<b>6.83</b>
<i>Inquirer</i>				
1836–40	—	—	—	—
1841–45	—	—	—	—
1846–50	4, 3, 4(2), 2, 2	2.5	5, 6, 8, 7, 1, 8(2), 8, 4	5.2
1851–55	—	—	5, 8, 8	7
1856–60	3, 1.75, 4, 8(2), 5, 10.5(3)	4.25	10, 8.75, 12	10.25
1861–65	—	—	10	10
1866–70	—	—	—	—
<b>Mean</b>		<b>3.38</b>		<b>8.11</b>
<i>Blue Books</i>				
1853	4, 1.5	2.75	24(3), 5.5	7.37
1854	—	—	14(4)	3.5
1860	20(6)	3.3	—	—
1862	24(6), 1	2.5	—	—
<b>Mean</b>		<b>2.85</b>		<b>5.4</b>



to 5 tons of bone (20:1). Once the whale species had been established, Bannister then determined the number of individuals from the reported oil return by an using an average of 5 tuns of oil per right whale, based on three instances where the oil yield from a single animal was reported in the Blue Books. He acknowledges that this is low in comparison with other areas and may be as much as two tuns lower than the average figure obtained using a much wider range of reports from Western Australian newspapers (see also Table 8, discussed below).

Table 7 presents the species of whales caught from the various south and west coast stations as reported in contemporary newspapers between 1845 and 1865.

### Oil yield

An analysis of reported oil yields from individual whales caught throughout Western Australia, taken from newspaper and Blue Book accounts (Table 8), shows that while right whales were frequently reported as producing eight tuns of oil or more (up to a maximum of 12 tuns), humpbacks did

not usually produce more than four tuns. The mean yield by individuals (Table 8) represents a combination of bulls, cows and calves, and should not be confused with an average yield from an adult of either species. There are, unfortunately, insufficient data to see if the mean yields for humpbacks and right whales change over time.

### Oil and bone export

Table 9 shows the reported production of oil and bone by the Western Australian shore-whaling stations on the south and west coasts over the period 1836–79. An overall decline is evident, despite a brief resurgence in the early 1870s due to a late surge in whaling activity, mostly in the newly-opened Dampier Archipelago area (north-west coast).

### Impact of foreign whaling

Bannister's analysis of the logbooks of American whaling vessels operating in the 'Coast of New Holland Ground' suggested that by the mid-1840s, right whales were becoming shy of whaling vessels or the population itself had

Table 9  
Reported oil and bone production (Source: *Blue Books*).

Year	Oil (tuns)				Bone (tons)				Total value (£)
	West	South	Total	Value (£)	West	South	Total	Value (£)	
1836		13	13	520	—	7	7	630	1,150
1837	71	45	116	—	4	2	7	540	—
1838	57	48	105	—	—	—	—	—	—
1839	—	—	—	—	—	—	—	—	—
1840	—	—	—	—	—	—	—	—	—
1841	—	—	—	—	—	—	—	—	—
1842	—	—	—	—	—	—	—	—	—
1843	—	—	90	—	—	—	—	—	—
1844	94	13	107	—	—	—	5	800	—
1845	—	—	100	2	—	—	7	910	2,935
1846	98	77	163	3,871	—	—	4	848	4,719
1847	141	55	196	2,972	1	1	2	300	3,272
1848	46	71	118	1,820	0	6	6	570	2,390
1849	—	—	90	1,450	—	—	2	290	1,740
1850	42	60	102	2,119	2	2	3	209	2,328
1851	38	63	101	2,660	2	2	4	735	3,395
1852	20	47	68	2,501	0	2	2	222	2,723
1853	39	25	64	3,038	1	1	3	345	3,383
1854	46	30	76	2,940	1	0	1	206	3,146
1855	113	18	131	4,983	0	0	0	30	5,013
1856	104	0	104	3,962	2	0	2	560	4,274
1857	53	41	94	3,438	0	0	0	0	3,439
1858	—	—	40	—	0	0	0	0	—
1859	60	55	115	2,364	1	1	2	637	3,001
1860	20	21	41	1,408	1	1	1	276	1,684
1861	31	22	54	1,940	1	0	1	138	2,078
1862	25	35	60	2,060	0	0	1	140	2,200
1863	20	21	42	1,770	1	0	1	110	1,870
1864	40	40	80	4,180	1	1	2	397	4,827
1865	84	46	130	5,424	1	0	2	250	5,674
1866	49	26	75	3,025	1	3	4	154	3,179
1867	39	4	43	1,070	0	0	0	0	1,070
1868	32	1	34	1,340	0	0	0	0	1,340
1869	43	6	50	1,725	0	0	0	0	1,725
1870	96	13	109	3,620	0	0	0	0	4,370
1871	100	19	119	6,867	0	0	0	38	6,905
1872	61	24	84	2,754	1	0	1	54	2,809
1873	45	7	52	1,733	0	0	0	52	1,785
1874	0	10	10	312	0	0	0	0	312
1875	5	40	45	1,350	0	0	0	0	1,350
1876	—	14	14	397	0	0	0	0	397
1877	21	12	32	402	0	0	0	0	402
1878	—	—	—	—	—	—	—	—	—
1879	—	—	—	185	—	—	—	—	185

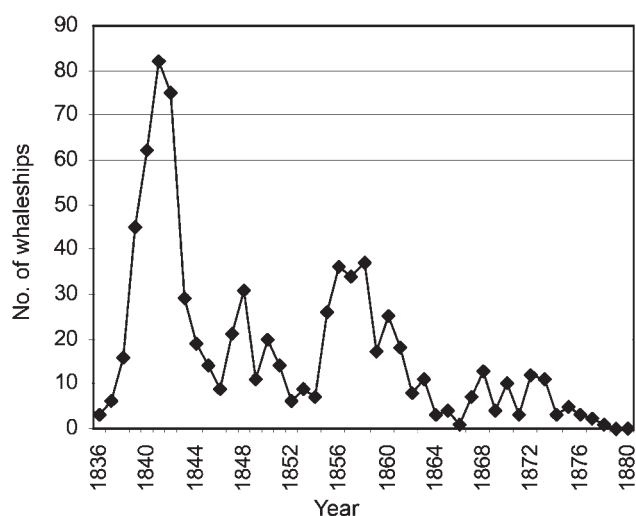


Fig. 2. Foreign whaleships reported in Western Australian waters 1835–1880 (Source: Gibbs, 1996).

decreased (Bannister *et al.*, 1981, p.257). Although it was not possible to extend Bannister's logbook research, a database of foreign (i.e. non-Australian) whaling ships known to have visited the south and western Australian coasts was compiled as a means of further defining periods where fishing by pelagic whalers may have had an impact (Fig. 2). Although the database only recorded presence rather than activity, it does indicate a significant peak in the early 1840s which presumably also suggests heavy fishing in the region (Gibbs, 1998).

## CONCLUSION

While the data from the historical Western Australian whaling records are insufficient to make any clear contribution on the nature or decline of right and humpback whale populations along the Western Australian coasts during the 19th century, they do provide further details of the nature of the whaling activity in the region. Analysis of the Castle Rock records clearly indicates an emphasis on the capture of humpbacks during the mid-1840s to mid-1850s, while consideration of other contemporary records confirms more humpbacks than right whales being caught by colonial shore parties elsewhere in the region in that period. Based on the presence of large numbers of American pelagic vessels operating near and on the Western Australian coasts in the early 1840s, immediately before the colonial shore whalers began operation, it is possible likely the right whale population had already suffered serious impacts, in line with the generally accepted trajectory of Southern Hemisphere right whales over the period 1815–1850 (Best *et al.*, 2001, p.25).

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# Euthanasia of beached humpback whales using explosives

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## ABSTRACT

A method for the safe and effective euthanasia of large beached humpback whales using explosives is described. Five recent case studies involving live stranded humpback whales measuring 9.1–12.7m are described to show how the method was applied, and the capacity of the method to deal with the varying conditions encountered when dealing with large baleen whales. Issues relating to the wider application of this method to other species of baleen whale and large odontocete species are discussed along with key safety implications for the safe use of this method.

KEYWORDS: HUMPBACK WHALE; EUTHANASIA; ANIMAL WELFARE

## INTRODUCTION

The live-beaching of a great whale presents a complex problem for wildlife managers and local government officials. It raises issues of animal welfare, public safety and the personal safety of the public officials involved. In some parts of the world, it is also often the subject of intense outpouring of public opinion and sentiment and can result in extensive media scrutiny during and after the event. As with many complex problems confronting government agencies, this one can be effectively managed only through cooperation as there are invariably multiple jurisdictions involved with multiple pieces of legislation in play.

With the protection of humpback whales (*Megaptera novaeangliae*) in 1963 and southern right whales (*Eubalaena australis*) since 1935 (Tønnessen and Johnsen, 1982), there have been encouraging increases in the number of both species visiting coastal Australian waters (e.g. Bannister, 2008; IWC, 2011). With the recovery in the numbers of these species, there is an increased likelihood of these animals coming ashore due to natural and human induced causes (Bannister *et al.*, 1996; Coughran and Gales, 2010). Kemper *et al.* (2005) reported more than 20 species of cetaceans as live-beaching in South Australia, including three species of great whale (sperm *Physeter macrocephalus*, Bryde's *B. edeni* and fin *B. physalus*). In Western Australia during the period 1981–2010 inclusive, several species (humpback, Bryde's, southern right, fin, blue *B. m. musculus*, pygmy blue *B. m. brevicauda*, Antarctic minke *B. acutorostrata* and sperm whales) have been recorded live-beaching (Department of Environment and Conservation (DEC) unpublished data).

Relocating live large whales weighing in the tens of thousands of kilograms is difficult and dangerous even under calm sea conditions. During inclement weather, the task can become extremely hazardous especially if the whales are beached on rocky substrates. If the risks are too great to allow a rescue team to work, or the logistics of moving the animal are unviable, then serious welfare issues arise. In circumstances where the whale faces a lingering death, euthanasia becomes a valid option (IWC, 2010).

Euthanasia of small cetaceans has been achieved using a range of techniques, including barbiturate overdose (intravenous or intra-cardiac injection), lancing of major heart blood vessels and shooting (brain or heart shot) using large calibre centre-fire firearms (Needham, 1993). While these methods are useful for smaller species (<6m; see Øen and Knudsen, 2007), they are inappropriate or unfeasible for the euthanasia of larger species such as baleen whales (Blackmore *et al.*, 1997). Data presented to the International Whaling Commission via workshops on whale killing methods (e.g. IWC, 2003) suggest that the use of firearms cannot guarantee a quick or humane death in all circumstances, but can have emergency application in some cases (IWC, 2010). Whales of a number of species are shot with large calibre bullets (7.62mm, 9.3mm, 30.06, .375 or .458 inch) in a number of whaling operations and for euthanasia (IWC, 2003).

The use of explosive charges such as penthrite (pentaerythritol tetranitrate or PETN) in the hunting of whales is well documented. Typically 30g charges are delivered into a whale's body via 50 or 60mm boat-mounted harpoon guns, which fire harpoons weighing between 12–18kg (Øen, 1995a; 1995c; 1999). Harpoons are aimed at the thorax of the whales and can result in up to nearly 80% of the target animals dying instantaneously (Øen, 2002). Death usually results from blast-induced trauma to the vital organs, the central nervous system or the brain (Knudsen and Øen, 2003). The use of penthrite grenades on larger whales, such as bowhead whales taken during indigenous hunting, has resulted in times to death ranging from instantaneous up to a median time of 15 minutes (Øen, 1995b). Reference has been made in the published literature to the use of a range of methods for euthanasing large (>6m) whales (e.g. Dierauff, 1990; Hyman, 1990). The few publications that mention the use of explosives for the euthanasia of whales either provide no working details on specifics of the method, only mention the existence of field research (e.g. Needham, 1993), or largely dismiss the method for reasons not related to the capacity of the method to deliver a quick and humane death (e.g. Greer *et al.*, 2001).

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This paper documents a highly effective and safe method of euthanasing humpback whales using explosives and the process that needs to be undertaken to safely apply it. Five case studies are presented to demonstrate the likely range of issues that can be expected in the field and some of the problems that have been encountered during the refinement of this methodology. This method was developed and refined over a 20 year period to the point where an instantaneous death can be delivered with minimal risk to the public and the wildlife management staff involved. The research was conducted by the Department of Environment and Conservation (DEC) on the lower west and south coast of Western Australia between 1990 and 2010.

## MATERIALS AND METHODS

In Western Australia, the DEC is responsible for the administration of the Wildlife Conservation Act 1950 and managing fauna issues, including whales. In this capacity, the DEC has adopted the Australian Inter-Service Incident Management System, which provides a total systems approach to all incident management involving risk<sup>1</sup>. The state police department is responsible for the critical issues of public safety that emanate from public proximity to powerful animals and from the use of explosives, while local government authorities are responsible for public health issues associated with the management of each whale beaching incident.

The process that leads to a decision to euthanase a great whale is relatively straightforward and arrived at following a clinical assessment of each whale (Gales *et al.*, 2008), based on 'Behaviour Criteria' (alert, weakly responsive, non-responsive) and 'General Condition Criteria' (behaviour in water, respiration, heart rate, body temperature and reflexes) of each whale. While there can be difficulty in interpreting every one of the categories during each assessment, the wide array of parameters observed offers the best clinical assessment to determine the prognosis for each whale. Where there is doubt over interpretation, time is allowed in order to ascertain trends in condition. A whale may be in good physical condition but impossible to save. Under these conditions euthanasia is also important. The basic pathways to managers are straightforward and should not be complicated by public expectations and media influences that have no scientific basis.

In all cases reported here, every opportunity was taken to obtain independent veterinary advice either following on-site assessment or telephone discussions. During case 1, DEC staff consulted with a senior veterinary officer from the Western Australian Department of Agriculture and Food on site. For cases 2–5 inclusive, DEC staff on site consulted the senior veterinary officer at the Perth Zoo by telephone with regard to the prognosis and palliative care of the whales. Death of each whale was confirmed using the criteria described in case 1 and in case 5 a local veterinarian who was able to attend the site for the purposes of learning from the exercise was also able to confirm that an instantaneous death had been achieved from the detonation of explosives in that case.

Over the 20-year development period, some of the materials (type of explosive, detonator system) used have

changed as technology has advanced. The most up-to-date materials being used are reported here, but the authors (DKC) can be contacted for details of the earlier types of materials used should that information be required.

## RESULTS FROM CASE STUDIES

### Case 1

On 9 October 1990, a yearling male humpback whale live-beached at 1630h, 200m south of 'The Cut' at Koombana Bay (33°18'S, 115°31'E) Bunbury, Western Australia. An unfavourable prognosis from the attending veterinarian, deteriorating weather conditions and the size of the whale (length 9.11m, weight *ca* 10t) precluded any rescue attempt. A decision was made to euthanase the whale. On the evening of 10 October, an explosive charge was detonated over the area dorsal to the cranium and immediately to the rear of the blow-hole (Fig. 1). Six sticks of AN60 (0.2m long × 25mm diameter) explosive were used in this controlled detonation. AN60 explosive has now been replaced by more advanced products such as Powergel Magnum<sup>®</sup> explosive (Orica Ltd). Detonation occurred as planned, resulting in a neat circular hole, approximately 300mm in diameter that completely removed the underlying skin, blubber, skeletal muscle and the top of the cranium. The brain showed evidence of severe trauma, indicating that the whale had most likely died instantly. Death was determined on the basis of a lack of corneal reflex, the relaxation of the jaw muscles, an absence of response to tactile stimulus of the tongue, an absence of visible signs of respiration and visual confirmation of significant damage to the brain. It was noted that the lower cranium was still intact indicating the appropriate amount of charge to achieve the desired result had been used. The force of the blast had been contained and directed downward and into the brain and apart from the blast wound there was no other physical damage to the whale.

### Case 2

On the afternoon of 24 September 2008, a 10.5m, *ca* 15t sub-adult female humpback whale live-beached in shallow water 1km south of Jurien Bay (30°18'S, 115°02'E), Western Australia. The whale beached in shallow inshore waters after being washed in over a limestone reef and sustaining superficial injuries during this process. It came to rest in the shallows of a sandy bay in a weak and debilitated condition. Following an assessment of the animal's condition, it was determined that the whale was too weak to move and as it

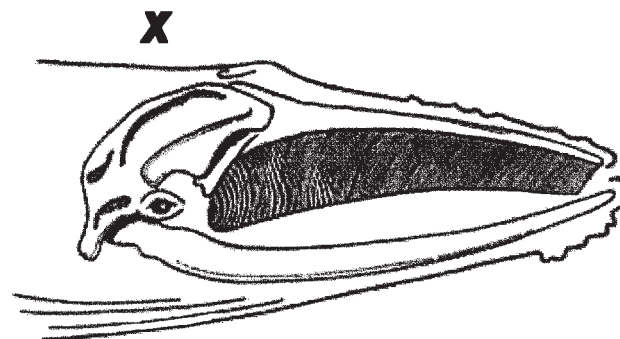


Fig. 1. Profile of humpback whale's head; X shows placement of charge.

<sup>1</sup> <http://knowledgeweb.afac.com.au/training/aiims> accessed 15 March 2010.

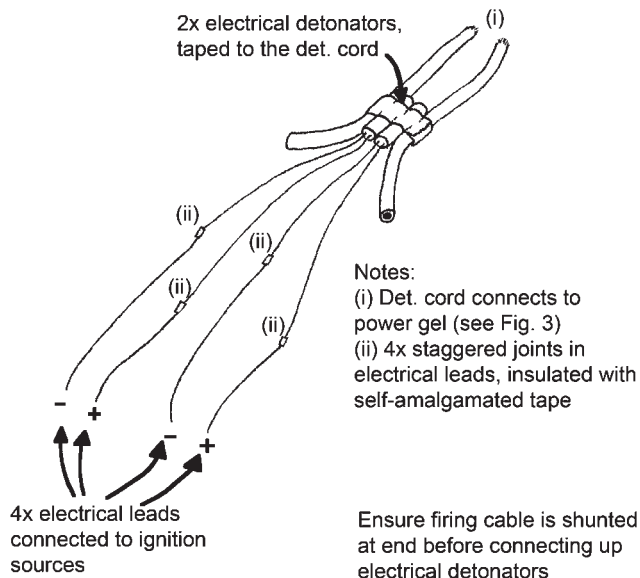


Fig. 2. Arrangement of wiring harness and electronic detonators and detonation chord.

had not made any attempt to dislodge itself from the shallows, it was unlikely to survive any rescue attempt. Due to the size and weight of the animal and the fact that it was lying on the bottom, it would probably sustain additional physical injury and expose staff to a high workplace risk if attempts were made to tow or move the animal back out into deeper waters.

As the stranding was a natural event and there were no immediate public safety concerns, the initial decision was made to allow nature to take its course. DEC officers were on site to ensure that there was minimal disturbance to the whale and to re-assess the situation as needed. A media statement was released by DEC on the morning of 25 September 2008 informing the media of the incident and the management strategy in place. Whilst media response to the strategy was mostly positive, there were some calls from the public, including some international calls, wanting to know why the DEC was not taking more direct action to either 'rescue' the whale or to 'put it down' to prevent it suffering<sup>2</sup>.

DEC chose to maintain the palliative care strategy, and to re-assess the position and consider other options in the coming days. On the morning of 30 September 2008, following a re-assessment of the whale, a decision was made to euthanase it using explosives.

Five sticks of 125g Powergel<sup>®</sup> explosive with two electric detonators connected to two electric firing cables were used in this detonation (Figs 2–6). The initial detonation on the afternoon of 30 September 2008 made a crater approximately 200mm in diameter in the whale's head. The whale was only stunned; no externally visible damage had occurred to the cranium or brain, and a short time later it became active. A 0.300 inch Winchester Magnum rifle was used to place five rounds into the area to the rear of the blow-hole aimed in the direction of the brain. This had no visual effect other than to cause a significant amount of arterial bleeding. A second explosive charge, double the size of

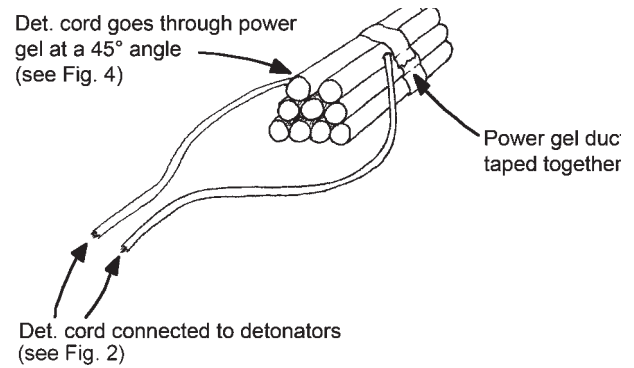
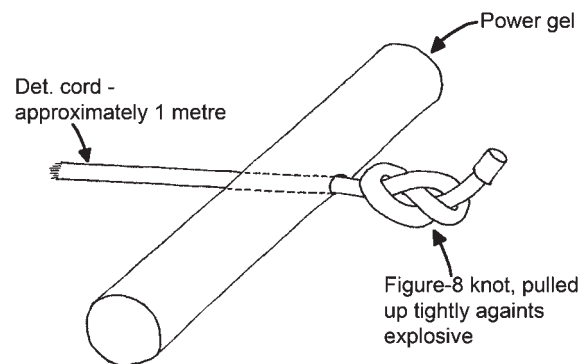


Fig. 3. Configuration of Powergel and detonation chord.



Skewer 2 sticks of power gel with a wooden skewer at a 45° angle to the centre, run the det. cord through and put a figure-8 knot in the end. One for each stick.

Fig. 4. Initiation charges and placement of detonation chord through the uppermost stick of Powergel.

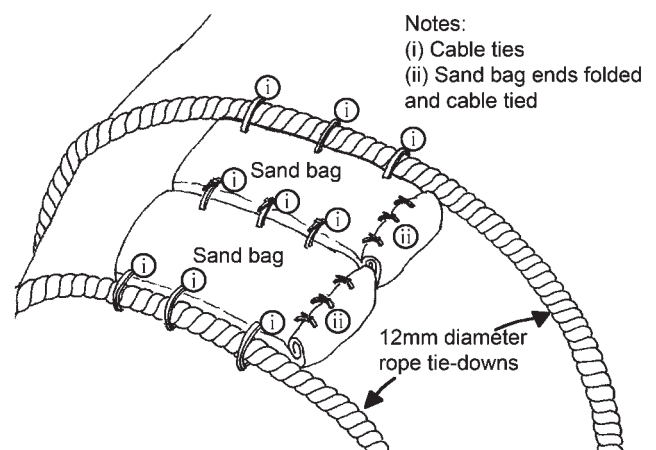


Fig. 5. Placement of tamping bags and tie-down ropes on the dorsal surface of the head immediately to the rear of the blowholes.

the first, was quickly prepared and detonated in the same area as the first charge. The second charge caused an approximately 500mm diameter hole in the whale's head removing all blubber and tissue dorsal to the cranium along with the dorsal part of the cranium and causing severe trauma to the brain, apparently killing the whale instantly. Death was confirmed using the criteria described in case 1.

### Case 3

On the morning of 20 October 2009, a 9.8m, ca 15t, sub-adult female humpback whale live-beached in shallow water

<sup>2</sup> <http://latimesblogs.latimes.com/outposts/2008/10/hard-times-for.html> accessed 15 March 2010.

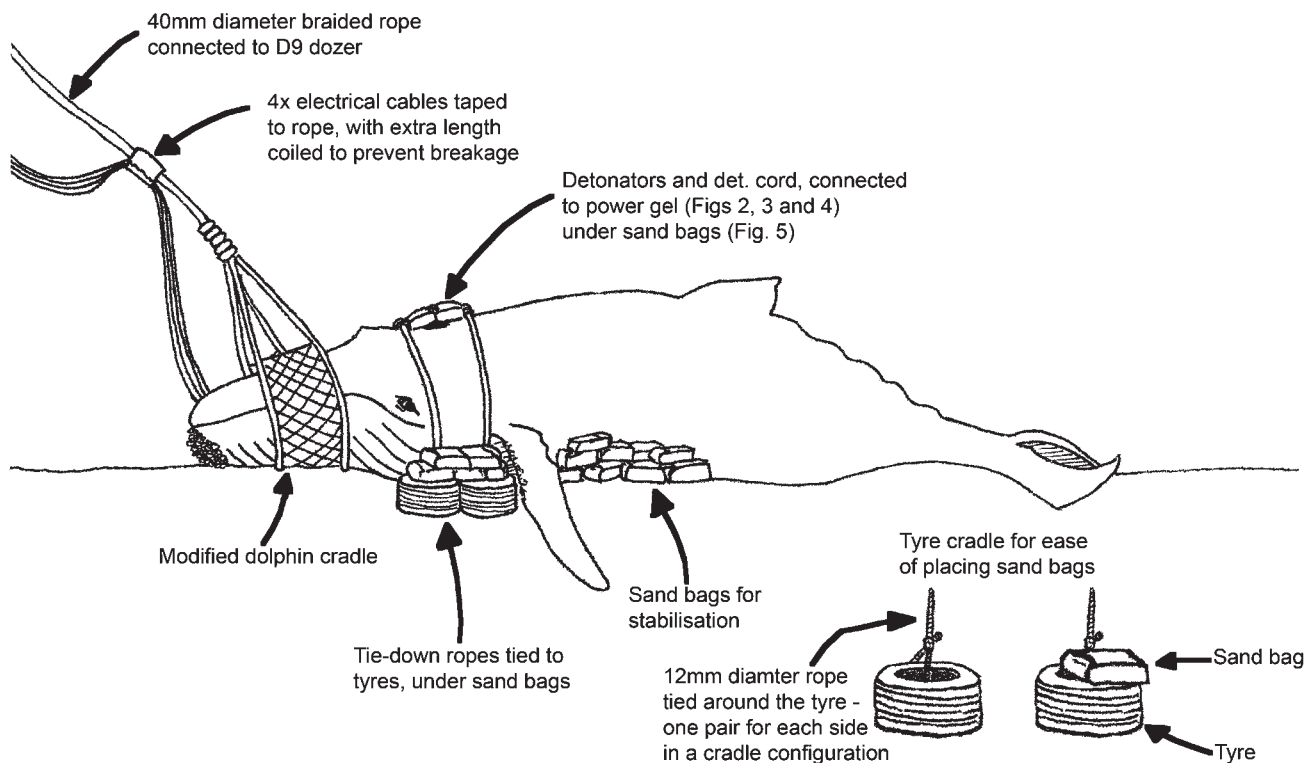


Fig. 6. Overall plan of materials used to secure whale, support wiring harness and placement of charge.

500m east of Windy Harbour (34°50'S, 116°02'E), Western Australia. The whale beached in shallow inshore waters after being washed in and sustaining superficial injuries during this process. It came to rest in the shallows of a sandy bay in a weak and debilitated condition. Following an assessment of the whale's condition it was determined that the whale was too weak to move and as it had not made any attempt to dislodge itself from the shallows, it was unlikely to survive any rescue attempt. Due to the size and weight of the animal and the fact that it was lying flat on the sand and almost high and dry on a low tide, it would likely sustain additional physical injury and expose staff to a high workplace risk if attempts to move the animal back out into deeper waters.

As the stranding was a natural event and there appeared to be no immediate public safety concerns, the initial decision was made to allow nature to take its course. DEC officers were on site to provide palliative care (covering the animal with wet cloth to protect it from the sun) and to ensure that there was minimal disturbance to the whale and to re-assess the situation as needed.

The whale was constantly monitored by DEC staff and veterinary assessments were carried out. The whale's general condition and prognosis was deemed very poor and a decision was made on 21 October 2009 to euthanase the whale using explosives on the morning 23 October 2009 if the animal was still alive at that time. Fourteen sticks of 125g Powergel Magnum explosive were used in this detonation. Detonation occurred as planned, resulting in a neat circular hole approximately 300mm in diameter that completely removed the skin, blubber, skeletal muscle and the top of the cranium (Fig. 7). The brain suffered severe trauma caused by the blast along with fragments of the upper cranium, apparently killing the whale instantly. Death was confirmed using the criteria described in case 1, above.

#### Case 4

On the evening of 12 January 2010, a 12.7m male humpback whale beached at Kennedys Beach (33°54'S, 122°51'E), Western Australia. It was assessed late that night and was still alive by the morning of 13 January 2010. Its body condition was very poor and the post-cranial depression was such that a pronounced hump was visible posterior to the blowholes. A significant depression was visible along the lateral flanks and a significant sub-dermal protrusion of the scapulae was visible. By 14 January more than 30% of its dorsal body surface had blistered from exposure to the sun. By late on 14 January 2010 it was obvious this animal was terminal and with high temperatures (>40°C) forecast over the ensuing days the decision was made to euthanase the whale using explosives. The challenge with this case was the fact that this animal would be the largest animal the technique had been applied to. With increased size and body mass there was an expectation that the dorsal bone structure of the cranium would be more substantial and that a larger explosive charge would be required. The charge consisted of 22 sticks of 125g Powergel Magnum, assisted by two 50g



Fig. 7. Photograph of the dorsal head area of the whale from case 3 after detonation of the explosive charge.



boosters. At 1610 hours on 15 January 2010, the charge was detonated, instantly killing the whale. The blast penetrated the upper cranium, causing severe trauma to the brain but did not sever the head from the body, leaving the bottom half of the skull intact. Death was confirmed using the criteria described in case 1, above.

### Case 5

On 19 August 2010, a 9.5m, 15t (weight post death) humpback whale beached on a sandbar within the port of Albany (35°03'S, 117°53'E) on the south coast of Western Australia. This whale was in a debilitated condition but still quite active. On high tide this whale could have swum into deep water but never attempted to do so. Its condition was slowly deteriorating, but the site and the activity of the whale did not allow for safe management for palliative care or early euthanasia. This whale was monitored daily by DEC staff until the tide, weather conditions and activity levels of the whale were deemed manageable. On 1 September 2010, the decision was made to euthanase the whale using explosives.

The whale was on a sand bar approx 1.2km from the nearest shoreline and it was noted to be lying on its left side. The right pectoral fin was in less than 0.5m of water whilst the left was in approximately 1m. The whale's blow-holes were submerged which meant it had to raise its head to breathe. The whale's breathing rate increased when first approached but settled down to a slower rate after a short period.

There were several factors associated with this case that had not been encountered in previous cases, necessitating minor modifications to the standard procedure. As the whale was resting on its side, in a left leaning aspect, it was not possible to place the charge to the rear of the blow-holes above the cranium as in cases 1 to 4, above. The whale was raising its head to breathe and there was some concern that this movement may dislodge the charge and sand bag tamping.

As the whale was so far from a beach it was difficult to stabilise the whale's head. An attempt was made to position sand bags under the whale's jaw to support it, without success. The whale would not leave its head up long enough to allow the sand bags to be safely positioned beneath the mandible. Truck tyres and a number of sand bags were positioned on the left side of the whale to stabilise the animal. It was decided to try putting a sand bag on the whale in the position of the charge to see if the sand bag would move when the whale lifted its head. The sand bag did not move in response to this activity, so more sand bags were positioned on the right side of the whale's head, in a line between the eye and to the rear of the blow-holes. These sand bags did not move so it was decided to go ahead with the placement of the explosive charge and detonation on 2 September.

Little information was available on the likely thickness of the lateral part of the skull that was presenting in the dorsal aspect, or the precise distance from the skin to the cranium from the position. Accordingly, three extra sticks of Powergel were used in the charge. The total charge consisted of 15 sticks of 125 gram Powergel explosive. The sticks were taped together forming a pyramid. These were initiated by two lines of detonation chord running through the stick at the apex.

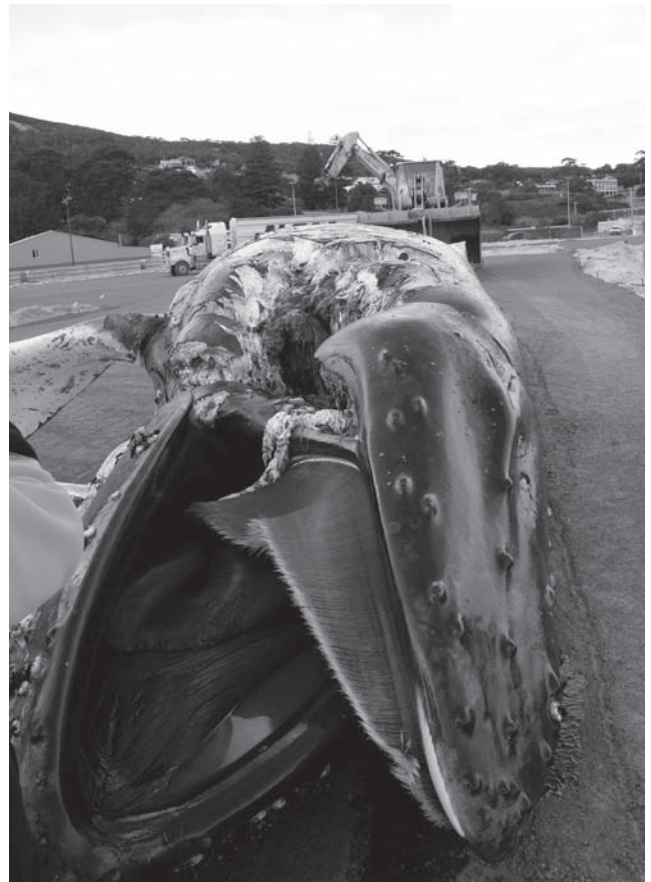


Fig. 8. Photograph of the lateral head area of the whale from case 5 after detonation of the explosive charge.

Due to the fact that no heavy machinery could be located close to the whale, no bulldozer blade was available to use as a blast shield. Initiation of the charge by a timed safety fuse was considered, however this would have required leaving a burning detonation chord for two minutes with the possibility of the whale smelling the black powder smoke and becoming agitated and dislodging the charge. A decision was made to detonate the charge electrically from behind a dinghy 50m away. The tamping sand bags were checked to ensure that only wet sand had been used for filling and that there was no chance of 'fly' from the charge. The wet sand in the bags was used to further assist in containing the explosive force to the target area. Two electric detonators were connected to the firing cable in parallel and then taped to the two lines of detonation chord. The area was checked to ensure no unauthorised people had entered the exclusion area and that it was safe to fire the charge, an air horn was sounded and the charge fired. Upon examination of the whale it was found that the charge had been successful with a 1.0m × 1.5m elliptical hole punched through the blubber and right dorso-lateral section of the skull, causing severe trauma to the cranium and brain (Fig. 8).

### OVERVIEW OF THE PROCESS

Circumstances at each site where whales beach vary and as such the range of equipment used, in particular heavy and light vehicles, differ slightly<sup>3</sup>.

<sup>3</sup> The recommended equipment list to successfully and safely euthanase whales is available from the principal author (DKC) on request.



### Public safety and information

In cases where whales have beached in close proximity to populated areas, DEC routinely requests the local police (assisted by State Emergency Service (SES) personnel) to secure and control the site before any operations begin on the whale. The presence of uniformed officers provides a distinct advantage in obtaining crowd compliance with requests to keep a required distance from operations involving heavy and light machinery, potentially inclement sea conditions, firearms and explosives. In remote areas where access to police and SES personnel is not always possible, the DEC incident controller delegates crowd control responsibilities to authorised DEC staff. Authorised DEC staff have powers under state legislation to compel members of the public to comply with given directions. The public are excluded to ensure safety rather than prevent them from gaining an appreciation of the events that are to take place.

Prior to any work related to the preparation or placement of the explosive charge, a briefing is provided to all essential personnel, members of the public (if present) and any media representatives. The briefing covers issues such as the species of whale involved, the conservation status of the whale, the animal welfare issues at hand (including any independent veterinary advice available), why the whale cannot be saved or returned to the sea, what course of action will be taken to end the whale's suffering and what will be asked of the public/media in order to ensure the safe operation of the euthanasia protocol.

### The process

It is important to shape the explosive charge into a triangular pyramid (see Fig. 3) to ensure maximum explosive force is directed downward onto the smallest area of the whale's head, directly above the cranium. For very large whales such as the one described in Case 4, it is recommended that two 50g boosters be added on top of the charge to ensure optimal detonation of the explosive charge and to direct the blast downwards. The boosters are installed with two lines of detonating cord and detonate before the primary charge. The electrical firing cables should be shorted out to discharge any static current within the wiring system, and the charge watched closely to ensure it is not dislodged from the main explosive charge, and that the charge does not move from its central position over the mid-line of the whale's head (Fig. 5). The electrical firing cables are laid out back to the bulldozer or protective sand dune (Fig. 6). Two electric detonators are connected to two electrical firing cables using self-amalgamating tape. The electric detonators are then taped to the detonating cord using plastic electrical tape.

Heavy machinery (e.g. D9 or D65EX bulldozers) is used to achieve four important functions. The first is to assist in manoeuvring the whale into a position on the beach where it can be stabilised. The second is to provide a secure point of attachment for the wiring harness to keep it clear of rocky substrates, surging wave action and personnel. The third function is to provide protection to the shot-firing team from the effects of the blast, and the final function is to remove the whale carcass from the beach, if necessary.

All non-essential persons are moved 500m back from the detonation site prior to the explosive charge being prepared or placed on the whale. All essential personnel take cover

behind the heavy machinery (if available) or the first line of sand dunes present on the beach, prior to the trigger mechanism being connected to the wiring harness. A transmission on the universal emergency and calling marine radio frequency (marine VHF channel 16) is made once all non-essential personnel are moved 500m back from the site and prior to the commencement of the preparation of the explosive charge.

After this point in the process, no electronic communication devices, including mobile telephones, are used or left on to ensure that the explosive charge is not detonated prematurely. It is important to note that electronic communications from aircraft over-flying the site could present a real risk of premature detonation. Military aircraft (or base installations) typically generate much stronger electronic transmissions than commercial or private aircraft and may make the use of electrical detonating systems impractical under some circumstances. Under such circumstances the charge should be detonated using a non-electric system.

Once the charge has been prepared and secured on the whale the shot-firer then provides a visual signal to the police/SES (if present) to activate their flashing emergency lights and siren. The shot-firer then takes cover behind the heavy machinery or sand dune, arms the system and detonates the explosives. No personnel are permitted to approach the whale carcass until the shot-firer has determined the site safe.

### DISCUSSION

Current use of explosives in killing whales at sea is limited to penthrite grenades (typically 30g charges) that are attached to whale harpoons. The harpoons are fired into the body of the whale and typically penetrate 600–700mm before the delayed fuse mechanism detonates the explosive (Knudsen and Øen, 2003). The method described in this paper uses up to 2,750g of Powergel explosive placed strategically above the cranium to achieve a better and more reliable outcome on beach stranded whales.

Explosives work by the virtual instantaneous conversion (detonation) of a mixture of chemical compounds into gas and heat. This detonation of the explosive is achieved by sending a shock or detonation wave through the explosive compound. A detonator is used to initiate the detonation wave which once started will propagate through the explosive at speeds of up to  $8,000\text{ms}^{-1}$ . The gas volume produced by a 30g penthrite charge is between 768–790L. The more gas produced by the explosive the greater the destructive power of the explosion. Military bombs confine the gas produced by the explosive detonation in iron cylinders allowing it to build up. In civilian utilisation of explosives such as mining, the gases are contained by placing the explosive in a bore hole and positioning 'tamping' over it. The greater the pressure build-up, the more productive the blast (i.e. the more rock that will be fractured and dislodged). If the blast is not contained or directed in some manner the gases will take the least line of resistance, dissipating into the atmosphere mainly as heat and noise with little blast effect.

Powergel is a more stable explosive and is less expensive than penthrite. Powergel has a reasonably high velocity of

detonation of  $6,337 \text{ ms}^{-1}$  compared with penthrite's  $7,400\text{--}8,300 \text{ ms}^{-1}$  (dependent on the density of the penthrite). When euthanasing stranded whales it is not possible to contain the explosive charge inside the animal and neither can the explosive charge be placed in a metal container in the manner of traditional military style bomb, which when shattered would cause dangerous fragments that could be propelled for quite some distance (1000m). The dying whales do not always choose to beach themselves in places that allow a 1,000m safety envelope for wildlife authority staff to operate with. The combination of layered sand bags containing wet sand as tamping to 'contain' the explosive gases produced, along with the larger amount of explosive (compared to the small amount of penthrite) and the careful shaping of the charge, addresses the issue that the majority of the explosive gases will escape when used in the manner described here. The sand from the disintegrating sandbags, with its low mass and very small particle size will not be propelled by the explosion any more than 30m from the blast site.

In Western Australia a shot-firer's licence, issued by the Department of Mines and Petroleum under the provisions of the Explosives and Dangerous Goods Act 1961, is required to handle and use explosives. The safe and efficient use of explosives requires considerable expertise, for which DEC relies heavily on outside personnel and agencies, including the military. Matching legislation will most likely need to be complied with in other jurisdictions. Most members of the police or military who have experience with explosives have learnt to use these materials on inanimate structures such as concrete, metal and the like. The physical properties of these inanimate materials respond very differently to the biological materials of blubber, muscle and bone. It is our experience that there is a strong tendency to underestimate the amount of explosive charge necessary to achieve a humane death of a living great whale.

The potential clearly exists to use this implosion technique on a range of large whale species. There is a wide range in head shape and the volume of tissue mass dorsal to the cranial anatomy within different whale species (and possibly even within species and between the sexes). The example provided in case 5 demonstrates that this method has application when the explosive charge needs to be placed on a section of the head other than directly above the cranium and posterior to the blow holes. Beached whales are encountered in a wide range of physical conditions, and this can greatly influence the amount of explosive required to ensure destruction of the cranium and brain. Further field trials involving already deceased animals are strongly recommended. This is particularly important if the technique is to be applied to odontocete whale species such as the sperm whale. The results of any such field trials, whether successful or not, should then be communicated to the wider scientific community either through publicly available fora such as the International Whaling Commission workshops on whale killing methods and/or through peer-reviewed journals.

During Case 2, a media helicopter presented a serious safety breach by over flying the site as the charge was being set on top of the whale's cranium as electrical detonators were at that time in place within the charge. Presumably the

pilot was unaware of the risk of premature detonation caused by electronic devices such as aircraft electronic transmitters and radios. Clearly serious thought needs to be given to how to manage any aircraft movement in close proximity to field operations involving the use of electrical detonators. There may also be situations where the safe use of explosives, especially when combined with electrical detonators, will not be possible and alternative euthanasia methods will need to be considered or nature allowed to run its course.

Management of cases such as these would benefit from professional advice from suitably qualified veterinarians. In many parts of Western Australia where these types of stranding events occur, it is not possible to access the services of a veterinarian, other than by telephone or radio. Added to this is the problem that few veterinarians have any practical experience in the treatment or palliative care of cetaceans, and in particular baleen whales. It is our experience that being able to receive any advice available provides reassurance, but an inability to access quality advice from a veterinarian should not be considered an impediment to applying this technique.

The management of beached whales evokes strong public emotions. It is important that public perceptions and lack of appreciation for the facts surrounding beaching events do not prevent responsible wildlife agencies from making science-based decisions about the welfare of beached whales. There is ample opportunity to apply palliative care actions such as covering whales with damp cloths to prevent blistering from exposure to the sun. However, just because a whale is larger than most animals that the public has experience with does not in any way mean that it should be treated any differently. Large animal euthanasia involves issues dictated by physics, and euthanasia by explosives is a feasible and safe response to the issue. The data presented here clearly demonstrate that euthanasia of large humpback whales (and potentially other species) can be achieved safely and humanely with modern commercial explosives. The broader application of this method should be investigated whenever opportunities present, ideally via field trials on already deceased animals.

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