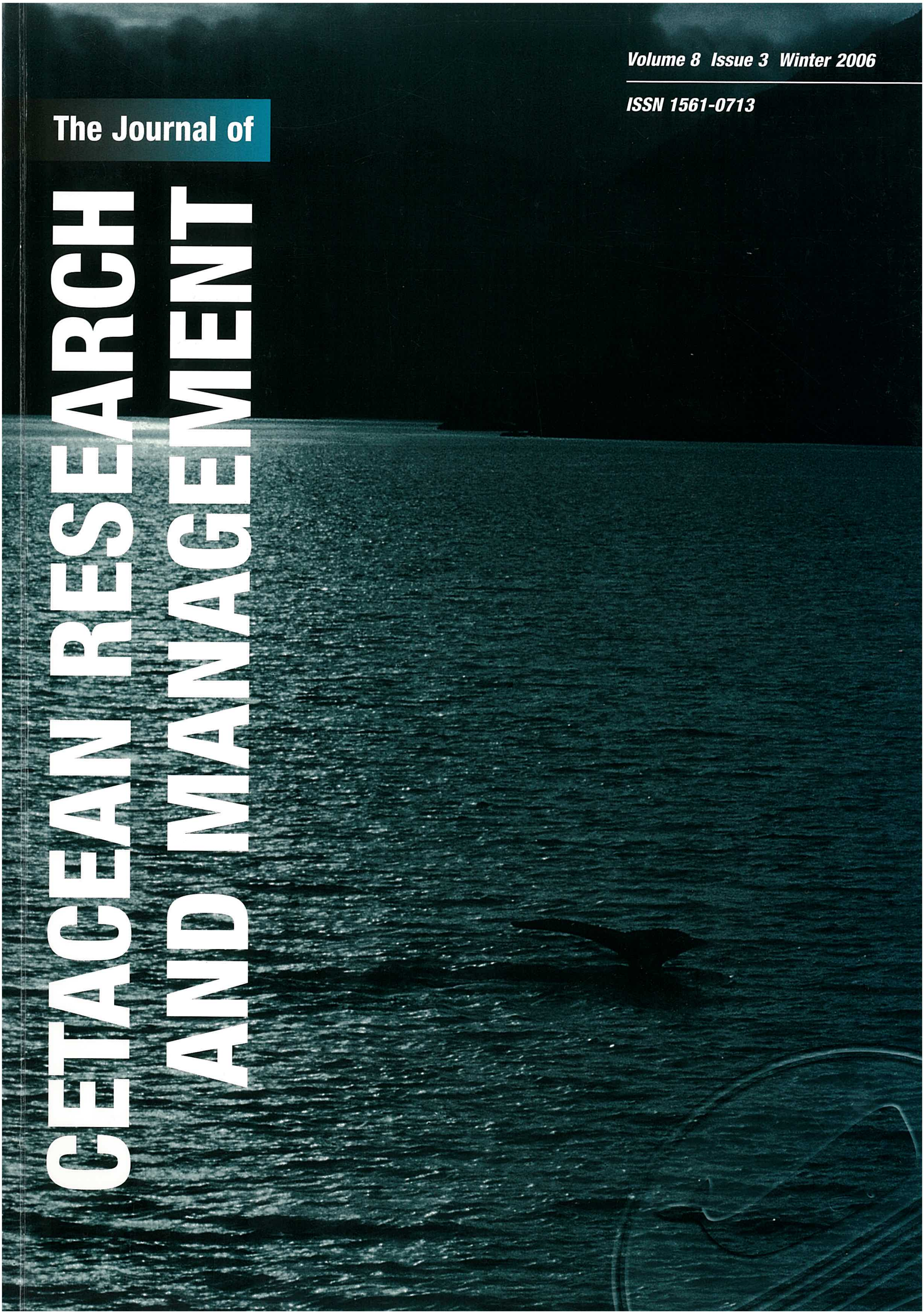
Volume 8 Issue 3 Winter 2006

ISSN 1561-0713

The Journal of
CETACEAN RESEARCH AND MANAGEMENT



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Editorial

Welcome to this the final issue of Volume 8 of the *Journal of Cetacean Research and Management*.

Despite certain logistical problems in timing, 2006 has been another successful year for the Journal. A total of 32 papers have been published this year covering a wide range of subjects related to the conservation and management of cetaceans. There have been a total of 104 authors from Europe, Asia, Africa and North and South America. This year's Supplement included the full report of the Scientific Committee held in Ulsan, Korea as well as the results of five important intersessional workshops. The author and subject index can be found at the end of this issue.

An essential part of providing wise management advice is the incorporation of scientific uncertainty into the assessment process. The IWC Scientific Committee has played a pioneering role in this work and I am pleased to include a paper that uses a new technique for incorporating uncertainty into the assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales which are subject to aboriginal subsistence whaling (Brandon and Wade). There has been considerable recent interest in the topic of man-made noise (such as that created by certain types of naval sonar and seismic activities) and its actual and potential effects on cetaceans; two of the papers in the present volume (Stone and Tasker; Wang and Yang) consider aspects of this important conservation issue. Assessing the status of cetaceans and the potential impact of human activites requires *inter alia* good estimates of abundance and this issue includes a paper providing the first abundance estimates of fin and sei whales in an area of northwest Scotland that is also an area of expanding oil industry operations (Macleod *et al.*) and another providing the first aerial survey abundance estimate for humpback whales off Brazil (Andriolo *et al.*). Understanding distribution, movements and stock structure is also of great importance to management and conservation and this issue includes a number of relevant studies, including papers illustrating the value of collaborative photo-identification studies for showing movements between feeding and breeding grounds (Stevick *et al.*, and Rock *et al.*), a paper providing the first comprehensive look at the distribution in Antarctic waters of the poorly studied spectacled porpoise (Sekiguchi *et al.*), a note on the first record of a dwarf minke whale from Chilean waters (Acevedo *et al.*), a paper evaluating the use of data from whalewatching operations for examining the distribution of killer whales (Hauser *et al.*) and a paper examining the use of stable isotope analysis to provide insights into the seasonal distribution and habitat use of the critically endangered North Atlantic right whale (Summers *et al*).

Finally, I would like to thank the 48 scientists that have acted as anonymous reviewers for the papers published in Volume 8 (Baker, C.S.; Ballance, L.T.; Bannister, J.L.; Barlow, J.; Barros, N.B.; Best, P.B.; Bravington, M.; Buckland, S.T.; Calambokidis, J.; Carlson, C.; Clapham, P.J.; Clark, C.W.; Cañadas, A.; Cooke, J.; DeMaster, D.; Fernandez, A.; Gales, N.; George, J.C.; Gerrodette, T.; Hammond, P.S.; Jefferson, T.A.; Jepson, P.D.; Katona, S.; Laake, J.L.; Larsen, F.; Leaper, R.; Martin, A.R.; Moore, S.E.; Natoli, A.; Northridge, S.; Nowacek, D.; O'Hara, T.; Raftery, A.; Rankin, S.; Read, A.J.; Reeves, R.R.; Reilly, S.B.; Schweder, T.; Secchi, E.R.; Siciliano, S.; Stone, G.; Strindberg, S.; Tanabe, S.; Van Waerebeek, K.; Wells, R.S.; Whitehead, H.; Zeh, J.E.; Zerbini, A.). Without their diligence and hard work, the papers in the *Journal*, and more importantly the contribution they make to the wise management and conservation of cetaceans, would be considerable poorer. A full list of the reviewers and their affiliations can be found at: *http://www.iwcoffice.org/publications/contents_reviewers.htm#review*.

G. P. DONOVAN
Editor

Assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales using Bayesian model averaging

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ABSTRACT

Bayesian estimation methods are used to fit an age- and sex-structured population model to available data on abundance and stage-proportions (i.e. calves/mature animals in the population) for the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). The analyses consider three alternative population modelling approaches: (1) modelling the entire population trajectory from 1848**,** using the 'backwards' method where the trajectory is back-calculated based on assigning a prior distribution to recent abundance; (2) modelling only the recent population trajectory, using the 'forwards from recent abundance' method, where the population is projected forwards from a recent year and the abundance in that year is not assumed to be at carrying capacity; and (3) a version of (2) that ignores density-dependence. The 'backwards' method leads to more precise estimates of depletion level. In contrast, the 'forwards from recent abundance' method provides an alternative way of calculating catch-related quantities without having to assume that the catch record is known exactly from 1848 to the present, or having to assume that carrying capacity has not changed since 1848. Not only are all three models able to fit the abundance data well, but each is also able to remain consistent with available estimates of adult survival and age of sexual maturity. Sensitivity to the stage-proportion data and the prior distributions for the life history parameters indicates that use of the 1985 stage-proportion data has the greatest effect on the results, and that those data are less consistent with data on trends in abundance and age of sexual maturity. The analyses indicate that the population has approximately doubled in size since 1978, and the 'backwards' analyses suggest that the population may be approaching carrying capacity, although there is no obvious sign in the data that the population growth rate has slowed. Bayes factors are calculated to compare model fits to the data. However, there is no evidence for selecting one model over another, and furthermore, the models considered in this study result in different posterior distributions for quantities of interest to management. Posterior model probabilities are therefore calculated and used as weights to construct Bayesian model-averaged posterior distributions for outputs shared among models to take this ambiguity into account. This study represents the first attempt to explicitly quantify model uncertainty when conducting a stock assessment of bowhead whales.

KEYWORDS: ARCTIC; BOWHEAD WHALE; MODELLING; WHALING – ABORIGINAL; NORTHERN HEMISPHERE; BERING SEA; BEAUFORT SEA; CHUKCHI SEA

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) have been caught by Alaskan Eskimos in an aboriginal fishery for hundreds of years or more and active whaling started along the arctic coast around 1,800-1,700 years before present (Braham, 1989; Dinesman and Savinetsky, 2003). A commercial fishery began takes from the Bering-Chukchi-Beaufort Seas (B-C-B) stock of bowhead whales in 1848, and the population is thought to have been severely depleted by the substantial commercial catches that occurred during the 1800s (Bockstoce and Botkin, 1983; Breiwick and Braham, 1990; Breiwick *et al.*, 1984). Although the commercial fishery almost completely collapsed early in the 1900s, aboriginal catches of B-C-B bowhead whales continue (e.g. Braham, 1995; George *et al.*, 1988; Suydam and George, 2004).

Most of the B-C-B bowhead whale stock migrates seasonally along the north slope of Alaska between wintering areas in the Bering Sea and summer feeding areas in the Beaufort Sea. Surveys have been conducted during the spring migration past Point Barrow during eleven years since 1978, to estimate the abundance and trends of this population (George *et al.*, 2004). The ice-based counts have resulted in abundance estimates substantiated by estimates using mark-recaptures of individually identifiable whales in aerial photographs (da Silva *et al.*, 2000). These abundance estimates have served as the primary basis for assessments of the status of and management advice for the B-C-B bowhead whale stock by the Scientific Committee of the International Whaling Commission (IWC).

Given a history of catches, it was possible to conduct an initial assessment of the status of the population once the first abundance estimate was made in 1978. This assessment suggested that the population had experienced some recovery since its depletion in the 1800s, but that it was still below its carrying capacity (Breiwick *et al.*, 1984). Breiwick and Braham (1990) noted that estimates of carrying capacity and depletion level are sensitive to the current estimated population size. However, it is now possible to make more precise estimates of these quantities (conditional on the accuracy of the catch data and population dynamics model) because the number and precision of the abundance estimates has increased substantially.

Givens *et al*. (1993) and Raftery *et al*. (1995) introduced Bayesian methods (e.g. Press, 1989) to the assessment of bowhead whales. These methods can make use of multiple sources of data and fully characterise uncertainty. Bayesian assessments of the B-C-B bowhead whale stock (e.g. Givens *et al.*, 1995) using the *BALEEN II* model (de la Mare, 1989) have consequently been used extensively by the IWC Scientific Committee (Punt, 1999b). Although there was general agreement that using multiple sources of data in assessments was desirable, considerable debate ensued in the IWC Scientific Committee regarding the details of the statistical methods to be used in bowhead whale

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assessments (e.g. Butterworth and Punt, 1995; Poole and Givens, 2001; Poole *et al.*, 1999; Punt and Butterworth, 1999; 2000; Schweder and Ianelli, 2000). One troublesome outcome of the results in the standard 'forwards from *K*' assessment (i.e. projecting the population dynamics model forwards from a prior distribution for the population size in 1848, which is assumed to be carrying capacity) was that the observed rate of increase of the population (ROI) differed substantially from the resulting posterior distribution for the ROI, even though the data on ROI were the main data source used in the analysis (e.g. Punt and Butterworth, 1999; Raftery and Poole, 1997). This and other related issues were determined to be due in part to a methodological issue associated with the forwards method and the specification of prior distributions. It was also determined that these issues could essentially be resolved by the use of the 'backwards' method, in which no prior is specified for the population size in 1848; instead, a prior distribution is specified for abundance in a recent year, and the population level in 1848 (assumed to be carrying capacity) is then back-calculated from that recent abundance (Butterworth and Punt, 1995; Poole and Raftery, 1998; Punt and Butterworth, 1999).

An important assumption made in bowhead whale assessments is that the catch history is known without error. It has been found that the catch record going back to 1842 for the eastern North Pacific stock of gray whales cannot be reconciled with the population's current dynamics (Punt and Butterworth, 2002), without assumptions that the catch record has been substantially under-estimated and/or that carrying capacity has changed since the mid 1800s. While it appears from past assessments that the bowhead whale catch record can be reconciled with the current dynamics, it is still appropriate to investigate an alternative assessment that does not make use of the historical catch record. This can be achieved using the method developed by Wade (2002a) for gray whales, where a model is projected forwards from a prior distribution for abundance in a recent year, with a separate prior distribution specified for carrying capacity. Such an assessment does not use the historic catch record prior to 1978, and does not need to assume that carrying capacity has remained constant since the mid 1800s; therefore, it should be robust to problems with these assumptions.

The 1998 assessment of the B-C-B bowhead whale stock (IWC, 1999; Punt, 1999a) used 'backwards' Bayesian estimation based on the *BALEEN II* model, and the then-available abundance estimates and the data on the proportion of calves and mature animals in the population during 1985-94 (the 'stage-proportion' data). New information available for this stock since the 1998 assessment includes: (1) a mark-recapture estimate of adult survival from aerial photographs (Zeh *et al.*, 2002); (2) an estimated age at sexual maturity and an estimate of maximum age (George *et al.*, 1999); (3) a recalculation of the stage-proportion data (Koski *et al.*, 2004); and (4) an estimate of abundance for 2001 (George *et al.*, 2004).

This paper examines the sensitivity of the results of the B-C-B bowhead whale assessment to modelling: (1) the entire population trajectory from 1848 (using the 'backwards' method); and (2) only the recent period (where the population is projected forwards from a recent year, and the abundance in that year is not assumed to be at carrying capacity). A third set of analyses is conducted using a Leslie matrix with no density-dependence. The population model used in this assessment is the density-dependent Leslie matrix model (Leslie, 1945; 1948) developed by Breiwick *et al.* (1984) except that reproduction and natural mortality are assumed to occur before removal by catches. When parameterised in equivalent ways, the results of the *BALEEN II* model and this Leslie matrix model are almost identical (Punt and Butterworth, 2002; Wade, 2002a).

This paper also examines the sensitivity of the model outputs to the sources of data included in the assessment and the specifications for the prior distributions. Scenarios are specified to investigate the sensitivity of the results to data-based informative vs. uniform (less informative) prior distributions, as well as to how the stage-proportion data are constructed. The stage-proportion data are excluded altogether in some analyses, and varied in others based on whether the aerial photographic survey data from 1985[1] are included in their calculation or not. Within a scenario, identical prior distributions are assumed for the life-history parameters and matching data-sets are used in the likelihood function for each of the three modelling approaches to enable comparisons to be made among them.

Model uncertainty is accounted for within a Bayesian framework, and Bayes factors (Kass and Raftery, 1995) are calculated to quantify the evidence provided by the data in favour of the different modelling approaches. For the 'reference scenarios' there is no evidence for selecting one model over another, but there are important differences in the estimates of quantities that would be of interest to management. Therefore, we follow the philosophy outlined by a number of authors (e.g. Buckland *et al.*, 1997; Durban *et al.*, 2005; Hoeting *et al.*, 1999; Kass and Raftery, 1995; Patterson, 1999; Raftery *et al.*, 2005) and present quantities of interest as Bayesian model averages; weighting the output of contending models based upon their relative likelihoods, as opposed to selecting between them.

METHODS

Available data

The population dynamics models were fitted to three sources of data: (1) abundance estimates from ice-based surveys at Point Barrow, Alaska between 1978 and 2001 (Table 1); (2) proportion calves/mature animals in the population from 1985 to 1994 (Table 2); and (3) annual catches in individuals from 1848 to 2002 (Table 3).

All of these sources of data were used in the 1998 assessment but have been updated since. The first ice-based survey since 1993 was conducted in 2001 and has provided an abundance estimate for that year of 10,545 with a coefficient of variation of 0.128 (updated from George *et al.*, 2004 by Zeh and Punt, 2005). The catch data have been updated with the post-1998 catches and revisions to the catches for 1994-96. Two additional years of aerial photographic data have been analysed since the previous assessment and the stage-proportion data have been recalculated (Angliss *et al.*, 1995; Koski *et al.*, 2004).

Additional information available for this stock since the 1998 assessment includes a mark-recapture estimate of survival (Zeh *et al.*, 2002) and a recent estimate of age of sexual maturity and the maximum age (George *et al.*, 1999). This information was included in the analyses of this paper as data-based informative priors (see the section on Model parameters and prior distributions).

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[1] 1985 appears to have been an anomalously late migration year; the aerial survey in 1985 is believed to have ended too early to have sampled the tail-end of the migration, typically when most cow/calf pairs are in the study area (Koski *et al.*, 2004).

Table 1

Estimates, coefficients of variance (CVs) (actually the standard errors of the log abundance estimates, which are approximately equal) and the correlation matrix for the indices of abundance for the B-C-B Seas stock of bowhead whales (Zeh and Punt, 2005).

Year	Estimate	CV	Correlation matrix										
1978	4,765	0.305	1.000										
1980	3,885	0.343	0.118	1.000									
1981	4,467	0.273	0.056	0.050	1.000								
1982	7,395	0.281	0.094	0.084	0.035	1.000							
1983	6,573	0.345	0.117	0.104	0.049	0.084	1.000						
1985	5,762	0.253	0.070	0.062	0.020	0.078	0.062	1.000					
1986	8,917	0.215	0.072	0.064	0.017	0.092	0.064	0.113	1.000				
1987	5,298	0.327	0.124	0.110	0.052	0.088	0.110	0.065	0.067	1.000			
1988	6,928	0.120	0.028	0.025	0.013	0.017	0.024	0.009	0.007	0.026	1.000		
1993	8,167	0.071	0.001	0.001	0.001	0.000	0.001	-0.001	-0.002	0.001	0.000	1.000	
2001	10,545	0.128	0.008	0.007	0.005	0.001	0.007	-0.004	-0.008	0.008	0.003	0.000	1.000

Table 2

The proportion of observed calves (p_c^{obs}) and mature (p_m^{obs}) animals with associated standard errors, over the years 1985-1994. Proportions are given based on including and ignoring the anomalous 1985 data set, as well as those used in the previous assessment (IWC, 1999; Koski *et al*., 2004).

Scenario	p_c^{obs}	σ_{p_c}	p_m^{obs}	σ_{p_m}
Exclude 1985	0.0580	0.0062	0.4366	0.0106
Include 1985	0.0309	0.0034	0.4160	0.0096
1998 assessment	0.052	0.0164	0.411	0.0286

Table 3

Catches of B-C-B Seas bowhead whales, 1848-2002. Values in parenthesis are the catches used by Punt and Butterworth (1999) in the 1998 assessment where these catches differ from those used in the present analyses.

Year	Total kill	Year	Total kill	Year	Total kill	Year	Total kill
1848	18	1887	240	1926	35	1965	14
1849	573	1888	160	1927	14	1966	24
1850	2,067	1889	127	1928	30	1967	12
1851	898	1890	136	1929	30	1968	27
1852	2,709	1891	284	1930	17	1969	32
1853	807	1892	346	1931	32	1970	48
1854	166	1893	180	1932	27	1971	25
1855	2	1894	234	1933	21	1972	44
1856	0	1895	117	1934	21	1973	51
1857	78	1896	118	1935	15	1974	42
1858	461	1897	130	1936	24	1975	32
1859	372	1898	309	1937	53	1976	74
1860	221	1899	234	1938	36	1977	72
1861	306	1900	148	1939	18	1978	15
1862	157	1901	55	1940	20	1979	20
1863	303	1902	162	1941	38	1980	32
1864	434	1903	116	1942	26	1981	26
1865	590	1904	86	1943	14	1982	14
1866	554	1905	105	1944	8	1983	16
1867	599	1906	69	1945	23	1984	16
1868	516	1907	96	1946	20	1985	14
1869	382	1908	123	1947	21	1986	22
1870	637	1909	61	1948	8	1987	29
1871	138	1910	37	1949	11	1988	28
1872	200	1911	48	1950	23	1989	25
1873	147	1912	39	1951	23	1990	41
1874	95	1913	23	1952	11	1991	47
1875	200	1914	61	1953	41	1992	46
1876	76	1915	23	1954	9	1993	51
1877	270	1916	23	1955	36	1994	39 (38)
1878	80	1917	35	1956	11	1995	56 (57)
1879	266	1918	27	1957	5	1996	42 (45)
1880	480	1919	33	1958	5	1997	62
1881	435	1920	33	1959	2	1998	51
1882	242	1921	9	1960	33	1999	47
1883	42	1922	39	1961	17	2000	42
1884	160	1923	12	1962	20	2001	67
1885	377	1924	41	1963	15	2002	44
1886	168	1925	53	1964	24		

Population dynamics model

The underlying population model is a simplified age- and sex-structured Leslie matrix (Leslie, 1945; 1948) projected as:

$$\underline{n}_{t+1} = \left(\mathbf{A_t}\underline{n}_t\right) - \underline{h}_t \qquad (1)$$

where:

$\underline{n}_t$	is vector of population size in each age class at the start of year t (defined when calving and natural mortality occur);
$\mathbf{A_t}$	is the Leslie matrix for year t;
$\underline{h}_t$	is the vector of age-specific catches during year t.

The catches and birth rates are assumed to be equal for both males and females (i.e. the vectors above are divided equally by sex). The parameters that define the entries of the Leslie matrix are: (1) S_{juv}, the survival rate of immature whales (assumed identical for calves and juveniles); (2) a_T, the last age with survival rate S_{juv}; (3) S_a, the survival rate of mature whales; (4) a_m, the age at sexual maturity (the last age class with zero fecundity); (5) f_{max}, the maximum fecundity rate; and (6) a_{max}, the maximum age, after which survival becomes zero. Fecundity is assumed identical for all mature animals, and is calculated as the number of female calves per mature female. Recruitment to the fishery is assumed to be knife-edged and to occur at age 1, and the catch is distributed uniformly over all recruited age-classes (i.e. uniform selectivity across recruited age-classes).

The projections are initialised from a stable age distribution for the population in the year prior to that with the first catch (e.g. 1977 or 1847) based on the values for the parameters sampled from the prior. This population vector is then projected one year forward without catch, and the population vector re-scaled so that the 1+ population size in the year with the first catch equals that generated from the prior for 1+ abundance for that year.

Density dependence is assumed to affect fecundity according to:

$$f_t = f_0 + \left(f_{\max} - f_0\right)\left[1 - \left(\frac{N_t^{1+}}{K^{1+}}\right)^z\right] \tag{2}$$

where:

f_t is the fecundity during year t;
f_{max} is the maximum fecundity (in the limit of zero population size);
N_t^{1+} is the (1+) population size at the start of year t;
K^{1+} is the pre-exploitation (1+) population size;
z is the shape parameter;
f_0 is the fecundity at carrying capacity.

Given values of life-history parameters in the model, the value for f_0 is determined from the characteristic equation of the Leslie matrix given equilibrium conditions:

$$f_0 = \frac{1 - S_a}{S_{juv}^{(a_T)}\, S_a^{(a_m - a_T)}\left[1 - S_a^{(a_{\max} - a_m - 1)}\right]} \tag{3}$$

Model parameters and prior distributions

Table 4 lists the parameters and their priors used in three ‘reference’ scenarios. The population trajectory is modelled in three ways: (1) a density-dependent model initialised in 1848 (abbreviated: ‘1848 DD’); (2) a density-dependent model initialised in 1978 (‘1978 DD’); and (3) a density-independent model initialised in 1978 (‘1978 NON DD’). The six life-history parameters of the Leslie model are included in each of three models, but the remaining parameters differ among models. The ‘1848 DD’ model includes a parameter for the population size in 1993, N_{1993}^{1+}, and one for the maximum sustainable yield level, $MSYL^{1+}$. The ‘1978 DD’ model also includes the parameter $MSYL^{1+}$ but instead of placing a prior on N_{1993}^{1+} places one on N_{1978}^{1+}. This model also includes an additional (explicit) prior on the carrying capacity, K^{1+}. The ‘1978 NON DD’ model includes priors on N_{1978}^{1+} and the maximum population growth rate in the absence of density dependence, r. For this model, fecundity and population growth rates apply only to the specified period, and where the distinction is appropriate, they are referred to as f and r. However, when methods are consistent across models, these rates are referred to as $f_{\max}$ and $r_{\max}$ for the sake of simplicity.

‘Data-based’ prior distributions are assigned to adult survival rate and the age at sexual maturity and the maximum age of the Leslie matrix is determined from the results of recent research on ageing. The informative prior for S_a (Table 4) approximates the Bayesian posterior calculated for this parameter based on a mark-recapture analysis of photo-identification data (Zeh *et al.*, 2002). Information on age-at-maturity is taken from a study by George *et al.* (1999) that estimated ages of caught animals based on the chemistry of eye lenses. Those authors fitted a growth curve to these ages from known lengths and combined this relationship with previous data on length at sexual maturity to provide an estimate of the age-at-maturity. The ageing results also estimated some animals were older than the previously accepted maximum age, and this result is supported by the recent recovery of traditional whaling tools in five whales (reported in the same study). The maximum age in the Leslie matrix is therefore set to 200 to reflect this information.

Punt and Butterworth (1999) noted that due to the functional relationships among the life-history parameters in an age-structured population model, placing a prior on S_{juv} would be an instance of Borel’s Paradox (i.e. effectively placing two priors on the same parameter); instead the value of S_{juv} is solved for analytically in this study by rearranging the characteristic equation of the Leslie matrix given the values for the remaining five parameters and λ, the dominant eigenvalue of the Leslie matrix (i.e. r_{max} + 1) (Breiwick *et al.*, 1984):

$$S_{juv} = \left[\frac{\lambda^{(a_m+1)} - S_a \lambda^{(a_m)}}{S_a^{(a_m - a_T)} f_{\max}\left\{1 - \left(S_a / \lambda\right)^{(a_{\max} - a_m - 1)}\right\}}\right]^{\frac{1}{a_T}} \tag{4}$$

The value for S_{juv} is forced to be less than that of S_a. If necessary, values for f_{max} and S_a are re-sampled (see below), until this condition is met, or 1,000 re-samples occur. If this maximum is reached, a new value for r_{max} is re-sampled, and the process repeated until an acceptable sample from the prior occurs.

The priors for the remaining life history parameters are also based on available information. The prior distribution for f_{max} is based on an assumed range of a 2.5- to 4-year calving interval for large baleen whales (IWC, 1998). Note that f_{max} is specified in the standard Leslie matrix formulation as female calves per female per year (i.e. a fecundity rate of 0.125 implies a female calving interval of 8 years, and therefore a total calving interval of 4 years, assuming an equal sex ratio of calves). The age of transition from immature to adult survival is assigned a discrete uniform prior over the interval 1 to 9 years.

Output quantities

Posterior distributions are calculated for several output quantities that are functions of the parameters in Table 4. The maximum sustainable yield rate ($MSYR^{1+}$) is calculated as $\lambda - 1$ based on the f_t value associated with $MSYL^{1+}$. Maximum sustainable yield (MSY^{1+}) is calculated as the product, $MSYR^{1+} \cdot MSYL^{1+} \cdot K^{1+}$. Current replacement yield (RY^{1+}) is calculated as the difference between the number of 1+ animals in 2002 (prior to the removal of catches in that year) and the number of such animals at the end of 2001. The quantity Q_1^{1+}, designed to meet the intent of aboriginal whaling management objectives (Wade and Givens, 1997), is also calculated. This quantity has the property that the proportion of net production allocated to recovery increases at higher levels of stock depletion[2]. Specifically:

$$Q_1^{1+} = \min\left(MSYR^{1+} * N_{2002}^{1+}, 0.9MSY^{1+}\right) \tag{5}$$

The post-model-pre-data distribution is reported for the parameters. This distribution arises after conditioning the specified priors on the model (i.e. by eliminating combinations of parameters for which the juvenile survival rate implied by equation (4) exceeds the adult survival rate drawn from the joint prior distribution). Likewise, post-model-pre-data distributions for output quantities are calculated as the distributions for these quantities in the sampled joint prior space.

Parameter estimation

The Sampling-Importance-Resample (SIR) algorithm (Rubin, 1988; Smith and Gelfand, 1992; Wade, 2002a) is used to generate samples of parameter vectors (and output quantities of interest) from the posterior distribution. This

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[2] This definition applies to a population above some minimum level, $P_{\min}$ (assumed here to be $0.1K^{1+}$), below which catches are set to zero.

Table 4

Prior distributions used for the reference scenarios for each model type. Dashes (-) represent prior distributions that are equal to those from the model in the column to the left (e.g. the 1978 NON DD model had the same prior on the size of the 1+ population in 1978 as the 1978 DD model). 'N/A' represents a prior that was not applicable to a certain model or models. Fecundity is defined as female calves per mature female. For the 1978 NON DD model $r_{\max}$ and $f_{\max}$ are not maxima, but constant values. Results from the reference scenario were used in all figures and when performing the Bayesian model averaging. The reference scenarios are based on the stage-proportion data set that ignores the data for 1985.

Parameter		Model type		
		1848 DD	1978 DD	1978 NON DD
S_a	Adult survival	N(0.990, 0.02), truncated at 0.940 and 0.995[a]	-	-
$f_{\max}$	Maximum fecundity	U[0.125, 0.200][b]	-	-
a_T	Age-at-transition to adult survival	U[1, 9][c]	-	-
a_m	Age-at-sexual maturity	N(20.0, 3.0) truncated at 13.0 and 26.0[d]	-	-
$r_{\max} = \lambda$ -1	Intrinsic population growth rate	U[0.005, 0.075][e]	-	-
$N^{1+}{}_{1978}$	1+ population size in 1978	N/A	U[3,000, 9,000][f]	-
$N^{1+}{}_{1993}$	1+ population size in 1993	N(7,800, 1,200)[g]	N/A	N/A
K^{1+}	1+ carrying capacity	N/A	U[8,000, 30,000][h]	N/A
$MSYL^{1+}$	*MSYL* in terms of the 1+ component	U[0.40, 0.80][i]	-	-

[a] Based on the posterior distribution for adult survival rate obtained by Zeh *et al.* (2002).

[b] The prior for the maximum number of calves (of both sexes) per mature female selected by the Scientific Committee of the International Whaling Commission was U[0.25, 0.4] (IWC, 1995). This is the corresponding prior given fecundity has been defined here as female calves per mature female per year.

[c] Selected by the Scientific Committee of the International Whaling Commission (IWC, 1995) although there is little information on the value of this parameter (Givens *et al.*, 1995).

[d] Based on a best estimate of 20 years and a lower confidence for the age-at-maturity of 14 years (IWC, 1995).

[e] Preliminary trials indicated there was no posterior probability outside this range, which was confirmed in the final analyses. This range was therefore selected to improve the efficiency of the numerical integration while not affecting the results.

[f] Selected to encompass a plausible range of values for 1+ population size in 1978.

[g] Selected by the Scientific Committee of the International Whaling Commission (IWC, 1995) based on the prior distribution assumed for the Bayes empirical Bayes estimate of abundance (Raftery and Zeh, 1991).

[h] Based on the range selected by the Scientific Committee of the International Whaling Commission (IWC, 1995).

[i] Selected to encompass the range of values commonly assumed when conducting assessments of cetacean populations.

algorithm involves randomly sampling a large number of parameter vectors $\underline{\theta}_i$ (draws) from the prior distribution. A population trajectory is then calculated for each vector of parameter values, and this trajectory is used to determine the likelihood of the data for each random draw. 10,000 draws (which form the numerical representation of the posterior distribution) are then selected by sampling (with replacement) from the initial samples from the prior, with probability proportional to the likelihood. Following Punt and Butterworth (1999) and Raftery *et al.* (1995), the SIR algorithm is considered to have converged if the number of unique parameter vectors in the sample from the posterior is fairly high (>5,000) and if the most frequently re-sampled parameter vector did not occur in the posterior sample more than ten times.

The total negative log-likelihood of a model trajectory, given a vector of parameters and the data, consists of contributions from four data sources: (1) the estimate of abundance for 1993; (2) the estimates of abundance for the remaining years; (3) the proportion of calves in the population; and (4) the proportion of mature animals in the population. The abundance estimates are assumed to be indices of the 1+ component of the population. The scientific surveys at Point Barrow are assumed to have occurred after the aboriginal catch, and the likelihood function is calculated accordingly (i.e. catches are removed before calculating the likelihood of the data for a given year). Model-predicted proportions are calculated over the period 1985 to 1994, as the actual stage proportions are based on data for these years.

The estimate of abundance for 1993 is assumed to be independent of the remaining estimates (Punt and Butterworth, 1999) and to have normally as opposed to log-normally distributed sampling error. The contribution of the abundance estimates to the negative of the log-likelihood function (ignoring constants independent of model parameters):

$$L_1 = 0.5\frac{\left(\hat{N}_{1993} - 8293\right)^2}{626^2}$$

$$L_2 = 0.5\sum_{t_1}\sum_{t_2}\left(\ell\text{n}\hat{N}_{t_1} - \ell\text{n}N_{t_1}^{obs}\right)^T \sum\nolimits_{t_1,t_2}^{-1}\left(\ell\text{n}\hat{N}_{t_2} - \ell\text{n}N_{t_2}^{obs}\right) \tag{6}$$

where:

N_t^{obs} is the estimate of abundance for year t;
$\hat{N}_t$ is the model estimate of 1+ abundance for year t;
Σ is the variance-covariance matrix for the logarithms of the estimates of abundance (excluding 1993).

The estimates of abundance (Table 1) are based on combining the data from visual counts at Point Barrow, Alaska, and estimates of the proportion of animals which passed within visual range based on acoustic data. Eqn. 6 accounts for the correlation among the non-1993 estimates of abundance that arises because the proportion within visual range is treated as a random effect when constructing the estimates of abundance (Zeh and Punt, 2005).

The contribution of the proportion data to the likelihood function follows Punt (2006), i.e. given the bootstrapping approach adopted to calculate the length-frequency distributions from which the proportion data were calculated (Koski *et al.*, 2004), it was reasonable to assume that the estimates are normally distributed (ignoring constants):

$$L_3 = \frac{1}{2\left(\sigma_{p_c}\right)^2}\left(p_c - p_c^{obs}\right)^2 \qquad L_4 = \frac{1}{2\left(\sigma_{p_m}\right)^2}\left(p_m - p_m^{obs}\right)^2 \tag{7}$$

where:

p_c^{obs} is the observed fraction of the population that consisted of calves between 1985 and 1994;
σ_{p_c} is the standard deviation of p_c^{obs};

p_c is the model-estimate of the fraction of the population that consisted of calves between 1985 and 1994;
p_m^{obs} is the observed fraction of the population that consisted of mature animals between 1985 and 1994;
σ_{p_m} is the standard deviation of p_m^{obs};
p_m is the model-estimate of the fraction of the population that consisted of mature animals between 1985 and 1994.

Model comparison

The three models considered in this paper are compared using Bayes factors (Kass and Raftery, 1995). The Bayes factor is calculated as the probability of observing the data given one hypothesis (model) divided by the probability of observing the same data given an alternative hypothesis, i.e.:

$$B_{12} = \frac{pr\left(D\middle|H_1\right)}{pr\left(D\middle|H_2\right)} \tag{8}$$

In the context of model comparison, the hypotheses represent competing models and the Bayes factor is used as the evidence provided by the data in favour of one model over another. Although Eqn. (8) has the form of a likelihood ratio, if there are unknown parameters in either of the competing models, the probability densities must be found by integrating, as opposed to maximising, over the parameter space. Therefore, for a given model, the probability of the data is:

$$pr\left(D\middle|H\right) = \int pr\left(D\middle|H,\theta\right) pr\left(\theta\middle|H\right) d\theta \tag{9}$$

This integration is based on the sample from the prior using the equation:

$$\hat{pr}\left(D\middle|H\right) = \frac{1}{n_1}\sum_{i=1}^{n_1} pr\left(D\middle|\underline{\theta}_i, H\right) \tag{10}$$

where $\underline{\theta}_i$ is the ith (of n_1) samples from the prior distribution.

Model averaging

Model uncertainty is accounted for by calculating the posterior probability of each model conditioned on the data and the priors, and then combining results across models as a weighted average of the posterior densities for a quantity of interest (Kass and Raftery, 1995). Hoeting *et al.* (1999) provide a convenient method of calculating the posterior probability of model H_k (where, k=1, …, K models are being considered) based on Bayes' theorem:

$$pr\left(H_k\middle|D\right) = \frac{pr\left(D\middle|H_k\right) pr\left(H_k\right)}{\sum_{i=1}^{K} pr\left(D\middle|H_i\right) pr\left(H_i\right)} \tag{11}$$

where $pr(H_k)$ is the prior probability that H_k is the true model and $pr(D|H_k)$ is the estimate of the probability of the data (Eqn. (10)). All of the probabilities are conditional on the set of models being considered (Hoeting *et al.*, 1999). For f_{max}, r_{max} and quantities related to carrying capacity, only the two models incorporating density dependence could be used to derive model averages. Under the set of models considered, these posterior model probabilities were used to determine model-averaged posterior probability distributions for the model outputs, θ:

$$pr\left(\theta\middle|D\right) = \sum_{i=k}^{K} pr\left(\theta\middle|H_k, D\right) pr\left(H_k\middle|D\right) \tag{12}$$

In the context of the SIR algorithm used here, Bayesian model averaging was accomplished by selecting a number of random draws from the posterior for each model and combining them to form a model-averaged posterior. This number was determined by the posterior probability for each model. All models were considered equally probable *a priori* (i.e. objective ignorance regarding the true model), so the posterior probability of a given model is determined using the values from Eqn. (10) normalised to sum to one over models.

RESULTS AND DISCUSSION

Fits to the data

Fig. 1 shows the fits to the abundance estimates for three reference scenarios and the Bayesian model average. All three models provide a relatively good fit to these data, although the abundance estimate for 2001 falls well above the upper 90% credibility limit from the '1848 DD' model. This occurs because the median of the posterior distribution for 1+ population size in 2002 for this model (9,496) is smaller than the posterior medians for the other two models (Fig. 2, Table 5).

The abundance estimates indicate the population has been increasing steadily over 1978-2001, and the data on adult survival, age of sexual maturity, and the stage-proportion data (excluding 1985) are all relatively consistent with this increase (i.e. the inclusion of those data in the analysis does not lead to the model being unable to mimic the abundance data).

Backwards to 1848 (density dependent model): 1848 DD

The upper left panel of Fig. 1 shows the posterior median time-trajectory of 1+ population size along with its 90% credibility interval for the reference scenario. The population size is estimated to have declined dramatically during the 1800s, being reduced to approximately half of its pre-exploitation level within five years of the start of the commercial fishery, and 10% of this size by the early 1900s. However, the population recovered steadily thereafter. The 90% credibility interval for the post-model-pre-data distribution for K^{1+} is [8,000-30,000], with lower values favoured (Fig. 2). In contrast, the 90% credibility interval for the posterior distribution of K^{1+} is [9,000, 14,000] (Table 5) indicating that the data update the prior distribution substantially. The 2002 population size is estimated to be above 50% of K^{1+}, and there is a high probability of it being above $MSYL^{1+}$ (Fig. 3, Table 5). The posterior distribution for replacement yield in 2002 has a mode around 200, with a lower 5th percentile of 61 (Fig. 4, Table 5). In contrast, the lower 5th percentile for Q_1^{1+} is 99 (Fig. 4, Table 5). These two quantities differ because the current population size is estimated to be larger than $MSYL^{1+}$, and approaching K^{1+}. Therefore, density dependence has slowed population growth and RY^{1+} has decreased. This is the same situation that led to the use of Q_1^{1+} as a more appropriate measure of sustainable catch (to achieve IWC management goals) for the eastern North Pacific stock of gray whales (Wade, 2002a).

The constraints imposed by the relationships among the life-history parameters constrained r_{max} to be less than about 0.07 (Fig. 3), although they also reduced the (prior) probability of values of r_{max} larger than 0.06. The posterior for r_{max} assigns most support to values larger than 0.03 (posterior median 0.041, Table 6). The posterior distributions for adult and immature survival favour higher

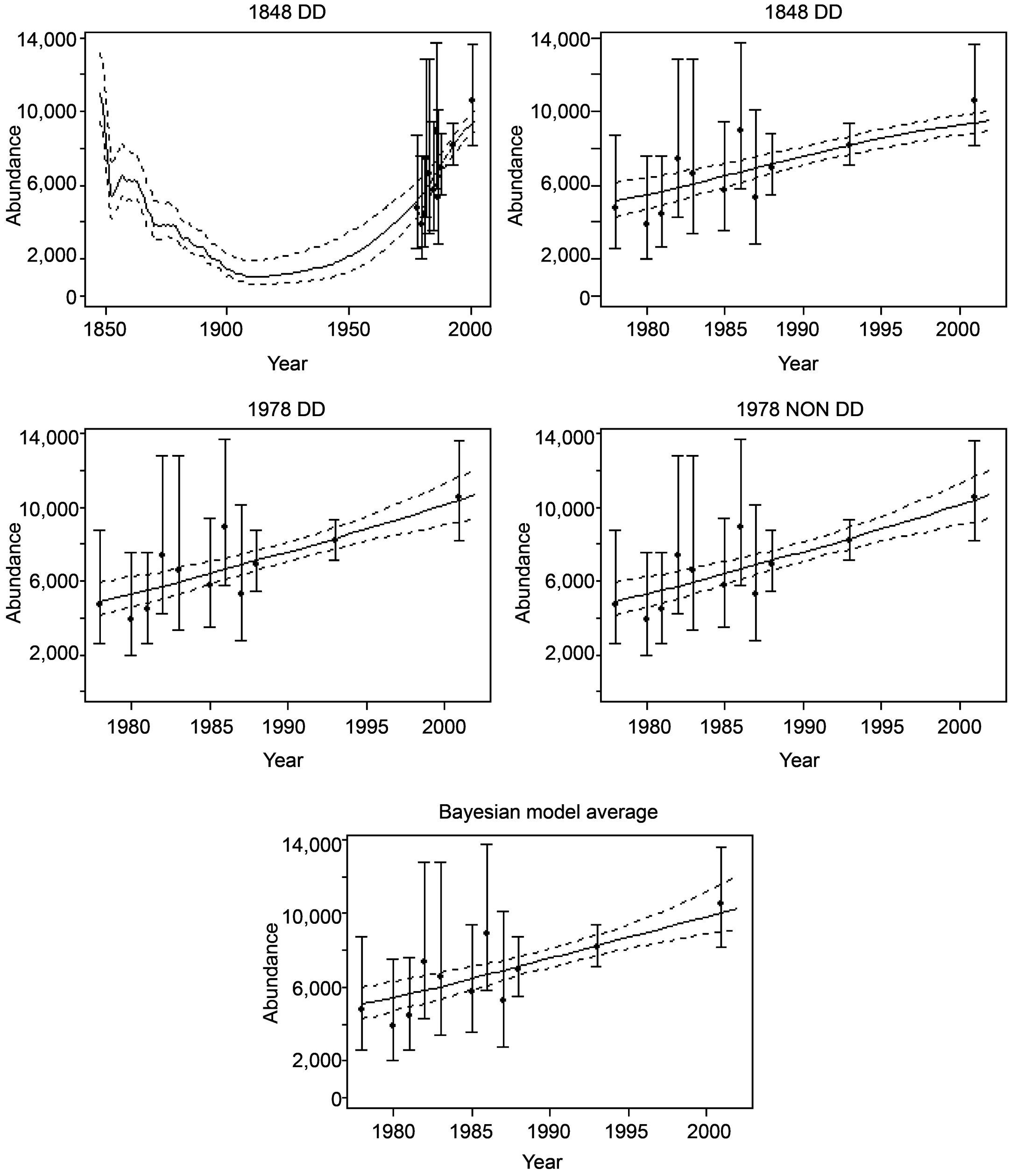

Fig. 1. Time trajectories (medians and 90% credibility intervals) for 1+ population size for the three reference scenarios and the Bayesian model average. The two uppermost plots are for the 1848 DD model, showing the entire trajectory from 1848, and only the recent trajectory from 1978 for comparison. Error bars represent 95% CIs, and are assumed to be log-normally distributed for all abundance estimates except 1993 (second to last), which is assumed to have a normally distributed error structure.

values than implied by the prior distributions for these parameters, and that for a_m values lower than implied by the prior distributions (Figs 5 and 6). The post-model-pre-data distribution for fecundity favours higher values (~0.20, Fig. 6), but the posterior median is 0.171, or a calving interval of approximately three years (Table 6). The results in Figs 3, 5 and 6 show that the data are clearly capable of updating the prior distributions for the life-history parameters.

The results for this model are not particularly sensitive to changing the prior distributions for S_a and a_m and to ignoring the proportion data (Table 5). The most noteworthy feature of these sensitivity tests are the changes to the catch-related outputs (RY^{1+}, Q_1^{1+} and MSY^{1+}). Results are not shown in Table 5 for the case in which the 1985 stage-proportion data are included in the analyses due to computational difficulties in achieving convergence. Preliminary analyses including these data indicated, however, that they are inconsistent with what is known about bowhead whale life history and the time series of abundance estimates. This inconsistency was the cause of the inability to achieve convergence.

Forwards from 1978 (density dependent model): 1978 DD

The posterior for K^{1+} from this analysis is much more uncertain than that from the '1848 DD' analysis (Fig. 2). This is because this analysis ignores the information contained in the 1848-1977 catch record, and because the abundance estimates show no evidence for a reduction in trend (which would be expected as the population approaches carrying capacity) and, unlike the '1848 DD' model, the '1978 DD' model does not make the assumption that the population size in 1848 was K^{1+}. Therefore, although this model confirms that the population is

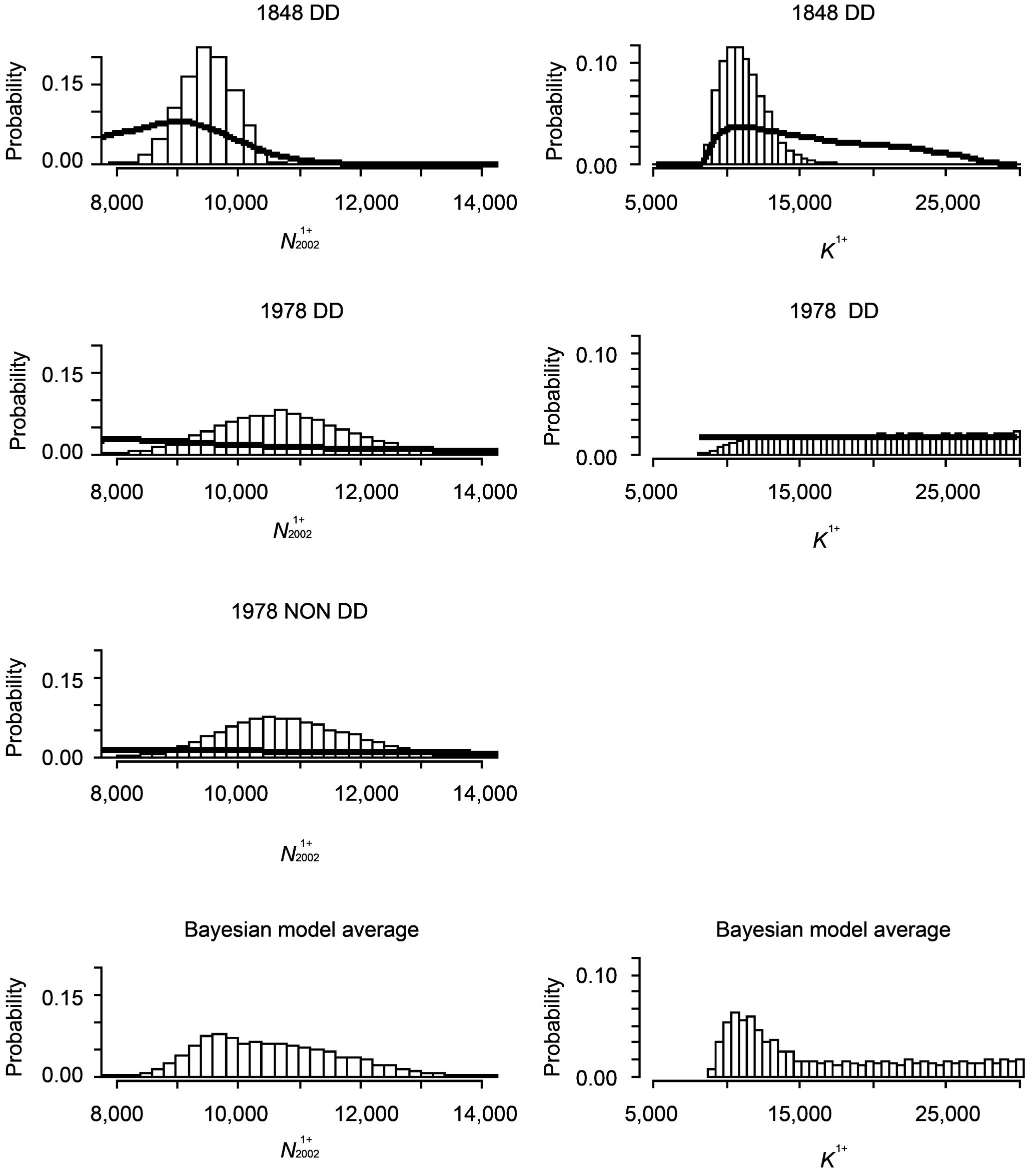

Fig. 2. Posterior (vertical bars) and post-model-pre-data (solid lines) distributions for 1+ population size in 2002, N^{1+}_{2002} (left panels) and 1+ carrying capacity, K^{1+} (right panels). Results are shown for only two of the three reference scenarios for K^{1+}, and the Bayesian model average for K^{1+} is based on the results of these two scenarios only.

increasing (Fig. 1), it infers that the population is currently at a much lower fraction of its (current) carrying capacity than the ‘1848 DD’ model (Fig. 3; Table 5). The posterior for N^{1+}_{2002}/K^{1+} is strongly influenced by the prior distribution assumed for K^{1+} given the inability of the data to place an upper bound on K^{1+}. This is clearly evident from the results of the sensitivity test in which the upper limit of the prior for K^{1+} is increased from 30,000 to 100,000. The results for this sensitivity test imply an increase to the median of the posterior for K^{1+} of 165% and a reduction to the posterior median for N^{1+}_{2002}/K^{1+} of 62% (Table 5) as the upper bound for K^{1+} is increased by 233%.

Given that there is little independent information on which to base a prior distribution for K^{1+}, the choice of the prior for K^{1+} is essentially arbitrary, and it should be recognised that this ‘forwards’ analysis consequently does not provide robust estimates of quantities related to K^{1+} (such as N^{1+}_{2002}/K^{1+}). However, Punt and Butterworth (1999) noted that some key management-related quantities (e.g. RY^{1+} and Q^{1+}_{1}) are relatively insensitive to the prior assumed for K^{1+}, so this approach still has some value. The implicit (post-model-pre-data) distribution for RY^{1+} favours (is skewed towards) values less than 200 (Fig. 4). Despite this, the posterior median is 324, with a lower 5th percentile of 147 (Table 5). A similar result is evident for Q^{1+}_{1}, with low values favoured by the post-model-pre-data distribution, but higher values supported by the data (median=295, lower 5th percentile=160) (Fig. 4, Table 5). In essence, the joint prior distribution for the parameter values, conditioned on the population dynamics model, is not neutral (non-informative) with respect to these catch-related quantities, but the data are influential enough to move the posterior distribution away from the mode of the prior distribution.

The posterior distributions for $r_{\max}$, $MSYR^{1+}$, and the life history parameters for this model are generally similar to those for the ‘1848 DD’ model. The most noteworthy difference between the posterior distributions for the ‘1978 DD’ and ‘1848 DD’ models in Table 6 relates to the posterior median for S_{juv} which is larger for the ‘1978 DD’ model. As was the case for the ‘1848 DD’ model, there is again little sensitivity to changing the priors for S_a and for a_m, and ignoring the stage-proportion data (Tables 5 and 6). In contrast, inclusion of the 1985 survey data when calculating the stage-proportion data has a large impact on

Table 5

Posterior medians (5th, 95th percentiles) for eight management-related quantities. This table includes results for all models and scenarios, and Bayesian model-averaged results for the reference scenarios. Model averages for all quantities, except RY and N^{1+}_{2002} (i.e. the two quantities not dependent on *K*), could only be based on the 1848 and 1978 DD models. Where noted, additional scenarios are based on the reference scenarios in Table 4, but changed to examine the sensitivity of the results to different proportion data sets and less informative priors. The uniform prior for S_a is U[0.940, 0.995], and that for a_m is Discrete U[13, 26]. Unique draws and the maximum number of times an individual draw is included in the final SIR resample are listed in the rightmost two columns.

	N^{1+}_{2002}	K^{1+}	RY^{1+}	Q_1^{1+}	N^{1+}_{2002}/K^{1+}	$MSYL^{1+}$	MSY^{1+}	$MSYR^{1+}$	Unique draws	Max sampled draw (*n*)
1848 DD										
Reference scenario	9,496 (8,750, 10,180)	10,960 (9,190, 13,950)	171 (61, 233)	228 (149, 296)	0.888 (0.647, 0.985)	0.734 (0.639, 0.793)	253 (166, 329)	0.033 (0.019, 0.048)	7,399	9
No proportion data	9,380 (8,652, 10,070)	10,980 (9,245, 14,710)	160 (63, 222)	216 (132, 283)	0.874 (0.602, 0.983)	0.703 (0.555, 0.791)	240 (147, 315)	0.032 (0.017, 0.047)	9,456	4
Uniform priors on S_a and a_m	9,488 (8,782, 10,180)	10,580 (9,112, 13,610)	159 (59, 229)	241 (158, 301)	0.921 (0.674, 0.986)	0.740 (0.644, 0.795)	267 (176, 335)	0.035 (0.020, 0.049)	6,527	9
1978 DD										
Reference scenario	10,670 (9,042, 12,410)	20,510 (11,010, 29,120)	324 (147, 501)	295 (160, 439)	0.530 (0.356, 0.925)	0.651 (0.573, 0.779)	368 (206, 599)	0.030 (0.018, 0.043)	8,992	5
No proportion data	10,410 (8,740, 12,380)	20,350 (10,600, 29,070)	297 (119, 519)	270 (136, 457)	0.524 (0.348, 0.930)	0.661 (0.528, 0.785)	341 (169, 644)	0.029 (0.016, 0.043)	9,519	3
Include 1985 proportion data	9,294 (7,780, 10,720)	13,510 (8,110, 28,890)	166 (44, 280)	193 (74, 289)	0.705 (0.299, 0.990)	0.607 (0.459, 0.784)	225 (89, 333)	0.025 (0.009, 0.048)	8,034	8
Uniform priors on S_a and a_m	10,820 (9,124, 12,600)	19,870 (10,750, 29,090)	336 (138, 525)	309 (168, 459)	0.554 (0.362, 0.947)	0.654 (0.570, 0.781)	379 (215, 624)	0.032 (0.019, 0.045)	7,493	9
U[8,000, 100,000] prior on *K*	10,830 (9,160, 12,690)	54,430 (14,990, 95,500)	363 (188, 566)	267 (136, 426)	0.201 (0.110, 0.710)	0.606 (0.523, 0.777)	712 (282, 1,737)	0.025 (0.014, 0.038)	7,554	7
1978 NON DD										
Reference scenario	10,740 (9,130, 12,700)	N/A	366 (204, 588)	N/A	N/A	N/A	N/A	N/A	9,262	5
No proportion data	11,020 (9,199, 13,130)	N/A	402 (206, 654)	N/A	N/A	N/A	N/A	N/A	9,809	3
Include 1985 proportion data	10,280 (8,796, 12,090)	N/A	310 (166, 511)	N/A	N/A	N/A	N/A	N/A	6,264	9
Uniform priors on S_a and a_m	11,110 (9,265, 13,050)	N/A	414 (217, 644)	N/A	N/A	N/A	N/A	N/A	8,374	6
Bayesian model average	10,276 (8,907, 12,406)	13,854 (9,466, 28,475)	297 (92, 539)	257 (155, 412)	0.720 (0.372, 0.980)	0.695 (0.581, 0.788)	302 (180, 555)	0.031 (0.018, 0.046)	-	-

the results. Specifically, K^{1+} and $MSYR^{1+}$ are estimated to be lower, and N^{1+}_{2002}/K^{1+} higher, with the population estimated to be above $MSYL^{1+}$ with almost 100% probability. r_{max} is estimated to be higher (as the population is estimated to be closer to K^{1+} and therefore experiencing a growth rate much lower than r_{max}). The estimates of the catch-related quantities are considerably lower for this scenario (e.g. the posterior median and the lower 5% percentile for RY^{1+} are 166 and 44 respectively).

Forwards from 1978 (density independent model): 1978 NON DD

The posterior median for RY^{1+} for this model ranges from 310 to 414 across the scenarios (166-217 for the lower 5th percentile for RY^{1+}). The posterior for for the '1978 NON DD' model is centred on lower values than those for the other two models (Fig. 3). This is to be expected because the *r* for the '1978 NON DD' model' pertains to the current rate of increase rather than the increase rate in the limit of zero population size. The inclusion in the analyses of the 1985 stage-proportion data is again very influential. For example, the posterior distribution for fecundity for the 'include 1985 proportion data' sensitivity test does not overlap with that for the reference scenario.

Model comparison and Bayesian model averages

Bayes factors based on pair-wise comparisons of models range from 1.10 to 1.51, and indicate that there is no evidence for selecting one model over another (Table 7). Rather, these Bayes factors imply that the best approach to summarising the state of the B-C-B bowhead whale stock is to consider all three models, e.g. through Bayesian model averaging. Average likelihoods of draws from the initial sample range from 0.522 ('1848 DD') to 0.789 ('1978 NON DD'). The two models that involve forward projection from recent abundance ('1978 DD' and '1978 NON DD') have slightly higher average likelihoods, and hence posterior model probabilities, than the model which started the population projection in 1848, although differences are not large (Table 8).

The time-trajectory of 1+ population size (medians and 90% credibility intervals) from the Bayesian model-averaged posterior provides, as expected, a good fit to the abundance estimates (Fig. 1, lower panel). The fit to the estimate of abundance for 2001 for the model-averaged posterior is not quite as good as for the '1978 DD' and '1978 NON DD' models because of the impact of including the '1848 DD' model in the average. The model-averaged posterior distribution for K^{1+} (Fig. 2) has a mode close to

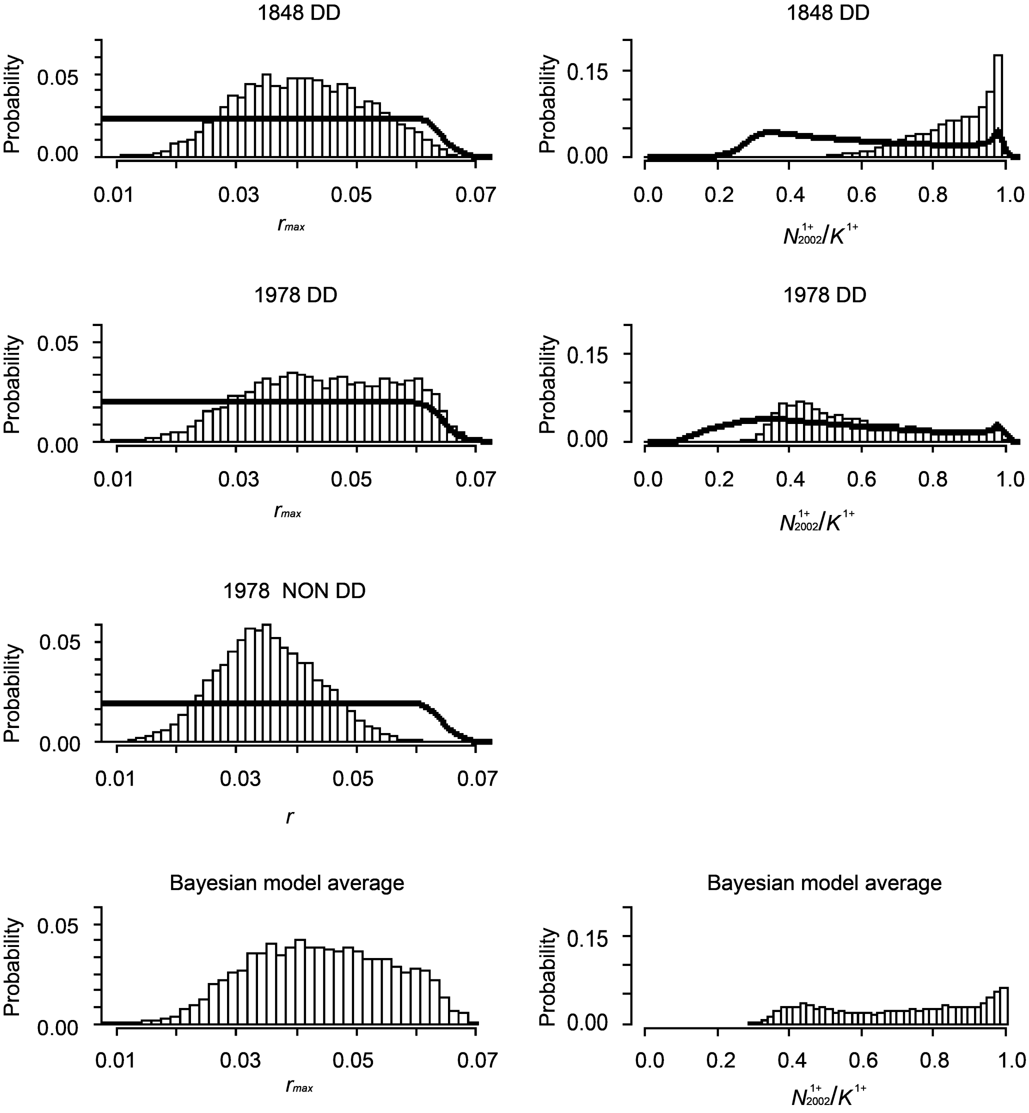

Fig. 3. Posterior (vertical bars) and post-model-pre-data (solid lines) distributions for intrinsic population growth rate, r_{max} and r (left panels) and recent depletion in terms of the 1+ component, N^{1+}_{2002} /K^{1+} (right panels). The Bayesian model average is based only on the two models with density dependence.

that of the posterior median for the '1848 DD' model, and a long tail caused by the uncertainty associated from the '1978 DD' model. The model-average posterior for N^{1+}_{2002} / K^{1+} (Fig. 3) is wide, but less so than that for the '1978 DD' model. The model-averaged posterior for RY^{1+} is slightly irregular because it consists of the combination of a bimodal posterior (for the '1848 DD' model) and a symmetric posterior (for the '1978 DD' model). In contrast to the model-average posterior for RY^{1+}, that for Q^{1+}_{1} is actually quite symmetric (Fig. 4, Table 5).

The '1978 NON DD' model estimates only the recent fecundity and rate of increase for the population, whereas the two density-dependent models estimate the maximum fecundity and rate of increase. Therefore, the posterior for f_{max} and r_{max} is averaged across the two models with density dependence only. Maximum fecundity and population growth rate are relatively consistent across these two models and have a median of 0.171 and 4.3% respectively (Fig. 6 and Fig. 3, Table 6). Likewise, both adult and juvenile survival rates are consistent across models, with a median for adult survival of 0.990 and for juvenile survival of 0.932 (Fig. 5, Table 6).

It is straightforward to calculate model-averaged posterior probability distributions given different prior probability distributions for the models. For example, the models based on starting the projections in 1978 could be assigned probabilities of 0.25 and that which starts the population projections in 1848, a prior probability of 0.5 to indicate, for example, that the assumption that carrying capacity has not changed over the last 150 years is equally as likely as some shift in the equilibrium population size during this time. Alternatively, the models with density-dependence could be assigned prior probabilities of 0.25 each, and that which ignores density-dependence a prior probability of 0.5.

General discussion

The three models have shown good concurrence. However, use of the historic catch record leads to lower estimates of RY^{1+} because the analysis estimates the population to be close to carrying capacity and so the growth rate is reduced compared to that at low population size. However, there is no (visual) evidence in the abundance estimates for a reduction in trend. It therefore appears that it is the

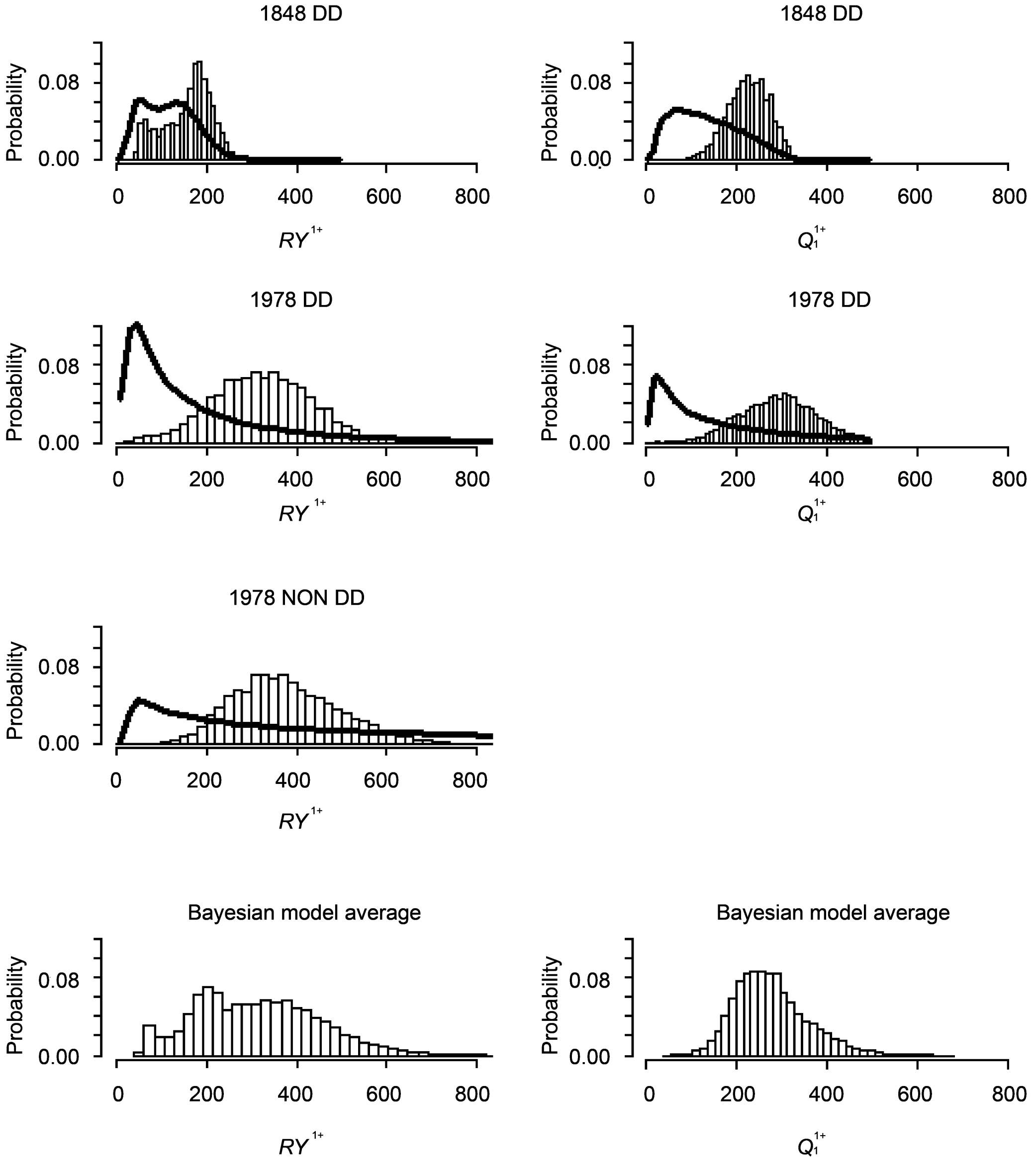

Fig. 4. Posterior (vertical bars) and post-model-pre-data (solid lines) distributions for replacement yield, RY^{1+}(left panels) and Q_1^{1+} (right panels). Results are shown for only two of the three reference scenarios for Q_1^{1+}, and the Bayesian model average for Q_1^{1+} is based on the results of these two scenarios only.

combination of the magnitude of the historical catches and the values for the biological parameters that determines the estimate of the carrying capacity. One implication of starting the population projection in 1848 is that the model underpredicts the 2001 estimate of abundance (probably because if the population is approaching carrying capacity, a near-linear growth in population size could not still be occurring). The '1848 DD' model is assigned less weight than the '1978 DD' and '1989 NON DD' models using Bayes factor, but the discrepancy between the predictions of the '1848 DD' model and the data remains sufficiently small that the '1848 DD' model cannot be rejected. It should be stressed that the results in this paper do not suggest that changes are required to the *Bowhead SLA* used to provide management advice on bowhead whales (e.g. IWC, 2003)

RY^{1+} is the catch that will keep a population at its current size. This quantity is less useful as the basis for management advice for the B-C-B bowhead whale stock now that at least some of the analyses suggest the recruited population may be approaching K^{1+}. Obviously RY^{1+} will be zero if the population stops increasing because it reaches carrying capacity. Q_1^{1+} is therefore a more appropriate catch-related quantity to examine because it does not become zero at carrying capacity. Furthermore, this quantity represents a catch level that has been argued to meet the requirements of aboriginal subsistence management (Wade, 2002b; Wade and Givens, 1997). The fact that there is no evidence to select one model over the others and not all models result in similar estimates of catch quantities is a reason why model uncertainty is important to include when conducting assessments of marine renewable resources. The lower 5th percentile of the Bayesian model-averaged posterior of Q_1^{1+} is 155 whales, and represents our best estimate of the catch level that would meet the intent of aboriginal whaling management objectives, taking into account both parameter, and model uncertainty (to the extent that model uncertainty can be captured by the three models considered in this study). It should be noted, in light of recent discussions regarding stock structure (IWC, 2005), that the results presented here are based on the assumption that the B-C-B bowhead whales comprise a single stock.

The actual aboriginal catch quotas are driven by need, and have averaged 36 whales per year from 1978-2002. There appears to be little effect on population size due to this catch

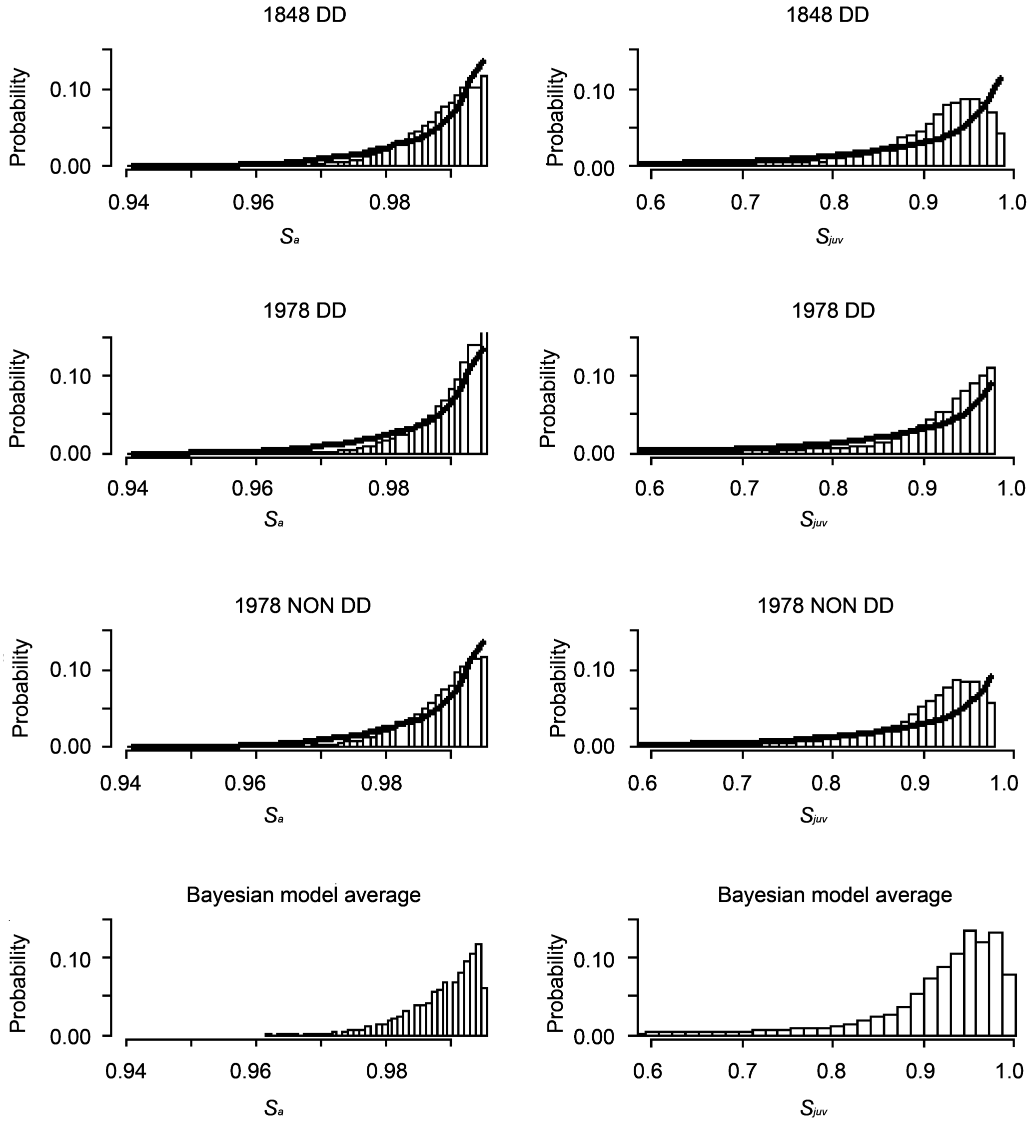

Fig. 5. Posterior (vertical bars) and post-model-pre-data (solid lines) distributions for adult survival rate, S_a (left panels) and calf and juvenile survival rate, S_{juv} (right panels). Results are shown for the three reference scenarios and for the Bayesian model average.

level. In fact, during this timeframe the B-C-B stock of bowhead whales is estimated to have more than doubled. Another way of putting an average take of 36 whales per year into perspective is to examine the annual net production over the last 25 years. If it is assumed that the population was increasing at a constant 3.5% per year (the median rate estimated from the density independent Leslie matrix analysis), the population increased by about 175 whales per year in 1978 (population size ~5,000), about 260 whales per year in 1990 (population size ~7,500), and about 350 whales per year in 2002 (population size ~10,000). Given that the population has increased from about 5,000 whales to about 10,000 whales, in this timeframe an average kill of 36 whales per year represents an annual catch rate between 0.35-0.70% of the total population size.

What is known about B-C-B bowhead whale life-history vital rates (survival, fecundity, etc.) appears consistent with the available data on trends in abundance and the proportion of the population in three stages (calves, immature and mature). Overall, the results support a value of r_{max} of between 0.03-0.05, a range often assumed for cetaceans, particularly species with delayed sexual maturity and a longer than 2-year calving interval (Reilly and Barlow, 1986; Wade, 1998; 2002a). In light of the reproductive life-history of this species, the results make clear that the observed population growth rates can only be supported by extremely high survival rates, as already suggested by the estimates of adult survival (0.990) in Zeh *et al.* (2002), and the observations of exceptionally old individuals (George *et al.*, 1999).

The analyses of this paper are based on the same types of data that were available for the 1998 assessment of this stock. Several other sources of data exist. For example, Schweder and Ianelli (2000) examined whether the data on the age-composition of the 1973-93 catches are consistent with the abundance and proportion data. Punt (2006) shows that it is possible to reconcile the abundance, proportion, length-frequency and age-composition data within a Bayesian framework. It would be straightforward conceptually (but perhaps computationally challenging) to use the approach outlined in this paper to compare models that utilise these additional data sources. Bringing in those additional data, as well as doing a full model comparison of a variety of models, was beyond the scope of this paper, but we agree this would be important future work, particularly in light of the methods now developed in Punt (2006).

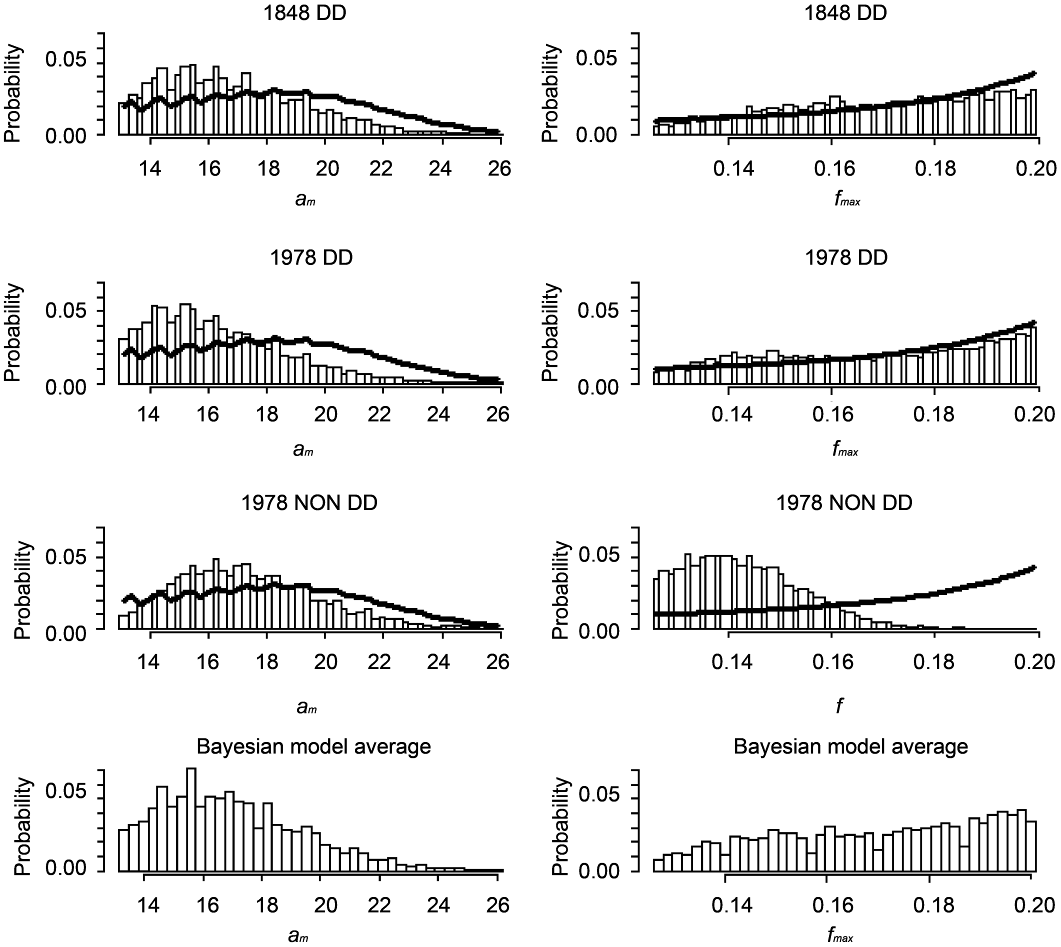

Fig. 6. Posterior (vertical bars) and post-model-pre-data (solid lines) distributions for the age-at-maturity, a_m (left panels) and fecundity, f_{max} or f (right panels). Results are shown for the three reference scenarios and for the Bayesian model average, which is based only on the two models with density dependence for fecundity.

Table 6

Posterior medians (5th, 95th percentiles) for eight life history-related quantities for all models and scenarios, and the Bayesian model-averaged results for the reference scenario. For the 1978 NON DD model, fecundity and population growth rate only apply to the specified period, and are referred to here as f and r. The model-averaged results for these rates are based only on the two models with density dependence, and refer to $f_{\max}$ and $r_{\max}$.

	S_a	S_{juv}	$f_{\max}$(or f)	$r_{\max}$(or r)	a_m	a_T	P_c	P_m
1848 DD								
Reference scenario	0.989	0.926	0.171	0.041	16	5	0.055	0.436
	(0.977, 0.995)	(0.718, 0.980)	(0.135, 0.198)	(0.024, 0.059)	(14, 21)	(1, 9)	(0.046, 0.065)	(0.418, 0.453)
No proportion data	0.991	0.957	0.181	0.046	17	5	N/A	N/A
	(0.978, 0.995)	(0.739, 0.990)	(0.136, 0.199)	(0.024, 0.062)	(13, 23)	(1, 9)		
Uniform priors on S_a and a_m	0.988	0.943	0.174	0.044	15	5	0.056	0.437
	(0.972, 0.994)	(0.786, 0.981)	(0.138, 0.198)	(0.026, 0.059)	(13, 20)	(1, 9)	(0.048, 0.065)	(0.420, 0.454)
1978 DD								
Reference scenario	0.991	0.945	0.171	0.045	16	5	0.057	0.435
	(0.979, 0.995)	(0.765, 0.988)	(0.133, 0.198)	(0.025, 0.063)	(13, 21)	(1, 9)	(0.048, 0.066)	(0.418, 0.452)
No proportion data	0.991	0.957	0.181	0.045	17	5	N/A	N/A
	(0.978, 0.995)	(0.753, 0.990)	(0.136, 0.199)	(0.025, 0.062)	(13, 23)	(1, 9)		
Include 1985 proportion data	0.993	0.981	0.182	0.049	20	5	0.034	0.424
	(0.979, 0.995)	(0.750, 0.993)	(0.126, 0.199)	(0.027, 0.065)	(13, 25)	(1, 9)	(0.025, 0.040)	(0.394, 0.663)
Uniform priors on S_a and a_m	0.989	0.956	0.171	0.047	15	5	0.058	0.436
	(0.974, 0.995)	(0.816, 0.988)	(0.135, 0.198)	(0.027, 0.064)	(13, 19)	(1, 9)	(0.050, 0.066)	(0.419, 0.453)
U[8,000, 100,000] prior on K	0.990	0.940	0.162	0.042	16	5	0.057	0.435
	(0.978, 0.995)	(0.752, 0.987)	(0.130, 0.197)	(0.025, 0.061)	(14, 21)	(1, 9)	(0.049, 0.067)	(0.417, 0.453)
1978 NON DD								
Reference scenario	0.990	0.923	0.141	0.035	17	5	0.060	0.434
	(0.977, 0.995)	(0.717, 0.978)	(0.127, 0.163)	(0.022, 0.049)	(14, 22)	(1, 9)	(0.054, 0.068)	(0.417, 0.450)
No proportion data	0.989	0.936	0.173	0.038	19	5	N/A	N/A
	(0.975, 0.995)	(0.684, 0.985)	(0.132, 0.198)	(0.022, 0.053)	(14, 23)	(1, 9)		
Include 1985 proportion data	0.989	0.823	0.197	0.031	18	4	0.081	0.424
	(0.976, 0.995)	(0.477, 0.899)	(0.191, 0.200)	(0.018, 0.044)	(14, 22)	(1, 9)	(0.080, 0.084)	(0.414, 0.437)
Uniform priors on S_a and a_m	0.988	0.943	0.144	0.038	15	5	0.061	0.435
	(0.973, 0.995)	(0.783, 0.982)	(0.128, 0.166)	(0.023, 0.052)	(13, 21)	(1, 9)	(0.054, 0.069)	(0.418, 0.452)
Bayesian model average	0.990	0.932	0.171	0.043	16	5	0.058	0.435
	(0.978, 0.995)	(0.733, 0.984)	(0.133, 0.198)	(0.025, 0.062)	(14, 21)	(1, 9)	(0.049, 0.067)	(0.417, 0.452)

Table 7

Bayes factors for comparison of paired models. Evidence categories are modifications of the original categories of Jefferys (1961), as presented by Kass and Raftery (1995) and used by Wade (2002a) in an assessment of the eastern North Pacific gray whales: >150 is decisive evidence, 12-150 is strong evidence, 3-12 is positive evidence, and 1-3 is not worth more than a bare mention. All comparisons are based on the results of the reference scenarios.

Models	Bayes factor	Evidence for the first model
1978 DD *vs* 1848 DD	1.37	Not worth more than a bare mention.
1978 NON DD *vs* 1848 DD	1.51	”
1978 NON DD *vs* 1978 DD	1.10	”

Table 8

The average likelihood (Eqn. (10)) and posterior model probabilities used in the Bayesian model averaging. It was only possible to consider the two DD models for averaging quantities related to carrying capacity. All models were considered equally likely *a priori*.

Model	Average likelihood	Posterior model probabilities for models considered	
		All three	1848 DD and 1978 DD
1848 DD	0.522	0.258	0.422
1978 DD	0.715	0.353	0.578
1978 NON DD	0.789	0.389	N/A

This study represents the first attempt to quantify model uncertainty when conducting assessments of the B-C-B bowhead whale stock. The analyses consider three alternative models and take model uncertainty into account by weighting alternative models based on their posterior model probabilities and by calculating a Bayesian model-averaged posterior. The only previous attempt to consider model uncertainty when conducting assessments of whale stocks was by Wade (2002a), who compared models for the Eastern North Pacific stock of gray whales with and without additional variance about the abundance estimates. In that case, one model received almost all the weight making model-averaging redundant. In contrast, in this study all three models were assigned non-negligible weight and this led to different estimates of quantities of interest (e.g. carrying capacity and related measures). The Bayesian model-averaged posterior distribution clearly represents our best efforts to incorporate all levels of uncertainty in the estimates of these quantities.

ACKNOWLEDGMENTS

Support for JB was provided by Minerals Management Service and NOAA Fisheries. Many thanks to André Punt for suggesting Bayesian model averaging and tireless reviews during the drafting process. Thanks also to Dave Rugh (NOAA Fisheries) and two anonymous reviewers for their very useful comments which greatly improved this paper. Fellow students in the Punt Lab provided necessary input and computing support for JB. Arni Magnusson provided assistance with R coding for the graphics. This work would not be possible were it not for the many colleagues in the field who have collected and analysed the data used in the analyses, in particular the North Slope Borough and National Marine Mammal Laboratory.

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Date received: April 2006
Date accepted: July 2006

J. CETACEAN RES. MANAGE. 8(3):241–245, 2006

A note on geographic and seasonal fluctuations in the isotopic composition of baleen in four North Atlantic right whales (*Eubalaena glacialis*)

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ABSTRACT

Despite management efforts, studies suggest that the North Atlantic right whale (*Eubalaena glacialis*) population may still be in decline. Due to its endangered status and propensity for human interactions, it is critical that all habitats and migratory routes utilised by the right whale are identified and protected. We conducted incremental stable isotope analysis along the baleen plates of three North Atlantic right whales, an adult female, a juvenile male and a neonate male, showing seasonal oscillation patterns in $\delta^{15}N$ and $\delta^{13}C$ values associated with migrations between summer and winter habitats. The $\delta^{15}N$ and $\delta^{13}C$ values displayed seasonal variability with enriched values occurring in the winter and depleted during the summer. Comparisons with published values for a fourth adult female (NEAq1014) showed that summer values differed significantly between adults. While the small sample size prevents firm conclusions, these data suggest differential habitat use between adult individuals as well as age classes. Isotopic ratios from plankton in the Labrador Sea indicate that portions of the population may be utilising this habitat as an alternative summer feeding ground.

KEYWORDS: NORTH ATLANTIC RIGHT WHALE; MIGRATION, MOVEMENTS; FEEDING GROUNDS; HABITAT; NORTHERN HEMISPHERE

INTRODUCTION

Prior to the 15th century, right whales were abundant throughout the western North Atlantic, ranging from Florida to as far north as the southern waters of Greenland (Knowlton *et al.*, 1992; Kraus and Brown, 1991; Kraus and Kenney, 1991; Winn *et al.*, 1986). However, extensive whaling over the next four and a half centuries depleted these populations to recent estimates of 300 animals, making the North Atlantic right whale one of the most endangered species of baleen whales (IWC, 2001; Knowlton *et al.*, 1994; Kraus *et al.*, 2001). Despite management efforts, some studies suggest that the population may still be in decline (Caswell *et al.*, 1999; IWC, 2001). Therefore, it is critical that all habitats and migratory routes utilised by the right whale are identified and protected.

Incremental stable isotope sampling along the length of the baleen is an effective way of tracing the migratory and feeding patterns of whales (e.g. Best and Schell, 1996; Hobson and Schell, 1998; Lee *et al.*, 2005; Schell *et al.*, 1989a; Schell *et al.*, 1989b), as isotopic ratios in the baleen directly reflect the diet of the animal during the tissue's formation. Migratory related changes in $\delta^{13}C$ and $\delta^{15}N$ values have been reported in the Arctic bowhead whale, *Balaena mysticetus* (Schell *et al.*, 1989a; 1989b) and the Southern right whale, *E. australis* (Best and Schell, 1996). Northern right whales are known to undergo annual migrations from calving grounds in Florida to feeding and nursery grounds in Cape Cod Bay (Hamilton and Mayo, 1990), the Great South Channel (Kraus and Kenney, 1991; Winn *et al.*, 1986), the Bay of Fundy and Roseway Basin (Gaskin, 1987; Kraus *et al.*, 1988; Murison and Gaskin, 1989) (Fig. 1). However, despite continuous research, substantial portions of the population remain unaccounted for in known winter and summer habitats (Kraus *et al.*, 1986; Mead, 1986), suggesting alternative residency and migratory patterns. Northern right whales feed primarily on late stages (IV and V) of *Calanus finmarchicus* copepods (Gaskin, 1982) and do not change their feeding preference as they age. Any variability in the stable isotopic signatures of their tissues, therefore, would reflect geographical differences in the isotopic signatures of food webs that individuals encounter during migration. This provides a unique method of tracking seasonal patterns in habitat use.

This study explores the value of stable isotope analysis as a determinate for differential migratory behaviours between age classes and same sex adult individuals in the North Atlantic right whale population.

MATERIALS AND METHODS

Attempts were made to locate North Atlantic right whale baleen plates for sampling from a number of museums and agencies around the US, Canada and Europe, but for only three plates could the proper permitting for destructive sampling be obtained. The three plates were sampled for stable ^{13}C and ^{15}N isotopic analyses (Table 1). An adult plate was obtained from NOAA Fisheries, Beaufort, NC (VMSM2004-1004; female, 1,600cm total length). This individual was estimated to be at least 25 years old when killed by a ship strike and stranded off the coast of Cape Hatteras, NC in 2004. The length of the plate, including the unerupted portion, was 193cm. A plate from a juvenile male was sampled at Harvard Museum of Natural History (MCZ 62052; 1,030cm total length). Age estimations indicated that this animal was 2.5 years of age when it stranded in Rhode Island due to line entanglement. The baleen plate measured 108cm. Lastly, a neonate (UF 28470; male, 417cm total length) that stranded in Florida after complications during parturition was sampled through the Florida Museum of Natural History. The baleen plate measured 12cm.

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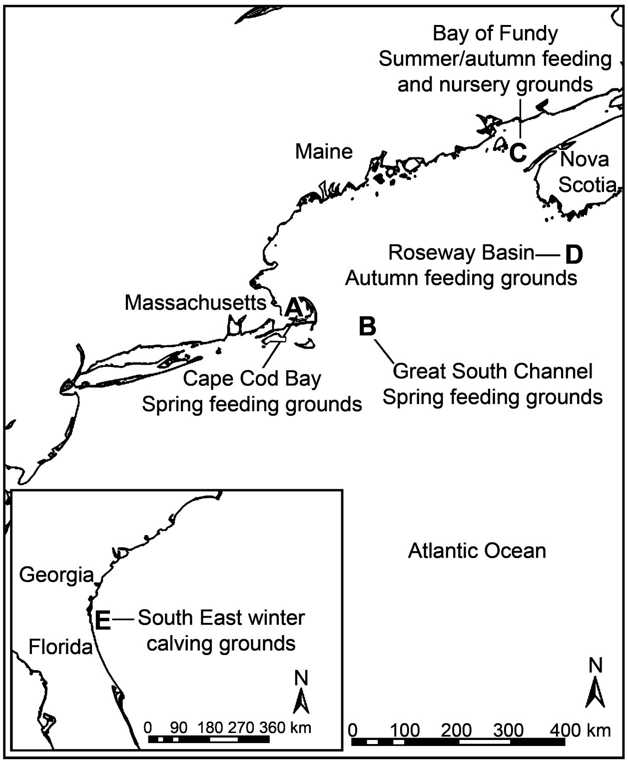

Fig. 1. Right whale critical habitat areas of the western North Atlantic.

The baleen plates, from the unerupted portion to the tip, were sampled along the outside edge in 2cm intervals, which corresponds to about one month of growth in adults (Schell and Saupe, 1993). All samples were obtained by using a flexible shaft hand-held drill fitted with a 1.6mm bit. The resulting powder was collected and dried at 55°C for 24hrs.

Approximately 1mg of ground tissue was used for carbon and nitrogen isotopic analysis. Samples were combusted using a Finnigan *MAT Delta Plus* mass spectrometer plumbed to a Carlo Erba NC2500 elemental analyser through a Conflo II open split interface. Stable isotope abundances were measured by comparing the ratio of the two most abundant isotopes (^{13}C/^{12}C and ^{15}N/^{14}N) in the baleen tissue to the standard reference material. Results are expressed in terms of parts per thousand (‰) deviation from the standard using the equation:

$$\delta X = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1{,}000‰$$

where X is the heavy isotope (^{13}C or ^{15}N) and R is the isotopic ratio ^{13}C/^{12}C or ^{15}N/^{14}N. Standards used for carbon and nitrogen analysis were Pee Dee Belemite (PDB) and atmospheric nitrogen (N_2) respectively. Seasons and years were assigned to the various sampling locations on the baleen plate using the distance between annual oscillations, the date of stranding, and estimated rates of growth as taken into account in the sampling interval (Best and Schell, 1996).

In addition to these three animals, the results from an adult female right whale, NEAq1014, were reconstructed from Wetmore (2001). This animal was estimated to be more than 28 years old when it was found dead in Cape Cod Bay in April 1999; likely due to a ship strike. This baleen plate measured 247cm and was sampled similar to the above methods. Those methods can be found in Wetmore (2001). A single-factor analysis of variance (ANOVA) was used to compare the summer and winter peak isotopic values for VMSM2004-1004 to published values for NEAq1014.

Vertical plankton tows were conducted in the Labrador Sea 26 May-7 June 2005 aboard the CCGS *Hudson* (Fig. 2), using 200µm mesh nets from a depth of 100m. Sampling locations ranged from coastal to deep basin habitats with depths ranging from 135-3,570m. Samples were immediately picked for *C. finmarchicus*, with priority given to stages IV and V. Copepod preparation and analysis for stable isotope ratios were identical to those for baleen.

RESULTS

Temporal oscillation patterns in δ^{15}N and δ^{13}C values were apparent along the baleen plate of VMSM2004-1004 with the enriched values for each isotope occurring during winter months and the depleted values during the summer (Fig. 3a). Values fluctuated broadly, ranging from 6.0 to 11.9‰ for ^{15}N and –21.9 to –17.4‰ for ^{13}C.

One notable exception existed in the oscillation pattern of δ^{13}C values. During a period between the 142 and 174cm sampling locations, the δ^{13}C values, with the exception of one smaller peak, fluctuated by less than 0.5‰ while nitrogen continued with the typical oscillation pattern (Fig. 3a). This anomaly occurred during winter months.

The δ^{13}C values for NEAq1014 fell mostly within the range of VMSM2004-1004, fluctuating between –20.9 and –16.6‰ (Fig. 3b). However, values of δ^{15}N were slightly heavier in NEAq1014, ranging 8.2 to 12.5‰. A single factor ANOVA yielded a significant difference between the two adults' summer δ^{15}N values ($p<0.01$). Summer δ^{13}C values were not significantly different when all values were included. However, when one outlier from VMSM2004-1004 was removed, the ANOVA showed significant differences between individuals ($p<0.05$). Results showed no significant differences in either δ^{15}N or δ^{13}C during winter months.

The beginning of the temporal oscillation pattern seen in the two adults was evident in the baleen plate of the juvenile MCZ 62052 (Fig. 3c). ^{15}N and ^{13}C values showed less

Table 1

Summary information taken from the stranding records of VMSM2004-1004, NEAq1014, MCZ 62052 and UF 28470.

	VMSM2004-1004	NEAq1014	MCZ 62052	UF 28470
Sex	Female	Female	Male	Male
Estimated age (yr)	25+	28+	2 ½	Neonate
Stranding date	Feb. 2004	Apr. 1999	Jul. 1995	Jan. 1997
Stranding location	Cape Hatteras	Cape Cod Bay	Rhode Island	Florida
Total length (cm)	1,600	?	1,030	417
Baleen length (cm)	193	247.65	108	12
Notes	Ship strike	Ship strike	Entanglement	Died during parturition

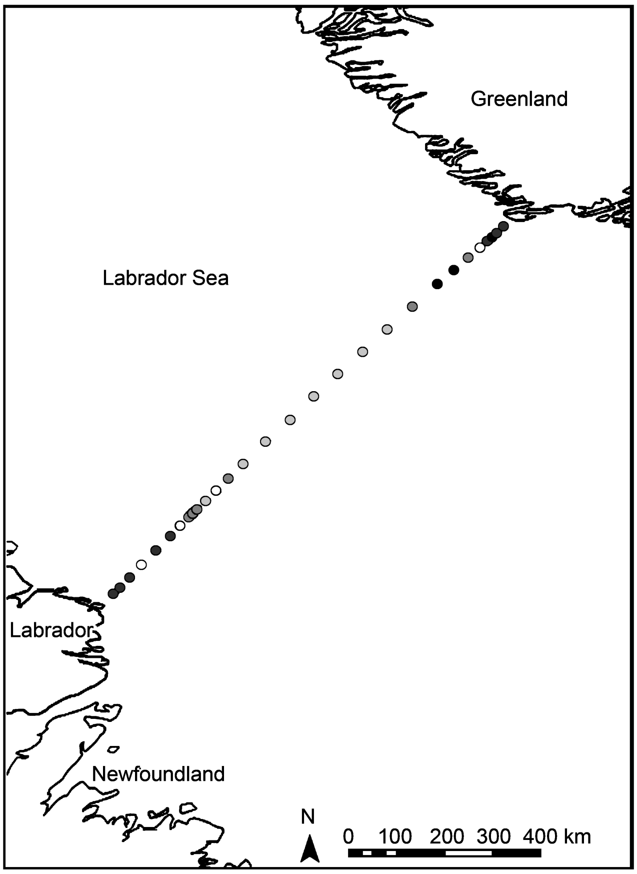

Fig. 2. Stations sampled for *Calanus finmarchicus* during the DFO Canada's *CCS Hudson* cruise May 26-June 7. $\delta^{15}N$ is given in parts per million.

variability, ranging 10.4 to 12.3‰ and –19.8 to –17.0‰, respectively. Encompassing two years of growth, the plate records the end of the nursing period and subsequent weaning from the 60-96cm sampling locations (Fig 3c). The annual oscillation pattern was apparent from the 6-60cm sampling locations, with the first residence in summer feeding grounds occurring around 36cm. A similar pattern to the anomaly in the ^{13}C values of VMSM2004-1004 was seen between the 46 and 82cm sampling locations, where ^{13}C values levelled off and fluctuated by less than 0.5‰. Additionally, samples taken from the most recently laid down baleen (2-12cm) become erratic. This time period corresponds to the entanglement event that led to the stranding of the individual.

Values for the neonate male UF28470 (Fig. 3d) showed very little variation, ranging 10.9 to 11.1‰ in ^{15}N and –18.9 to –18.5‰ in ^{13}C. These values corresponded only to baleen formed during late gestation and fell within the ranges of the two adults during the proposed winter periods.

$\delta^{15}N$ values for *C. finmarchicus* sampled in the Labrador Sea ranged from –1.2 to 13.3‰. Values were consistent in deep waters (>2,000m) in the centre of the trackline, ranging from 2.0 to 4.2‰. Nitrogen values became highly variable along either shelf, but were generally higher in the coastal waters, with values between 5.9 and 7.9‰. Anomalies occurred in areas characterised by steep slopes at or around the shelf break resulting in some negative $\delta^{15}N$ values.

DISCUSSION

The baleen record of VMSM2004-1004 details eight years of monthly seasonal migratory behaviour (Fig. 3a). This annual oscillation pattern is reflective of dietary changes due to migrations between winter and summer habitats, with values fluctuating between enriched and depleted ratios respectively. In fasting animals, the catabolism of body tissues produces substantial enrichments in $\delta^{15}N$ values (Hobson *et al.*, 1993). Since right whales are thought to fast during the winter, this would appear to be a likely explanation for the enriched ^{15}N values during these months. Additionally, each peak in ^{15}N is associated with a cluster of $\delta^{13}C$ values that differ by less than 0.5‰ (Fig. 3a), indicating that the diet of the whale is not changing during this time. This pattern of peaks in nitrogen during periods in which the carbon isotope remains constant has been linked to migratory-related fasting in the Arctic bowhead whale (Hobson and Schell, 1998) and the southern right whale (Best and Schell, 1996). However, the broad range in $\delta^{15}N$ values between summer and winter months suggests that fasting is not solely responsible for this enrichment. Typically, the breakdown of body tissue would be expected to produce a ^{15}N enrichment of approximately 3.0 to 4.0‰, roughly the equivalent of one full trophic position (Post, 2002; Tiezen *et al.*, 1983). In several years, VMSM2004-1004 shows an enrichment of nearly 6.0‰, a two-level trophic shift. Lee *et al.* (2005) found similar broad ranges in the isotopic values of bowhead whales and suggested that this pattern may be due to sporadic feeding during early migratory movements coupled with seasonal fasting. Wetmore (2001) found that copepod prey in Cape Cod Bay and Bay of Fundy were substantially enriched, when compared to those found off the shelf of Nova Scotia. Therefore, it is likely that winter enrichments in $\delta^{15}N$ values represent opportunistic feeding during the start of the southward migration, followed by a subsequent period of fasting prior to arrival in winter habitats.

The $\delta^{15}N$ values of VMSM2004-1004 are highly depleted in the late summer, sometimes dropping to as low as 6.0‰. Assuming a trophic enrichment of 3.0 to 4.0‰ for ^{15}N, this would suggest that this whale is utilising a summer feeding ground in which the primary prey has a $\delta^{15}N$ value of 3.0 to 4.0‰. However, copepod data presented by Wetmore (2001) indicate that prey values in the common summer habitat in the Bay of Fundy are substantially more enriched at this time, ranging from 7.1 to 10.6‰ (Table 2). Additionally, the summer $\delta^{13}C$ (outlier removed) and $\delta^{15}N$ values for VMSM2004-1004 were found to be statistically different than those of NEAq1014, which was commonly sighted in the Bay of Fundy during the summer (S. Kraus, pers comm). Therefore, it seems likely that VMSM2004-1004 is utilising a different habitat during this season. Isotopic analysis of copepods taken near the shelf break of Nova Scotia during August of 1998 by Wetmore (2001) (Table 2) and samples taken in the Labrador Sea basin during May and June 2005 (Fig. 2), indicate that VMSM2004-1004 may have been using this region as an alternative summer feeding habitat. For the latter, $\delta^{15}N$ values between 2.0 and 4.1‰, approximately one full trophic level below VMSM2004-1004, occurred through the deepest part of the trackline (Fig. 2), an area that is within the historic range of the North Atlantic right whale (Aguilar, 1986; Knowlton *et al.*, 1992; Lien *et al.*, 1989; Mead, 1986). It is possible that certain segments of the population are still exploiting this region as a feeding ground and as a result are displaying lower summer ^{15}N values and broader seasonal ^{15}N fluctuations than other segments of the population.

One exception to the seasonal patterns of VMSM2004-1004 can be seen in samples between 142 and 174cm (Fig. 3a). Here, carbon changes only slightly during a one-year period, indicating little, if any, migration during this period.

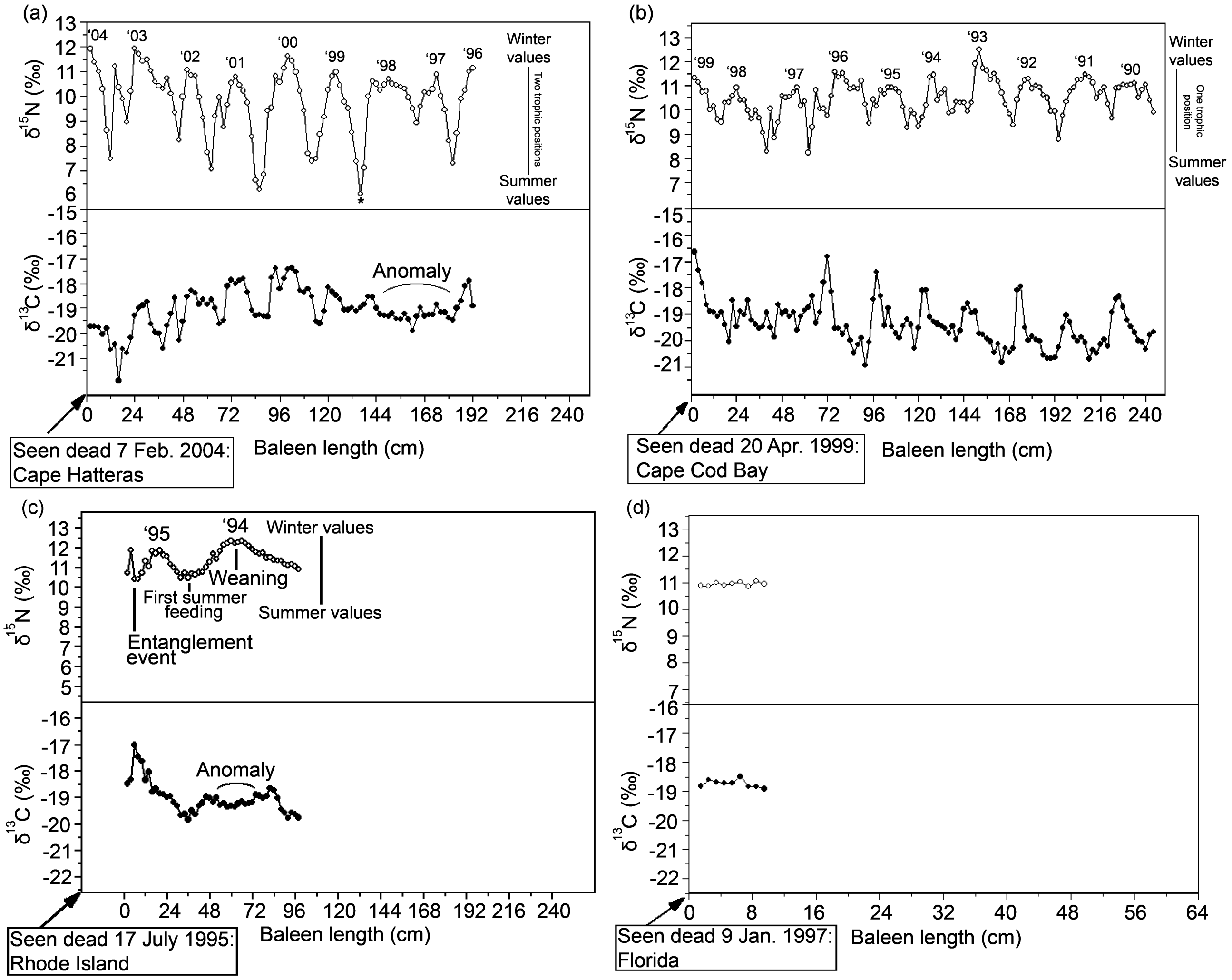

Fig. 3. Time series for adult female VSMS2004-1004 (a), adult female NEAq1014 (b), juvenile male MCZ 62052 (c) and neonate male UF28470 (d); δ^{15}N and ^{13}C ‰ versus baleen length in centimetres. All peaks represent winter values, while all valleys correspond to summer values. VSMS2004-1004 (a) stretches over two trophic positions with the asterisk identifying an exceptionally depleted δ^{15}N value. NEAq1014 (b) is reconstructed for comparison purposes from Wetmore (2001) published values. Both MCZ 62052 (c) and UF28470 (d) fall within the adults' value ranges, with MCZ 62052 detailing the first feeding cycle of a calf's life.

Table 2

δ^{15}N and δ^{13}C values (‰) of plankton taken from Wetmore (2001). Samples taken in the Bay of Fundy (BOF), Roseway Basin (RB), and the Nova Scotia Shelf (NSS) were taken during July and August over the three year period 1998-2000. Plankton samples from Cape Cod Bay (CCB) were taken in January and March of 2001.

	CCB	BOF	RB	NSS
Min. δ^{13}C	-21.27	-22.69	-24.59	-23.59
Max. δ^{13}C	-9.97	-20.12	-20.18	-18.30
Mean δ^{13}C	-17.48	-21.16	-22.64	-21.99
Min. δ^{15}N	6.94	7.12	5.40	3.14
Max. δ^{15}N	9.97	10.60	9.84	9.96
Mean δ^{15}N	8.15	8.16	8.05	7.24

Since this occurred over the course of two winter seasons, we hypothesise that this anomaly is due to a calving event and prolonged residency in Florida waters. This hypothesis is supported by the isotopic values in the baleen of MCZ 62052 and UF 28470. MCZ 62052's baleen recorded residency time in the calving ground during its first year of life. This period corresponds to the section of baleen between the 46 and 82cm sampling locations (Fig. 3c). Here, the lack of fluctuation indicates little to no migratory movement and closely matches the ^{13}C values and pattern of the adult, VMSM2004-1004, between 142-174cm. Additionally, UF 28470's ^{15}N and ^{13}C values correspond to the adult's values immediately prior to the hypothesised parturition (sample location 174cm in VMSM2004-1004; Fig. 3a). Baleen, being formed directly from amino acids in the bloodstream (Schell and Saupe, 1993), has a high turnover rate and shows no fractionation from mother to fetus, suggesting that the values of UF 28470's baleen correspond directly to the calving ground. The smaller fluctuations in the summer isotope values of VMSM2004-1004 during this period also support the proposed calving event. δ^{15}N and δ^{13}C at 166cm closely match summer values from NEAq1014, which can be linked to the Bay of Fundy. This suggests that VMSM2004-1004 may have undergone a shorter migration to the Bay of Fundy when she was with her calf, but extended her migration further north in subsequent years. However, the summer isotopic values of MSC 62052 are higher than those of VMSM2004-1004 even in the proposed calving year. It is plausible that since the recorded summer would have been this juvenile's first attempt at feeding, it was utilising a different portion of the water column or habitats closer to shore and therefore had different isotopic values.

Winter values for δ^{15}N and δ^{13}C were not significantly different between adults. This would be expected since calving females are known to winter in Florida waters. However, females only calve approximately once every two to five years (Kraus *et al.*, 1986), leading to speculation regarding their residency patterns in non-calving winters. The sighting record of NEAq1014 during years in which she was not seen with a calf (1998 and 1999) indicates that she was seen feeding in Massachusetts Bay in January and February (Wetmore, 2001). This behaviour has also been identified in several other right whales (Schevill *et al.*, 1986; Watkins and Schevill, 1982; Wetmore, 2001). Plankton sampled by Wetmore (2001) during this time from Cape Cod Bay showed ^{15}N values ranging from 6.9 to 9.7‰, which is approximately one trophic level below NEAq1014's corresponding values of around 11.0‰ (Table 2). Therefore, it seems plausible to assume that in non-calving years some females may be feeding on locally dense patches of copepods in Cape Cod Bay or other northern habitats.

By using stable isotopes to compare two adult females, as well as different age classes, it is apparent that while there may be substantial overlap in habitat usage in some regions, such as the calving and spring feeding grounds, many of their migratory patterns differ and remain unknown. While NEAq1014 appears to utilise the same specific habitats throughout multiple seasons, VMSM2004-1004 has a more variable record with broader fluctuations. These fluctuations indicate the use of alternative habitats in different years, including the potential for utilisation of an unidentified summer feeding ground and periods of fasting. These results demonstrate that while sampling a single animal is useful in gaining information about that individual, many animals will need to be analysed before conclusions regarding the behaviour of the population can be drawn. Future studies on northern right whale baleen involving isotopes should focus on comparing multiple individuals that differ in sex and matrilineal lines in order to determine how much variability exists within the population and how each segment is using habitats differently. A more complete understanding of the migratory and residency patterns of North Atlantic right whales will have significant impacts on the future conservation and management protocols for this endangered species.

ACKNOWLEDGEMENTS

We thank G. Lovewell and the Cetacean and Sea Turtle team at the NOAA Fisheries Beaufort Laboratory for providing samples and assistance, T. Williamson for copepod sampling and processing, A. Rice for editing and suggestions, S. Kraus and M. Bertrand for ideas and lab support and Fisheries and Oceans Canada through Glen Harrison, Erica Head and the staff and crew of the *CCGS Hudson* for providing space, equipment and guidance aboard their research vessel. NASA Research Grant NAG13-03027 funded this project.

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Date received: September 2005
Date accepted: July 2006

J. CETACEAN RES. MANAGE. 8(3):247–254, 2006

Abundance of fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) amid oil exploration and development off northwest Scotland

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ABSTRACT

A ship-based line transect survey was conducted during July-August 1998 to assess the distribution and abundance of cetaceans off northwest Scotland. Limited information from dedicated surveys exists for this area and the lack of baseline data is cause for concern given the expanding oil industry in these waters. Historical whaling records show that large numbers of baleen whales, particularly fin and sei whales, were captured in these waters during summer. The waters surveyed included former whaling grounds and currently licensed oil blocks to the west of the Outer Hebrides and the Faroe-Shetland Channel and both fin and sei whales were encountered. Neither species was recorded to the west of the Outer Hebrides whereas relatively high densities of both were recorded further north in the Faroe-Shetland Channel. The density of fin and sei whales was 0.021km^{-2} and 0.022km^{-2}, respectively. Abundance was estimated as 933 (CV=0.38) fin whales, 1,011 (CV=0.35) sei whales and 1,923 (CV=0.33) 'large whales'. The high density of whales recorded in the Faroe-Shetland Channel supports the idea that it is an important summer feeding ground for both species and the potential for acoustic disturbance associated with increasing industrialisation of this area is a concern. Factors affecting the distribution and abundance of these whales are discussed.

KEYWORDS: FIN WHALE; SEI WHALE; ABUNDANCE ESTIMATE; ATLANTIC OCEAN; SURVEY-VESSEL; MOVEMENTS; DISTRIBUTION; WHALING-HISTORICAL

INTRODUCTION

The distribution of fin (*Balaenoptera physalus*) and sei whales (*B. borealis*) is cosmopolitan, they both occur almost worldwide, with populations in the Atlantic, Pacific and Southern Oceans (e.g. Rice, 1998). Both species may also be vagrant to the Indian Ocean (Rice, 1998). Most mysticetes are typically believed to undertake seasonal migrations between high latitude productive feeding grounds and low latitude breeding grounds. The predictable nature of some of these migrations has contributed to their exploitation. Commercial whaling began in the late 19th and 20th centuries and led to population declines of many of the great whales. Fin and sei whales were amongst those species that were heavily exploited and since the 1860s an estimated 79,000 fin whales and 16,000 sei whales have been taken globally (Sigurjónsson, 1995). The worldwide status of both species is currently listed as 'endangered' on the World Conservation Union (IUCN) Red List of Threatened Species (IUCN, 2004), primarily due to the decline in the Southern Hemisphere (Reeves *et al.*, 2003).

In the early 20th century, fin and sei whales were regularly caught in British waters. Between 1903-04, four whaling stations opened on the Shetland Islands and one in the Outer Hebrides. The Scottish whaling season extended from April to September and operations took part annually until whaling from these stations ended in 1929. The Hebridean whaling station completed a further two seasons in 1950 and 1951. Fin whales constituted the largest proportion of catches (Brown, 1976; Thompson, 1928) with 2,418 fin whales and 1,283 sei whales captured between 1908-14 and 2,164 fin and 439 sei whales captured between 1920-27 (Thompson, 1928). Whaling records suggest that these species were relatively abundant off northwest Scotland and it is considered likely that this area is still important for these species. Recent opportunistic sightings (e.g. Stone, 2003; Weir *et al.*, 2001), acoustic detections (Clark and Charif, 1998) and dedicated surveys (Buckland *et al.*, 1992; Macleod *et al.*, 2003; Sigurjónsson *et al.*, 1989) confirm that fin and sei whales still occur in these waters. Visual records of fin and sei whales off western Britain are largely restricted to the summer months (Macleod, 2001; Weir *et al.*, 2001), although fin whales have been recorded acoustically throughout the year in temperate North Atlantic waters (Clark and Charif, 1998).

During summer, the highest densities of large whales to the west of Great Britain occur further north in the Faroe-Shetland Channel (Pollock *et al.*, 2000). The productivity of the cold water Faroe-Shetland Channel is enhanced by eddies and meanders formed by strong currents and mixing of the relatively warm, saline continental slope current flowing northeast, and the deeper, cooler, less saline Nordic waters flowing south. The speed of the continental slope current also increases as it enters the Faroe-Shetland Channel (Hopkins, 1991), because of the restriction in flow and enhanced mixing over the Wyville-Thomson Ridge (Burrows *et al.*, 1999). Therefore, it is reasonable to assume that prey resources would be abundant during summer and provide a rich feeding area for fin and sei whales. Sei whale diet consists almost exclusively of copepods (Flinn *et al.*, 2002; Nemoto and Kawamura, 1977), especially *Calanus finmarchicus* in the North Atlantic (Ingebritsen, 1929), whereas fin whale diet includes euphausiids, copepods and fish (Nemoto, 1959; Sigurjónsson, 1995; Woodley and Gaskin, 1996).

The historical whaling grounds (and presumed feeding grounds) for fin and sei whales off northwest Scotland lie within licensed oil blocks and the area is undergoing rapid

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exploration and exploitation. Mysticetes produce loud, species-specific low frequency signals and are adapted for low-frequency hearing (Ketten, 1992). They are thought to be particularly susceptible to the powerful, predominantly low frequency seismic noise produced by airguns, typically with broadband source levels of 220-255dB re: 1μPa-m (Richardson *et al.*, 1995). Low frequency, underwater pulses from airguns are often audible many tens of kilometres away (Richardson *et al.*, 1995). Intense anthropogenic underwater sound may adversely affect the behaviour and hearing of marine mammals (Gordon *et al.*, 2003). It may also lead to their displacement from an area and mask communication and other sounds (Finneran *et al.*, 2000; Gordon *et al.*, 2003; Gordon and Moscrop, 1996; Richardson *et al.*, 1985; Richardson *et al.*, 1995). Short-term behavioural responses of cetaceans to anthropogenic noise include changes in dive-surfacing cycles (Richardson *et al.*, 1985), respiration rates (Richardson *et al.*, 1986) and swimming speeds and direction (Borggaard *et al.*, 1999). Short-term vocal responses have also been noted, such as changes in calling rates (Watkins *et al.*, 1985) or cessation of calls in response to unfamiliar or intense anthropogenic sounds (Finley *et al.*, 1990; Goold, 1996).

Summer abundance of fin and sei whales has been estimated within some areas of their eastern North Atlantic range (Fig. 1). Although survey strata have included waters to the west of the UK, survey effort was relatively low. Information on the abundance and seasonal distribution of cetaceans off northwest Scotland is limited but given the considerable interest in oil and gas exploration and development in the area, gaining baseline information is important. This paper presents an abundance estimate for fin and sei whales and a combined estimate of large whales off northwest Scotland. The data were collected during a dedicated survey conducted in summer 1998 (Macleod *et al.*, 2003). The distribution of both species was restricted to the Faroe-Shetland Channel, where relatively high densities were encountered. The importance of this information is discussed in the context of findings from previous surveys and implications for management of industrial activities off northwest Scotland.

METHODS

Survey methods

A line transect survey was conducted from 14 July-15 August 1998, in predominantly offshore waters (>200m) to the west of the Outer Hebrides (Stratum A) and in the Faroe-Shetland Channel (Stratum B) (Fig. 2). The survey strata were chosen to coincide with areas of historical whaling grounds and those currently licensed for oil exploration. The survey was conducted onboard the vessel M.V. *Neptun*, travelling at an average speed of 10 knots. The ship followed saw-tooth tracklines, designed from a random start point in an east-west direction to avoid paralleling depth contours. Surveying was conducted in Beaufort sea state 4 and below with good visibility. The survey was carried out in 'passing mode' meaning that the vessel did not approach sighted cetaceans.

Surveying was conducted using an Independent Observer (IO) method (Palka, 1995) involving two teams of observers on visually and acoustically separated platforms. The primary and secondary platforms were 5.7m and 8m above sea level, respectively. Three observers searched primarily with the naked eye on each platform, rotating around observation positions (port, centre, starboard and rest) every 30 minutes. Binoculars were used intermittently to search at distance and during sightings to aid species identification and school size estimation. Effort and environmental data were recorded every 30 minutes and when conditions changed. Radial distances (km) and angles to each sighting were measured using Fujinon 7×50 reticle binoculars and angle boards mounted on the ship's railings. Minimum, maximum and best estimates of school size were recorded. Automated recording of survey data was aided with the *Logger* software (IFAW 1994) run on a laptop connected to the ship's Global Positioning System (GPS) via an NMEA interface.

A two-day training period for observers to practise angle and distance estimation using the equipment and by eye was conducted before the survey. Estimates to surrounding vessels or headlands were taken and checked against the ships radar.

Abundance estimation

The conventional distance sampling estimator of animal abundance, $\hat{N}$, for line transects is (Buckland *et al.*, 2001):

$$\hat{N} = \frac{n_s \cdot \bar{s}}{2L\hat{\mu}} A = \frac{n \cdot \hat{f}(0) \cdot \bar{s}}{2L} A$$

with variance,

$$\widehat{\mathrm{var}}(\hat{N}) = \hat{N}^2 \left[\frac{\widehat{\mathrm{var}}(n_s)}{n_s^{\,2}} + \frac{\widehat{\mathrm{var}}(\hat{f}(0))}{\hat{f}(0)^2} + \frac{\widehat{\mathrm{var}}(\hat{\bar{s}})}{\hat{\bar{s}}^2} \right]$$

where, n_s = number of sightings (schools) after truncation; $\bar{s}$ = mean size of detected schools; L = length of transect surveyed (km); A = survey area (km^2); $\hat{\mu} = 1/\hat{f}(0)$ (estimated effective strip half-width) where $\hat{f}(0)$ is the estimated probability density function of perpendicular distance evaluated at zero distance. This estimator assumes that all animals are detected on the survey trackline with certainty and there is no movement, random or responsive, to the survey vessel. The theory further assumes that measurements of sighting distances and angles in the field are accurate (Buckland *et al.*, 2001).

Double platform surveys enable data to be collected to estimate the probability of detecting animals on the trackline. However, small numbers of fin and sei whale sightings during this survey precluded a double platform analysis and the data were analysed using conventional distance sampling methods (Buckland *et al.*, 2001). Sightings of each species from the two observation platforms were combined and one of the duplicate pair was removed to form data sets of unique sightings. Definite and probable sightings of both species and across all sea states (Beaufort 0-4) were included in the analysis.

Estimating *f(0)*, *μ* and group size

Reticle binocular measurements taken in the field were converted to radial distances using the equation given in Lerczak and Hobbs (1998). Radial distances (r) and sighting angles (θ) were converted to perpendicular distances, x, using basic trigonometry (i.e. $x = r \times \sin\theta$). Histograms of perpendicular distances to the detected whale schools, under various groupings, were used to assess the need for truncation to remove outliers and to detect any obvious rounding of measured distances.

The detection probability, $f(x)$, was modelled by pooling the perpendicular distance data for both fin and sei whale sightings. Considering the similarity in the detection cues of

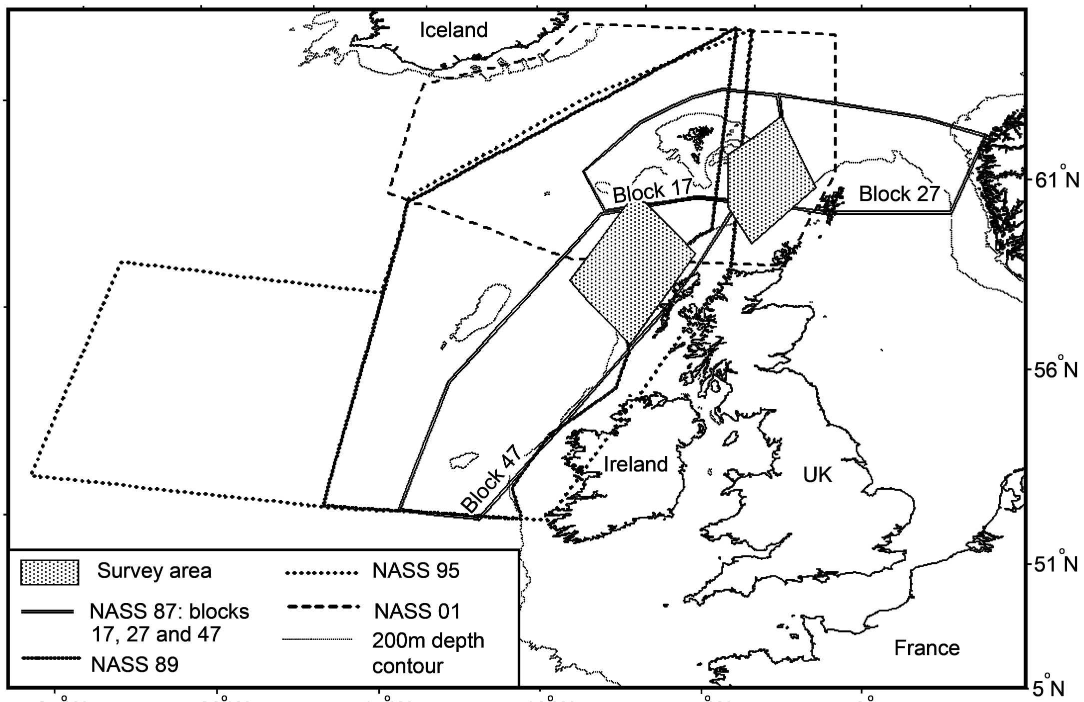

Fig. 1. Areas surveyed during the North Atlantic Sighting Surveys, 1987-2001 with coverage to the north and west of Scotland in relation to the position of the survey blocks for this study (survey area).

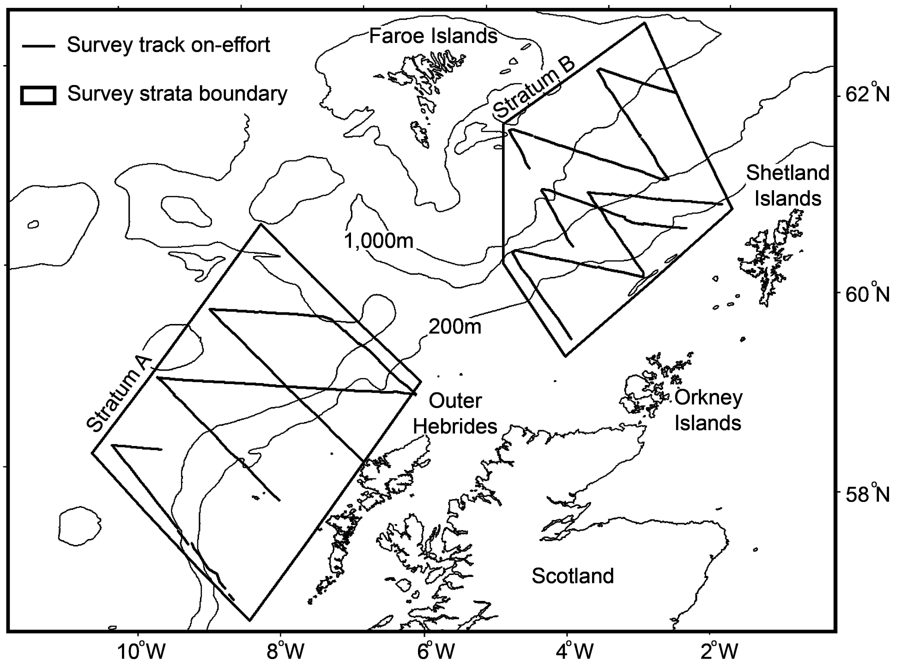

Fig. 2. Survey blocks and effort in Stratum A to the west of Outer Hebrides and Stratum B in the Faroe-Shetland Channel.

these species (e.g. blow height and shape) we considered it reasonable to assume that they would have similar detection functions. Perpendicular distances were modelled using the *Distance* 4.1 software (Thomas *et al.*, 2003). Several models were fitted to the data using combinations of key functions (half-normal and hazard rate) and series expansions (cosine, Hermite and simple polynomial) identified as model robust (Buckland *et al.*, 2001). The need for, and number of adjustment terms in the series expansion was determined using the Likelihood Ratio Test (Buckland, 1987; Buckland *et al.*, 2001). Selection of the best model was based on visual inspection of model fit (QQ-plot), goodness-of-fit statistics (Kolmogorov-Smirnov test) and the lowest value of the Akaike Information Criterion (AIC) (Buckland *et al.*, 2001).

School size was estimated for each species either from the regression of the log of school size against the fitted detection function if significant (α = 0.05) or as the observed mean school size. Best estimates of school size were used for the analysis. Density and abundance were estimated for each species using the estimated *f*(0) from the pooled species perpendicular distance data and the estimated or observed mean school size. Abundance was also estimated for ‘large whales’ by pooling sightings of fin and sei whales and including further sightings recorded as fin or sei whale. Variance was estimated analytically, as described above, and 95% confidence intervals were calculated assuming that estimated density was log-normally distributed.

RESULTS

During the survey, 136 cetacean sightings of seven species were recorded (Macleod *et al.*, 2003). Fin and sei whales were only encountered in the Faroe-Shetland Channel (Stratum B) and none was identified to the west of the Outer Hebrides (Stratum A) despite over 1,000km of survey effort in Beaufort sea state 4 and below. In Stratum B, 1,057.6km of transect was surveyed in the 43,578km^2 area of the Faroe-Shetland Channel. This was only 54% of the planned survey effort; fog and consequently poor visibility was the primary cause of survey downtime. Most sightings occurred beyond the continental shelf (Fig. 3). The mean depth of fin whale sightings was 1,089.9m (SD=415.7) and 822m (SD=168.5) for sei whale sightings.

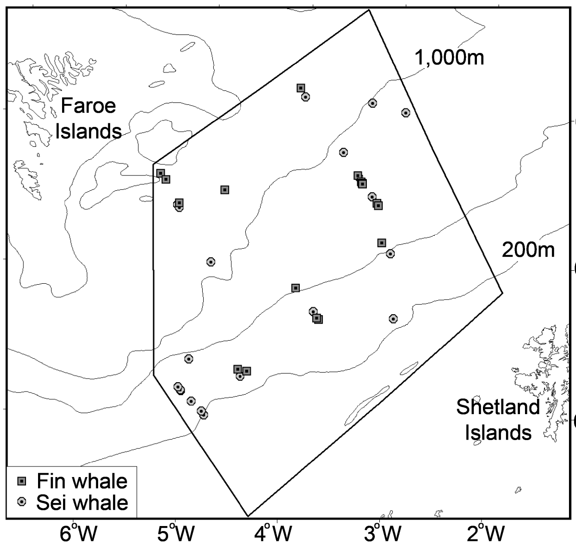

Fig. 3. Distribution of sightings of fin and sei whales in the Faroe-Shetland Channel.

The upper team of observers recorded 13 fin whales and 15 sei whales. The lower team recorded 12 fin whales and 8 sei whales. The combined dataset (FS) from both platforms of unique fin and sei whale encounters (definite and probable) resulted in a sample size of 40 (20 fin and 20 sei whales) and they were the most frequently recorded baleen whales in the area. A further 7 schools of large whales were classified as fin or sei whales and were used to estimate a combined 'large whale' (LW) abundance. Additionally, 43 unidentified whales were recorded in the Faroe-Shetland Channel but these were not used in the analysis. These observations were mainly of blows and may have been fin and sei whales but could also have been blue (*B. musculus*), sperm (*Physeter macrocephalus*) or humpback whales (*Megaptera novaeangliae*). The combination of species in the 'unidentified whale' category would weaken the assumption that pooling sightings to estimate the detection function was valid. Identifying species from blows alone, which was the most common sighting cue of large whales, can be extremely difficult, particularly in windy weather conditions or moderate visibility. Conducting the survey in closing mode would have helped species identification.

Density and abundance of whales could not be estimated for Stratum A and estimates are presented for Stratum B only. For both the FS and LW datasets, histograms of the distribution of perpendicular distances to sightings (Figs 4 and 5) showed that detections within 100m of the trackline were low. This suggests that some whales ahead of the ship may have moved away from the survey trackline prior to detection. Alternatively, the low number of detections close to the trackline may have been due to rounding problems or sampling errors. Outliers were removed by truncating both datasets at 1.5km.

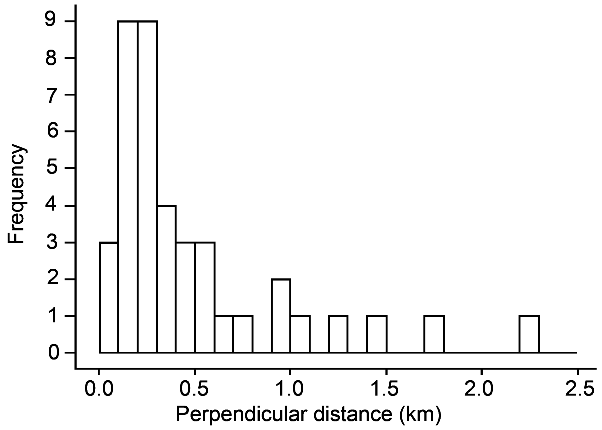

Fig. 4. Frequency histogram of the perpendicular distance data for pooled fin and sei whale sightings (FS data).

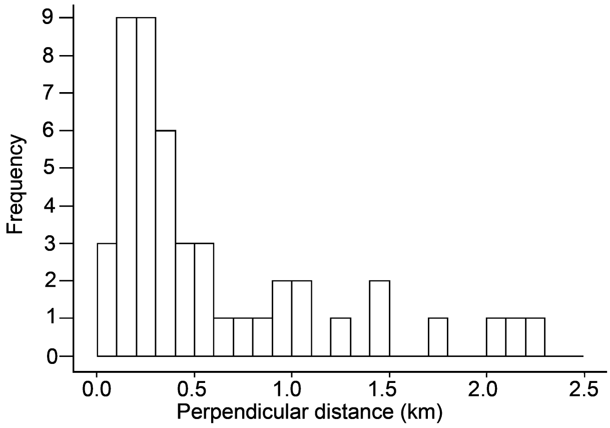

Fig. 5. Frequency histogram of the perpendicular distance data for all large whale sightings (LW data).

The resulting sample size for analysis of the FS data was 38 observations ($n_{s\ \mathrm{fin}}$=19 and $n_{s\ \mathrm{sei}}$=19). The probability density function of the perpendicular distances was modelled with a hazard rate key function without adjustment terms (Fig. 6) and was a good fit to the data (Kolmogorov-Smirnov, *p*=0.466). The point estimate of *f*(0) was 1.82 (CV=0.21) and the estimated effective strip half-width was 550m (SE=116) (Table 1). The size-bias regression estimates of school size for FS data were not significant (P_{fin}=0.755, P_{sei}=0.417) and the mean school size for each species was used. Mean school size was slightly smaller for fin whales than sei whales (Table 1) but school sizes ranged from 1-3 individuals for both species. Animal density was estimated to be 0.021 fin whales km^{-2} and 0.022 sei whales km^{-2}. Fin whale abundance was estimated as 933 (CV=0.38, 95% CI=435-2,003) individuals and sei whale abundance was slightly higher at 1,011 (CV=0.35, 95% CI=497-2,058) individuals (Table 1).

Forty-three observations from the LW dataset were used to estimate abundance after truncation. A hazard rate function without adjustment terms (Fig. 7) was used to fit the probability density function (Kolmogorov-Smirnov, *p*=0.519) (Table 1). Abundance of large whales was estimated as 1,923 animals (CV=0.33, 95% CI=994-3,721) (Table 1).

Table 1

Summary of the estimates for fin, sei whale and large whale abundance estimation, where $\hat{\mu}$ = effective strip half-width, s = average school size, n_s = number of schools, n_sL^{-1} = encounter rate ($n_s$km^{-1}), $\hat{D}_s$ = density of schools, $\hat{D}$ = density of whales and $\hat{N}$ = abundance of whales.

	Estimates (*CV*)		
	Fin whale	Sei whale	Large whales
$\hat{\mu}$	0.550 (0.21)	0.550 (0.21)	0.612 (0.22)
s	1.26 (0.10)	1.37 (0.10)	1.28 (0.06)
n_sL^{-1}	0.018 (0.30)	0.018 (0.27)	0.041 (0.24)
$\hat{D}_s$	0.016 (0.36)	0.016 (0.34)	0.033 (0.32)
$\hat{D}$	0.021 (0.38)	0.022 (0.35)	0.042 (0.33)
$\hat{N}$	933 (0.38)	1011 (0.35)	1923 (0.33)

DISCUSSION

The effects of sea state on whale detection were not considered in this analysis. Sample sizes were too small for stratification by sea state or for selecting effort and sightings recorded only in low sea states (0-2, for example). Borchers and Burt (1997) found that $\hat{\mu}$ for sei and fin whales detected in Beaufort sea states 4-6 was half that in sea states 0-3, although they were not significantly different. About 97% of the survey effort in Stratum B in this study was in sea state 3 or below and so the effects of sea state on whale detection would be expected to be small.

There are potential sources of bias in the abundance estimates presented. Animals can go undetected because observers miss them (perception bias) or because they are diving and underwater (availability bias). Missing whales on the survey trackline causes negative bias. However, the large size and tall blows of fin and sei whales are very visible and easy to detect. Fin and sei whales can be detected far from the ship and mean dives times are also relatively short (Croll *et al.*, 2001). It is reasonable to assume, therefore, that the probability of detection on the trackline is close to one and that any bias in abundance estimates is small.

Responsive movement of animals away from the survey vessel before they are detected will also cause negative bias. A suggestion of this was found in these data (Figs 4 and 5). Avoidance of ships has been documented for fin whales and in general it is particularly strong when ships head directly towards the whale or vessel noise is changing rapidly because of changes in speed (Richardson *et al.*, 1995). If animal orientation data are collected, methods are available to correct for responsive movement during analysis (Palka and Hammond, 2001). These data should be collected in future surveys.

Abundance estimates and previous surveys

The only dedicated cetacean surveys of offshore waters to the north and west of Scotland are the international North Atlantic Sighting Surveys (NASS). NASS have been conducted during the summers of 1987, 1989, 1995 and 2001 (Fig. 1), primarily to assess abundance of minke whales (*B. acutorostrata*), pilot whales (*Globicephala macrorhynchus*), fin and sei whales (Pike *et al.*, 2003), although all species sighted were recorded. The results of the early NASS surveys suggested that the numbers of fin and sei whales to the northwest of Britain were relatively low compared to East Greenland/Iceland stocks (Borchers and Burt, 1997; Buckland *et al.*, 1992). In previous surveys with survey effort off northwest Scotland (Fig. 1), no sightings (NASS-87) and a single sighting (NASS-89) of sei whales were made (Joyce *et al.*, 1990). Sei whale abundance has only previously been estimated from NASS-95 survey data to the west of the UK and Ireland (Borchers and Burt, 1997). An abundance of about 9,250 sei whales was estimated for the entire NASS-95 survey region, including waters around Iceland in the central North Atlantic. The highest densities occurred to the southwest of Iceland (mean density over three strata = 0.034 whales km^{-2}, CV=0.79) and are comparable to estimated density in the Faroe-Shetland Channel from this study (0.022 whales km^{-2}, CV=0.35) (Table 1). NASS surveys (1987-1995) show that the highest densities of fin whales have consistently occurred in the Irminger Sea off southwest Iceland. However, in 2001, the highest density was recorded off northwest Iceland (0.34 km^{-2}). The estimates of fin whale density in the northeast Atlantic suggest an increasing trend and the increases in abundance between Iceland and Greenland account for nearly all the increase in abundance over the entire NASS area (Pike *et al.*, 2003). However, full

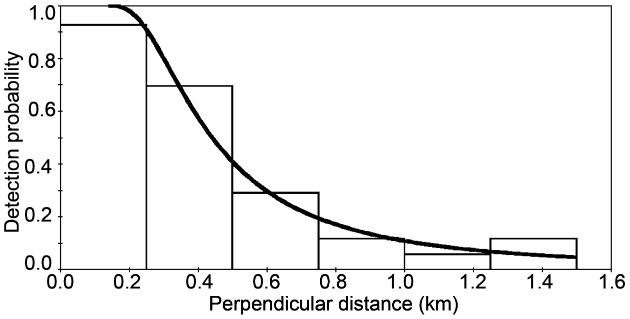

Fig. 6. Detection probability of pooled fin and sei whale sightings against perpendicular distances. The data are fitted with a hazard-rate key function and the fitted curve indicates the estimated probability density function.

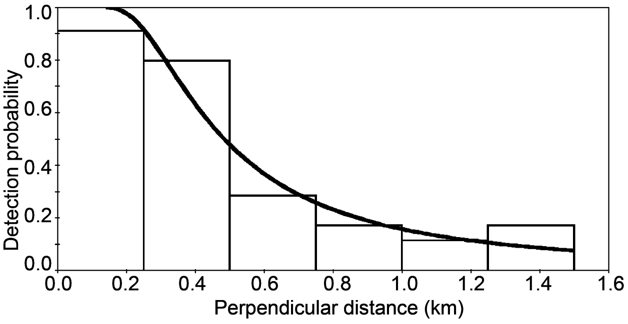

Fig. 7. Detection probability of all large whale sightings against perpendicular distances. The data are fitted with a hazard-rate key function and fitted curve indicates the estimated probability density function.

interpretation of the NASS estimates is complicated by the fact that stratification and coverage have changed in every survey, as have analytical methods (Pike *et al.*, 2003). There are insufficient data to interpret trends in sei whale abundance. Migrations of sei whales have been described as 'erratic' (e.g. Ingebritsen, 1929) and high densities in an area in one year would not necessarily hold for subsequent years.

The density of fin whales (0.021 km^{-2}) and sei whales (0.022 km^{-2}) in the Faroe-Shetland Channel estimated in this study are the highest recorded off western and northern Britain and Ireland since dedicated surveying began in 1987. The high densities of fin and sei whales in the Faroe-Shetland Channel in July 1998 indicate that this area is an important feeding ground and/or migration route to feeding grounds further north.

The high density of large whales in the Faroe-Shetland Channel contrasts with the complete absence of fin and sei whale sightings further south to the west of the Outer Hebrides. Both species were once caught in considerable numbers off the Hebridean shelf. The Scottish whaling season extended from April to September with peak catches of fin and sei whales occurring in June and July. However, by the end of July, the 'sei-season' closed for Hebridean whalers, but continued off the Shetland Islands until September (Brown, 1976; Thompson, 1928). Fin whale catches peaked in July at all stations. The absence of sightings off the Outer Hebrides may be a true reflection of the very low density of animals in these waters compared to numbers present historically or it may have been caused by some other factors. Changes in the timing of fin and sei whale migrations off the Scottish continental shelf may have occurred since whaling ceased, perhaps resulting in most whales now passing through Hebridean waters earlier to concentrate at the Faroe-Shetland Channel in July. Stone (1998) noted movements of fin whales throughout the area and found that, in June, most fin whales were near the Wyville-Thomson Ridge at the mouth of the Faroe-Shetland Channel. In July, most sightings occurred to the north and west of Shetland and this continued until October.

Changes in prey distribution and availability off the Outer Hebrides may also have contributed to the apparent lack of fin and sei whales in Hebridean waters compared to the Faroe-Shetland Channel. The calanoid copepods, *C. finmarchicus* and *C. helgolandicus* constitute one of the major components of the northeast Atlantic Ocean zooplankton (Planque, 1996). Since the 1960s, there has been a dramatic decline in abundance of *C. finmarchicus* in the northeast Atlantic Ocean and North Sea. Significant declines have occurred off the northwest of the UK and one of the areas where the decline is most evident is on the Malin Shelf, southwest Hebrides (OSPAR QSR, 2000). For almost four decades, the decline in *C. finmarchicus* was linked to the warmer seawater temperatures of the mainly positive North Atlantic Oscillation Index (NAOI) over this period. However, in 1996, there was a pronounced drop in the NAOI and it was predicted that there would be a corresponding increase in *C. finmarchicus* abundance. However, this did not occur and abundance continues to decline. The preference of *C. finmarchicus* for cooler water temperatures limits its distribution ever further north with increasing sea temperatures. A corresponding shift in marine predators feeding on this species might also be predicted.

However, anthropogenic factors, such as seismic surveys, may also influence the distribution and abundance of these species. During summer 1998 (June-August inclusive), the number of seismic surveys reported to the UK Joint Nature Conservation Committee (JNCC) was four times as many to the west of the Outer Hebrides than in the Faroe-Shetland Channel (Barton, pers. comm.). In each month, seismic activity was consistently greater to the west of the Outer Hebrides than further north. However, since reporting to the JNCC is not mandatory this can only be used as rough indicator of seismic activity in the area. Fin and sei whales may have avoided the area or passed through it because of the noise from seismic surveys. The impact of low-frequency noise from seismic surveys on the distribution of these species is unknown because of the lack of studies. The impact has been studied in other Balaenopterids such as the bowhead (*Balaena mysticetus*) and gray whale (*Eschrichtius robustus*). Evidence of avoidance behaviour in response to seismic activity, even at several kilometres away from the source, is well documented for bowhead whales in the Bering, Chuckchi and Beaufort Seas (Richardson *et al.*, 1995). Gray whales off Sakhalin Island, Okhotsk Sea shifted their distribution away from an area of seismic activity within their feeding ground (Weller *et al.*, 2002). Similarly, indirect effects on prey distribution and abundance may also be an important consideration.

Conservation concerns in the Faroe-Shetland Channel

The Faroe-Shetland Channel is an important habitat for large baleen whales. The Faroe-Shetland Channel and west coast of Scotland is undergoing industrialisation and the numbers of animals potentially at risk in these waters becomes an important factor for assessing both short- and long-term impacts to populations. In total, 24 species of cetacean have been recorded off western Scotland (Parsons *et al.*, 1999) and the list includes other large baleen whales, such as blue and humpback whales. A major concern is the effect of acoustic disturbance on cetaceans from seismic exploration and the associated noise from development and production. Mysticetes are thought to be particularly susceptible to the predominantly low frequency noise associated with oil and gas development because it is likely to be within the range of their hearing sensitivity. Two Floating Production Storage and Offloading facilities (FPSOs) are currently in production in the Faroe-Shetland Channel anchored at 4-600m. Swift *et al.* (2003) studied ambient noise levels and tracked fin whales in the vicinity of these FPSOs with autonomous bottom mounted recording systems. Low frequency noise associated with the dynamic positioning system of the FPSOs and from supply vessels and tankers characterised recordings. Seismic activity dominated summer recordings. In two fin whale frequency vocalisation bands (18-22Hz and 22-28Hz), noise levels ranged from 120dB re: 1mPa^{2}Hz^{-1} to 49dB re: 1mPa^{2}Hz^{-1} at distances of 8.5 and 40km, respectively. In 50% and 25% of the data, noise levels exceeded the predicted lower and upper limits, respectively, of mysticete hearing (Swift *et al.*, 2003).

Seismic exploration off northwest Scotland is likely to increase over the coming years with the success of the fields in the Faroe-Shetland Channel and the continual advancement of technology, which enables these deep waters to be exploited. Peak seismic activity coincides with peak densities of fin and sei whales in this region. The seismic zone of influence on these whales should be considered in the context of the amount and availability of suitable feeding habitat for them. If seismic surveys and industrial development were to reach such a level as to acoustically swamp feeding grounds off northwest Scotland, then fin and sei whales may be displaced. The theoretical zone of audibility for seismic pulses can be large, reaching distances of over 50km (Richardson *et al.*, 1995; Richardson and Würsig, 1997) although the maximum radius of influence is normally expected to be much less than the maximum radius of audibility (Richardson *et al.*, 1995). An immediate means of mitigating the effects of seismic activity on cetaceans is by avoiding areas with high cetacean densities (Harwood and Wilson, 2001). As densities are lower in September and October (Stone, 1998; Weir *et al.*, 2001) any seismic operators wishing to survey offshore waters off northwest Scotland could survey at this time with a reasonable expectation of having a lesser impact on these species. In addition, exploitation licences could be limited to reflect the sensitivities of the wildlife of the region and guidelines for minimising acoustic disturbance (e.g. JNCC, 1998) strictly adhered to as a minimum protective measure. Other management measures, which may include time-area closures (Macleod, 2001), should be considered to ensure disturbance to cetaceans off northwest Scotland is minimised.

The populations of fin and sei whales are still thought to be recovering from overexploitation. Baseline abundance estimates are crucial for monitoring populations and assessing the impacts of potentially harmful activities. However, it is important that surveys try to capture the entire range of populations, as 'regional' estimates are difficult to interpret at the population level. Future surveys to assess the summer abundance of northeast Atlantic fin and sei whales should ensure that areas off northwest Scotland are included.

ACKNOWLEDGEMENTS

The survey was made possible by funding from the Greenpeace Environmental Trust and the Whale and Dolphin Conservation Society. We would especially like to thank the survey team, H. Arnold, M. De Boer, R. Irish, C. Mackins, K. Norris, J. Pert and M. Stanley. Thanks also to the captains and crew of the MV *Neptun* and Carolyn Barton, Joint Nature Conservation Committee, for information on reports of seismic surveys. These data were partly collected using the software, *Logger*, developed by the International Fund for Animal Welfare (IFAW) to promote benign and non-invasive research.

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Date received: July 2006
Date accepted: September 2006

J. CETACEAN RES. MANAGE. 8(3):255–263, 2006

The effects of seismic airguns on cetaceans in UK waters

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ABSTRACT

Observations undertaken during 201 seismic surveys in UK and adjacent waters were analysed to examine effects on cetaceans. Sighting rates, distance from the airguns and orientation were compared for periods when airguns were active and when they were silent, both for surveys with airgun arrays of large volume and surveys with smaller volume arrays. The results demonstrate that cetaceans can be disturbed by seismic exploration. Small odontocetes showed the strongest lateral spatial avoidance (extending at least as far as the limit of visual observation) in response to active airguns, while mysticetes and killer whales showed more localised spatial avoidance. Long-finned pilot whales showed only a change in orientation and sperm whales showed no statistically significant effects. Responses to active airguns were greater during those seismic surveys with large volume airgun arrays than those with smaller volumes of airguns. It is suggested that the different taxonomic groups of cetaceans may adopt different strategies for responding to acoustic disturbance from seismic surveys; some small odontocetes move out of the immediate area, while the slower moving mysticetes orient away from the vessel and increase their distance from the source but do not move away from the area completely.

KEYWORDS: NOISE; EUROPE; CONSERVATION; SURVEY-VESSEL; SHORT-TERM CHANGE; MONITORING

INTRODUCTION

Cetaceans use sound to communicate and, in some cases, to echolocate. Their ability to detect calls from conspecifics, echolocation signals and other natural sounds is likely to be of paramount importance. Man-made sounds have the potential to interfere with their natural functions, such as feeding, social interactions and navigation, as well as the potential to cause physical harm. Seismic surveys use airguns to generate sound for the purpose of exploration of geological features beneath the seabed; seismic surveys are commonplace in the world's oceans, with noise from seismic airguns being recorded frequently over large distances (Nieukirk *et al.*, 2004). The airguns used produce sound at low frequencies that overlap with those used by mysticetes; these species are therefore considered to be vulnerable to disturbance from seismic surveys. Seismic operations also emit incidental high frequency sounds (Goold and Fish, 1998) that could potentially disturb odontocetes which communicate and echolocate using high frequencies. Several reports have called for more research into the effects of anthropogenic noise on marine mammals (Cox *et al.*, 2006; National Research Council, 2000; 2003; 2005). More specifically, Richardson *et al.* (1995) concluded that information is needed about reactions of odontocetes to underwater noise from airgun arrays used for seismic exploration. Kastelein and Wartzok (2004) also highlighted the need for information on the behavioural responses of marine mammals to current mitigation measures.

To address conservation concerns that have arisen in relation to seismic surveys, in 1995 the UK government and the Joint Nature Conservation Committee (JNCC) issued guidelines for seismic operations (latest version: JNCC, 2004). The guidelines have requirements for operators at the planning stage and during the operation of a seismic survey. For example, for at least 30 minutes prior to using airguns, onboard observers should check for the presence of marine mammals within 500m of the airgun array; if any are detected then use of the airguns must be delayed until at least 20 minutes after the last sighting. Whether marine mammals are detected or not, a 'soft start' procedure should be employed, where airgun array power is gradually built up over at least 20min from a low energy starting level. Seismic operators should submit a report to JNCC, using standard recording forms that are used to assess the implementation of the guidelines and the effects of seismic airguns on marine mammals. Previous analyses of annual data sets (Stone, 1997; 1998b; 2000; 2001; 2003) have been limited by small sample sizes. This paper uses data combined over four years (1997-2000) to investigate further the effects of seismic airgun activity on cetaceans.

METHODS

Visual monitoring for marine mammals was conducted during daylight on seismic survey vessels operating in UK and some adjacent waters, to ensure implementation of the JNCC guidelines. Observers ranged from biologists experienced in marine mammal surveys, to non-scientific personnel who had usually received training that included the implementation of the guidelines, data recording and marine mammal identification. Data from 201 seismic surveys during which weather conditions were recorded were used, enabling the influence of weather on the detection of cetaceans to be controlled when analysing the data. The surveys covered 152 quadrants (1° × 1° rectangles), including those passed in transit (Fig. 1). All except two surveys (in 1997) took place between 1998 and 2000. Survey effort was not evenly distributed spatially or temporally, peaking during summer and in the northern North Sea and to the west of Shetland. The proportion of time when the seismic sources were active (shooting) also varied spatially and temporally.

A total of 110 surveys used large airgun arrays with volumes in excess of 1,300 cubic inches (cu.in.), with most (79%) using volumes of at least 3,000cu.in. The noise characteristics of these large volume airgun arrays varied between surveys, but typically frequencies used were 3-218Hz, with a peak energy output from the source of around 65-70 bar metres, equating to a peak source level of around 250dB re. 1μPa @ 1m in the dominant bandwidth. A total of 39,168hr 06min was spent watching for cetaceans during these 110 surveys with large volumes of airguns, with the airguns being active for 38% of this time. The remaining 91 surveys, hereafter collectively termed site surveys, used low

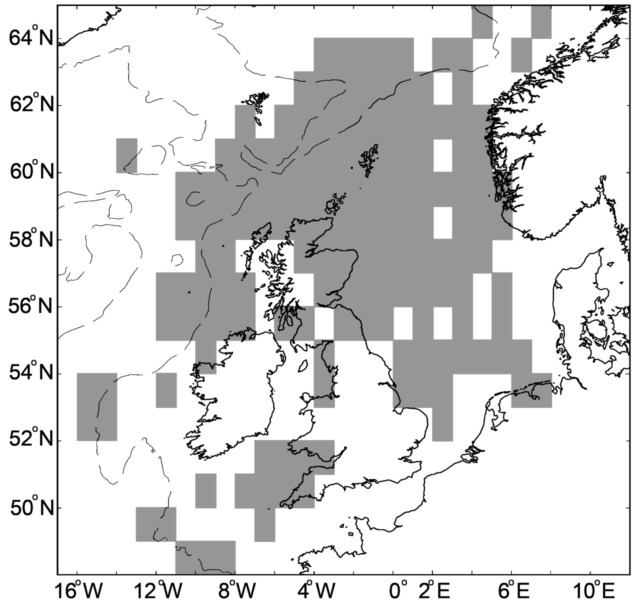


Fig. 1. Quadrants surveyed for cetaceans from seismic surveys, with 1,000m isobath.

power output to survey small areas to shallow depth (e.g. for rig site, pipeline, cable route, debris or anchor search surveys). On most (87%) site surveys the total array volume was 180cu.in. or less; the maximum array volume for these surveys was 820cu.in. The frequencies used during site surveys were typically 3-250Hz, with a peak energy output of around 10 bar metres, equating to a peak source level of around 235dB re. 1μPa @ 1m. Data from site surveys were analysed separately from surveys with large volume airgun arrays. Most site surveys were of short duration; observations during site surveys totalled 5,383hr 44min, with the airguns active for 17% of this time.

Observers routinely recorded information including the duration of the watch for marine mammals and the duration of airgun activity during the watch. Weather conditions, including sea state, swell and visibility, were recorded. When marine mammals were encountered, the information recorded included date, time, airgun activity, location, depth, species, number, direction of travel (relative to the vessel and in compass points), behaviour and the closest distance of approach to the airguns. Observers were asked to provide descriptions of marine mammals to support their identification. Where descriptions were not sufficient to confirm the identification, the taxonomic level of the identification was downgraded (e.g. from common bottlenose dolphin (*Tursiops truncatus*) to dolphin sp.). Videos or photographs, where available, were used to verify identification. Sometimes sightings that could not be identified to the species level could nevertheless be identified as being one of a group of morphologically similar species, e.g. fin/sei whale (*Balaenoptera physalus/ B. borealis*), white-beaked dolphin/Atlantic white-sided dolphin (*Lagenorhynchus albirostris/L. acutus*). At times, particularly with distant or brief sightings, it was impossible to identify animals beyond the level of small odontocete (i.e. excluding sperm whale (*Physeter macrocephalus*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melas*) and beaked whales) or a mysticete. For some groups of morphologically similar species there were considerable numbers of sightings and in order to gain as much information from the data as possible these species groups were included in the analyses.

Weather conditions varied considerably and influenced the ability of observers to detect cetaceans, with sighting rates increasing as sea state and swell decreased and as visibility increased. As the proportion of time spent shooting also varied in relation to weather conditions, periods of poor weather were discarded when comparing sighting rates or distance of animals from the source in relation to airgun activity. In these cases only periods with sea states of ‘slight’ (equivalent to sea state 3) or less, swell of less than 2m and visibility of more than 5km were used.

RESULTS

Sighting rate of cetaceans

There were 1,625 sightings of cetaceans (Table 1). Sighting rates were calculated per unit effort (1,000 hours of observations), and were compared between periods of shooting and periods when the airguns were silent. Variations in sighting rate due to location, season or observer ability were controlled by using matched pairs within each day of each survey. Only periods of good weather conditions were used, as defined above.

Sighting rates of all cetaceans combined, all small odontocetes combined, and the *Lagenorhynchus* species (both individual species and a group comprising all *Lagenorhynchus* species combined) were significantly reduced during periods of shooting on surveys with large volume airgun arrays (Fig. 2; Table 2). For site surveys, a significant reduction in sighting rate during periods of shooting was found for all small odontocetes combined (z =2.116, n=14, p=0.0170; Fig. 3).

Sighting rates through the course of surveys were examined for evidence of exclusion from survey areas due to the continued use of seismic airguns, using only periods of good weather conditions. The influence of location and season was controlled by using only data from known areas and months of peak abundance, established using various sources (e.g. Bloor *et al.*, 1996; Clark and Charif, 1998; JNCC, 1995; NERC, 1998; Northridge *et al.*, 1995; Pollock *et al.*, 2000; Pollock *et al.*, 1997; Reid *et al.*, 2003; Skov *et al.*, 1995). Kruskal-Wallis analysis of variance showed that variations in sighting rate (over a maximum of 18 weeks) during surveys with large volume airgun arrays were non-significant for all species. For site surveys the results (over a maximum of four weeks) were also non-significant.

Distance of cetaceans from the airguns

The median closest distance of approach to the airguns was compared between periods of shooting and periods when the airguns were not firing, using only periods of good weather conditions (as defined above). Only species where the sample size equalled or exceeded 10 sightings were used.

All small odontocetes tested, killer whales and all mysticetes combined remained significantly further from the source during periods of shooting on surveys with large volume airgun arrays (Fig. 4; Table 3). The only species found to approach closer to the airguns during periods of shooting was the sperm whale, but this result was not statistically significant. During site surveys no significant differences in the closest distance of approach of animals to the source were found (Fig. 5).

The proportion of sightings of small odontocetes within a given range of large volume airgun arrays was significantly reduced during periods of shooting (Fig. 6; Kolmogorov-Smirnov test χ^2 approximation = 21.021, df=1, $p<0.001$), while for other cetaceans no significant differences were found (χ^2 approximation = 3.056, df=1). During site surveys

Table 1

Summary of cetacean sightings from seismic survey vessels.

Species		Number of sightings	Number of individuals
Unidentified cetacean sp.		41	358
Unidentified whale sp.		59[1]	163
Unidentified large whale sp.		54[1]	129
Northern right whale (probable)	*Eubalaena glacialis*	1	1
Humpback whale	*Megaptera novaeangliae*	8	10
Blue whale	*Balaenoptera musculus*	4[1]	4
Fin whale	*Balaenoptera physalus*	116[1]	244
Sei whale	*Balaenoptera borealis*	13	16
Unidentified fin/blue whale		10	18
Unidentified fin/sei whale		56[1]	97
Unidentified fin/sei/blue whale		6	9
Unidentified fin/sei/humpback whale		27	40
Unidentified fin/sei/blue/humpback whale		17	36
Common minke whale	*Balaenoptera acutorostrata*	79[1]	103
Sperm whale	*Physeter macrocephalus*	123[1]	191
Unidentified humpback/sperm whale		12	17
Unidentified medium whale sp.		8	13
Unidentified beaked whale sp.	*Mesoplodon/Ziphius/Hyperoodon* spp.	3	3
Northern bottlenose whale	*Hyperoodon ampullatus*	2	11
Sowerby's beaked whale	*Mesoplodon bidens*	1	1
Long-finned pilot whale	*Globicephala melas*	172[1]	3,384
Killer whale	*Orcinus orca*	61	357
Unidentified dolphin sp.		226[1]	6,203
Unidentified dolphin sp. not porpoise		34	432
Risso's dolphin	*Grampus griseus*	10	28
Common bottlenose dolphin	*Tursiops truncatus*	34[1]	321
Unidentified unpatterned dolphin sp.[2]		2	12
White-beaked dolphin	*Lagenorhynchus albirostris*	172[1]	1,365
Atlantic white-sided dolphin	*Lagenorhynchus acutus*	198[1]	12,879
Unidentified *Lagenorhynchus* sp.[3]		44[1]	815
Common dolphin	*Delphinus delphis*	24[1]	246
Striped dolphin	*Stenella coeruleoalba*	5[1]	255
Unid. common/Atlantic white-sided dolphin		4	143
Unidentified common/striped dolphin		5	39
Unidentified common/Atlantic white-sided/striped dolphin		1	65
Unidentified patterned dolphin sp.[4]		5	18
Harbour porpoise	*Phocoena phocoena*	37	111
Total		**1,625**	**28,137**

[1]Includes mixed species sightings; [2]unpatterned dolphin = Risso's/common bottlenose dolphin; [3]*Lagenorhynchus* sp. = white-beaked/Atlantic white-sided dolphin; [4]patterned dolphin = white-beaked/ Atlantic white-sided/common/striped dolphin.

Table 2

Difference in sighting rate of cetaceans in relation to the use of large volume seismic airgun arrays (Wilcoxon signed ranks test).

Species	*z*	*n*	*P*
All cetaceans combined	2.005	193	0.0222
All mysticetes combined	0.585	65	n.s.
Humpback whale	-1.604	3	n.s.
Fin whale	0.082	30	n.s.
Fin/sei whale[1]	0.228	36	n.s.
Common minke whale	0.547	23	n.s.
Sperm whale	0.578	23	n.s.
Long-finned pilot whale	0.735	31	n.s.
Killer whale	1.244	9	n.s.
All small odontocetes combined	2.290	128	0.0110
Common bottlenose dolphin	-0.908	9	n.s.
Lagenorhynchus spp.[2]	3.685	85	0.0001
White-beaked dolphin	1.916	35	0.0274
Atlantic white-sided dolphin	2.806	49	0.0025
Harbour porpoise	0.345	14	n.s.

[1]Includes fin whales, sei whales and unidentified fin/sei whales; [2]includes white-beaked dolphins, Atlantic white-sided dolphins and unidentified *Lagenorhynchus* sp; n.s.= not significant.

there were no significant differences in the proportion of sightings within a given range of the airguns in relation to airgun activity for any cetaceans (small odontocetes: χ^2 approximation = 0.097, df=1; other cetaceans: χ^2 approximation=1.214, df=1).

Orientation of cetaceans

The orientation of some species or species groups (all cetaceans combined, all mysticetes combined, all small odontocetes combined, long-finned pilot whale, *Lagenorhynchus* spp., white-beaked dolphin and harbour porpoise (*Phocoena phocoena*)) varied significantly with airgun activity (Table 4); partitioning showed that significantly fewer animals were travelling towards the vessel and/or more were travelling away from the vessel during periods of shooting. Orientation during site surveys differed with airgun activity for all species or species groups tested (Table 5), with significantly fewer animals travelling towards the vessel and/or more travelling away from the vessel during periods of shooting.

Although precise data on other aspects of behaviour were not collected, observers' records suggested that fewer cetaceans were feeding, fewer were interacting with the vessel or its equipment (e.g. bow-riding) and more were altering course when airguns were active. Observers also gained the impression that small odontocetes tended to swim faster when airguns were active and some mysticetes remained submerged more when airguns were silent.

Sightings during the soft start

Sightings occurring only during the soft start were compared with those only occurring at other times during surveys with large volume airgun arrays (no

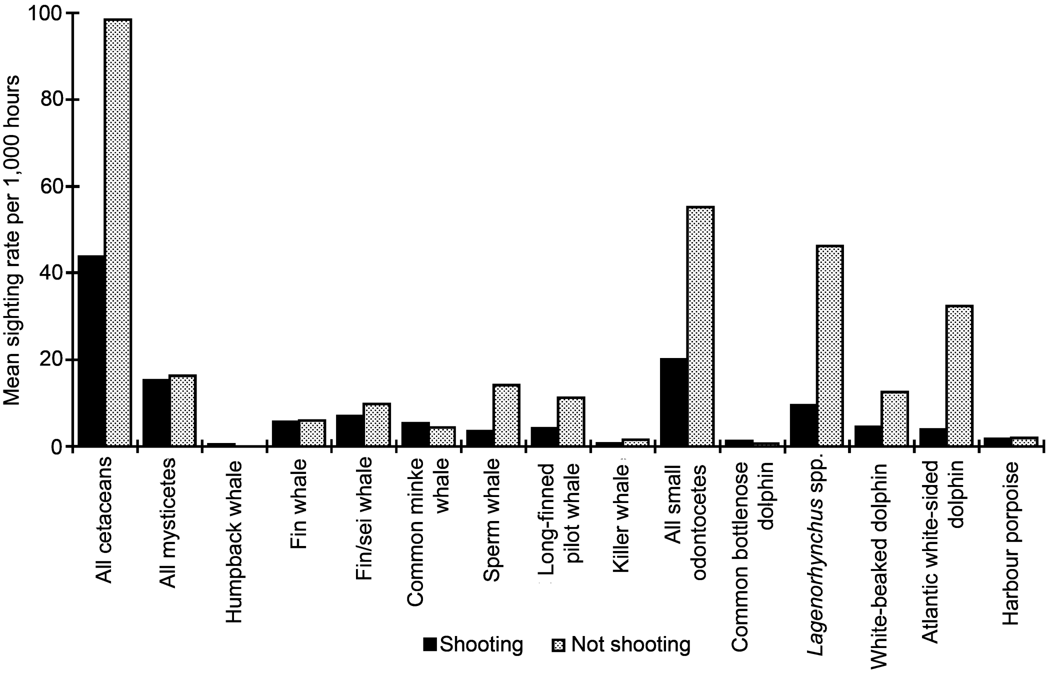


Fig. 2. Sighting rates of cetaceans in relation to the use of large volume airgun arrays.

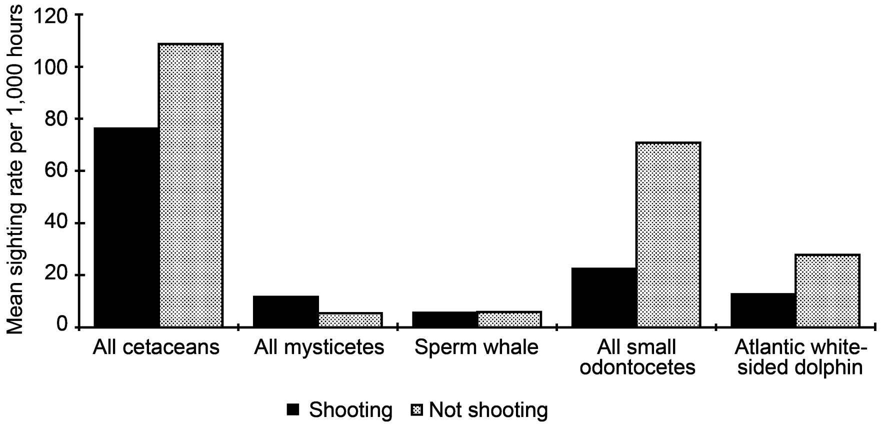


Fig. 3. Sighting rates of cetaceans in relation to the use of airguns during site surveys.

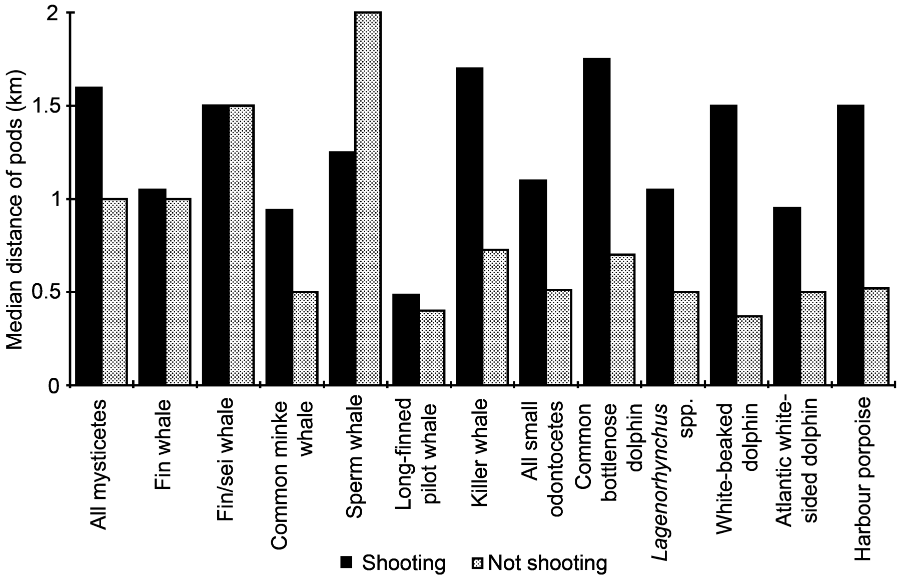


Fig. 4. Median closest distance of approach of cetaceans to large volume airgun arrays in relation to airgun activity.

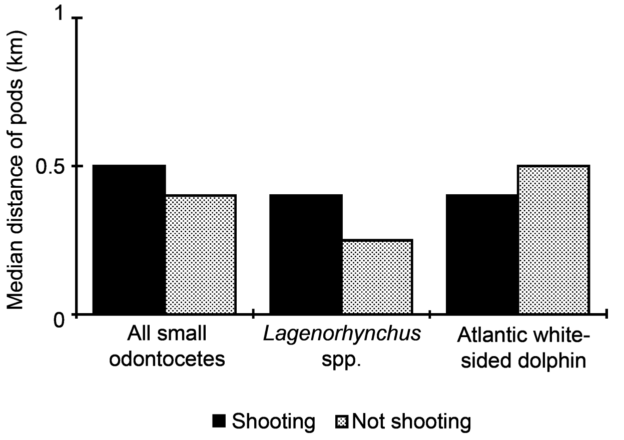


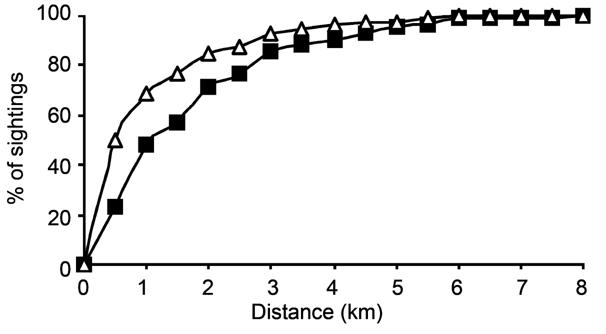
Fig. 5. Median closest distance of approach of cetaceans to airguns in relation to airgun activity during site surveys.

Table 3

Difference in closest distance of approach of cetaceans to the airguns in relation to the use of large volume seismic airgun arrays (Wilcoxon test).

Species	*z*	*n*	*P*
All mysticetes combined	2.529	148	0.0057
Fin whale	1.546	57	n.s.
Fin/sei whale	1.226	78	n.s.
Common minke whale	1.206	42	n.s.
Sperm whale	-0.445	51	n.s.
Long-finned pilot whale	-0.243	59	n.s.
Killer whale	1.843	14	0.0329
All small odontocetes combined	4.707	292	<0.0001
Common bottlenose dolphin	-1.701	14	0.0446
Lagenorhynchus spp.	4.464	164	<0.0001
White-beaked dolphin	3.702	71	0.00011
Atlantic white-sided dolphin	2.428	80	0.0075
Harbour porpoise	2.503	21	0.0062

(a) Small odontocetes



(b) Medium and large cetaceans*

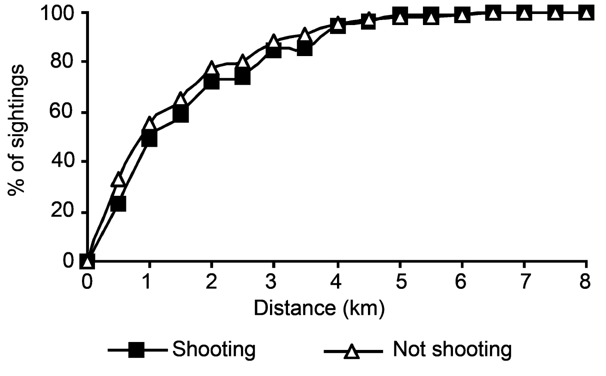


Fig. 6. Proportion of cetacean sightings occurring within specified distances of large volume airgun arrays, in relation to airgun activity. * Medium and large cetaceans = long-finned pilot whale, killer whale, beaked whales, sperm whale and mysticetes.

sightings occurred during the soft start on site surveys). As sample sizes were small, all cetaceans were combined.

The median closest distance of approach of cetaceans observed during periods of good weather varied according to the activity of the airguns (median distance when shooting at full power=1.1km, during soft start=900m, when not shooting=700m; Kruskal-Wallis statistic=18.970, n=569, df=2, p<0.001). Multiple comparisons revealed significant differences between the distance of cetaceans when the airguns were not firing and during shooting at full power levels, but the distance of cetaceans during the soft start did not differ significantly from either shooting at full power or not shooting.

Although sample sizes were too small to test differences in orientation of cetaceans during the soft start, more small odontocetes were seen heading away from the vessel (29%) during the soft start than in any other direction, although it was also noted that there were occasional instances of white-beaked dolphins bow-riding. Mysticetes were also more often seen heading away from the vessel (22%) than towards it (11%) during the soft start, while the few long-finned pilot whales seen during the soft start tended to head towards the vessel (67%).

Of 12 sightings that were present at the onset of a soft start, two exhibited startle responses. A pod of long-finned pilot whales 290m from the airguns altered course and swam away from the vessel as the soft start commenced. In another case, a sperm whale at 2km from the airguns had previously been swimming slowly and had dived; it resurfaced as the soft start began and swam rapidly at the surface.

DISCUSSION

The responses observed here indicate that there is some level of disturbance of cetaceans by seismic airguns. The observations suggest that small odontocetes show the strongest lateral spatial avoidance of active airguns, with mysticetes and killer whales showing some localised spatial avoidance, long-finned pilot whales showing only a change in orientation and sperm whales showing no statistically significant effects from these data.

Most of the energy from seismic airguns is at frequencies below the optimum hearing range of small odontocetes, whose greatest auditory sensitivities lie within the range 10-150kHz; consequently they are sometimes regarded as being relatively insensitive to seismic sounds (Richardson *et al.*, 1995). However, high frequency noise is emitted incidentally during seismic operations. Seismic exploration generally utilises frequencies up to 220Hz, but Goold and Fish (1998) found that noise from seismic airguns also dominated the 200Hz-22kHz bandwidth at ranges of up to 2km from the source and that even at 8km airgun noise exceeded background noise at frequencies of up to 8kHz. They concluded that seismic emissions would be audible to dolphins out to ranges of at least 8km. Furthermore, dolphins may be able to detect low frequency sounds using some mechanism other than conventional hearing. Turl (1993) found that a common bottlenose dolphin responded to sounds of 50-100Hz and suggested that this was due to detection of particle velocity or a combination of pressure and velocity in the near-field.

Those small odontocetes tested showed a greater range of responses to seismic surveys than mysticetes or larger odontocetes. Amongst these responses, significant declines in sighting rates during periods of shooting were observed

Table 4

Direction of travel of cetaceans relative to the survey vessel in relation to airgun activity, during surveys with large volume airgun arrays (χ^2 calculated from frequencies).

Species	Airgun activity	Towards ship	Away from ship	Crossing path of ship	Parallel to ship in same direction	Parallel to ship in opposite direction	Milling or variable	χ^2	*n*	*d.f.*	*P*
All cetaceans combined	Shooting	6.81%	20.43%	22.57%	10.89%	30.74%	8.56%	58.933	1,368	5	<0.001
	Not shooting	19.20%	10.19%	20.49%	11.12%	31.38%	7.61%				
All mysticetes combined	Shooting	4.35%	21.74%	18.84%	10.87%	34.78%	9.42%	12.037	304	5	<0.05
	Not shooting	9.64%	9.64%	21.69%	11.45%	40.96%	6.63%				
Fin whale	Shooting	6.12%	26.53%	16.33%	10.20%	32.65%	8.16%	3.955	108	2	n.s.
	Not shooting	6.78%	11.86%	16.95%	3.39%	54.24%	6.78%				
Fin/ sei whale	Shooting	3.61%	24.10%	13.25%	13.25%	37.35%	8.43%	6.605	174	5	n.s.
	Not shooting	4.40%	13.19%	17.58%	7.69%	50.55%	6.59%				
Common minke whale	Shooting	7.69%	11.54%	34.62%	7.69%	34.62%	3.85%	3.160	73	2	n.s.
	Not shooting	21.28%	6.38%	23.40%	10.64%	31.91%	6.38%				
Sperm whale	Shooting	10.00%	25.00%	7.50%	25.00%	25.00%	7.50%	3.732	104	5	n.s.
	Not shooting	9.38%	21.88%	18.75%	15.63%	23.44%	10.94%				
Long-finned pilot whale	Shooting	7.89%	14.47%	22.37%	10.53%	43.42%	1.32%	12.031	162	5	<0.05
	Not shooting	19.77%	4.65%	13.95%	10.47%	45.35%	5.81%				
All small odontocetes combined	Shooting	8.10%	20.95%	28.57%	7.62%	22.86%	11.90%	45.035	646	5	<0.001
	Not shooting	25.23%	8.49%	22.48%	11.01%	24.77%	8.03%				
Common bottlenose dol.	Shooting	8.33%	33.33%	25.00%	0.00%	25.00%	8.33%	2.556	30	1	n.s.
	Not shooting	22.22%	5.56%	22.22%	11.11%	27.78%	11.11%				
Lagenorhynchus spp.	Shooting	11.11%	18.18%	28.28%	9.09%	21.21%	12.12%	29.676	350	5	<0.001
	Not shooting	32.27%	4.78%	25.50%	9.96%	20.72%	6.77%				
White-beaked dolphin	Shooting	6.12%	26.53%	28.57%	8.16%	16.33%	14.29%	33.081	153	5	<0.001
	Not shooting	48.08%	4.81%	21.15%	6.73%	10.58%	8.65%				
Atlantic white-sided dol.	Shooting	12.50%	12.50%	30.00%	7.50%	27.50%	10.00%	5.211	154	4	n.s.
	Not shooting	21.93%	5.26%	30.70%	8.77%	28.95%	4.39%				
Harbour porpoise	Shooting	0.00%	45.45%	27.27%	0.00%	27.27%	0.00%	4.289	34	1	<0.05
	Not shooting	4.35%	30.43%	4.35%	13.04%	47.83%	0.00%				

Table 5

Direction of travel of cetaceans relative to the survey vessel in relation to airgun activity during site surveys (χ^2 calculated from frequencies).

Species	Airgun activity	Towards ship	Away from ship	Crossing path of ship	Parallel to ship in same direction	Parallel to ship in opposite direction	Milling or variable	χ^2	*n*	*d.f.*	*P*
All cetaceans combined	Shooting	3.29%	14.75%	14.75%	11.48%	45.90%	9.84%	19.380	230	5	< 0.01
	Not shooting	23.08%	7.69%	15.98%	15.98%	25.44%	11.83%				
All small odontocetes combined	Shooting	0.00%	16.67%	10.00%	13.33%	50.00%	10.00%	21.783	124	4	< 0.001
	Not shooting	31.91%	6.38%	20.21%	11.70%	19.15%	10.64%				
Lagenorhynchus spp.	Shooting	0.00%	15.79%	15.79%	10.53%	47.37%	10.53%	10.127	59	1	< 0.01
	Not shooting	37.50%	10.00%	22.50%	7.50%	12.50%	10.00%				
Atlantic white-sided dol.	Shooting	0.00%	17.65%	11.76%	11.76%	47.06%	11.76%	8.410	42	1	< 0.01
	Not shooting	20.00%	12.00%	36.00%	8.00%	16.00%	8.00%				

for the *Lagenorhynchus* species and all small odontocetes combined. This implies that effects persist at least as far as the limit of visual observation. Studies of the effects of seismic airguns on small odontocetes are rare, with most previous work concentrating on mysticetes and sperm whales; one study found that common dolphin (*Delphinus delphis*) populations were apparently temporarily disturbed by seismic surveys (Goold, 1996), while another found a reduction in cetacean diversity, mainly amongst members of the family Delphinidae, during a period of intensification of seismic surveys (Parente and de Araújo, 2005).

Mysticetes have often been considered to be vulnerable to anthropogenic noise (e.g. Ketten, 1998; Richardson *et al.*, 1995), as the frequencies they use overlap with those produced by many industrial sources. Although the auditory sensitivities of mysticetes are not known, there is an assumption that hearing will occupy approximately the same range of frequencies that these animals produce sounds at. Fin whales, for example, produce calls around 20Hz (Watkins, 1981) and would be expected to be sensitive to sounds at these frequencies.

In spite of their anticipated vulnerability, few responses to airgun activity have been recorded for mysticetes in UK waters. No obvious effects on the occurrence of individual species were found in the present study. However, when all species of mysticetes were combined to permit inclusion of sightings that were not identified to species level, it was found that they occurred further from the airguns during periods of shooting and tended to head away from the vessel at these times. These results indicate that there may be at least some level of localised spatial avoidance of operating airguns by mysticetes. Avoidance of airguns has previously been observed in mysticetes in other regions (e.g. Ljungblad *et al.*, 1988; Richardson *et al.*, 1985; Richardson and Greene, 1993; Richardson *et al.*, 1999; Weller *et al.*, 2002).

The absence of any reduction in sighting rates of mysticetes should not be taken as confirmation that there was no or minimal disturbance. As discussed above, there were other indications of localised spatial avoidance, and in addition there may be effects not able to be detected using these data. For example, effects on vocalisations would not be apparent from visual observations. Changes in call detection rates in response to airgun activity have been found for bowhead whales, *Balaena mysticetus* (Greene *et al.*, 1999; Richardson, 1997). Other studies have also indicated some level of stress, with alterations in surfacing, respiration and dive cycles being observed in mysticetes in response to the use of seismic airguns, sometimes at considerable distances from the source (Ljungblad *et al.*, 1988; Richardson *et al.*, 1985; Richardson *et al.*, 1995; Richardson *et al.*, 1986). Although effects of active airguns on the physiology of the mysticetes found around the UK are largely unknown, in one study, shorter blow intervals indicated an increase in the respiration rate of fin whales within 1km of the airguns during periods of shooting (Stone, 1998a).

No statistically significant effects of airgun activity on sperm whales were found during this study, although a startle response was noted at the onset of shooting on one occasion. Some studies have found that the use of seismic airguns resulted in a decrease in abundance of sperm whales (Mate *et al.*, 1996; Stone, 2006) and negative effects on their communication and orientation (Bowles *et al.*, 1994; Rankin and Evans, 1998), while other studies have shown no response to operating airguns (Madsen *et al.*, 2002; Tyack *et al.*, 2003). Cetaceans hear as well at depth as they do near the surface (Ridgway *et al.*, 1998), so deep-diving species such as sperm whales will be vulnerable to acoustic disturbance throughout the water column. It may be difficult to observe effects on their occurrence or behaviour simply from surface observations due to the relatively small proportion of time they spend at the surface.

Long-finned pilot whales also showed little response to operating airguns. The only observed effect was on their orientation, with more heading away from and fewer towards the vessel during periods of shooting. However, any avoidance appeared to be relatively minor as there was no significant difference in their distance from the airguns in relation to airgun activity. Bowles *et al.* (1994) noted that pilot whales were not vocalising during periods of airgun noise.

For the first time, some effects of airgun activity on killer whales have been assessed. As with the mysticetes, sperm whales and long-finned pilot whales, no reduction in the sighting rate of killer whales was found in response to operating airguns. However, killer whales were found to remain further from the source when it was active, which may indicate some level of spatial avoidance. As with small odontocetes, studies on the effects of airgun activity are rare for medium-sized odontocetes; however, seismic surveys may have been implicated in at least one beaked whale stranding (Peterson, 2003; Taylor *et al.*, 2004).

It is possible that the different cetacean species react to the use of seismic airguns in different ways. It has been suggested that species variation in auditory processing is so important that a distinction should certainly be made between taxonomic groups that have widely different hearing and sensitivity frequencies (National Research Council, 2005). Most of the taxonomic groups examined here have shown at least some response during periods of shooting. The fast moving small odontocetes not only orient away from the source and increase their distance from it, but are able to move out of the immediate area (as indicated by reduced sighting rates during periods of shooting). However, although mysticetes orient away from the survey vessel and increase their distance from the source, they do not move away from the area completely. It is possible that these slower moving species, rather than moving out of the area, have adopted a different strategy in response to anthropogenic noise. Some studies have suggested that cetaceans may remain near the surface during periods of noise – received sound levels near the surface are generally lower than at greater depths (Richardson *et al.*, 1995; Urick, 1983). McCauley *et al.* (1998; 2000) offered this as an explanation for humpback whales spending much of their time at the surface during a period of seismic surveying, and it could also explain an increased tendency for cetaceans to be logging at the water surface during periods of shooting (Stone, 2006). Observations during the present study hinted that some mysticetes may submerge less during periods of shooting; it would be useful to collect precise behavioural data to investigate this further.

The avoidance exhibited by small odontocetes, and to a lesser extent other cetaceans, appears to be temporary. There was no consistent evidence of declining sighting rates throughout the course of seismic surveys. However, it is not known whether animals seen later in a survey are the same individuals that were present earlier, or whether they have left and new animals have arrived. It is also possible that animals may have no choice but to remain in an area, if there is some reason (e.g. food) that they need to be there.

Site surveys had some effects on cetaceans, although less than surveys with large volume airgun arrays. Effects on orientation were evident for all species tested.

Barlow and Gisiner (2006) have stated that marine mammal responses to the soft start are unknown and that since the effectiveness of the method is untested, there is a need for more research. The value of the present study in this respect was limited by small sample sizes – larger sample sizes of sightings during the soft start are needed to assess the effectiveness of this procedure as a mitigation tool. Obtaining larger sample sizes should be feasible by continuing the present programme of data collection from seismic surveys, and would present an economical first step towards evaluating the effectiveness of the soft start.

Although the present study found that more cetaceans were heading away from the vessel than towards it during the soft start (with the exception of long-finned pilot whale), sample sizes were too small to test the significance of this result. Another study found that significantly more cetaceans were heading away from the vessel during the soft start than at any other time, including when airguns were shooting at full power (Stone, 2006). Swimming away from the vessel during the soft start may reduce the potential for disturbance; although in the present study some cetaceans swam away from the vessel during the soft start, conversely some dolphins engaged in bow-riding. Noise levels ahead of the vessel may be less than those abeam of it (McCauley *et al.*, 2000; Richardson *et al.*, 1995), but animals bow-riding during low power shooting may be vulnerable to disturbance if they have insufficient time to move away before full power levels are reached.

As well as minimising disturbance, the aim of the soft start is to reduce the risk of physical injury to undetected animals close to the source, and this risk may increase if shooting were to commence at full power levels with no soft start. Encounters with cetaceans have been noted as occurring at increasing distances from the airguns during the first two-thirds of the soft start, when relative increases in power are greatest, then closer to the airguns again during the latter stages, when relative increases in power are low (Stone, 2006); a secondary peak in the closest distance of approach has been observed at the commencement of the soft start, perhaps due to a startle response. Instances where a startle response was observed during the present study also support the need for a soft start; startle responses would presumably be more severe and/or more frequent if shooting were to commence at full power.

This study concentrated on examining short-term effects of airgun activity on the occurrence and orientation of cetaceans. Other potential effects remain largely unknown, for example long-term effects, effects on vocalisations, behaviour and physiology, consequences of auditory masking and the potential for damage to hearing. The lack of an observed response in some species does not therefore imply that the use of seismic airguns has no effect on those species. Furthermore, although those responses that were observed were short-term effects, it is not known whether these may have been biologically significant: effects that persisted beyond the time of disturbance, responses that affected the ability of animals to engage in essential activities (e.g. breeding, feeding, caring for young, migrating, etc.), or effects that had consequences at the population level. The difficulties of determining the biological significance of observed effects are recognised (National Research Council, 2003; 2005). Until the biological significance of the observed effects can be determined, precautionary guidelines to minimise disturbance should continue to be applied.

ACKNOWLEDGEMENTS

This work was made possible by the cooperation of the oil and gas industries, seismic exploration companies, and the crews of the seismic survey vessels. Numerous observers, including dedicated marine mammal observers, fishery liaison representatives and members of ships' crews, recorded the data, and their contributions are gratefully acknowledged. The map was plotted using *DMAP* for Windows. Zoë Crutchfield (JNCC) and Tim Barton (University of Aberdeen) are acknowledged for their comments and suggestions during the preparation of the manuscript.

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Date received: September 2005
Date accepted: November 2006

J. CETACEAN RES. MANAGE. 8(3):265–271, 2006

The spectacled porpoise (*Phocoena dioptrica*) in Antarctic waters

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ABSTRACT

Most knowledge on the biology and ecology of the spectacled porpoise (*Phocoena dioptrica*) has been obtained from stranded specimens, with less than fifteen confirmed sightings in the sea. Published photographs of live animals in their natural environment are also very rare. In this study, 28 live sightings are summarised, from Antarctic and sub Antarctic waters (mainly from the 1978-2004 IWC-IDCR/SOWER cruises). These sightings supported the suggested circumpolar and offshore distribution of this species; however, this was extended further south than previously thought, into Antarctic waters. The sea surface temperature recorded at the time of each sighting ranged from 0.9-10.3°C, with most of the sightings (52.0%) in waters 4.9-6.2°C. Group size was small, averaging 2.0 (SD=0.92) animals per group. A total of six cow-calf pairs were observed and all such pairs were accompanied by one or two additional adults, always including a mature male. Based on observations at sea and new photographs of live animals, a pale 'saddle' around the dorsal fin was noticed and is described for the first time. The porpoises generally showed fast swimming behaviour when the vessel approached, resembling the swimming behaviour of harbour porpoises.

KEYWORDS: SPECTACLED PORPOISE; SOUTHERN OCEAN; ANTARCTIC; SCHOOL SIZE; SURVEY-VESSEL; DISTRIBUTION; COLOURATION

INTRODUCTION

The spectacled porpoise (*Phocoena dioptrica*, Lahille, 1912) is one of the cetacean species about which least is known. Its limited biological data are based mainly on opportunistic records of stranded specimens, while the understanding of its distribution is based on only a few sightings at sea (Goodall and Schiavini, 1995 and also see below). No studies have been carried out on this species in the wild and only a few photographs of live animals are known of a live stranded calf (Goodall and Schiavini, 1995); one animal at sea (Read, 1999 and also see below); two live strandings at South Georgia (Goodall, pers. comm.); and one adult male at sea (Bastida and Rodriguez, 2005).

Despite the lack of live sightings, stranding records indicate that the spectacled porpoise has a widespread distribution in the Southern Ocean and may be more common in some regions than previously thought. Confirmed osteological remains or strandings have been recorded from the coasts of Uruguay, Argentina, the Falkland Islands (Islas Malvinas) and South Georgia in the Atlantic Ocean; southern Chile and the Auckland Islands in the Pacific Ocean, southern Australia and Tasmania in the Tasman Sea; and the Macquarie and Heard Islands in the Indian Ocean (Baker, 1977; Brownell, 1975; Brownell and Clapham, 1999; Brownell *et al.*, 1989; Evans *et al.*, 2001; Fordyce *et al.*, 1984; Fraser, 1968; Goodall, 1978; Goodall and Cameron, 1979; Goodall and Schiavini, 1995; Guiler *et al.*, 1987; Hamilton, 1941; Lahille, 1912; Marelli, 1922; Pagnoni and Saba, 1989; Perrin *et al.*, 2000; Pinedo *et al.*, 2002; Praderi, 1971). Despite the wide geographic distribution of these records, most strandings have been concentrated between the Atlantic coast of Tierra del Fuego and the coast of southern Argentina, with more than 270 records to date (Goodall, pers. comm.).

In comparison with the number of osteological/stranding records reported for this species, sightings of live spectacled porpoises at sea are very rare. Goodall and Schiavini (1995, table 3) summarised fifteen known live sightings at sea or from shore: one sighting from South Georgia; six off the south-eastern coast of South America; two from the Drake Passage; five off the Auckland Islands; and one off the Kerguelen Islands (Fordyce *et al.*, 1984; Frost and Best, 1976). Most of the sightings involved solitary individuals, however, some included up to five individuals.

Overall, based on stranding and sighting information, it was inferred that spectacled porpoises inhabit cold, temperate waters (5.5-9.5°C) of the Southern Ocean, with a circumpolar distribution at sub-Antarctic latitudes (33-58°S), from near-shore to deep offshore waters (Brownell and Clapham, 1999; Goodall, 2002; Goodall and Schiavini, 1995; Pinedo *et al.*, 2002).

Spectacled porpoises are known to be strongly sexually dimorphic. Adult males appear to be larger than females, as occurs in many odontocete species (Ralls, 2002). The largest male studied measured 224cm and the largest female measured 203.5cm (Goodall, 2002; Goodall and Schiavini, 1995). A further striking difference is the size and shape of the dorsal fin (Bruch, 1916; Fraser, 1968; Goodall and Schiavini, 1995). Adult males present a broad based, oval dorsal fin, which is significantly higher than the triangular dorsal fin of adult females.

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Nearly all other biological information is also based on information from strandings. The general external colouration is well reported from stranded animals, but to date there have been no detailed descriptions of the appearance and behaviour of live animals at sea. Since almost no behavioural observations have been reported to date, it is usually assumed that spectacled porpoises, like the other porpoises (except Dall's porpoise, *Phocoenoides dalli*), are normally rather undemonstrative.

In this paper, the at-sea distribution of spectacled porpoises is reviewed based largely on sightings made during International Whaling Commission (IWC)/ International Decade of Cetacean Research (IDCR)/ Southern Ocean Whale and Ecology Research (SOWER) cruises in Antarctica from 1978 to 2004. Furthermore, the sightings of this species in Antarctic and sub-Antarctic waters are discussed in regards to group composition, reproduction, external morphology and behaviour.

MATERIALS AND METHODS

The majority of the sightings reported here were recorded during IWC IDCR/SOWER cruises. These cruises started in 1978 as the Southern Hemisphere minke whale assessment cruise (IDCR), which became the SOWER in 1996. By March 2004 a series of three circumpolar surveys have been completed. The histories and survey methodologies of these cruises have been reviewed elsewhere (Matsuoka *et al.*, 2003). In summary, the main sighting effort during surveys was conducted by two crew members at the top of the barrel (20m above sea level), and two other crew observers at the upper bridge (12m above sea level), all using 7×50 handheld binoculars. Additionally, three researchers and a further crew member also undertook sighting effort from the upper bridge. All cetacean sightings were confirmed and recorded by researchers on board.

During both the IDCR and SOWER cruises, the main surveys have focused their efforts in the Antarctic area south of 60°S, but also sighting surveys has been conducted during the transit period to/from home ports (35-55°S) and the main surveyed areas (see table 1 in Matsuoka *et al.* (2003) for list of home ports between 1978/79 and 2000/01 cruises). Hobart was the home port for cruises 2001/02 to 2003/04. Therefore, the surveys covered not only Antarctic waters but also the sub-Antarctic regions of cold temperate water north of the Polar Front, around 50-60°S (Gross, 1996; Orsi *et al.*, 1995; Shirihai, 2002).

All spectacled porpoises sighting information was extracted from the IWC database (part of the Database and Estimation Software System (DESS)). This contains all the information obtained during the IDCR and SOWER cruises between 1978/79 and 2003/04. Copies of all original sighting data sheets were examined. Additionally, data from the 2000-2004 SOWER cruises were complemented by our personal records, since most of the authors of this work participated in those cruises (Ensor *et al.*, 2001; 2002; 2004).

Only data from confirmed sightings of spectacled porpoises were used in this study. On most occasions, especially during the transit period, the vessels approached the animals to confirm the species identification. The sighting data considered here included: date, time, geographic position, sea surface temperature, school size, presence or absence of calf, closest distance to vessels, observation time, photographs taken and general behaviour. Photographs obtained during the SOWER 2001/02 and 2003/04 cruises were taken using a Single-Lens Reflex (SLR) camera with a 75-300mm or 100-400mm zoom lens, and 400 or 200 ASA colour slide films. Video footage of swimming behaviour observed in record 24 was recorded using a Canon *Elura 40mc* digital video camcorder.

Three sightings considered in this paper were collected opportunistically during other cruises in Antarctica (by Seitre, Pitman and Findlay, onboard *M/V Bahia Paraiso*, *M/V Explorer* and *R/V Africana*, respectively).

RESULTS

Distribution

A total of 25 sightings, representing 54 individual spectacled porpoises (including 5 sightings of 11 individuals previously reported by Kasamatsu *et al.*, 1990), were extracted from DESS. The sightings were from IDCR and SOWER cruises from 1978/79 to 2003/04 (Table 1). Additionally, three sightings of one individual each were included (observed by Seitre, Pitman and Findlay respectively). The 2003/04 SOWER cruise had the highest number of sightings compared to the other cruises, with ten out of a total of 28 confirmed sightings.

All sightings were distributed in the vicinity of the Polar Front (Fig. 1). The northernmost sighting was at 48°30.35'S (record 7, Table 1) and the southernmost sighting was 64°33.5'S (record 26). Sightings revealed a circumpolar distribution; however, longitudinally they were somewhat concentrated in the Pacific Ocean sector (60°W-130°E) of the Antarctic. Fifteen records (53.6%) were from the region between New Zealand and the Ross Sea. These clumped sightings were recorded on three different cruises and five different vessels. Most of these sightings (*n*=10) were recorded during the 2003/04 SOWER cruise (Table 1). The sea surface temperature (SST) recorded at the time of each sighting ranged between 0.9°C and 10.3°C (mean=4.7°C, SD=2.52); however, the most frequent ranked temperatures were between 1.0-1.9°C and 5.0-5.9°C, which were recorded in half (52%) of the sightings.

Group size and composition

Group sizes of the 28 sightings were small, averaging 2.0 (SD=0.92) individuals (ranging 1-4 individuals). The most frequent group size was one (*n*=10), followed by three (*n*=9), two (*n*=8), and four individuals (*n*=1).

A calf was present in six of the sightings (21.4%). Cow-calf pairs were always accompanied by either one or two other adults (records 2, 13, 14, 16, 17 and 27). The size of a calf was approximately one half to two thirds of the size of the closest associated animal (a cow, based on proximity, behaviour and dorsal fin morphology). If one other adult was present in the group (*n*=6), it was a mature male, based on size and dorsal fin morphology (Bruch, 1916; Fraser, 1968; Goodall and Schiavini, 1995). On one occasion when two adults were present, the second animal was a female (record 16).

Groups including a calf were only temporarily stable. For record 6, the group dispersed at the end of the 16min observation. For records 13 and 14, groups also dispersed at the end of the observation (41min and 26min, respectively), the male left the group, but the cow-calf pair stayed together until the end of the observation. During the 22min observation of record 17, the trio was initially very close; keeping the calf in the centre of the group (Fig. 2), however, the adult male left the group at the end of the encounter. For record 27, the male left the group while the vessel approached within 20m; the cow-calf pair remained in close proximity during the 25min observation.

Table 1

Sighting data of spectacled porpoise (*Phocoena dioptrica*) observed in the Southern Ocean.

			Position				Sea condition				
Record no.	Date	Time (hrs)	Latitude	Longitude	School size	SST (°C)	Sightability	Sea state	Swell	Notes	Data source
1	22 Dec. 1985	13:55	54°54’ S	167°12’ E	1	6.0	Good	2	-	A female/juvenile?	IDCR 85/86
2	19 Feb. 1986	09:48	56°12’ S	174°36’ W	3	8.4	Moderate	2	-	One adult male and a cow-calf pair, photos	IDCR 85/86
3	19 Feb. 1986	14:33	55°41’ S	175°14’ W	2	10.3	Moderate	0	-	A male and a female, photos	IDCR 85/86
4	28 Dec. 1986	18:40	58°02’ S	62°19’ W	3	5.5	Moderate	1	-	Possibly all females. In 1.2m TL, photograph taken	IDCR 86/87
5	28 Dec. 1986	19:28	58°05’ S	62°09’ W	2	5.5	Moderate	1	-	At the edge of Antarctic Convergence	IDCR 86/87
6	10 Dec. 1987	-	About middle of Drake Passage		1	-	Excellent	Calm	V. low	One photo published by Read (1999)	Seitre, pers. data
7	31 Mar. 1990	09:54	48°30’ S	15°50’ W	1	-	-	Calm	-	6 knot wind	Findlay, pers. data
8	1 Jan. 1991	17:30	58°03’ S	175°16’ W	2	6.2	Moderate	2	-		IDCR 90/91
9	1 Jan. 1991	17:48	58°05’ S	175°14’ W	1	6.2	Moderate	2	-	Possibly a female. Dive pattern recorded	IDCR 90/91
10	23 Jan. 2001	11:44	60°33’ S	135°15’W	1	1.9	Good	2	Low	A female or juvenile based on rounded dorsal fin	SOWER 00/01
11	23 Jan. 2001	15:03	60°01’ S	135°00’ W	2	2.8	Good	2	Low		SOWER 00/01
12	24 Jan. 2001	08:37	61°42’ S	134°03’ W	2	2.0	Moderate	2	Low	One male and a female	SOWER 00/01
13	22 Dec. 2001	13:50	50°53’ S	142°46’ E	3	9.5	Moderate	2	Low	One male and a cow-calf pair, photos	SOWER 01/02
14	24 Dec. 2001	09:41	58°51’ S	136°09’ E	3	1.6	Moderate	1	V. low	One male and a cow-calf pair. Fig. 5	SOWER 01/02
15	24 Dec. 2001	09:41	58°51’S	136°09’ E	2	1.6	Moderate	1	V. low		SOWER 01/02
16	24 Dec. 2001	10:49	58°55’ S	136°05’ E	4	1.8	Moderate	2	V. low	One male, one female and one cow-calf pair	SOWER 01/02
17	25 Dec. 2001	09:10	60°55’ S	133°18’ E	3	1.4	Good	2	V. low	One male and a cow-calf pair. Figs 2 and 3	SOWER 01/02
18	5 Jan. 2003	-	58°04’ S	65°48’ W	1	-	-	3-4	-		Pitman, pers. data
19	24 Dec. 2003	10:01	60°23’ S	170°56’ E	2	5.0	Poor	2	V. low		SOWER 03/04
20	24 Dec. 2003	12:34	60°36’ S	171°30’ E	2	4.9	Moderate	2	V. low		SOWER 03/04
21	24 Dec. 2003	12:46	60°36’ S	171°32’ E	3	4.9	Moderate	2	V. low	One male, one juvenile, one other, photos	SOWER 03/04
22	24 Dec. 2003	06:17	57°50’ S	172°21’ E	3	5.4	Moderate	2	Low	Photos	SOWER 03/04
23	24 Dec. 2003	07:10	57°55’ S	172°36’ E	3	5.7	Good	2	Low		SOWER 03/04
24	24 Dec. 2003	12:19	58°17’ S	173°51’ E	1	5.0	Good	1	Low	A female or juvenile. Video. Fig. 4	SOWER 03/04
25	24 Dec. 2003	14:44	58°25’ S	174°15’ E	1	5.5	Good	1	Low		SOWER 03/04
26	6 Jan. 2004	08:11	64°34’ S	176°19’ E	1	0.9	Good	2	Low		SOWER 03/04
27	8 Jan. 2004	12:00	61°40’ S	177°18’ W	3	3.6	Good	2	Low	One male and a cow-calf pair. Fig. 6	SOWER 03/04
28	2 Mar. 2004	11:09	58°25’ S	162°00’ E	1	5.4	V. poor	5	Moderate		SOWER 03/04

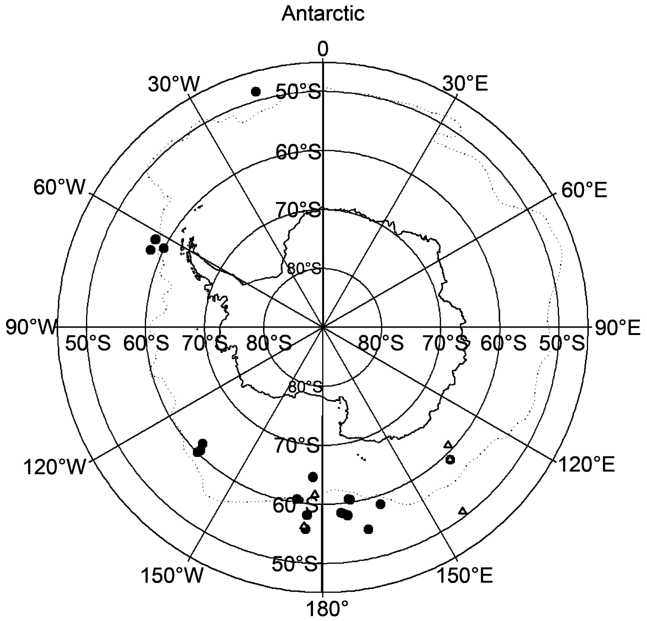

Fig. 1. Distribution of spectacled porpoise sightings in the Southern Ocean. Black circles indicate each sighting position and hollow triangles indicate a group with a calf. The dotted line shows the Polar Front.

Fig. 2. A group of three spectacled porpoises observed on 25 December 2001 at 60°54.58'S; 133°18.34'E. The group contained an adult male (background), showing the prominent dorsal fin, a cow and a calf (Photo Sekiguchi).

External morphology

Spectacled porpoises were readily identifiable by their small size, black and white pigmentation and, especially the remarkable dimorphism in the size and shape of the dorsal fin (Figs 2-4). The dorsal fin of an adult female (i.e. attending a calf) was lower and triangular in comparison with an adult male, with the apex placed near the trailing edge of the fin; both the leading and trailing edge of the fin appeared to be slightly convex (Fig. 2 foreground) as Goodall and Schiavinni (1995) described. The massive, almost oval-shaped dorsal fin of the adult male was unmistakeable as it was substantially larger than that of the female or juvenile, being both broader and taller (Figs 2 and 3); (Bruch, 1916; Fraser, 1968; Goodall, 2002; Goodall and Schiavini, 1995). One individual had a dorsal fin larger than that of an adult female, but smaller than that of a matured adult male; therefore, it might have been an immature male (Fig. 4).

Fig. 3. Another view of the adult male on 25 December 2001 at 60°54.58'S; 133°18.34'E (Photo Sekiguchi).

Fig. 4. A single spectacled porpoise (an adult female or a juvenile male) sighted on 24 December 2003, 58°17.21'S; 173°51.98'E. Note the light colour saddle around the base of the dorsal fin (Photo Sekiguchi).

In overcast conditions, body colour appeared to be mainly dark or even black (Figs 2 and 3). At very close range, the white ventral colouration, including above and below the black lips, and the white 'spectacles' were evident (Fig. 5). Under good lighting conditions, females and juveniles appeared lighter in colour; more grey (Fig. 4) than adult males (Fig. 6). When viewed from above, the tail stock appeared lighter on the sides as well as the dorsal side of the fluke, joining with the white colouration of the ventral part and along the sides of the tail stock (Fig. 5). A pale area was evident around the dorsal fin, which appeared to form a saddle (Figs 4-6). This saddle was only visible at a short distance, especially through the clear water column (Fig. 5). One mature male, which accompanied a cow-calf pair (record 27, Fig. 6), showed this cape clearly. Two lighter grey stripes from the blowhole to the apex of the melon were visible in a female (Fig. 5), forming a part of the 'bridle' as discussed by Perrin (1997).

Based on our observations, photographs and video at sea, the external morphology and colouration of spectacled porpoises shown in Fig. 7 were proposed.

Fig. 5. A female spectacled porpoise seen through the sea surface on 22 December 2001 at 50°53.16'S; 142°45.88'E. Note the white ventral surface, white lips and 'spectacles'. The light colour of 'the saddle' around the dorsal fin is clearly visible through the water (Photo Olson).

Fig. 6. An adult male showing a broad dorsal fin observed on 8 January 2004 at 61°39.49'S; 177°17.69'W. Note the light colour 'saddle' around the dorsal fin (Photo Sekiguchi).

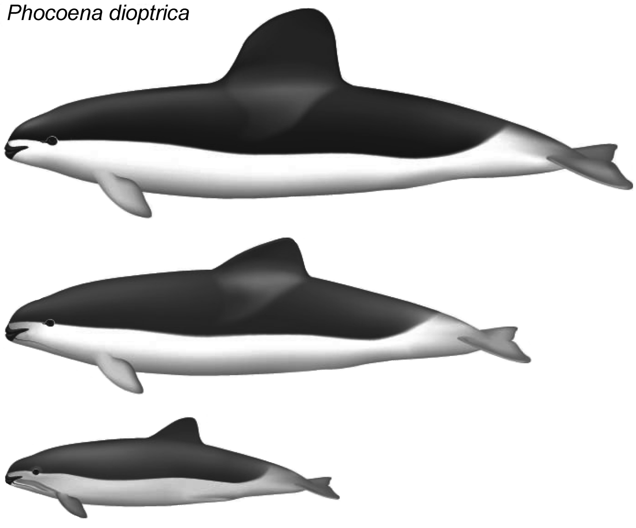

Fig. 7. Proposed external morphology and colouration of spectacled porpoise. Lateral views of an adult male, an adult female and a calf (Illustrated by Gorter).

Behaviour

When undisturbed, spectacled porpoises were observed swimming in a slow rolling motion, without any splash, similar to that of harbour porpoises (*P. phocoena*). However, when disturbed by the approach of the vessel they attempted to avoid it in a very distinctive fast swim, completely submerged but just under the sea surface, producing almost continuous 'fluke prints' on the surface, which were easy to follow by the vessel. When conditions were extremely good, the black and white colouration of the flukes and tail stock was clearly visible under the water as the tail beat rapidly (Fig. 5). After travelling for around 100 to 200m, the animal would reduce speed, then follow this with a slow roll at the surface, perpendicular to the original direction of travel, as if turning back to determine if it was being pursued. After one or more slow rolls, it would submerge again and continue to swim rapidly away from the vessel.

During only one encounter (record 14) 'porpoising' behaviour was observed, which was just before the group dispersed. No association with bow riding behaviour was noted in any record.

DISCUSSION

The 23 new confirmed sightings in this study (Table 1) double the previously reported number of sightings at sea (Goodall, 2002). These new sightings corroborate previous assumption that the spectacled porpoise has a circumpolar distribution around the Antarctic (Brownell and Clapham, 1999; Goodall, 2002; Goodall and Schiavini, 1995) in the vicinity of the Polar Front and that it inhabits mainly oceanic waters (Barnes, 1985; Kasamatsu *et al.*, 1990). The new data extends the distribution of this species south more than 400 n.miles than from previously known information, to 58°02'S (Goodall, 2002). The southernmost sightings also expand the range of SST that this species was known to inhabit (i.e. 0.9-10.3°C).

Spectacled porpoises are very difficult to sight at sea, mainly because of their small body and group sizes and inconspicuous behaviour. Almost all sightings of spectacled porpoises were recorded close to the vessels (ranging 0.03-1.5 n.miles) and under excellent survey condition (96.3% under Beaufort sea state 2). Thus, the paucity of sightings is considered to occur mainly due to the typically rough conditions in the vicinity of the Polar Front.

The concentration of sightings during IDCR and SOWER cruises, limited to the area of the Southern Pacific Ocean into Antarctic waters (60°W-130°E), may seem inconsistent with the distribution of most of the strandings, which were concentrated along the eastern coast of South America, especially Tierra del Fuego (Goodall, 2002). We believe that the geographical concentrations of live porpoises may reflect the real porpoise distribution, south of New Zealand during December to January, although they may reflect also the greater survey effort in that area. Despite the even coverage around Antarctica by the IWC cruises, the coverage of survey area during transits was longitudinally rather poor, compared with the main survey area (south of 60°S).

Despite a similar oceanic distribution to Dall's porpoise (Barnes, 1985), the behavioural observations of the spectacled porpoise at sea show greater similarity to the harbour porpoise, which is of the same genus *Phocoena* (Rosel *et al.*, 1995). The average group size was small (2.0 animals on average) and typical swimming behaviour was slow rolling, like a harbour porpoise.

The dorsal saddle observed has not previously been reported, although some field researchers have noticed this light colouration around the dorsal fin (R. Rowlett, pers. comm.), as well as a relatively light (grey/brown) dorsal body colour on some animals. This saddle has not been noted for stranded specimens, probably because this kind of subtle body colouration often disappears soon after death (Evans *et al.*, 2001). It was not clear from our observations if the calves had this 'saddle'. Similarly, the harbour porpoise has a complex external colour pattern but the animal looks plain grey and white in the field at a distance or after stranding (Reeves *et al.*, 2002).

A total of six small calves accompanied by a cow (22% of the total sightings) were sighted during late December to mid February. These observations indicate that birth may occur in late spring to summer (November to February) as suggested by Goodall and Schiavini (1995). Each of the cow-calf pairs sighted was accompanied by one or two other adults, which always included a mature male and, in one case, another female. It is unlikely that attendant males were biological fathers of the calves because no male parental care is known to exist in marine mammals (Mesnick and Ralls, 2002). These males might be suitors who were guarding females, as seen in bottlenose dolphins, *Tursiops truncatus* (Connor *et al.*, 1992; Wells, 1991) and humpback whales, *Megaptera novaeangliae* (Mesnick and Ralls, 2002).

The IDCR and SOWER cruises have provided excellent opportunities to observe rarely sighted spectacled porpoises at sea. The sighting data in this study suggest a concentration of spectacled porpoises to the south of Auckland Island, although effort biases might have arisen through sighting or oceanographic conditions. Intensive research in this region would provide more data for this little known cetacean species.

ACKNOWLEDGEMENTS

We would like to express our great appreciation to all researchers, captains, officers and all other crew involved in the IWC IDCR and SOWER cruises, especially to those of *Shonan Maru* and *Shonan Maru No 2* of the cruise 2003/04 for their hard work, cooperation and friendship during the longest cruise of the series. Mr. Roland Seitre kindly provided sighting data for his previously published photograph. We thank the IWC Secretariat for providing data from past IDCR and SOWER cruises and especially Marion Hughes for 'digging out' old data. Thanks to Ms. Rebecca Rademeyer from the University of Cape Town for kindly faxing some data to the first author, to Dr. Hirawake, National Institute of Polar Research, Japan, for providing Polar Front data, María José Pérez (University of Valparaíso) for data and reference searches and Emma Newcombe (University of Auckland) for reviewing different versions of this manuscript.

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Date received: February 2006
Date accepted: October 2006

Evaluating the use of whalewatch data in determining killer whale (*Orcinus orca*) distribution patterns

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ABSTRACT

Commercial whalewatching has been used as an opportunistic data source for studies of cetacean distribution, but there are few comprehensive analyses of the biases and assumptions implicit in such methodology. The goal of this study was to evaluate the use of data generated by commercial whalewatch operators using a case study of whalewatchers targeting killer whales (*Orcinus orca*) within Washington and British Columbia inshore waters. In this region, many whalewatch vessels work cooperatively in a small, semi-enclosed area to locate and identify well-known killer whales. To address search biases and cross-examine the accuracy in killer whale locations and pod identifications by whalewatchers, an independent field study was conducted. The whalewatch data were 91.7% accurate in locating killer whales, but only 74.1% of those sightings were correctly identified to the pod level. However, identification accuracy increased to 92.6% when errors due to sub-pod mis-identification were excluded and 96.3% when early morning (before 10:30), unknown pod sightings were also excluded. It is suggested that these data can be used to describe spatial use patterns by killer whales, with recognition of the dataset's limitations. Results of this study indicate that examination of biases is necessary before initiating research using data generated by commercial whalewatchers, but such data sources can be effective for specific study questions if the limitations are known. Although the whalewatch situation described here is relatively unique because it targets a small, well-known population, this study presents a practical methodology for evaluating the efficiency of whalewatch vessels in detecting and identifying cetaceans. Globally, whalewatching industries are increasing in numbers and geographic scope, and capitalising on these platforms of opportunity represents potentially valuable and accurate data for studies of cetacean distribution.

KEYWORDS: WHALEWATCHING; KILLER WHALES; NORTH AMERICA; MONITORING; DISTRIBUTION; SAMPLING STRATEGY; PACIFIC OCEAN; NORTHERN HEMISPHERE; SURVEY-SHORE BASED

INTRODUCTION

Assessing distributions of highly mobile, wide ranging marine mammals presents a challenge to marine ecologists. Depending on the species or population of interest and available resources, there are a number of possible assessment methods. Standardised line-transect aerial or vessel surveys are commonly used to determine distributions of cetaceans (e.g. Baumgartner *et al.*, 2003; Drouot *et al.*, 2004; Elwen and Best, 2004; Griffin, 1999; Zerbini *et al.*, 2004), but such methods may not be feasible for all populations due to budgetary constraints or other restrictions. Opportunistic information, such as historical stranding or whaling catch and sighting information, have been used to illustrate seasonal patterns in distribution (e.g. Clapham *et al.*, 2004; Dalebout *et al.*, 2003; Gregr and Trites, 2001; Jaquet *et al.*, 1996; Maldini *et al.*, 2005). Similarly, sightings data from platforms of opportunity, such as whalewatch vessels, have provided broad-scale information on distribution, without expensive survey effort (e.g. Darling *et al.*, 1998; Weinrich *et al.*, 2000). However, caution must be applied when using data collected from platforms of opportunity. Specifically, Evans and Hammond (2004) have argued that to generate useful data, observers must provide correct species identification and sighting biases must be limited in space and time. Potential biases in data collected from platforms of opportunity will be minimised with more observers and broad spatial coverage. Rapidly developing industries for commercial whalewatching, often with highly localised spatial and temporal effort, present a chance to test the applicability of data opportunistically collected by whalewatchers for studies of cetacean distribution.

Within the semi-enclosed marine waters of Washington and British Columbia (BC), an extensive whalewatching industry has developed for killer whales (*Orcinus orca*). Whalewatchers have established a centralised method for locating whales on a daily basis that is available to any subscriber, between mid-May and October each year. In 2004, fifty American and Canadian whalewatch companies were estimated to operate 91 vessels on a frequent basis in the region (K. Koski, pers. comm.). Centralised observers from these companies have accumulated location data for killer whales across several years, creating prospects for distribution analyses. The killer whales in this region have been researched intensively over the last four decades, and there is substantial information on their behaviour, population structure and demographics. Studies have identified three distinctive, sympatric ecotypes of killer whales, known broadly as 'residents' (or fish-eating), 'transients' (or mammal-eating) and 'offshores' (Bigg *et al.*, 1987; Ford, 1991; Ford *et al.*, 2000; Ford *et al.*, 1998; Hoelzel *et al.*, 1998; Hoelzel and Dover, 1991). Every individual resident and transient killer whale can be identified using photo-identification methods, based on unique pigmentation patterns and dorsal fin morphology (Baird and Stacey, 1988; Bigg *et al.*, 1987). Although whalewatch companies report sightings of any killer whale ecotype, the most frequently encountered is the so-called southern resident killer whale. Southern resident killer whales are particularly well-studied and every individual is separated into one of three pods of matrilinealy related families (termed J, K and L pods) (Ford *et al.*, 2000; van Ginneken *et al.*, 2004), although some argue that L pod can be further subdivided into multiple pods (Baird *et al.*, 2005; Hoelzel, 1993). Published identification guides, regular

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occurrence in the relatively benign waters of this region and proximity to urban centres facilitate viewing opportunities and identification of southern resident and transient killer whales from centralised observers and whalewatch vessels. Because the southern resident killer whales of the North Pacific Ocean are such a well-studied population, in which all individuals are uniquely photo-identified and reside during the summer in a region that can be surveyed easily from land, they provide a unique opportunity to study the accuracy and applicability of data garnered from whalewatching platforms. In addition, the whalewatching data could provide detailed information on habitat use in this region. However, there has not yet been any attempt to quantify effort biases, proper identification or limitations for distribution analyses in the data, all of which are necessary before the data can be used (Evans and Hammond, 2004).

This study was conducted in order to evaluate biases in whalewatch data on killer whales from inshore waters of Washington and British Columbia and to determine the quality and utility of this platform of opportunity for multi-scale analyses of distribution patterns. A validation study of these data was designed using independent field work with land-based spotters using a systematic search and identification of killer whale pods. This systematic search overlapped temporally and spatially with the opportunistic data from the whalewatch industry. Data from this land-based network were used to determine biases in whalewatcher effort and evaluate the applicability of whalewatch data to spatial analyses. The specific objectives were to: (1) quantify efficiency of killer whale group detection by whalewatch data; (2) quantify whalewatch data accuracy in southern resident killer whale identification; (3) identify inconsistencies in resident pod identifications; (4) describe general daily patterns in the whalewatch data; and (5) provide general and region specific recommendations for the use of whalewatch data for describing cetacean distribution patterns.

METHODS

Whalewatch data

Data on killer whale locations were compiled daily from May to October 2004 by monitoring reports of a commercial whalewatch sighting network, referred to hereafter as the Pager Network. Commercial whalewatch operators created this centralised spotting service to cooperatively locate whales for their customers. Searches were made daily from approximately 08:00-17:00 by at least one land-based observer near Victoria, BC and several Canadian and American whalewatch vessels from throughout the region (Fig. 1). Whale identifications (i.e. southern resident J, K or L pod, transient or unidentified), time of day, location and direction of travel were provided to subscribers of the Pager Network for all sightings. Sightings of unknown pod or ecotype were reported as unidentified killer whales. Location was described via pre-established grids throughout the study region and generalised to standard 5km^2 cells for analyses (Fig. 2).

The Pager Network represents a potentially useful platform of opportunity for collecting data on cetacean distributions, but search effort was not randomised. Effort was often concentrated in areas where whales were thought likely to be, and areas far from ports were less frequently searched. However, vessels were traversing throughout the region from home ports multiple times a day (morning, noon and evening) and had the opportunity to intercept any previously un-reported whales. Sightings by the Pager Network are also typically a series of related events on a given day. It is in the best interest of whalewatching companies to locate whales early in a day and follow them throughout it. The ability to locate killer whales 'early' may involve expectations of the location and direction of movement of groups at the end of the previous day or a higher likelihood of detecting larger groups. To maintain whale follows, sightings are reported approximately every 30 minutes to the Pager Network throughout a day. Although several participants cooperatively searched for whales, an observation of a whale pod was only reported by the Pager Network once per time unit as a matter of standard protocol, such that sightings of a pod were not artificially inflated by multiple reports of the same whales. The Pager Network data thus contain a variety of potential biases.

Field evaluation

An independent field study was conducted to address possible violations of key assumptions and consider biases in effort, in the context of assessing the use of the Pager Network data for distribution analyses. Misidentification and sampling bias are two common forms of error introduced by whalewatching platforms. Misidentification can be either fully incorrect identification or partial misidentification. The Pager Network assumed that every individual of a pod was present during each sighting, based on the definition of pods as long-term, stable associations (Bigg *et al.*, 1990). Sampling bias is affected by the lack of documentation on search effort. The Pager Network assumed that there was sufficient effort throughout the region during the summer such that a pod would be detected by the Pager Network during a given 24hr period if whales were anywhere within the study area (Fig. 1). Information was reported when whales were located, but it was rarely known when, for how long and where whalewatchers looked before locating whales. Therefore, it was difficult to determine if apparent pod distribution patterns reflect bias in searching patterns by commercial operators or true animal distribution.

To study the Pager Network data, a land-based survey was designed in order to provide a systematic spatial and temporal search for killer whales in the study region over the same time period as the Pager Network data. The survey used trained observers in a uniform search protocol. The field study examined: (1) whether pods were being misidentified, partially or wholly and if misidentification was affected by time of day or location; and (2) whether pods were present in areas less commonly seen by the Pager Network but not reported due to lack of effort and if missed sightings were related to a particular time period. The land-based study sites (Fig. 2) were primarily chosen to cover the maximum extent possible of the primary whalewatch operations within the inshore waters of Washington and BC. To identify whether lack of sightings by whalewatchers represented low search effort or a true deficiency of sightings in a particular area, some sites were chosen where there have been few killer whale sightings in past years (D. Hauser, unpublished data) but which are nonetheless visible, at least in part, by Pager Network participants.

From July to September 2004, the network of land-based observers scanned for killer whales on a daily basis for 10 days per month (separated into two distinct five-day blocks) for comparison with the Pager Network. At each of five spatially distinct sites (Fig. 2), observers simultaneously conducted an approximately 5min long scan of the surrounding area every 15min using 10×50 magnification binoculars. Visual surveying via binoculars is a standard

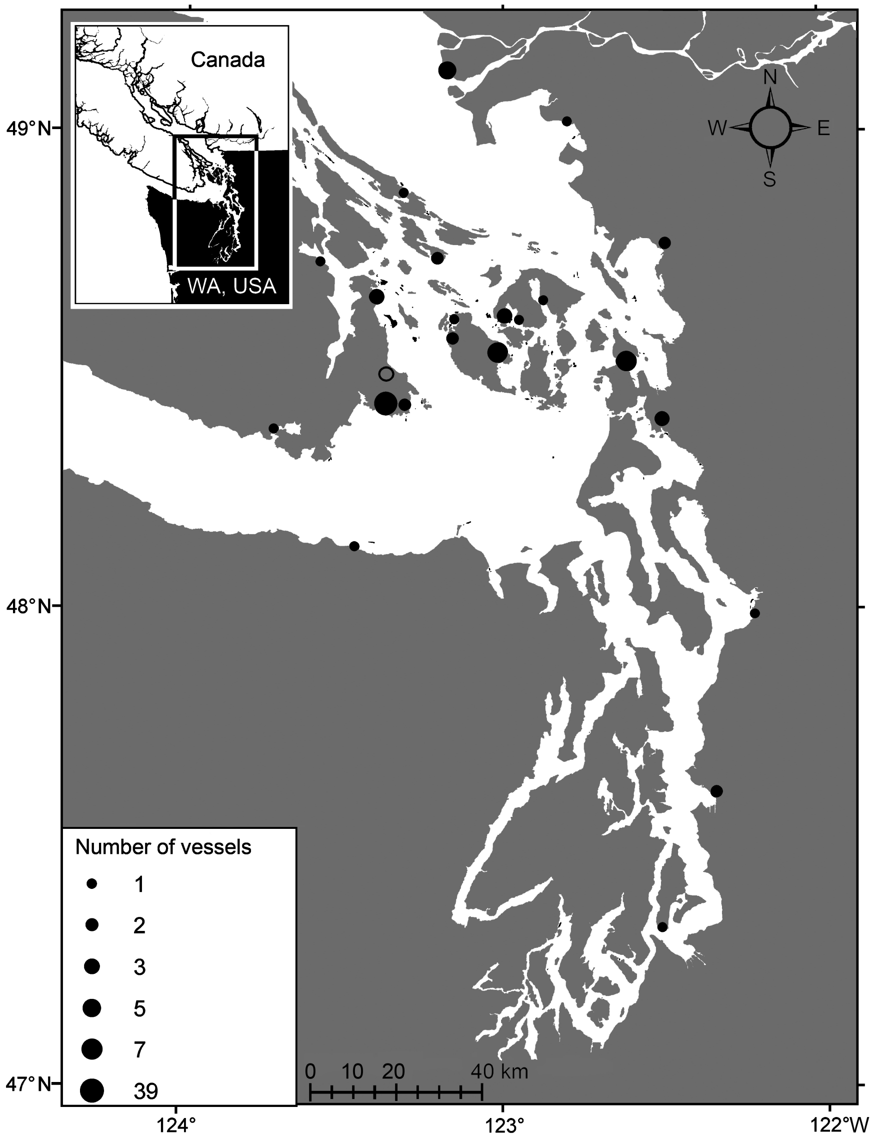

Fig. 1. Map of Washington and British Columbia 2004 whalewatch ports. Solid circle diameter indicates the total number of vessels originating from each port (data courtesy Kari Koski, The Whale Museum Soundwatch Program) and the open circle signifies the location of the land-based Pager Network observer. Vessels transit throughout the region and to/from their ports on a daily basis, contributing sightings to the Pager Network.

technique for spotting and censusing killer whales (Zerbini *et al.*, In press) and in addition the killer whales in this region are primarily resident killer whales, whose active surface behaviour and large pod size makes them especially visible (Ford *et al.*, 2000). Killer whale scans occurred throughout a 5hr period of each observation day. The start time of each daily 5hr scan period was staggered such that each hour from 08:00-17:00 was sampled at least once during a five-day survey period. Sighting conditions (i.e. Beaufort sea state, glare, visibility and cloud cover) were recorded for each scan, and scans were aborted if sighting conditions were poor (i.e. Beaufort sea state of three or more, less than 100m visibility). Killer whales were identified to the pod-level. The total number of individuals, number of adult and adolescent males, number of calves and any visually identified animals were recorded to determine pod identity and ecotype (i.e. resident, transient or offshore). Additionally, photo-ID pictures were taken when possible. Subset groups of L pod whales often occur separate from one another, so subset groups were identified to the sub-pod-level if necessary. Additionally, observations of other cetaceans (such as porpoises) and pinnipeds were also recorded. Regular spotting of other species helped confirm that the scans were successful at sighting animals in the water even if no killer whales were sighted. Pod location was estimated based on the same grid system used by the Pager Network to facilitate comparisons. Continuous daily killer whale monitoring occurred at a sixth site, Lime Kiln State Park on San Juan Island, where a large staff of researchers equipped with a hydrophone provided continuous visual and acoustic detection of whales. Hereafter, all scan and Lime Kiln data will be referred to as the land-based survey. Lime Kiln observations will be mentioned as ‘during survey’ for sightings co-occurring with the scheduled surveys at other sites and ‘non-survey’ periods for sightings occurring during times when there was not simultaneous sampling at other survey sites. Concurrently throughout the summer, sightings by the Pager Network were recorded independently from the field surveys. Although recorded independently from one another, it should be noted that the presence of whalewatch vessels could alert land-based observers to the presence of killer whales. However, scans were conducted systematically and for a fixed amount of time for killer

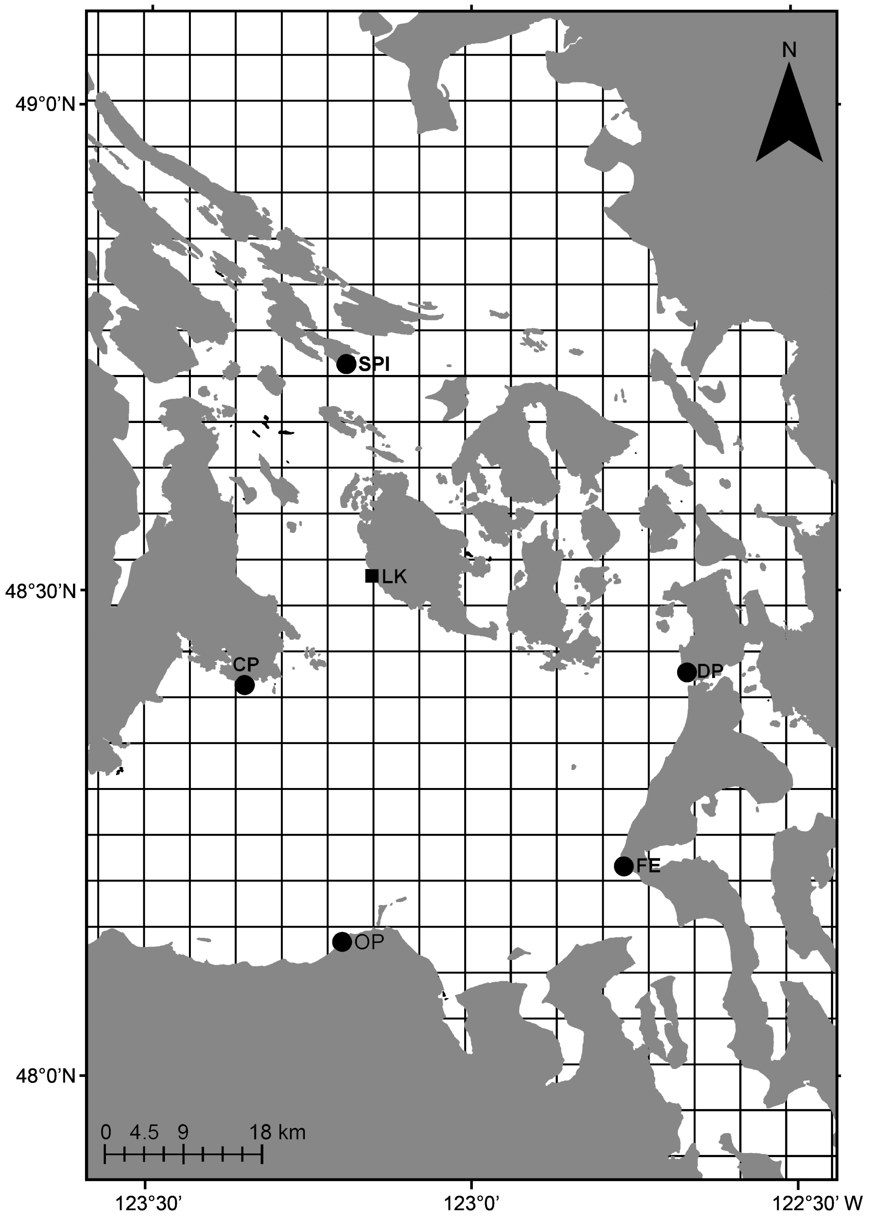

Fig. 2. Detailed map of study area and standardised grids indicating survey sites referenced in the text. Solid circles represent sites that were surveyed according to the study schedule and the square represents Lime Kiln State Park (LK) that was continuously surveyed (i.e. constant surveillance for killer whales). Study sites included Clover Point near Victoria, BC (CP), Deception Pass State Park, WA (DP), Fort Ebey State Park on Whidbey Island, WA (FE), Lime Kiln State Park on San Juan Island, WA (LK), Dungeness National Wildlife Refuge on the Olympic Penninsula, WA (OP) and Higg's Point on South Pender Island, BC (SPI).

whales regardless of the presence of whalewatch vessels and the land-based scans used standard survey methods that are regularly used to spot killer whales in the absence of vessels.

Data analysis

Land-based surveys at each of five land-based sites consisted of a total of 150hr, on 30 days (10 days per month July to September 2004), and comprised 2,941 scans. In cases where multiple sightings of a pod occurred during a day, the first Pager Network pod sighting on a sampling day at each site was selected to avoid pseudo-replication in analyses. There were a total of 34 independent killer whale group sightings during scans, 73% of which occurred at Lime Kiln Lighthouse. Killer whales were also observed at South Pender Island and Deception Pass survey sites. All killer whale sightings occurred in excellent-good sighting conditions (100% visibility, Beaufort sea state of two or less), and mean scan length was 5.1min (0.02 standard error). Only survey scans occurring in at least fair sighting conditions (three kilometre or more visibility, Beaufort sea state of three or less, little or no fog or glare) were used in comparisons to the Pager Network. Sightings of killer whale groups were identified to pod(s) using current, established North Pacific Ocean killer whale photo-ID guides (Ford and Ellis, 1999; Ford *et al.*, 2000; van Ginneken *et al.*, 2004). Percentages of pod sightings by land-based observers corresponding to the Pager Network were calculated to evaluate the land-based survey's ability to detect killer whale groups. Additionally, pod sightings were compared to the corresponding day of the Pager Network data to establish the percentage of correct locations and pod identifications by the Pager Network. It should be noted that the accuracy rates for the land-based survey and Pager Network were calculated in different ways; land-based accuracy looks for Pager Network sightings that occurred during the survey period and compares those to the actual land-based detections, whereas Pager Network accuracy first looks for the land-based sightings during the surveys and compares those to the actual Pager Network sightings. Therefore, the number of detections may be different for each comparative method.

Pager Network pod misidentification rates were examined by comparing Pager Network and land-based pod identifications for all sightings that corresponded in time and location. Observers from the land-based survey were assumed to have 'correct' killer whale identifications to test Pager Network identification accuracy against the land-based survey. This assumption is supported by: (1) the use of trained observers or experienced local killer whale researchers for sightings; (2) an explicit emphasis on pod identification by the land-based observers as opposed to the Pager Network observers who are primarily focused on killer whale presence rather than pod identification; (3) capture of photo-ID pictures when possible; and (4) observations of proportions of calves, juveniles, adult males, and easily identified individuals for comparisons with known pod compositions. Criterion (4) was particularly useful for establishing identification when land-based sightings occurred at a distance. The percentage of correctly identified pods by the Pager Network was calculated, and likely causes of any misidentification errors were considered. Identifications between the Pager Network and land-based surveys were compared directly by creating a matrix of concurrent sightings. The Pager Network did not distinguish among possible sub-pods, while the land-based study did. Therefore, the matrix recognised identification inconsistencies between the Pager Network and the land-based study related to sub-pod misidentification. Descriptive statistics of all 2004 Pager Network sightings were explored to produce Pager Network data use recommendations. Timing of daily sightings was described, and variations in mean sighting time were compared among pods and ecotypes.

RESULTS

The Pager Network searched for whales on 166 days from 19 May to 31 October 2004, resulting in a total of 2,554 killer whale sightings. Of all the 2004 Pager Network data, 74% of sightings were identified as southern resident killer whales, while transient and unidentified killer whales each contributed 13% of the sightings.

Killer whale detections by land-based survey

Before examining the accuracy of the Pager Network data, it was necessary to evaluate how well the land-based survey detected killer whale groups known to be present. In this case, whales reported by the Pager Network represented killer whales known to be present. Land-based sightings were compared to the number of Pager Network sightings co-occurring during the times and locations that were surveyed from shore. A total of 27 Pager Network observations occurred within areas visible from land-based sites during survey periods. During fair or better sighting conditions, the land-based survey detected 25 of the 27 Pager Network observations (92.6%). No Pager Network observations were made at survey locations in poor sighting conditions during the land-based study. These results indicate that the land-based surveys had a high detection probability for killer whale groups that are reported by the Pager Network. However, it is possible that a subset of killer whale groups, particularly transient killer whales, may exhibit highly cryptic behaviour that neither systematic land surveys nor opportunistic boat surveys would detect. It is unlikely, in our opinion, that killer whale groups would have been missed by the land surveys during good conditions, since smaller, more cryptic cetaceans like harbour and Dall's porpoise (*Phoceoena phocoena* and *Phocoenoides dalli*, respectively) and pinnipeds were routinely observed (Table 1, columns five and six). Scans were short but frequent, making it extremely unlikely that killer whale pods would pass the scan area undetected.

Killer whale presence/absence accuracy of the Pager Network

To address whether the Pager Network failed to observe detectable killer whales, killer whale sightings detected by the land-based observers were compared to killer whales detected by the Pager Network. The Pager Network detected 31 of 34 killer whale groups observed at land-based locations, (91.7%; Table 1, columns three and four). All sightings occurred in fair or better sighting conditions. Therefore, the Pager Network had a high probability (>90%) of detecting groups that were also detected as present by the

Table 1

Information on effort (number of scans) at each site, the Pager Network's accuracy in correctly locating killer whales (indicated as the number of land detections matched by the pager and percent accuracy) and the number of non-killer whale marine mammal observations (small cetacean and pinniped). Sites are Clover Point, near Victoria, BC (CP), Deception Pass State Park, WA (DP), Fort Ebey State Park on Whidbey Island, WA (FE), Lime Kiln State Park on San Juan Island, WA (LK) during the survey periods and non-survey periods, Dungeness National Wildlife Refuge on the Olympic Penninsula, WA (OP) and Higg's Point on South Pender Island, BC (SPI). Lime Kiln State Park was under continuous surveillance during Pager Network operations via acoustic and visual detection, but did not record non-killer whale sightings.

	Land-based effort	Pager Network accuracy		Non-killer whale marine mammal observations	
Survey site	Number of land-based scans	Number of land-based observations	Number of land-based observations detected by Pager Network (% accuracy)	Number of small cetacean observations	Number of pinniped observations
CP	474	0	0	9	75
DP	631	2	1 (50%)	309	255
FE	605	0	0	268	89
OP	599	0	0	11	95
SPI	632	8	8 (100%)	173	472
LK	Continuous	18	16 (88.9%)	N/A	N/A
LK non-survey	Continuous	6	6 (100%)	N/A	N/A
Total	2,941	34	31 (91.7%)	770	986

land-surveys. Additionally, when no killer whales were reported by the Pager Network in an area being surveyed from land, no whales were seen during nearly 3,000 scans of the systematic land surveys either (Table 1, column two). Overall, this suggests that deficient or low numbers of Pager Network reports within a particular area indicate a lack of killer whales rather than a lack of Pager Network search effort in that area. This is particularly important because prior to this study, it could be assumed that the presence of killer whales in the Pager Network data represented their actual presence, but absence of killer whales in the data could not be assumed to mean that no whales were present.

Pod identification accuracy of the Pager Network

Of the killer whale sightings that corresponded between the Pager Network and the land-based survey, the Pager Network correctly identified 74.1% (*n*=20 of 27) of the pods at land-based sites and Lime Kiln lighthouse (Table 2). Of the incorrectly identified sightings, problems associated with L sub-pods appeared to be the most common reason for incorrect identification by the Pager Network. Seventy-one percent (*n*=5 of 7) of incorrect pod identifications occurred when either: (1) all of L pod was reported when only a sub-pod was present; or (2) a sub-pod was not present during a sighting of the rest of L pod. An inability to identify pods early in the morning (before 10:30) was also associated with incorrect pod identifications (14% of incorrect identifications). Pod identification inconsistencies were further compared using a matrix with counts of identified pods from all land surveyed sites and times corresponding to Pager Network sightings (Table 3). When sightings that misidentified an L sub-pod were excluded, pod identification accuracy increased to a total of 92.6% (*n*=25 of 27) (Table 2, centre panel). Pods were further correctly identified a total of 96.3% (*n*=26 of 27) of the time when misidentifications of both L sub-pods and early morning unidentified killer whales were excluded (Table 2, right panel). Although the number of sightings (*n*=27) is small, the high correspondence suggests that the Pager Network has a high probability of correctly identifying southern resident pods, given exclusions of systematic misidentifications.

Temporal trends in Pager Network sightings

Trends in the timing of all (*n*=2,554) Pager Network sightings were also examined. Among all of the 2004 Pager Network data, sightings of killer whales occurred between 06:00-20:00. The majority of sightings (87.3%) occurred at and maintained a relatively constant frequency level from 10:00 to 16:30 (Fig. 3). There was no variation in mean time of sightings among southern resident pods and transients, except for unidentified killer whale sightings which occurred significantly earlier than all other pods (Analysis of Variance; ANOVA) with Tukey's 'Honestly Significantly Different' (HSD) *post hoc* test, *F*=80.3, *p*=0.000). Mean unidentified killer whale sighting time occurred at nearly 10:00 (mean=9.97, SD=1.77) and exhibited a positive skew (Fig. 4). Excluding unidentified killer whales, mean sighting time occurred at nearly 13:00 (mean=12.99, SD=2.00). This suggests that killer whale pod identification tends to be known by midday, and that unknown pod identifications are skewed to 10:00 and earlier.

DISCUSSION

Implications for the use of Pager Network data for study of southern resident killer whale distribution

These results suggest that the Pager Network can provide accurate locations of killer whale pods, but the Pager Network's ability to correctly identify southern resident pods is less certain. The primary cause of pod misidentification by the Pager Network occurred because the sub-structure of the L pod was not recognised by it. Instead, L sub-pods were reported only as 'L pod' even when the entire pod was not necessarily present. Pods are considered long-term and consistent social associations among southern resident killer whales; individuals spend 50% or more of their time together (Bigg *et al.*, 1990). Smaller groups, often referred to as sub-pods, also occur within the L pod. Although only three southern resident pods (J, K and L) are usually recognised, some suggest that the L sub-pods are actually two recently split pods (Baird *et al.*, 2005; Hoelzel, 1993). If the sub-pod concept is dissolved and instead it is assumed that at least 'some' of the L pod is present in a Pager Network L pod sighting, then accuracy in Pager Network sightings improves from 74 to 93% correct. While it is recommended that future Pager Network operators distinguish among L sub-pods, this allowance in sub-pod ambiguity facilitates confidence in past Pager Network identifications. Both J and K pod follow the Bigg *et al.* (1990) definition of pods, and it can be assumed that the entire pod is present during Pager Network sightings of J or K pod.

Unknown pod identity of early morning sightings was another reason for pod misidentification by the Pager Network. Identification is not necessarily a priority for operators, since killer whales, irrespective of their pod, are their target. Some animals are very distinctive and easily identified by experienced observers. Although published identification guides are available and used by whalewatchers, vessels cannot be assumed to have equal identification ability. Unknown identity killer whale sightings occurred significantly earlier in the day than all southern resident pod and transient sightings. These patterns

Table 2

Information on the Pager Network's accuracy to correctly identify Southern Resident killer whale pods at survey locations, including Lime Kiln State Park during and not during land-based survey periods, based on correctly located sightings as listed in Table 1. South Pender Island and Deception Pass sites were pooled for the non-Lime Kiln survey sites. Counts and relative percent accuracy are shown for all observations (left panel), those excluding errors due to mis-identification of an L sub-pod (centre panel) and for all excluding L sub-pod and early morning (before 10:30) errors (right panel).

	All observations			Excluding L sub-pod errors			Excluding L sub-pod and early morning errors		
Observation period	Total	No. correct	Percent	Total	No. correct	Percent	Total	No. correct	Percent
Non Lime Kiln survey	5	4	80.0	5	5	100	5	5	100
Lime Kiln: survey	16	13	81	16	15	93.8	16	16	100
Lime Kiln: non-surveys	6	3	50.0	6	5	83.3	6	5	83.3
Overall	27	20	74.1	27	25	92.6	27	26	96.3

Table 3

Matrix showing counts of killer whale identifications by pod (bold) for the land-based survey (correct identification) and Pager Network (test identification). Pods observed travelling together are noted with double (e.g. 'JK') or triple (e.g. 'JKL') pod designations. L sub-pod (called L12s) identification errors are shown. Survey information, listed horizontally, includes sightings corresponding to the Pager Network from all surveyed sites and Lime Kiln during survey and non-survey periods. The Pager Network sightings are listed vertically. Correct identification correspondence between the survey and Pager Network should fall along the highlight.

		Survey											
	Pod	J	JK	JKL	JL	K	KL	L	L12s	JKL12s	Transient	Un-ID	SUM
Pager Network	J	0	0	0	0	0	0	0	0	0	0	0	0
	JK	0	**7**	0	0	**1**	0	0	0	**1**	0	0	9
	JKL	0	0	**8**	0	0	0	0	0	**1**	0	0	9
	JL	0	0	0	0	0	0	0	0	0	0	0	0
	K	0	0	0	0	0	0	0	0	0	0	0	0
	KL	0	0	0	0	0	0	0	0	0	0	0	0
	L	0	0	0	0	0	0	**2**	**3**	0	0	0	5
	L12s	0	0	0	0	0	0	0	0	0	0	0	0
	JKL12s	0	0	0	0	0	0	0	0	0	0	0	0
	Transient	0	0	0	0	0	0	0	0	0	**3**	0	3
	Un-ID	0	0	**1**	0	0	0	0	0	0	0	0	1
	SUM	0	7	9	0	1	0	2	3	2	3	0	27

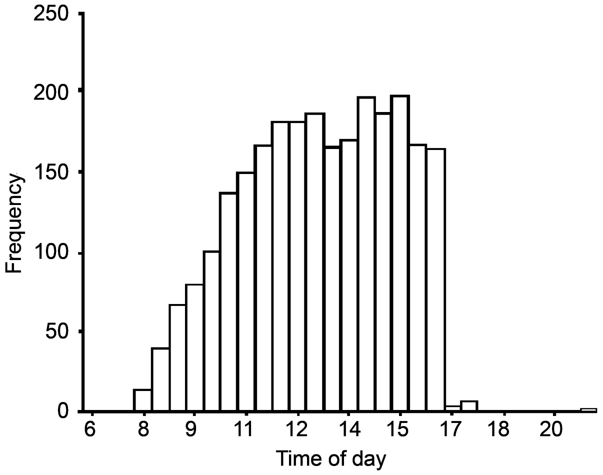

Fig. 3. Frequency histogram of all Pager Network killer whale sightings during 2004 (mean=12.6, SD=2.22, *n*=2,554).

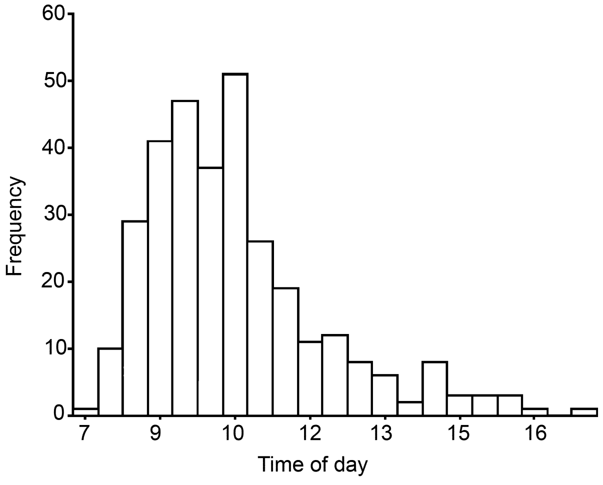

Fig. 4. Frequency histogram of all 2004 Pager Network sightings listed as un-identified killer whales (mean=9.97, SD=1.77, *n*=319).

likely represent the search strategy of whalewatch operators. Operators searched for killer whales until they were located in the morning and an increasing number of operators, and thus number of experienced observers, searched for whales throughout the day. There appears to be a short transition period before pod identity is determined and unknown killer whale sightings declined after 10:00. Whalewatchers often located whales in the morning and followed them throughout the day, thereby maintaining recognition of pod identity and location. This behaviour increases the whalewatcher's ability to locate and maintain relatively high confidence in pod identity after 10:00. The majority of sightings occurred from 10:30-16:00 and during this time period sighting frequency remained relatively constant before abruptly discontinuing after 16:00. This suggests that sighting effort throughout a day was consistent and stable among pods from mid-morning to afternoon and supports the conclusion that pod identity is typically determined by mid-morning. If the previous allowances for L sub-pods are accepted and unknown identity sightings before 10:30 are also excluded, the Pager Network identification accuracy increases to 96%.

In order to evaluate whether the observed killer whale distribution reflects bias in whalewatch operator search patterns, areas where sightings are rare must be sampled. In 166 days of surveys, no killer whales were sighted during the land-based surveys from Clover Point, Fort Ebey or Olympic Peninsula sites, and there were few sighted at Deception Pass. During the same periods, no killer whales were reported by the Pager Network for the grids which were searched from these sites. The possibility that whalewatch operators miss killer whales in these areas cannot be eliminated since we have few to no land sightings to compare the Pager Network data with. However, hundreds of scans were conducted at each site and no killer whales were ever observed, nor reported by the Pager Network. With nearly 100 vessels originating from over 22 ports throughout the study region, the area is transited by whalewatchers throughout the day. Therefore, it is suggested that there is sufficient effort throughout the region during the summer that a pod would be detected by the Pager Network during a 10:30-16:00 period if whales were anywhere within the study area.

Southern resident sightings occurred in the 2004 Pager Network data significantly more frequently than transient or unidentified killer whales. This pattern can be attributed primarily to the higher likelihood of sighting residents than transients (Ford *et al.*, 2000). The total transient population size within this region is unknown and is assumed to be in the low hundreds and there is a protracted resighting interval (up to ten years) for many individuals (Baird, 2001; Baird and Dill, 1995). Additionally, the divergent foraging strategies of transients and residents contribute to the overall likelihood of sighting animals. Average transient group size in this region is two individuals, ranging from between one and four individuals (Baird and Dill, 1996), while southern resident group sizes range from 11 individuals in an L sub-pod to all 91 individuals when the pods assemble as a single group (van Ginneken *et al.*, 2004). Larger group size presumably contributes to greater sighting probability of residents, but transients are also less vocal, have more erratic surface behaviour and are more difficult to detect at the surface than their resident counterparts (Ford and Ellis, 1999). Therefore, it is expected that the Pager Network is more likely to miss sightings of transients than residents and care should be taken in future research employing Pager Network transient sightings. Furthermore, variation in ecotype behaviour, with residents often exhibiting more noticeable surface behaviours and occurring in large groups (typically greater than 20 individuals), promotes sightability of southern residents. Poor weather could reduce sightability for both land and whalewatch observers, but was not a factor considered in this study since all land-based observations occurred in fair or better conditions.

The Pager Network can be used for future research of northwest Pacific killer whale distribution and habitat analyses, particularly for identified southern resident sightings. The Pager Network was able to detect whales within the region, and a lack of detection in an area was assumed due to a true lack of whales rather than poor effort. However, it is recommended that researchers recognise the limitations, biases and assumptions associated with these data. Specifically, it is proposed that researchers may rely on Pager Network pod identifications given three conditions: (1) awareness that a small (<5%) degree of error due to unambiguously incorrect pod identifications exists; (2) assumption that a Pager Network L-pod sighting does not necessarily represent all of the L-pod, but rather may represent only one of its sub-pods; and (3) restriction of analyses of Pager Network data to sightings occurring between 10:30 and 16:00, when there is consistent search effort and pod identity is more likely already known. Future studies should not extrapolate these results beyond the region bounded by the extent of the land-based survey sites.

Broader implications

Globally, whalewatching is a growing enterprise and research opportunities using whalewatching as a platform are likely to increase. In 1998, over nine million participants were involved in whalewatching in 87 countries and territories and the number of participants was growing by an average of 12% per annum (Hoyt, 2001). Although ecological tourism has been regarded by some as a possible disturbance source to cetacean populations, it is beyond the scope of this study to examine the potential impacts of whalewatching. If managed responsibly, ecological tourism may also have local economic and educational benefits. A more dispassionate analysis of such activities seems appropriate, and researchers should consider whether ecological tourism can be utilised to gather technical data of value in understanding, conserving and managing target species. Using whalewatching as an avenue of research represents a more affordable approach to distribution studies, which traditionally require labour and cost intensive line transect, aerial or vessel surveys.

In this case, whalewatching companies have a high level of self-interest in maintaining a sighting network. The Pager Network is a somewhat unique situation in which whalewatchers target a small, well-known population of a single species in a very localised, semi-enclosed area. However, as shown with the Pager Network, such data can be accurate enough to be useful for describing whale distribution. Particularly in developing nations with expanding ecotourism endeavours, whalewatch platforms may present a cost-effective method to accumulate basic information as a segue into more intensive research. There is clearly a need for testing data quality from platforms of opportunity, as well as acknowledgment of data limitations and biases before such research is pursued. These should be tested on a regular basis, if long-term use of platforms of opportunity is planned. Although there may be situation-specific considerations for each whalewatching platform, this research in the northeast Pacific provides an example of possible approaches to validation. It is proposed that data provided by commercial whale watch operations can be applied to spatial analyses, with proper evaluation and understanding of limitations.

ACKNOWLEDGEMENTS

Several volunteers helped during the field study and with data processing, particularly Teresa Mongillo, Sarah Ashworth and Toby Black. The Whale Museum supported the collection of Pager Network data, and Robert Otis provided data from Lime Kiln State Park. Kari Koski contributed information on vessel numbers and whalewatch operations during the 2004 season. Jennifer Marsh provided a supplemental dataset for secondary evaluation of Pager Network accuracy. Analyses of pod identification would not be possible without the long-term commitment to the annual killer whale census and survey by Ken Balcomb and the Center for Whale Research. This manuscript was greatly improved by comments from Peter Best, Robin Baird, Peter Westley, Heather Smith and an anonymous reviewer. The Washington Cooperative Fish and Wildlife Fisheries Research Unit provided logistical support for field operations, and this work was funded by the Northwest Fisheries Science Center, National Marine Fisheries Service and the Claire L. and Evelyn S. Egtvedt Fellowship to DDWH from the University of Washington's School of Aquatic and Fishery Sciences.

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Date received: November 2005
Date accepted: July 2006

Unusual cetacean stranding events of Taiwan in 2004 and 2005

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ABSTRACT

In early 2004 and in 2005, several unusual stranding events occurred in Taiwan during a period when large-scale naval exercises were conducted in and on nearby waters. Gross examination of the partial remains of two carcasses (a ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) and a pygmy killer whale (*Feresa attenuata*)) and an intact Risso's dolphin (*Grampus griseus*) revealed that the former two had internal injuries to structures associated with or related to acoustics or diving. The several unusual stranding events and the findings of the gross *post mortem* examination of the only specimens that were available for study were suggestive that nearby naval exercises may have contributed to or caused the death of at least one cetacean in this region and that species other than beaked whales may also be susceptible to such activities. With an increasing number of military exercises in this region, more attention to the impacts of such activities on cetaceans is needed.

KEYWORDS: ASIA; STRANDINGS; GINKGO-TOOTHED BEAKED WHALE; SHORT-FINNED PILOT WHALE; PYGMY KILLER WHALE; DWARF SPERM WHALE; BLAINVILLE'S BEAKED WHALE; LONGMAN'S BEAKED WHALE; PANTROPICAL SPOTTED DOLPHIN; STRIPED DOLPHIN; RISSO'S DOLPHIN; DISTRIBUTION

INTRODUCTION

In recent years, concern about the impact of military activities (especially usage and testing of naval sonar) on cetaceans and other marine life has been increasing rapidly. A considerable amount of military activities occur in Taiwanese and adjacent waters due to decades of political instability and military tension in the region. Until recently, Taiwan's navy did not possess warships with the AN/SQS-53C mid-frequency active sonar (see *www.globalsecurity.org*) that has been implicated in the mass stranding of cetaceans in the Bahamas in 2000 (Balcomb and Claridge, 2001; England and Evans, 2001). At the end of 2005, Taiwan began acquiring US-made Kidd-Class destroyers (which do possess the above sonar). Furthermore, military exercises involving the US Navy occur in regions adjacent to Taiwanese waters (e.g. Balikatan exercises in the Luzon Strait of the Philippines). It has also been reported that Taiwan has plans to purchase two units of low frequency active sonar for land-based deployment.

With regards to cetacean welfare and conservation, the number of naval exercises in East Asian waters is of concern. Past records and more recent, but limited, ship-based cetacean survey data show that the waters of Taiwan (especially off the eastern and southern coasts) are inhabited by many deep-diving cetaceans (Chen, 2001; Wang *et al.*, 1995; Wang *et al.*, 2001; Wang *et al.*, 2002; Yang *et al.*, 1999; Yeh, 2001), of which at least some may be particularly vulnerable to naval activities (e.g. see Cox *et al.*, 2006). Furthermore, the potential deployment of new powerful anti-submarine warfare sonar by the US navy in the western North Pacific including waters near Taiwan raises more concerns about the potential impact of military activities on cetaceans in this region.

In this paper, we present the chronology of three series of unusual cetacean stranding cases that occurred on the shores of Taiwan (and nearby regions) in 2004 and 2005 and the results of *post mortem* gross examinations of three of the stranded animals.

MATERIALS AND METHODS

Information on cetacean stranding events were obtained from newspaper articles, direct observations, photographs, people who attended to stranding events and unpublished stranding records. Information about military exercises was obtained from newspaper, television news reports and from official internet sources.

Three carcasses were provided by local county governments for examination: ginkgo-toothed beaked whale (*Mesoplodon ginkgodens*) – Pingtung County; pygmy killer whale (*Feresa attenuata*) – Tainan County; and Risso's dolphin (*Grampus griseus*) – Changhua County.

RESULTS

Chronology of the first series of events (see Fig. 1)

23 February 2004: Balikatan 2004 (large-scale US/Philippines joint military exercises) began; Taiwanese newspapers reported that naval exercises were conducted about 100km south of Taiwan on this day (also reported on the *US Marines in Japan* website: *http://www.okinawa.usmc.mil/*).

24 February 2004: Nine or ten short-finned pilot whales (*Globicephala macrorhynchus*) began stranding (alive) on a pebble beach south of Chengkung (Taitung County) in the morning. Other members of the group were seen swimming near the stranding site. Six carcasses were retrieved for display, education or research purposes by local institutions after rescue attempts failed.

29 February 2004: A female ginkgo-toothed beaked whale was found floating at sea near the town of Linbian (Pingtung County) by local coast guards at midday. It was uncertain if the animal was still alive when it was first discovered (reports were mixed). The specimen was sent to the National Museum of Marine Biology and Aquarium (NMMBA) where it was dissected by NMMBA staff but the intact head was frozen and later examined in detail by the authors (see below).

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1 March 2004: A fresh carcass of a striped dolphin (*Stenella coeruleoalba*) was found on a beach of Linbian (near the stranding location of the above ginkgo-toothed beaked whale). Photographs of the dolphin showed that it was not obviously emaciated and was bleeding from at least one (the left) eye. It was sent to the National Chengkung University for educational and research purposes.

7 March 2004: Balikatan 2004 military exercises ended (see *http://www.okinawa.usmc.mil/*).

7 March 2004: Although slightly beyond the geographical scope of this paper, an interesting event occurred in Zhejiang Province of the People's Republic of China. Seven short-finned pilot whales stranded alive on a beach. They were all assisted back to the sea by local residents but the cause of the stranding and the fate of the whales are unknown.

10 March 2004: One short-finned pilot whale stranded on the shores of Taishi (Yunlin County). The specimen was sent to the National Museum of Natural Sciences in Taichung City and examined by several researchers including staff of the Taiwan Cetacean Society.

These events are unusual because prior to 2004, there were only two other confirmed records of short-finned pilot whale strandings in Taiwan. Both events involved single individuals (females) and neither showed any obvious signs of internal injuries that could not be explained by natural causes such as pathogens, etc. (both specimens were dissected by the authors and the skeletons of these specimens are maintained at the NMMBA). The 24 February stranding was also the first mass stranding of short-finned pilot whales recorded in Taiwan. None of the animals examined by the authors at the stranding site exhibited typical signs of emaciation (such as the presence of a 'neck', loss of epaxial muscle mass, etc.). There is only one previously recorded stranding event of the striped dolphin in Taiwan (1, 2 and 5 dolphins stranded alive about 10-50km apart from each other over two consecutive days) and this species has only been observed in Taiwanese waters once (Yeh, 2001). Prior to 2004, there were at least 11 cases of stranded mesoplodonts (at least five were identified as ginkgo-toothed beaked whale and 1 as Blainville's beaked whale (*M. densirostris*). Unfortunately, for the previous stranded striped dolphins and mesoplodonts, there was no awareness of, or attention given to, injuries that may have been caused by acoustic or blast trauma or decompression sickness-like symptoms (e.g. see Fernández *et al.*, 2005; Jepson *et al.*, 2003).

Gross examination of the Linbian ginkgo-toothed beaked whale

General information

Only the intact head and partially cleaned post-cranial skeleton of the Linbian ginkgo-toothed beaked whale were available for the authors to dissect and examine. It was found floating at sea near Linbian (Pingtung County) on February 29. The specimen was female, at least 460cm long (measured from the flensed skeleton) and its mass was reported (in a newspaper) to be 870kg. The mammary glands were well-developed (but not lactating) and the epiphyses of all vertebrae were fused indicating sexual and physical maturity, respectively. The head was removed during initial necropsy by veterinarians and frozen for about one month before a detailed dissection was performed by the authors. Unfortunately, none of its visceral organs were available for examination of evidence of other lesions such as those described by Jepson *et al*. (2003).

The blubber weighed 201.7kg, which represented about 23% of the total reported mass of the whale. This was higher than the mean reported for mesoplodonts (Mead, 1989) and suggests that the Linbian ginkgo-toothed beaked whale was in good body condition before death. In addition, photographs of the whale did not reveal any obvious signs of emaciation. There was a substantial number of parasitic cysts (possibly *Phyllobothrium delphini*) in the blubber, particularly in the dorsal and ventral areas of the tailstock around the genital region. However, the level of infestation by this parasite in the blubber of the Linbian ginkgo-toothed beaked whale was not unusually heavy and similar levels have been observed in many presumably healthy cetaceans that were taken by local fisheries (J.Y. Wang, unpublished data).

The head

A circular area (about 20-25cm in diameter) of bruising in the left lower jaw region just ventral of the gape and some superficial damage to the skin were present. A longitudinal section of the melon along the midline revealed severe haemorrhaging in a pattern of several vertical stripes (or planes in three dimensions; Fig. 2a). The lower jaw fats also appeared to be discoloured by blood but this was not as striking as in the melon. Both tympanic bullae were shattered into many fragments (Fig. 2b) and a small amount of blood was observed in the tissues surrounding the bullae. Breakage of the tympanic bones occurred generally in the thinnest areas of the bones. Haemorrhage was found in the tissues lining the ventral regions of the pterygoid bones, the ventral margins of which were also severely fractured (and again breakage occurred generally in the thinnest portions of the bones; Fig. 2c). A considerable amount of dark blood was found under the skin lining the upper portion of both walls of the nasal septum of the external nares (Fig. 2d). The larynx appeared normal externally and no obvious signs of damage were found upon gross examination of this structure in longitudinal section. Haemorrhage in bone tissue was found in a wide band across the top of the anterior face of the cranial vertex and at the upper portions of the nasal septum. A fresh dark circular scar (about 1-1.5cm in diameter) that resembled knife damage to the bone was also observed on the right premaxilla on the anterior face of the cranial vertex and within the band of haemorrhage yet the tissue in this region was never removed by cutting (these injuries were discovered after the skull was cleaned of tissue using water maceration; Fig. 2e). The rest of the skull was undamaged with the exception of the fragile tip of the rostrum and the thin, brittle postero-ventral corner of both sides of the mandibles that were broken during skeleton preparation. A fully-healed fracture from a previous injury across the tip of the lower jaw was also found.

The body

On each side, there were 11 vertebral ribs (8 two-headed, 2 single-headed and 1 floating). The 10th vertebral rib on the right side was cut near the middle by veterinarians during necropsy. The vertebral formula was: C_e 7, T 11, L 10, C_a 20 = 48 (the last caudal vertebra was counted as one unit because its shape and size did not appear to be the union of two vertebrae). Some haemorrhage was found in the vertebral disk between the 9th and 10th lumbar vertebrae but the cause of the haemorrhage is unknown and may have been incurred during the stranding process, in the final moments prior to death.

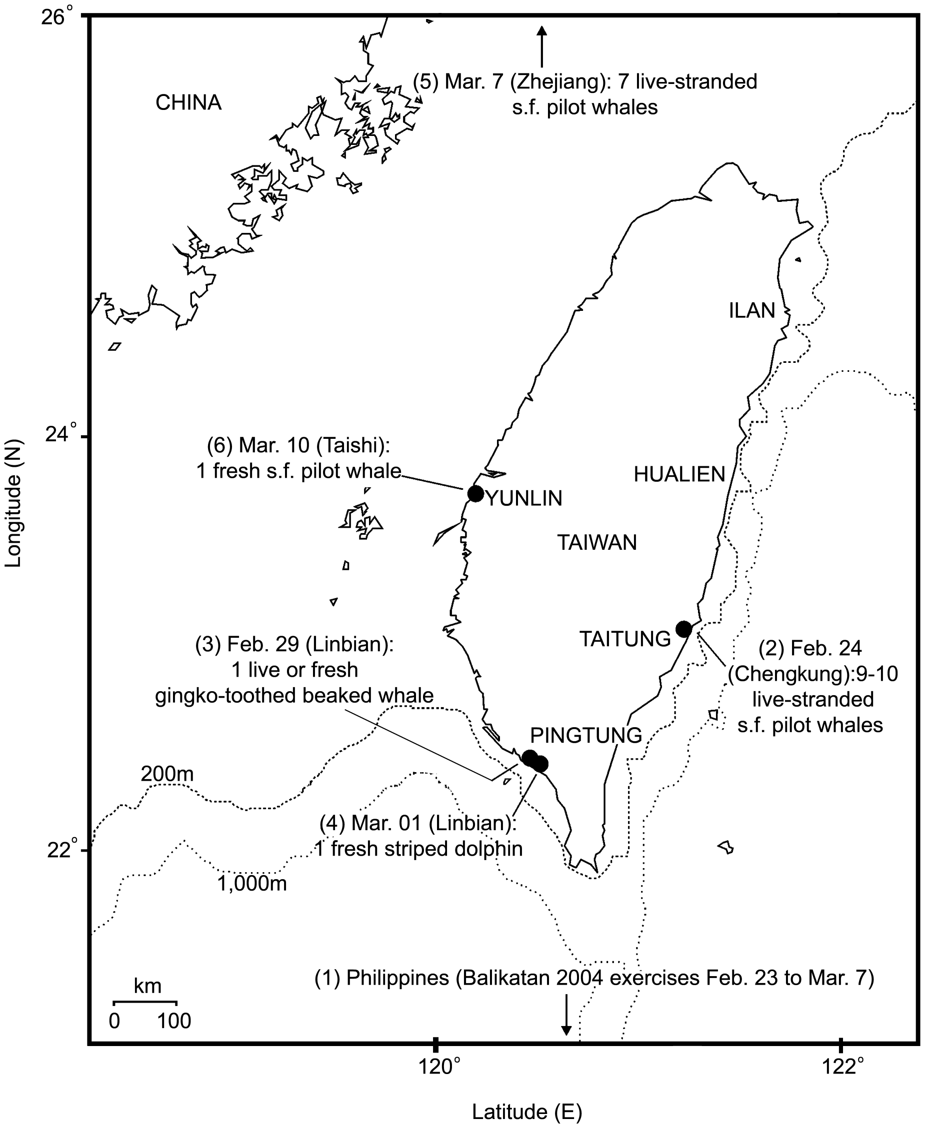

Fig. 1. Map showing a series of events that occurred on the island of Taiwan during the winter of 2004 (with one event being in Zhejiang Province, mainland China). Numbers represent the chronological order of the events.

Examination of the thoracic *rete* revealed extensive haemorrhage in the anterior approximately three-quarters of this structure. The vermiculate blood vessels in the anterior three-quarters of the thoracic *rete* were hardly, if at all, visible while the vessels in the posterior one-quarter were clear. The phalangeal formula of both flippers was: I 1, II 7, III 6, IV 5, V 4. Many metacarpal and phalangeal bones were broken at about the middle of the flippers but these injuries were likely incurred post-mortem, during the handling of the specimen.

The complete skeleton of this specimen was cleaned and is in the collection of the NMMBA (specimen code: JYW-04-02).

Chronology of the second series of events (see Fig. 3)

22 February 2005: Eight pygmy killer whales stranded alive on the shores near Jiangjun fishing port (Tainan County); three died, three were reportedly returned to sea and the other two were assumed to have been returned to sea. Initial reports misidentified these cetaceans as melon-headed whales (*Peponocephala electra*).

23 February 2005: 28 pygmy killer whales stranded alive on a beach near Chinshan fishing port, (Chiku village, Tainan County), which is about 5km south of the area above. Nine died, the remaining 19 were returned to sea.

23 February 2005: A Risso's dolphin stranded alive near Fangyuan village (Changhua County) and was sent to the NMMBA for rehabilitation, but died three days later.

26 February 2005: A school of 20-25 pygmy killer whales (species identification could not be confirmed from photos available) swam into the Nanxing industrial area of Hongmao port (Kaohsiung) around 10:00hrs.; coast guards herded them out at about 16:00hrs.

1 March 2005: A small Risso's dolphin was seen swimming in very shallow waters close to shore near Nanwan, Kenting National Park (Pingtung County). Attempts to catch it failed and it swam offshore.

Of all the stranded pygmy killer whales, two were kept for rehabilitation but died within a few days. All specimens were examined by local veterinarians and pathologists as commissioned by the Tainan County government.

Fig. 2. Internal injuries to the head of a ginkgo-toothed beaked whale that stranded on 29 February 2004. Arrows and ovals show the injuries: (a) vertical stripes of haemorrhage in the melon; (b) shattered tympanic bullae; (c) fractured pterygoid bones; (d) haemorrhage and blood clot under the skin lining the nasal septum; and (e) haemorrhage across the anterior face of the cranial vertex and nasal septum. (Photographs by John Y. Wang/*FormosaCetus*).

Only the Risso's dolphin of 23 February and one partially flensed, but completely eviscerated pygmy killer whale were available to the authors for *post mortem* examination (see below). Coincidentally, these events occurred during the same period (last week of February to first week of March) as the events of 2004.

Gross examination of the Tainan pygmy killer whale

General information

For the Tainan pygmy killer whale, only a partially intact head (area anterior of the blowhole and lower jaw were intact; the posterior part of the head was cut open and brain removed) and partially flensed and eviscerated body were available for examination. The accompanying information indicated this individual was involved in the 23 February mass stranding event. From the incomplete carcass, the body length was measured (piece meal) to be about 225cm and it was male. The thickness of the blubber of the animal was not unusually thin in any area of the body and appeared to be in good condition (note: photographs of most of the other dead specimens showed them to be fairly robust and none exhibited obvious signs of emaciation).

The head

There was a partially healed 'cookie-cutter' shark type wound on the right side of the anterior part of the head. The crater of missing flesh from the attack was about 3cm long, 2.5cm wide and 1.5cm deep. However, there were no other

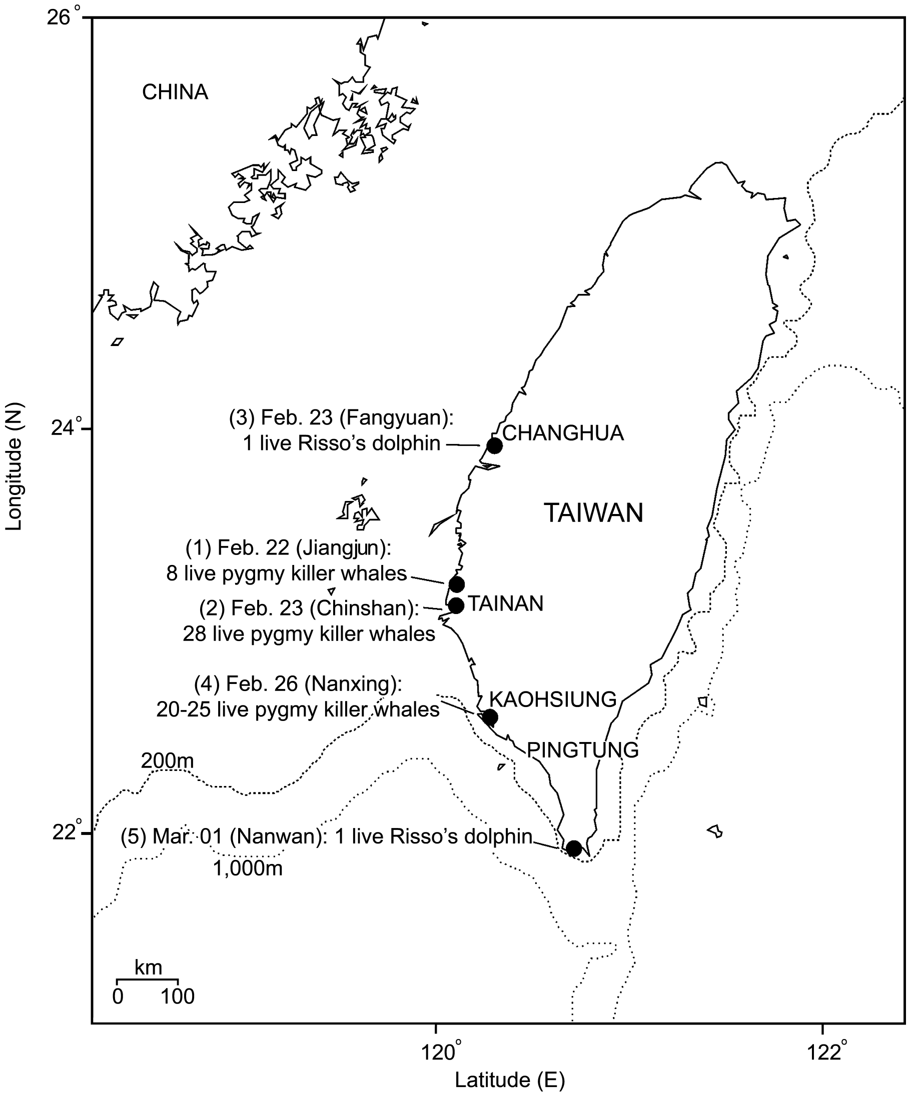

Fig. 3. Map showing a series of events that occurred on the island of Taiwan during the winter of 2005. Numbers represent the chronological order of the events.

obvious external injuries to the anterior part of the head and lower jaw regions. Fairly heavy loads of parasites were discovered in the auditory, pterygoids and orbital sinuses. In the melon, an unusual sheet of haemorrhage was found running parallel to and about 2cm above the plane of the rostrum and in a wedge shape. The wedge of haemorrhage was about 4-5cm wide, extended throughout almost the entire length of the melon and was thickest laterally on the right side and gradually became thinner medially and across to the left of the midline of the melon (Fig. 4). Given the incompleteness of the specimen, our examination was limited. The skull has not yet been prepared for examination or measurements and is being maintained in the freezers of the NMMBA (specimen code: JYW-05-09).

The body

Numerous completely healed 'cookie-cutter' shark type wounds were also found on the body, especially around the urogenital region. No obvious unusual internal or external injuries were noted but the material available was extremely limited. The skeleton has not been prepared and is being maintained in the freezers of the NMMBA (specimen code: JYW-05-09).

Gross examination of the Fangyuan Risso's dolphin

General information

The Fangyuan Risso's dolphin stranded on 23 February 2005, but died a few days later after unsuccessful rehabilitation efforts. It was a male measuring 262.0cm and 259.6kg (weighed after death). The entire carcass was frozen for 4.5 months before *post mortem* examination. There were no obvious gross signs of unusual injuries. The skeleton has not been prepared for examination or measurement and is maintained in the freezers of the NMMBA (specimen code: JYW-05-01).

Chronology of the third series of events (see Fig. 5)

It is important to note that the following list was compiled from local news sources and is only a subset of the many stranding events that occurred. A closed workshop aimed at examining the possible cause(s) of the large number of unusual stranding events in Taiwan was convened recently and included international cetacean pathologists, who examined the remains of some of the carcasses and histological preparations (see Anon., 2005a). During an open symposium on these unusual strandings in 2005, it was reported that from 19 July to 13 August, there were 22

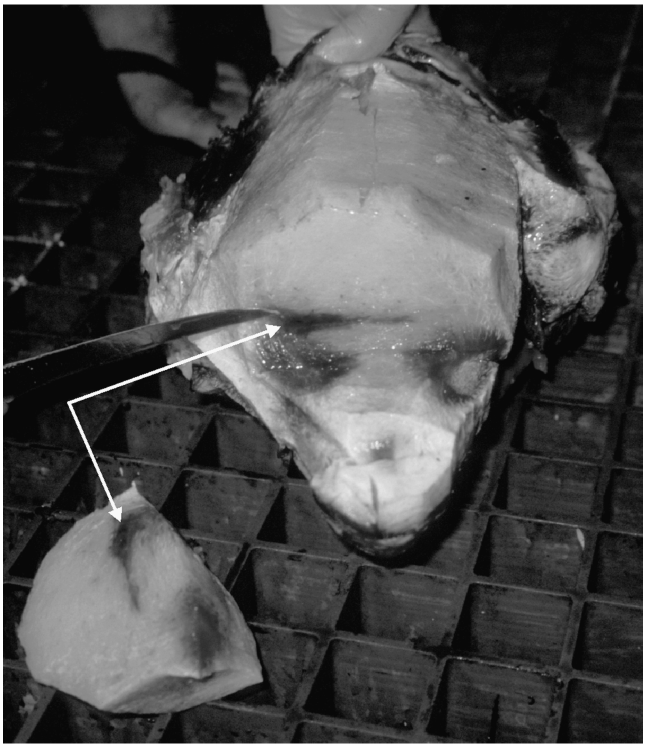

Fig. 4. A head-on view of a cross section of the melon at about mid-rostrum of a pygmy killer whale that stranded on 23 February 2005. Arrows point to the area of haemorrhage (Photograph by Shih-Chu Yang/*FormosaCetus*).

stranding events involving at least 7 species and 25 individuals (Yang, 2005). In five or six of the individuals examined, 'bubble-like' lesions were reported (Yang, 2005), but more detailed analyses of these lesions and other tissues were still being conducted by workshop participants.

19 July 2005: A single pantropical spotted dolphin (*Stenella attenuata*) was found dead on a beach of Chijin (Kaohsiung County). News reported the animal was discovered at about 16:30hrs and appeared to have been dead for about a day.

20 July 2005: A dwarf sperm whale (*Kogia sima*) was found dead on a beach near Aodi/Gongliao (Taipei County) in the evening.

21 July 2005: Two striped dolphins stranded alive on the shores of Toucheng (Ilan County) in the morning (one died, the other was returned to the sea on July 22).

21 July 2005: One *Kogia* sp. (species identification could not be confirmed by the authors) stranded alive on the shore near Aodi/Gongliao (Taipei County) and was discovered at about 15:00hrs; it was later returned to the sea.

22 July 2005: Two beaked whales were seen swimming close to shore in shallow waters off Ilan County in the afternoon.

22 July 2005: One cetacean of unknown species stranded alive near Suao (Ilan County) in the afternoon but was returned to the sea.

22 July 2005: One live or freshly dead dwarf sperm whale was found on a beach of Xiamen, Fujian province of mainland China (the news article reported it as a minke whale but the accompanying photograph clearly showed a dwarf sperm whale).

23 July 2005: Two (possibly mother and calf pair) Longmans's beaked whales (*Indopacetus pacificus*) stranded alive on a beach near Suao (Ilan County) in the afternoon and died. These animals were originally misidentified as ginkgo-toothed beaked whales.

24 July 2005: A Blainville's beaked whale was found alive on a beach at Wujie (Ilan County) at 12:30hrs but died shortly afterwards. This animal was also misidentified initially as a ginkgo-toothed beaked whale.

26 July 2005: The East China Sea (Donghai) Fleet of the People's Republic of China was reported to have held exercises in July[1] but no details (including dates) of the exercises were disclosed in the report.

29 July 2005: A dead *Kogia* (species identity could not be confirmed by the authors) washed into the port of Keelung City. However, there are mixed reports that claimed this was a dwarf sperm whale that was alive when discovered.

30 July 2005: One dwarf sperm whale was found swimming in Taichung Harbour (Taichung County).

30 July 2005: One dwarf sperm whale (species identity could not be confirmed by the authors) stranded alive on a beach of Hsinchu County and was returned to the sea.

3-4 August 2005: Taiwan's navy held exercises (Han-Kuang No. 21) off southwest Taiwan that involved depth charges (see *www.taipeitimes.com*, 04 August 2005).

7 August 2005: US/Japan joint exercises (JASEX) in and around the waters of Guam and Okinawa began (see US Pacific Command's official website[2]).

10 August 2005: A young Blainville's beaked whale stranded alive on a beach of Zhunan (Miaoli County) and kept for rehabilitation before dying about three days later.

13 August 2005: JASEX ended (see US Pacific Command's official website[2]).

This series of events was composed mainly of deep-diving and oceanic species. In Taiwan, striped dolphin records are relatively rare as stated earlier. The large number of *Kogia* spp. and beaked whale strandings over such a short period is highly unusual. This stranding rate is by far the highest ever recorded in Taiwan, where an active reporting network for cetacean strandings has operated since the mid 1990s. Because the first stranding (19 July, pantropical spotted dolphin) was located at a distance from all other earlier stranding events, the former case is unlikely to be related to the others. The strandings in July were not related to the naval exercises of Taiwan or the US and Japan listed above. However, it is unclear if military exercises were being conducted by the People's Republic of China. Investigations into potential causes of these unusual stranding events, including military activities and detailed pathological examinations of some of the carcasses, are being conducted presently (Anon., 2005a).

DISCUSSION

Many of the severe internal injuries sustained by the Linbian ginkgo-toothed beaked whale were extraordinary because there were no obvious signs of external injuries with the exception of bruising to the left lower jaw region ventral to the gape and superficial damage to the skin (the latter damage was almost certainly caused during post-mortem handling of the specimen). In addition, the well-protected (by soft tissue and bone) tympanic bones were shattered, yet there was no damage to the lower jaw bones or calvarium adjacent to this area. The pterygoid bones were also fractured even though this region of the head is also well protected from physical trauma by soft tissue and the lower jaw. Furthermore, all obvious injuries (except the vertebral disk haemorrhage) were to, or adjacent to, anatomical

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[1] *www2.chinesenewsnet.com/NewsPics/Reuters/Tue_Jul_26_19_42_29_2005.html*

[2] *http://www.pacom.mil/exercises/jasex05/index.shtml*

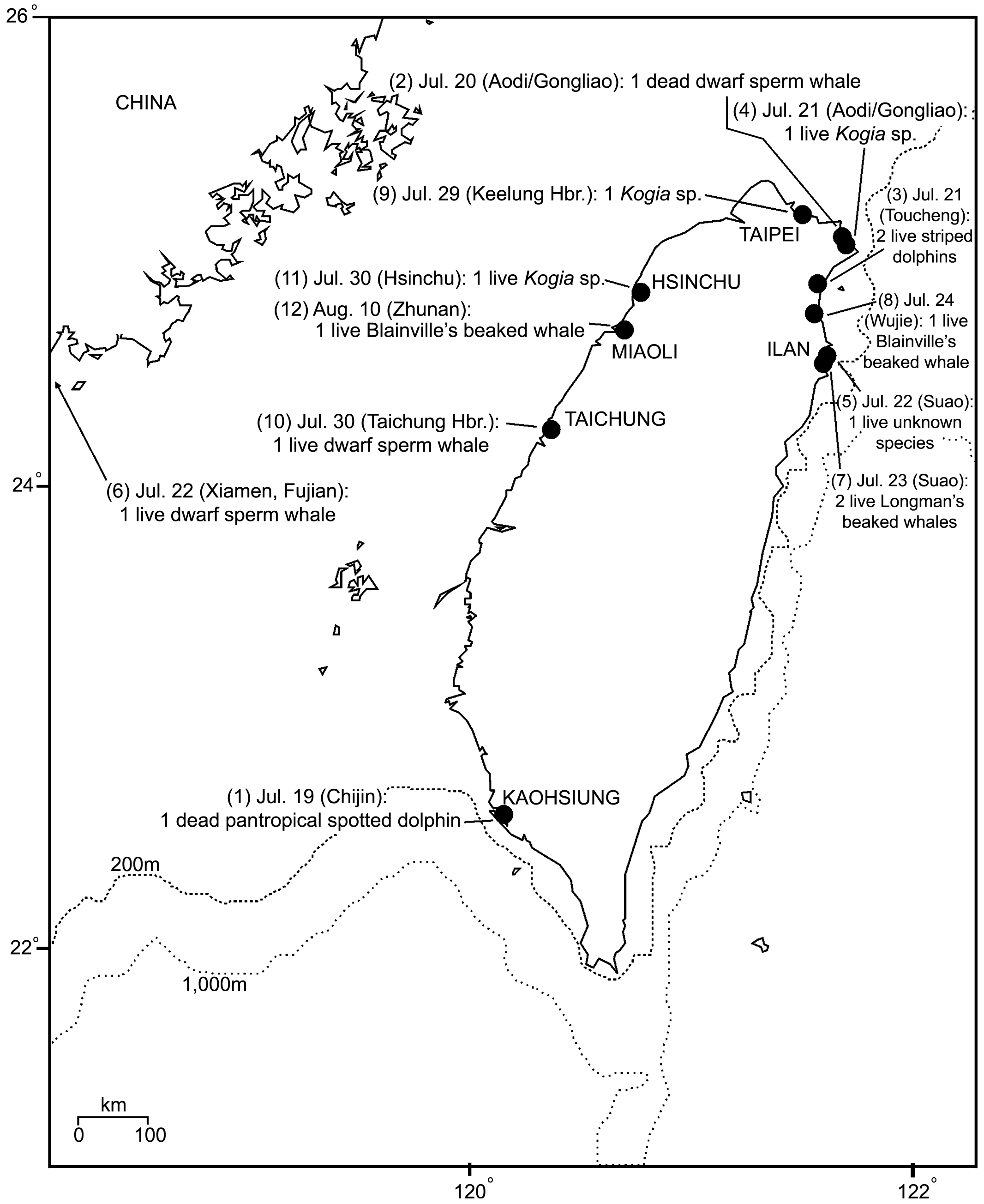

Fig. 5. Map showing a subset of a series of stranding events that occurred on the island of Taiwan during the summer of 2005 (with one event being in Fujian province, mainland China). Numbers represent the chronological order of the events.

structures associated with the animal's acoustic sense (i.e. melon, lower jaw fats, nasal septum, tympanic bones, anterior face of the cranial vertex) or likely involved in or related to diving (i.e. thoracic *rete*, pterygoid bones). Unfortunately, none of the visceral organs were available for examination. The freshness of the carcass, its discovery location and the coincidence of the event with nearby large-scale military exercises are suggestive that the energy source may have originated from these exercises.

The haemorrhage in the melon of the pygmy killer whale somewhat resembled the melon injuries observed in the Linbian ginkgo-toothed beaked whale but the haemorrhage was not as extensive or severe and in a different orientation than the latter case and no other soft tissue injuries were found during gross examination of the limited material available. We suspect that at least some of the other more than 30 individuals involved in the mass stranding events at Tainan on 22 and 23 February 2005 would also exhibit similar, and possibly more, injuries. It would be too coincidental that the only and incomplete specimen that we examined be the only one with such injuries. However, we can only await the findings of those who performed the *post mortem* examinations on the other specimens. Although the 2005 event involved the largest number of individuals, there have been prior cases of mass stranding events of pygmy killer whale in Taiwan such as in 1996, 1997 and 2002 (unpublished data). The causes of pygmy killer whale strandings in Taiwan are unknown and require more attention.

Live single stranding events involving Risso's dolphin are fairly common and it is one of the most commonly encountered species in Taiwanese waters (see Chen, 2001; Huang, 1996; Wang *et al.*, 2001; Yang *et al.*, 1999; Yeh, 2001) so the occurrence of the Fangyuan stranding event was not unusual, probably unrelated to the pygmy killer whale stranding events and maybe a ‘natural’ background event.

The number of unusual cetacean stranding events during and shortly after the end of nearby naval exercises suggests that stranding events involving cetacean species other than beaked whales (particularly, *Kogia* spp. and short-finned pilot whale) should also be examined in the context of military activities. However, unlike the Bahamas stranding events in 2000 (Balcomb and Claridge, 2001), a full suite of information is unlikely to be available for these Taiwanese cases. However, the following factors may be rejected for some of these cases.

Earthquakes

Most of the unusual strandings did not appear to be related to earthquakes. Earthquakes occur often and tectonic movements exceeding magnitude 5.0 (Richter scale) are fairly frequent in and around Taiwan, yet large numbers of strandings are not so common. On 29 February 2004, two earthquakes measuring magnitude >4.0 (at the epicentres) were recorded in the morning off Ilan County (northeast Taiwan) and off Hualien County (central eastern Taiwan) before the discovery of the Linbian ginkgo-toothed beaked whale (see Anon., 2004 for earthquake information). However, it is unlikely that these activities caused or contributed to the death of this animal because the earthquakes were relatively minor (for Taiwan) and the epicentres were situated about 200-275km (point-to-point distance across land) away from the town of Linbian in southwest Taiwan. Similarly, it is also unlikely that the Linbian striped dolphin stranding of 1 March 2004 was related to earthquakes (>4.0) that occurred off Hualien County in the evening of 29 February 2004 and the early morning of 1 March. The other stranding events on 7 and 10 March were distant, temporally and spatially, from sizeable seismic movements that occurred in March prior to the stranding events (Anon., 2004).

Two earthquakes measuring almost magnitude 5.0 (at the epicentres) were recorded on 23 and 24 February 2004 just north of the location of the 24 February 2004 mass stranding of short-finned pilot whales (see Anon., 2004 for earthquake information). Presently, with minimal information from the carcasses of the short-finned pilot whales, natural seismic activity cannot be eliminated completely as the cause of, or a contributing factor, to this mass stranding event.

From 20 February to 1 March 2005, five sizable earthquakes measuring over magnitude 4.0 were recorded (Anon., 2005b). In the early morning of 23 February, a 4.19 earthquake was recorded near Orchid Island, which is fairly distant from the stranding locations in Tainan County. Also, it is likely that the 23 February stranding of pygmy killer whales were related to the stranding event of the previous day so it seems unlikely this earthquake was the cause of the stranding of these pygmy killer whales. The other four large earthquakes occurred on 28 February off and along eastern Taiwan (Ilan and Hualien counties), quite distant (about 200-330km) from the location where a small Risso’s dolphin nearly stranded on 1 March. We conclude that earthquakes are unlikely to be the reason for any of the cetacean strandings during this series of unusual events.

There were 15 recorded earthquakes between 18 July and 10 August, 2005 that were at least magnitude 4.0 (of these two were >5.0) at their epicentres (Anon., 2006a). However, due to either the distance of the stranding locations from the epicentres of the earthquakes and time of the movements, only for the following six events would earthquakes be a potential factor: 21 July – two striped dolphins in Ilan County; 21 July – one *Kogia* sp. in Taipei County; 22 July – two beaked whales reported near the shore of Ilan County; 22 July – one stranded cetacean that was sent back to sea; 23 July – two Longman’s beaked whales in Ilan County; and 24 July – one Blainville’s beaked whale. There were five earthquakes that could be related to these stranding or near-stranding events. On 19 July, there was an earthquake off Hualien County (4.28). On 20 July, there were two earthquakes, one inland in Pingtung County at 18:48hrs (4.29) and one along the coast of Ilan County at 21:06hrs (5.22). On 22 July, there was an earthquake also along the east coast at Taitung County at 19:52hrs (4.17). Finally, on 23 July, there was a magnitude 4.41 earthquake at 01:18hrs (Hualien County). As there is little information available presently on these stranding victims, earthquakes can not be eliminated as at least a contributing factor to their stranding.

More research is needed to understand the effects, if any, of earthquakes on cetaceans. However, it is clear that earthquakes were not the main factor in causing most of the stranding events presented in this paper. It is also noteworthy that Taiwan is an area where natural seismic activities are common (Anon., 2004; 2005b; 2006a) but the recent numbers of stranding events have not been equally as common. For example, from 4 January to 29 June 2005, there were more than 50 earthquakes that were magnitude 4.0 or greater and more than ten that were greater than or equal to 5.0 (mostly off eastern Taiwan), but there were fewer stranded cetaceans during this period than between 19 July and 13 August 2005. If earthquakes do affect cetaceans, there does not appear to be any obvious temporal or spatial pattern between stranding events and the magnitude (as measured on the Richter scale) of the seismic activities.

Typhoons

For the first (February/March 2004) and second (February/March 2005) series of stranding events, typhoons were not a factor. Even though two typhoons (*Matsa* and *Haitang*, the latter being a super typhoon) battered Taiwan during the period of the third series of strandings (Anon., 2006b), severe weather was unlikely to have been the primary cause of all the strandings because typhoons are common in Taiwan from June to September but such large numbers of stranded cetaceans have not been recorded in previous years. Furthermore, there was an overwhelmingly high number of infrequently encountered species (e.g. kogiids and ziphiids) and almost none of the more common species in Taiwanese waters such as spinner dolphins (*Stenella longirostris*), Risso’s dolphins, pantropical spotted dolphins and bottlenosed dolphins (*Tursiops* spp.). However, it is possible that the typhoons led to the beaching of compromised individuals and although it may be possible that deep-diving cetaceans were more susceptible to these recent storms, it is difficult to explain why previous and subsequent powerful storms did not have a similar impact on local cetaceans.

Seismic research

The main research ship for seismic surveys in Taiwan is the *Ocean Researcher No. 1* and vessel equipment and activities are well documented (e.g. National Center for Ocean Research of Taiwan, *www.ncor.ntu.edu.tww* and *www.ntuio.oc.ntu.edu.tw*). The *Ocean Researcher No. 1* has seismic equipment and CHIRP sonar. Prior to the period of the first series of strandings, there were two student training (of physical oceanography) trips that were made by *Ocean Researcher No. 1* from 10-21 February 2004 and 25-27

February 2004 (in the coastal waters off SW Taiwan). These trips did not appear to involve seismic surveys using air guns or sonar.

During and just prior to the second series of stranding events (late February/early March 2005), *Ocean Researcher No. 1* did not conduct any research trips so could not have caused these strandings.

Around the period of the third series of stranding events, there were several research trips by *Ocean Researcher No. 1*: 16-20 July (OR1 759 – ODP surveys); 24-31 July (OR1 – 760 VANS surveys); 2-3 August (student training trip from Kaohsiung to Keelung); 4-5 August (student training trip from Keelung to Kaohsiung); and 6-17 August (South China Sea research). On July 16 and 17 and from 24-31, ocean floor surveys of the northern part of the South China Sea (off the continental shelf) were conducted using the CHIRP sonar. This sonar has a frequency range of 3-11kHz and a beam width of 25-50°. It seems highly unlikely this sonar system could have caused most, if any, of the strandings in the northern parts of Taiwan in the latter half of July. Furthermore, air guns were never used during or prior to any of the three series of unusual strandings. However, seismic research cannot be ruled out completely because smaller vessels are capable of conducting seismic surveys and seismic research vessels from mainland China may also be conducting surveys in adjacent waters. Oil/gas and mineral exploratory activities are increasing in the region and the impact of such surveys on cetaceans needs to be examined. Much more detailed information about seismic research equipment and activities in and around Taiwanese waters is required (see IWC, in press).

CONCLUSIONS

Although, some factors can be eliminated as the cause of some strandings, it is difficult to make solid conclusions about the causes of most of these events or the serious internal injuries that were found during gross examination of two of the animals involved. However, at least one, the Linbian ginkgo-toothed beaked whale, coincided with large-scale military exercises south of Taiwan and the internal injuries that were sustained by this whale were remarkable. Naval sonar and live ammunition exercises are two of many plausible causes that need to be investigated. However, given the paucity of *post mortem* results from other cetaceans that stranded and other supporting information (e.g. recordings of ocean sounds, details about the military exercises, etc.), it is impossible to determine the reason for the unusual stranding events. For the most recent series of events, more detailed *post mortem* results are expected, but information about human and natural activities in this region is also needed urgently.

Recommendations

It was unfortunate that the *post mortem* results of only one complete and two partial carcasses from the first two series of stranding events were available. To increase our knowledge and understanding of the impact of human and natural activities on cetaceans, all specimens need to be examined properly by experienced researchers. Given the large and increasing military presence of several nations in Chinese and adjacent waters, including the newly acquired Kidd Class destroyers (which possess the 53C mid-frequency sonar that has been implicated in the deaths of some cetaceans – see England and Evans (2001)) of the Taiwanese navy, it would not be surprising if more unusual cetacean stranding events occurred in the future. One of the aims of this paper is to bring attention to the possibility of an, as yet undocumented, impact of naval and seismic research activities on populations of cetaceans inhabiting Taiwanese and adjacent waters, which needs to be investigated with the help of international expertise. Below are several recommendations that can help to increase our understanding of anthropogenic and natural activities on cetaceans in this region.

(1) Local researchers and government authorities need to acknowledge that military activities may seriously injure or kill cetaceans and lead to stranding events.

(2) All efforts should be made to preserve entire carcasses of all stranded cetaceans (especially deep-diving or oceanic species) for examination by experienced researchers and to collaborate with international experts on cetacean pathology.

(3) All unusual stranding events should be examined with considerations of recent military or other activities emitting intense amounts of energy (e.g. live fire target practice, seismic research, etc.) in local and neighbouring waters.

(4) Information about military exercises needs to be obtained or made available if presently unavailable to improve the understanding of the issue(s).

(5) Taiwanese waters should be monitored acoustically on a continuous basis.

(6) Live stranded cetaceans (especially of deep-diving or oceanic species) should not be returned to the sea immediately because they are unlikely to survive. Release of an animal should only be conducted if the animal can be demonstrated to be healthy and can be tracked remotely (e.g. with satellite telemetry), as well as monitored visually after release for a minimum of one to two months as recommended by St. Aubin *et al.* (1996). Unless a released animal can be monitored, success of the release (and any rehabilitation efforts) cannot be determined.

ACKNOWLEDGEMENTS

We would like to thank the Pingtung, Changhua and Tainan County governments for providing the Linbian ginkgo-toothed beaked whale, the Fanyuan Risso's dolphin and the Tainan pygmy killer whale, respectively. We would also like to thank several people at the National Museum of Marine Biology and Aquarium (L.-S. Fang, J.-I. Liao, W.-J. Su and T-M. Hsiao) for their continued support of and help with our research and E.C.M. Parsons for providing information and encouragement. This paper was improved by A. Fernández and an anonymous reviewer who provided valuable suggestions.

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Date received: December 2005
Date accepted: July 2006

A note on the first record of the dwarf minke whale (*Balaenoptera acutorostrata*) in Chilean waters

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ABSTRACT

Two species of minke whale have been recognised, the larger Antarctic minke whale (*Balaenoptera bonaerensis*) restricted to the Southern Hemisphere, and the common minke whale (*B. acutorostrata*), which is distributed globally. The common minke whale of the Southern Hemisphere is referred to as the dwarf minke whale. The occurrence and identity of minke whales in the coastal waters of Chile are examined based on animals stranded and sighted in the Patagonia Channels. A total of three strandings and five sightings of the minke whale were examined in this study. Comparative analysis of external characteristics between the stranded animals and the two recognised species of minke whale identified these animals as dwarf minke whales. Of the five sightings, two were identified as Antarctic and two as dwarf minke whales based on observation of the presence/absence of the white patch on the flippers. This is the first record of the dwarf minke whale in the coastal waters of Chile. Based on available information on temporal distribution of sightings in the western south Atlantic, it is suggested that the population of dwarf minke whales wintering off Brazil may move to the south in summer, some moving into the Patagonia Channels.

KEYWORDS: SOUTH AMERICA; DWARF MINKE WHALE; ANTARCTIC MINKE WHALE; DISTRIBUTION; COLOURATION

INTRODUCTION

Rice (1998) reviewed morphological (e.g. Omura, 1975) and genetic (e.g. Pastene *et al.*, 1994; Wada *et al.*, 1991) data collected from extant minke whales and sub-divided them into two species; the larger Antarctic minke whale (*Balaenoptera bonaerensis*) restricted to the Southern Hemisphere and the common minke whale (*B. acutorostrata*), which is distributed globally. In the Southern Hemisphere the common minke whale is referred to as the 'dwarf' or 'diminutive' minke whale (Arnold *et al.*, 1987; Best, 1985).

Records of the dwarf minke whale are scarce but cover a wide longitudinal area: Paraiba, Brazil (da Rocha and Braga, 1982; Zerbini *et al.*, 1996); New Zealand (Baker, 1983); Durban, South Africa (Best, 1985); and northern Queensland, Australia (Arnold *et al.*, 1987). The dwarf minke whale was only believed to be found between 7-41°S (Best, 1985) as no dwarf minke whales had been identified in past commercial catches near the ice-edge. However, the occurrence of dwarf minke whales in the catches made during the earlier part of the JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) surveys in Areas IV and V was mainly between 55-61°S, although one individual was caught at 65°S (Kasamatsu *et al.*, 1993), showing that the dwarf minke whale can be found much farther south than previously thought.

Off the Chilean coast, minke whales have been reported in oceanic waters from Mejillones Bay (23°20'S) to the Drake Passage, including waters around Eastern Island (Aguayo-Lobo *et al.*, 1998a; Aguayo-Lobo *et al.*, 1998b). This study reports on strandings and sightings of minke whales in the Patagonia Channels and describes the first observed occurrence of the dwarf minke whale in Chile.

MATERIALS AND METHODS

Strandings

Three stranded minke whales were available for this study. The strandings occurred in April 2004 at Navarino Island (Fig. 1). The strandings were found by local fishermen and pilots of a local commercial air company (DAP) who informed the government authorities of Puerto Williams. The authorities then informed scientists of the Marine Biology Group of the CEQUA (Center for the Studies of the Quaternary), which is based in Punta Arenas and scientists from this group visited the strandings. No stranding network or systematic survey to search for carcasses exists in Chile.

External characteristics (morphological) and observations of the baleen plates of the stranded animals were recorded in the field. Species identification was made by comparing external morphology in photographs of the stranded individuals with those of known minke whale species. Tissues samples collected were preserved in 95% ethanol for future genetic analysis. Osteological material and external measurements were collected by the Puerto Williams Museum but were not available for this study.

Sightings

Marine mammal surveys in the Magellan Strait, Beagle Channel and Cape Horn areas were conducted in the spring and summer seasons during the period 1999-2004. Surveys were made from vessels. Some were systematic (e.g. those conducted by the Marine Biology Group of CEQUA since September 2002) and others were opportunistic (observations made from vessels transiting between Punta Arenas and the Antarctic Peninsula). Field observations were made by marine mammal specialists from the bridge or front bridge (bridge wings) of the vessel. For each sighting, geographic location, species identity, school size, estimated body length and behaviour were recorded.

RESULTS AND DISCUSSION

Strandings

Three whales were found stranded at Navarino Island (Table 1, Figs 1 and 2). One of the carcasses (UCM1 in Fig. 2) was found in an advanced state of decomposition while the other two (UCM2 and UCM3 in Fig. 2) were in a relatively fresh state. These individuals were identified as dwarf minke

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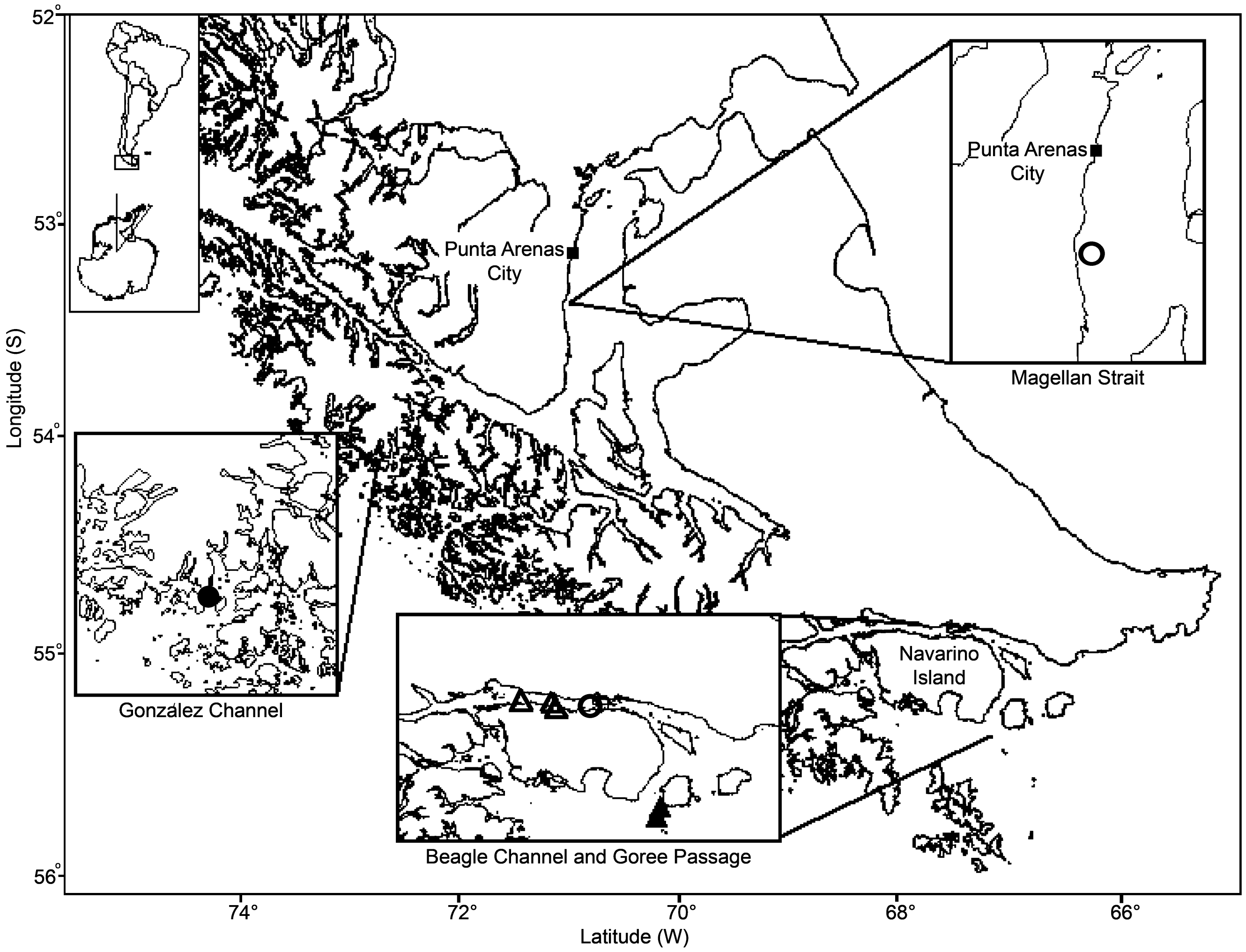

Fig. 1. Map showing the location of the stranding of dwarf minke whales (open triangle), sightings of dwarf minke whale (closed triangle), sightings of Antarctic minke whale (open circle) and unidentified minke whale (closed circle), in the waters off the southern tip of South America, Chile.

whales, based on the presence of a white patch on the flipper and white 'shoulder', and dark pigmentation on the ventral grooves (e.g. Arnold *et al.*, 1987; Best, 1985); Table 2.

Sightings

A total of five minke whale sightings were recorded during the 1999-2004 surveys in the Patagonia Channels (Table 3, Fig. 1): two were identified as dwarf, two as Antarctic minke whales and one remained unidentified. One of the Antarctic minke whales was sighted in the Beagle Channel and the other in the Magellan Strait, 40km southwest of Punta Arenas. In both cases there were good opportunities for observations; the closest distance between the vessel and the whale was about 25m. Whales were identified as Antarctic minke whales by absence of the white patch on the flippers. The animal observed near Punta Arenas was feeding very near to the coast probably on sardines, which occur in the area around the sighting. Both dwarf minke whales were sighted at Goree Passage (south of Navarino Island). There were good opportunities for observations; the closest distance from the vessels to the animals was 10m. Both animals were swimming to the north and the survey vessel was steaming to the south. These whales were identified as dwarf minke whales by the striking white patch observed on the flippers.

The results of this study suggest that both Antarctic and dwarf minke whales occur in the Patagonia Channel in summer and early autumn. One of the questions to be resolved is the location of the wintering grounds for these animals. Minke whales are rarely observed in the eastern South Pacific, but they are commonly observed in the western South Atlantic. This is similar to the situation in southern Africa where they are rare off southwestern Africa but are common off southeastern Africa (Williamson, 1975). Both species occur in the wintering ground off Brazil, indicating a degree of overlapping in their distributions (Zerbini *et al.*, 1996), but the dwarf minke whale is more commonly observed near the coast, as has also been

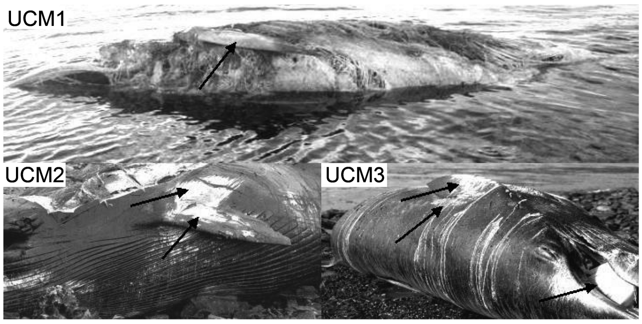

Fig. 2. Individual dwarf minke whales stranded at Navarino Island. UCM 1 shows a white patch on the flipper; UCM 2 shows a white patch on the flipper and white shoulder; UCM 3 shows a white patch on the flipper, white shoulder and white pattern of coloration of baleen plates.

Table 1

Place, date, geographical position and biological information for three minke whales stranded in southern Chile.

	Place	Date	Latitude	Longitude	Sex	Condition of the carcass
UCM1	Honda Bay	12/04/04	54°52'18''S	68°02'14''W	Unknown	Decomposed
UCM2	Robalo Beach	17/04/04	54°54'02''S	67°47'19''W	Male	Fresh
UCM3	Robalo Island	19/04/04	54°53'02''S	67°42'33''W	Male	Fresh

Table 2

Comparison of external characters between UCM2, 3 and dwarf and Antarctic minke whales examined by Best (1985) and Arnold *et al.* (1987).

	UCM2	UCM3	Dwarf minke whale	Antarctic minke whale
Body length	6.75m	6.87m	7.01m	9.50m
Baleen plate colouration	Predominantly white with a thin black band	Predominantly white; no black band	Predominantly white with a thin black band	Some white; some with a black band occupying 2/3 or 1/2 of the surface; some completely black
Proportion of white baleen plates	+80%	100%	70-100%	-50%
Size of largest baleen plate	19.0cm	20.5cm	18-20cm	<22cm
Flipper white patch	Present	Present	Present	Absent
Shoulder white patch	Present	Present	Present	Absent
Dark pigmentation in ventral grooves	Present	Present	Present	Absent

Table 3

Species, sighting date and location and school sizes of five sightings of minke whales recorded in the coastal waters of southern Chile.

Species	Date	Place	Latitude	Longitude	No. of whales
Antarctic minke whale	02/99	Beagle Channel	54°53'S	67°36'W	1
Common minke whale (dwarf)	14/02/01	Goree Passage	55°19'S	67°05'W	1
Common minke whale (dwarf)	14/02/01	Goree Passage	55°20'S	67°04'W	1
Unidentified minke whale	14/02/04	González Channel	54°06'S	72°34'W	1
Antarctic minke whale	12/03/04	Magellan Strait	53°29'S	70°52'W	1

reported for Durban in South Africa (Best, 1985). It seems therefore that the minke whales of both species observed in the southern tip of South America (Patagonia Channel) could be related to minke whales in the western South Atlantic off Brazil.

Dwarf minke whales have been observed in Brazil from July to February but with most individuals recorded in the austral winter and spring, suggesting that these whales present some degree of seasonal north/south movement (Zerbini *et al.*, 1996). The records of this species presented in this study were made mainly in April, a month when whales were not recorded further north in tropical latitudes. This suggests that the population of dwarf minke whales wintering off Brazil may move towards the south in the summer and that some whales move into the Patagonia Channels. Due to the scarcity of data, it is not possible to determine whether or not these whales are normally distributed within the channels in summer. Not all sighting surveys in the Patagonia Channels have been conducted in a systematic manner and the searching effort has been limited.

ACKNOWLEDGEMENTS

We thank H. Kato (National Research Institute of Far Seas Fisheries, Japan) for his assistance in identifying the dwarf minke whales from photographs. Our acknowledgements to E. Barros, Governor of the Antarctic Province, Chile, for continuous support, to the fishermen and DAP pilots of Puerto Williams for informing on the stranding. A. Zerbini provided valuable comments that notably improved this manuscript.

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Date received: December 2005
Date accepted: July 2006

J. CETACEAN RES. MANAGE. 8(3):297–300, 2006

A note on the movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia

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ABSTRACT

Most models of population structure for Southern Hemisphere humpback whales (*Megaptera novaeangliae*) assume that individuals feeding in the Scotia Sea migrate primarily to breeding and calving areas off Brazil. However data to support this are few and mostly indirect. Abrolhos Bank, Brazil, is the largest breeding and calving ground for humpback whales in the western South Atlantic Ocean. Historically, the waters near South Georgia held the largest concentrations of humpback whales in Antarctic Area II and were among the largest in the Southern Ocean. Photographs of individually distinctive natural markings on humpback whale flukes collected from the Scotia Sea (*n*=9) were compared with two collections of photographs from Brazilian waters (*n*=829 and *n*=735) to identify re-sightings. A humpback whale photographed in August 2000 at Abrolhos Bank was subsequently photographed in December 2004 near Shag Rocks off South Georgia. The migratory distance between these sightings is 3,945km. This finding constitutes the first long-distance individual re-sighting to be documented from either of these areas.

KEYWORDS: MIGRATION; HUMPBACK WHALE; SOUTHERN HEMISPHERE; PHOTO-ID

INTRODUCTION

Early modern industrial whaling operations severely reduced humpback whale (*Megaptera novaeangliae*) populations in the South Atlantic Ocean and corresponding areas of the Southern Ocean during the early decades of the 1900s (Mackintosh, 1942; Tonnessen and Johnsen, 1982; IWC, In press). Since this depletion occurred before biological data were routinely taken on killed whales and before the development of the Discovery tag (Brown, 1978), there are few data available with which to assess the movements and population structure of humpback whales in the region, although observed movement of individuals identified by natural markings (Katona and Beard, 1990) is an increasingly important tool in these waters.

Two principal low-latitude breeding and calving grounds for humpback whales occur in the South Atlantic Ocean; the coastal waters of eastern Brazil (Siciliano *et al.*, 1999; Zerbini *et al.*, 2006), and the west coast of Africa (Townsend, 1935; Walsh *et al.*, 2000). Abrolhos Bank, Brazil (16°40’-19°30’S, 38°35’-39°20’W), is the primary breeding and calving ground of humpback whales in the western South Atlantic Ocean. Mark-recapture abundance estimates for the period 1996-2000 range from 1,848 (95% CI; 725-2,971) to 3,871 (95% CI; 2,795-5,542) (Frietas *et al.*, 2004).

Humpback whale distribution within the high-latitude feeding grounds is less clearly delineated. While humpback whaling was widespread over the entire region (Mackintosh, 1942), most researchers suggest three primary concentrations, one to the west, associated with the Antarctic Peninsula and South Shetland Islands extending into the Bellingshausen Sea (‘Chilean Group’ – Mackintosh, 1942; ‘Area I’ – Donovan, 1991; ‘Group G’ – IWC, 1998), another in the Scotia Sea, principally near South Georgia and the South Sandwich Islands (‘Atlantic Group’ – Mackintosh, 1942; ‘Area II’ – Donovan, 1991; ‘Group A’ – IWC, 1998), with a third, and perhaps a fourth, south of Africa (‘African Group’ – Mackintosh, 1942; ‘Area III’ – Donovan, 1991; ‘Groups B and C’ – IWC, 1998). The waters near South Georgia (54.5°S, 37°W) and the South Sandwich Islands were a principal centre of early humpback whaling operations and historically were one of the primary concentration areas for humpback whales in the Southern Ocean (Tomilin, 1957; Mackintosh, 1965).

The migratory movements of whales from these areas have not been well documented. Most current models of population structure for Southern Hemisphere humpback whales assume that individuals feeding near South Georgia migrate primarily to the waters off Brazil (e.g. IWC, 1998; Siciliano *et al.*, 1999; IWC, 2005). However the data to support this are scarce and mostly indirect. Alternative migratory destinations have been suggested for individuals from both Brazil and South Georgia. Notably South Georgia has been linked to western Africa (Mackintosh, 1942), while some degree of movement from Brazil to the Antarctic Peninsula has been widely suggested, though with varying levels of uncertainty (Mackintosh, 1942; Slijper, 1979; Evans, 1987).

METHODS

Comparison of photographs of individually distinctive natural markings can provide direct evidence of whale movement. For this study, individual humpback whales were identified from photographs of natural markings and permanent scars on the ventral surface of the flukes (Katona *et al.*, 1979). A collection of identification photographs from throughout the Southern Hemisphere is maintained at College of the Atlantic (Bar Harbor, Maine, USA). This Antarctic Humpback Whale Catalogue (AHWC) is an international collaborative effort involving numerous individual or institutional contributors. Photographs from Brazil were systematically compared with identification photographs from the Scotia Sea to identify re-sightings.

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The AHWC sample of identified individuals from Brazil consists of 829 whales. These photographs were collected primarily by Projeto Baleia Jubarte (PBJ). PBJ conducts ongoing studies of humpback whales on the Abrolhos Bank using photographic identification. An additional 735 individual whales photographed by PBJ off Brazil were also used in these analyses. These photographs have not yet been fully compared with the AHWC so there is probable overlap.

Nine individuals were identified in the waters of the Scotia Sea, three from the bays of South Georgia Island, two from Shag Rocks to the west of South Georgia, two from offshore waters and two near the South Orkney Islands. For this analysis individuals identified west of ~55°W at Elephant Island were included with individuals from the Antarctic Peninsula and South Shetland Islands.

RESULTS AND DISCUSSION

An individual humpback whale (AHWC#2215, Fig. 1) was photographed on 4 August 2000 at 18°11.275’S, 038°37.034’W on the Abrolhos Bank (Fig. 2). The whale was a member of a pair that was observed from 11:40 to 12:30. There was a record of singing in this group. The same individual was subsequently photographed on 4 December 2004 at 53°33.04’S, 041°37.73’W off Shag Rocks near South Georgia. Approximately 10 humpback whales and 15 southern right whales were present and heavy traces of prey were reported on the echo-sounder at a depth of 30m. The migratory distance between these locations is 3,945km.

This observation constitutes the first long-distance re-sighting of an individual to be documented from either area. The small number of individuals identified on the Scotia Sea feeding grounds and the single observed re-sighting preclude statistical analyses. However, in contrast to this sighting, none of the catalogued individuals from Brazil were re-sighted in the Antarctic Peninsula (*n*=839) or any other Antarctic region (*n*=105).

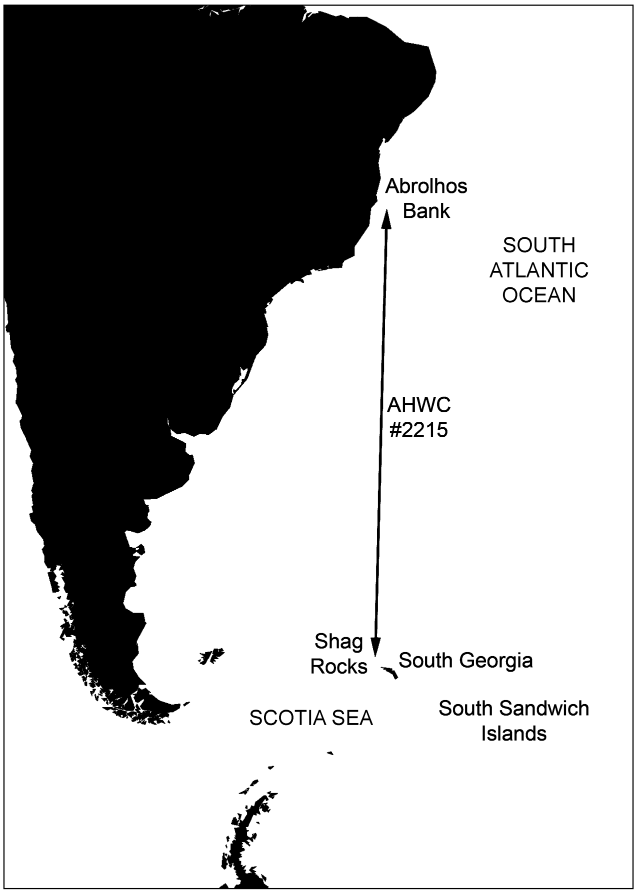

Fig. 2. The western South Atlantic Ocean and the Scotia Sea. The arrow marks the endpoints for the migratory transit of humpback whale AHWC#2215 that is documented here.

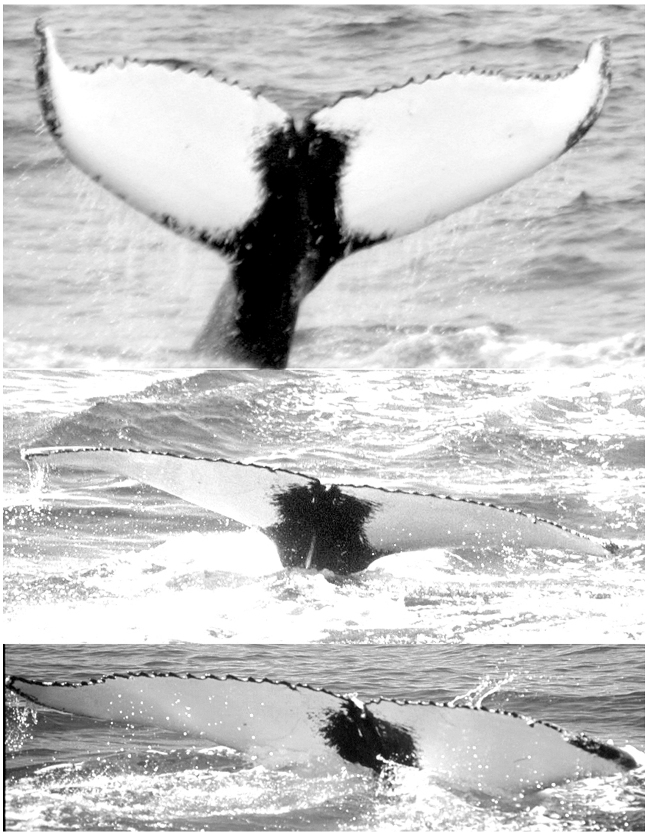

Fig. 1. Humpback whale AHWC#2215 photographed on 4 December 2004 off Shag Rocks near South Georgia (upper) and on 4 August 2000 on Abrolhos Bank, Brazil (centre and lower).

Only a single Discovery tag recovery has been reported from the South Georgia vicinity, and that was recovered after an interval of only 5 days and a distance of ~220km (IWC, 1998). A tag fired into an animal in the feeding grounds at 116°W has been reported as having been recovered by the former USSR off Brazil at 45°W (IWC, 1998), however it was recovered from the cooker, so the actual capture location of the whale is not known with certainty and in the absence of additional information the reported recovery location must be considered unreliable (IWC, 1998).

The movement of an individual between Brazil and South Georgia is not surprising. The migration of most animals from the South Georgia/South Sandwich/Scotia Sea area to Brazil and the majority of animals from the Antarctic Peninsula to the west coast of South America is consistent with current thinking regarding humpback whale population structure in the region (IWC, 1998; Siciliano *et al.*, 1999; IWC, 2000; IWC, 2005). This finding supports the results of other studies that have used natural markings and genetic markers to identify links between the Antarctic Peninsula and South America and found no evidence of movement from these areas to Brazil despite increasingly large sample sizes (Stone *et al.*, 1990; Olavarría *et al.*, 2000; Caballero *et al.*, 2001; Garrigue *et al.*, 2002; Dalla Rosa *et al.*, 2004;

Stevick *et al.*, 2004). Recent evidence from satellite-linked transmitters has demonstrated the movement of two individuals from the Abrolhos Bank to waters east of South Georgia and near the South Sandwich Islands (Zerbini *et al.*, 2006). Additionally, modern sighting and stranding patterns off Brazil do not support a coastal migration, but are more consistent with an offshore migration to a feeding area to the south or southeast (Siciliano *et al.*, 1999).

While the observation presented here supports growing evidence that humpback whales from Brazil migrate to the Scotia Sea, low humpback whale population densities are generally reported in the vicinity of South Georgia today. The primacy of South Georgia stations in the historic killing of humpback whales, with more than 18,000 humpback whales reported to have been taken there between 1909-1915 (Mackintosh, 1942; IWC, 2005) and the exceptionally high krill densities in this region, suggest that it was a primary feeding concentration area a century ago. In contrast, recent reports indicate that few humpback whales are sighted in these waters today, while greater densities are reported near the Antarctic Peninsula and east of 20°E (Kasamatsu *et al.*, 1996; IWC, 1998; Moore *et al.*, 1999). Thus there is little evidence to suggest that the number of humpback whales in the immediate South Georgia area today is comparable to the number sighted off Brazil. While it is possible that larger numbers of whales occur in poorly sampled waters offshore, near the South Sandwich Islands or elsewhere in the Scotia Sea, there are few data to confirm or refute this and the question deserves more scrutiny.

ACKNOWLEDGEMENTS

This project would not have been possible without the cooperation of many dedicated researchers, naturalists, tourists and tour operators throughout the world, who provided photographs that contributed to these analyses. We are deeply indebted to the captain, crew and staff of the ship *Endeavour* and to Lindblad Expeditions for making it possible to obtain the photographs from Shag Rocks. S. Ferreira and F. Fontes assisted with photo-identification studies in Brazil. Financial support for work in Brazil was provided by PETROBRAS S.A. and Aracruz Celulose. Financial support for photographic analyses was provided by the International Whaling Commission and contributors to the Antarctic Humpback Whale Catalogue programme, with additional logistical and financial support from Allied Whale, College of the Atlantic. We appreciate the thoughtful comments of S. Siciliano and an anonymous reviewer.

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Date received: November 2005
Date accepted: April 2006

J. CETACEAN RES. MANAGE. 8(3):301–305, 2006

A note on East Australia Group V Stock humpback whale movement between feeding and breeding areas based on photo-identification

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ABSTRACT

Documentation of humpback whale migratory movements between Australasia and the Southern Ocean has been limited almost exclusively to historical whaling data. This study examines photographic evidence documenting the movements of three individual humpback whales between their breeding grounds on the northeast coast of Australia and feeding grounds in Area V of the Southern Ocean. Although these individuals exhibited marked site fidelity to the same low latitude breeding grounds, their sightings in high latitude feeding grounds vary by 35° longitude, confirming dispersal of Eastern Australia Group V Stock humpback whales in the Antarctic feeding ground.

KEYWORDS: HUMPBACK WHALE; MIGRATION; DISTRIBUTION; PHOTO-ID; AUSTRALASIA; ANTARCTIC

INTRODUCTION

Early historical data from Discovery marks supported the hypothesis that humpback whales (*Megaptera novaeangliae*) wintering off the eastern coast of Australia (East Australia Group V Stock: EAGVS) spend their summer months in Antarctic waters in the vicinity of 150°E-180° (Omura, 1953; Dawbin, 1964; Chittleborough, 1965). However, since the late 1960s, no humpback whales from these stocks have been taken for commercial or scientific purposes and subsequently, recovery rate of these marks has been poor. Of 3,000 marks deployed over a 25 year period in this region, fewer than three percent were recaptured (Dawbin, 1964; Chittleborough, 1965).

The use of photo-identification (photo-ID) methodologies to document movements of humpback whales has since become well established and studies of migratory movement between Australasia and the Southern Ocean, in particular, have increased in recent years (Kaufman *et al.*, 1987; Kaufman *et al.*, 1990; Gill and Burton, 1995; Matsuoka *et al.*, 2001; Allen *et al.*, 2002). Despite this increase in effort, only two publications provide photographic documentation of humpback whale migration between these regions. They detail the movement of just two individual whales; one between western Australia and Antarctic Area IV (70°-130°E; Gill and Burton, 1995) and the other (Animal E0212; Kaufman *et al.*, 1993) between eastern Australia and the boundary area between Area V (130°E-170°W) and Area VI (170°-120°W) (Kaufman *et al.*, 1990). This note reports further photographic evidence for migratory movement of humpback whales between eastern Australia and Area V.

FIELD OBSERVATIONS

Humpback whales frequently congregate in coastal waters off eastern Australia during the austral winter. Hervey Bay, in southern Queensland (QLD≈ 24°S, 153°E; Fig. 1), has historically been one such congregation point and photo-ID has revealed that many individuals frequent this area over multiple years (Kaufman *et al.*, 1993; Forestell *et al.*, 2003), with occasional visits to other important areas of aggregation such as the Whitsunday Islands (≈ 20°S, 150°E), Point Lookout, North Stradbroke Island (≈ 27°S, 153°E) and Eden, New South Wales (NSW,≈ 37°S, 150°E; Fig. 1). This study focuses on three individuals, one that was described previously (Kaufman *et al.*, 1990) and two that are described here for the first time. All three whales have been photographed in QLD, NSW and in Antarctic Area V; two have been photographed multiple times over the past 15 years.

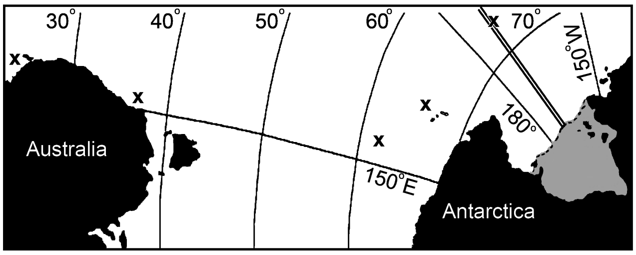

Fig. 1. Documented sightings of humpback whales E0212, E0502 and E1007 in Hervey Bay and off Eden, Australia and in Antarctic Area V. Locations of sightings are marked with dark crosses. Latitudinal markings are degrees south; double line indicates the boundary between Area V and Area VI.

Animal E0212 (Kaufman *et al.*, 1993) was first photographed in the Antarctic in 1986 and the following year was re-sighted over a four-day period in Hervey Bay (Kaufman *et al.*, 1990). Since that time, E0212 has been photographed in Hervey Bay in 1989, 1990, 1992, 1998 and 2002 (Table 1). In 1996 and 1998 it was also photographed off Eden, NSW. Although E0212's gender has not been verified by DNA analysis, behavioural observations off eastern Australia suggest it is a male. On nine of the twelve occasions in Hervey Bay, E0212 was in surface-active groups of four or more whales. On three of those occasions

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there was a mother and calf in the group. While not completely conclusive, such activities during the breeding season are indicative of male competitive mating behaviour (Clapham, 2000). Identifying features of E0212 have previously been published (Kaufman *et al.*, 1990).

Table 1
Documented sighting history of E0212, E0502 and E1007 in Eastern Australia and Antarctica.

Individual	Date	Location	Latitude (S)	Longitude (E)
E0212	07/02/1986	AN*	68° 46' 00"	170° 52' 00" W
	10/09/1987	HB*	24° 58' 00"	153° 06' 00"
	11/09/1987	HB*	24° 58' 00"	153° 06' 00"
	12/09/1987	HB*	24° 58' 00"	153° 06' 00"
	13/09/1987	HB*	24° 58' 00"	153° 06' 00"
	21/08/1989	HB*	24° 58' 00"	153° 06' 00"
	05/09/1990	HB*	24° 58' 00"	153° 06' 00"
	07/09/1990	HB*	24° 58' 00"	153° 06' 00"
	08/09/1990	HB*	24° 58' 00"	153° 06' 00"
	22/08/1992	HB*	24° 58' 00"	153° 06' 00"
	24/08/1992	HB	24° 45' 68"	153° 03' 82"
	15/10/1996	ED	37° 20' 00"	150° 02' 70"
	27/09/1998	HB	24° 59' 46"	153° 10' 35"
	22/10/1998	ED	37° 06' 66"	150° 04' 11"
	24/10/1998	ED	37° 05' 50"	149° 58' 16"
	21/09/2002	HB*	24° 58' 00"	153° 06' 00"
E0502[1]	27/09/1988	HB*	24° 58' 00"	153° 06' 00"
	25/09/1991	HB	25° 01' 45"	153° 11' 30"
	04/09/1996	HB	24° 59' 45"	153° 09' 07"
	07/09/1996	HB	24° 58' 13"	153° 09' 78"
	05/08/1997	HB	24° 59' 97"	153° 06' 54"
	06/08/1997	HB	24° 55' 78"	153° 07' 92"
	30/07/1998	WI	20° 04' 16"	148° 54' 22"
	19/09/1998	HB	24° 55' 37"	153° 11' 14"
	20/09/1998	HB	24° 55' 43"	153° 12' 99"
	23/09/1998	HB	24° 53' 87"	153° 10' 17"
	24/09/1998	HB	24° 55' 96"	153° 13' 30"
	20/02/1999	AN*	66° 11' 00"	163° 14' 00"
	19/09/1999	HB	24° 58' 24"	153° 12' 36"
	22/09/1999	HB	24° 54' 62"	153° 10' 19"
	02/11/1999	ED	37° 06' 40"	149° 57' 61"
	05/10/2000	HB	24° 56' 15"	153° 11' 15"
	06/10/2000	HB	24° 55' 06"	153° 08' 44"
	07/10/2000	HB	24° 57' 90"	153° 12' 77"
	10/10/2000	HB	24° 59' 15"	153° 11' 36"
	15/09/2002	HB	25° 06' 27"	153° 03' 12"
	16/09/2002	HB	25° 07' 73"	153° 04' 33"
	19/09/2002	HB	25° 00' 15"	153° 10' 91"
	24/09/2002	HB	25° 02' 38"	153° 09' 06"
E1007[2]	02/08/1991	PL*	27° 25' 58"	153° 33' 47"
	16/01/1995	AN*	62° 49' 00"	155° 55' 00"
	10/11/2002	ED*	37° 04' 75"	149° 57' 05"

Notes: [1]AHWC #0978; [2]AHWC #0958. *Represents locations for which generalized approximations are given (although data are available for each observation with regard to the general location, exact GPS fixes were not determined); AN = Antarctica; WI = Whitsunday Islands; HB = Hervey Bay; PL = Point Lookout; ED = Eden.

The humpback whale individual E0502 (Kaufman *et al.*, 1993) was first identified in Hervey Bay in 1988 and was re-sighted in 1991, 1996-2000 and 2002 (Table 1). E0502 was also photographed in the Whitsunday Islands (1998) and in Eden, NSW (1999). Identifying features of this individual are shown for the ventral fluke and both left and right dorsal fin/flank regions in Figs 2a-c, respectively. Pigmentation patterns on both fluke and flank remained relatively unchanged over the fifteen-year re-sight period (Pacific Whale Foundation (PWF), unpublished data), however the animal suffered significant injury to the left side of its dorsal fin in 2002. E0502 was photographed in association with a calf in every year of its sighting history in eastern Australia, a total of eight seasons, including a period spanning five consecutive years (1996-2000). In all but one of those years the calf was newborn (<one year old); in 1997 a yearling, assumed to be the calf born the previous season, was in accompaniment.

The humpback individual E1007 was first identified at Point Lookout, ≈ 160 n.miles south of Hervey Bay in 1991 (Table 1; Kaufman *et al.*, 1993) and was re-sighted in Eden in 2002. Identifying features are shown for ventral fluke and left dorsal fin/flank region in Figs 3a-b; there is little sign of modification over the 11 year re-sight period.

Fig. 2. Identifying features of E0502 including, (a) fluke (2002) and both left (b) and right (c) dorsal fin/flank areas (2002 and 1997, respectively) in Hervey Bay, Australia and (d) fluke (1999) in Antarctic Area V.

Fig. 3. Identifying features of E1007 including, (a) and (b) fluke and left dorsal fin/flank area (both 1991) in Australia and (c) fluke (1995) in Antarctic Area V.

As was the case with E0212, both E0502 and E1007 were photographed in Antarctic Area V of the Southern Ocean. Animal E0212 was photographed at 68°46'S, 170°52'W on 7 February 1986 (Kaufman *et al.*, 1990). Animal E0502 was sighted at 66°11'S, 163°14'E (Fig. 1) on 20 February 1999, during the 1998/1999 JARPA cruise (Japanese Whale Research Program under Special Permit in the Antarctic). Animal E1007 was sighted at 62°49'S, 155°55'E (Fig. 1) on 16 January 1995 during the 1994/1995 JARPA cruise. As was done earlier with animal E0212, ventral fluke photographs of E0212 and E1007 (Figs 2d, 3c) were submitted to the Antarctic Humpback Whale Catalogue (AHWC; curated at Allied Whale, College of the Atlantic, Maine, USA). The flukes of all three animals were compared with catalogued individuals from Antarctic sectors I-VI (*n*=696), as well as Western Australia (*n*=239), East Australia (*n*=2250), Oceania (*n*=2), Gabon (*n*=46), Brazil (*n*=288), Costa Rica (*n*=38), Colombia (*n*=102), Ecuador (*n*=252) and Chile (*n*=8). No further matches were made between E0212, E0502 or E1007 and catalogued individuals from these regions; E0502 and E1007 were assigned AHWC catalogue numbers 0978 and 0958, respectively.

E0502 was confirmed as a female by genetic analysis of a biopsy skin sample obtained in Area V (Pastene *et al.*, unpublished data). At the time of sampling in Area V, E0502 was observed in a group of three individuals that included a yearling. The estimated length of each whale was 13.4m (E0502), 11.9m (genetic analysis indicated this animal was also female) and 10.4m. They were observed to be swimming slowly, approximately 25 n.miles from the edge of the pack ice. No feeding activities were observed and the animals spent periods of time resting with just the blowhole region of the rostrum at the surface. Although E0502 had been observed approximately 8 months earlier in Hervey Bay with a calf, it is not certain at this point that this animal, rather than the second female in the group of three whales, was the mother of the accompanying yearling in the Antarctic.

DISCUSSION OF MOVEMENTS BETWEEN FEEDING AND BREEDING GROUNDS

Photographs of E0212, E0502 and E1007 along the QLD coast during the breeding season (at Hervey Bay and Point Lookout), the NSW coast during the southward migration (near Eden) and in the Southern Ocean during the feeding season at 155°E-170°W, provides further documentation that humpback whales wintering along the east coast of Australia spend their summer months feeding in the Southern Ocean in Area V (Dawbin, 1964; Chittleborough, 1965). The latter two sightings add to the only other photo-documentation of a humpback whale moving between eastern Australia and the Area V region (E0212, photographed in Hervey Bay and in the Ross Sea, Kaufman *et al.*, 1990). These sightings are compared with respect to their significance to our understanding of the longitudinal distribution of humpback whales in the Southern Ocean.

Animals E0212, E0502 and E1007 were photographed at similar locations in the low latitude breeding grounds (i.e. in Hervey Bay and Point Lookout during the breeding season and near Eden late in the southward migration). They were also documented at similar latitudes in Area V of the Southern Ocean (68°46'S, 66°11'S and 62°49'S respectively). There is, however, a marked longitudinal difference of 35° (approximately 817 n.miles) between the sightings of these humpback whales in Area V. Animal E0502 was observed at 163°14'E and E1007 was observed at 155°55'E, in the vicinity of the Balleny Islands. In contrast, E0212 was photographed far to the east at 170°52'W, in the open Ross Sea region on the boundary between Area V and Area VI. These data provide photographic evidence that East Australia Group V Stock (EAGVS) humpback whales tend to disperse more widely in their high latitude feeding grounds, as first concluded by Chittleborough (1965) and Dawbin (1966).

In general, little is known about the movements of Southern Hemisphere humpback whales within their summer feeding grounds. Data from Discovery marks document longitudinal movements of individuals within Areas I (120°-60°W), III (0°-70°E) and VI across years (IWC, 1998). Additional, more comprehensive, data come from long-term photo-ID efforts in Area I of the Antarctic Peninsula (Stevick *et al.*, 2004). Here, some individual humpback whales are regularly re-sighted at similar latitudes and longitudes in different years (AHWC, unpublished data). Little other information exists on the movements of individual humpback whales within other areas of the Southern Ocean, where there are few or less significant landmasses to concentrate the resources that contribute to feeding site fidelity. In Area VI, one individual has been photo-documented twice in similar geographic positions, with a span of six years between sightings

(JARPA, 1 January 1997 at 65°33'S, 167°29'W; IWC, 3 January 1991 at 64°56'S, 171°43'W, AHWC, unpublished data). There is also a single case of a molecular marker match for a female humpback whale first sampled in the western part of Area V (January 1995) that was subsequently re-sampled in the eastern part of Area IV (January 2000; Pastene *et al.*, 2002).

A broad distribution of humpback whales at high latitudes increases the likelihood of an overlap of breeding populations, resulting in the mixing of discrete low latitude populations, as suggested by Omura (1953) and Chittleborough (1959). Mixing between stocks is less likely to occur through within-season changes in breeding locations; such movements have been documented only rarely and in populations not separated by large landmasses (e.g. movements of an individual between Mexico and Hawaii (PWF, unpublished data) and between eastern Australia and New Zealand (Dawbin, 1964)). Thus the primary site for population stock mixing is most likely to occur in the Southern Ocean. Such mixing of stock has been documented, by a variety of methodologies, between EAGVS and both western Australia Area IV stock and Oceania Area VI stock. Historical whaling data shows that a small percentage (5%) of marks deployed in EAGVS were recovered in animals in western Australia (Chittleborough, 1965; Dawbin, 1966) and several mark recaptures of EAGVS have occurred well into Area VI (160°W; Dawbin, 1966). At least eight marks deployed in New Zealand/Oceania animals have also been recaptured in Area V (between 162-177°E; Dawbin, 1964). Further evidence for interchange has been established more recently by the discovery of overlap in song characteristics between eastern and western Australian stocks (Noad *et al.*, 2000), photographic documentation in Hervey Bay of an animal also identified near Perth, Western Australia (Pacific Whale Foundation and D. Coughran, unpublished data) and photographic matches between eastern Australia and western Oceania (including New Caledonia and Tonga; Garrigue *et al.*, 2000; 2002). Genetic studies have also confirmed that Southern Hemisphere humpback populations are generally more discrete in their breeding grounds than in their feeding grounds (Pastene and Baker, 1997).

Mark recapture results do not necessarily suggest mixing of stocks on an ongoing basis, but may indicate transitory patterns associated with unusual fluctuations in prey distribution in the Southern Ocean (Chittleborough, pers. comm.). The proclivity of humpback whales to shift distribution in response to changes in prey availability has been well documented in the North Atlantic (Weinrich *et al.*, 1997). In the Southern Ocean, the distribution of baleen whales is highly correlated with availability of euphasiids and humpback whales, in particular, have been shown to follow prey concentrations irrespective of bottom topography (Murase *et al.*, 2002). Matsuoka *et al.* (2003) demonstrated that high-density areas of humpback whales occur along the large (and temporally flexible) meander of the southern boundary of the Antarctic Circumpolar Current. Large-scale changes in prey distribution, such as those associated with significant El Niño-Southern Oscillation events, would set the stage for animals converging on areas of dense prey availability to include transitory whales from relatively distant feeding groups (Chaloupka *et al.*, 1999; Forestell *et al.*, 2003). Such an event may have occurred, for example, in 1958 when one of the strongest El Niños on record in the last 55 years occurred (International Research Institute for Climate Prediction, 2004) and mark recoveries documented expansion of the EAGVS feeding range into Area IV, with some EAGVS individuals migrating north with the western Australia breeding population (Chittleborough, 1965).

The present data, in combination with previously published photographic evidence (Kaufman *et al.*, 1990), show examples of broad dispersal in high latitude feeding grounds for EAGVS whales, providing support for the earlier findings based on Discovery mark analyses. The data do not exclude the possibility that breeding populations from both eastern and western Australia and Oceania are subject to some low level of mixing on the feeding grounds during summer months. Clearly, continued effort to photo-ID humpback whales in the Southern Ocean (particularly in Areas II-VI) and collaborative exchange between the disparate international groups expending effort in high latitudes, are necessary to clarify important questions about the population biology of Southern Hemisphere humpback whales.

ACKNOWLEDGEMENTS

Research in Australia was conducted by the Pacific Whale Foundation (PWF) between 1984 and 2002 under permits from the Commonwealth of Australia, the States of Queensland and New South Wales and the Great Barrier Reef Marine Park Authority. The members of PWF, the QLD Environmental Protection Agency (Parks and Wildlife Service) and a number of whale watch vessels including FantaSea Cruises, Lady Musgrave, Matilda Cruises, Sea Spray and Cat Ballou Cruises provided financial and logistical support. R. Butts and C. Smith provided additional photographs from NSW; B. Lagerquist, P. Naessig and A. Hellrung curated the Australian catalogue and L. de la Paz assisted in matching. We thank countless individuals who facilitated research in Australia by working as volunteers and research assistants and by contributing identification photographs. In Antarctica, research was conducted by JARPA under special permit in the Antarctic (Matsuoka and Ohsumi, 1995). We would like to thank JARPA researchers H. Murase, S. Otose and S. Machida who took the pictures in the Antarctic with assistance of captains K. Matsuzaka and M. Yamada of *Kyoshin Maru No 2* and *Toshio Maru No 25*, respectively. The AHWC receives curation support from the IWC under Research Contract 16. Its maintenance also relies on considerable support donated by C. Carlson (International Fund for Animal Welfare) and by staff and students at Allied Whale (College of the Atlantic), among whom we particularly thank R. Seton and B. Holm, as well as S. Katona and P. Stevick for their contributions to this manuscript.

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Date received: January 2005
Date accepted: November 2005

The first aerial survey to estimate abundance of humpback whales (*Megaptera novaeangliae*) in the breeding ground off Brazil (Breeding Stock A)

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ABSTRACT

In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) were heavily exploited from both coastal stations and in pelagic waters in all major ocean basins. About 200,000 whales were taken after 1900, causing declines of populations to small percentages of their pre-exploitation levels. The study presented here aimed to investigate humpback whale abundance in the Brazilian coastal breeding ground, in order to provide information to support further analysis of the population recovery. Between 25 August and 2 September 2001, a fixed wing, flat window, aircraft was used to survey transect lines along the northern limit of Bahia State (12°10'S), to the southern limit of Espírito Santo State (20°42'S). All on-effort sightings were recorded and abundance was estimated according to standard distance sampling methodology (Burnham *et al.*, 1980; Buckland *et al.*, 1993). Group sizes of humpback whales ranged between 1-5 and the mean group size was 1.52 (±0.06). The model that best fitted the perpendicular distance data, based on the minimum Akaike Information Criterion, was the hazard rate model. The population size estimated using uncorrected data was 1,493 (CV=0.21) whales. Surface time was used to correct the estimates for $\hat{g}(0)$, resulting in a correction factor of 0.67 (±0.15). The corrected analysis for each block and combined result, increased the population size estimate to 2,229 (CV=0.31) individuals. The data from this study could be used to identify new areas appropriate for whalewatching, to monitor the status and dynamics of the humpback whale population off the Brazilian coast and to provide information for the establishment of new protected areas.

KEYWORDS: SURVEY-AERIAL; HUMPBACK WHALE; ABUNDANCE ESTIMATE; BREEDING GROUND; SOUTH AMERICA; SOUTHERN HEMISPHERE

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) occur in all major oceans of the world. In the Southern Hemisphere they usually migrate from summer feeding grounds in the Antarctic to mating and calving grounds in tropical and subtropical regions (e.g. Mackintosh, 1965). Its coastal habitat has made the humpback whale especially vulnerable to modern whaling methods and the species was heavily exploited in the Southern Hemisphere from both coastal stations and in pelagic waters in all major ocean basins (e.g. Chittleborough, 1965; Gambell, 1973; Williamson, 1975; Tonnessen and Johnsen, 1982; Best, 1994). About 200,000 whales were taken after 1900, causing declines of populations to small percentages of their pre-exploitation levels (e.g. Gambell, 1973). The International Whaling Commission (IWC) has afforded the species virtually complete protection since 1966 and currently recognises seven humpback whale breeding populations in the Southern Hemisphere (IWC, 1998). Breeding stock 'A' is one of the least known and corresponds to whales wintering off Brazil.

Current information on the distribution of humpback whales shows that the species is abundant in the Abrolhos Bank (16°40'-19°30'S), possibly the main breeding area for the species in the western South Atlantic Ocean (e.g. Siciliano, 1997; Engel, 1996; Freitas *et al.*, 1998; Martins *et al.*, 2001). The size of the population breeding in the Abrolhos Bank has been estimated for 1995 as 1,634 individuals, using an empirical Bayes closed mark-recapture model with photo-identification data (Kinas and Bethlem, 1998). Recently, abundance estimates of the population of whales available for marking within the study area were obtained from across year mark-recapture data between 1996 and 2000. A closed population, multiple-recapture model resulted in an estimate of 2,393 whales (approx. CV=0.12). An alternative open population model suggested a population increase over the study period and an estimated population size of 3,871 (CV=0.18) whales in 2000 (Frietas *et al.*, 2004).

The first population estimate for humpback whales off part of northeastern Brazil using line transect methodology (628 individuals; CV=0.33) was for the year 2000 (Zerbini *et al.*, 2004). The study confirmed that humpback whales are regularly found in coastal waters, as far north as 5°S, along the northeastern coast of Brazil. In addition, a whale that stranded in Ceará (3°43'S, 38°30'W) (Furtado-Neto *et al.*, 1998), west of the northwestern tip of South America, suggests that humpback whales may be moving west along the northern coast of Brazil. Non-systematic sightings and strandings of humpback whales have been reported for other areas of the coast, from the Fernando de Noronha Archipelago (~3°S) to Rio de Janeiro (~23°S) (e.g. Lodi, 1994; Siciliano, 1997; Pizzorno *et al.*, 1998). Despite this information, humpback whale distribution and density are still poorly known for a large proportion of the Brazilian coast.

Surveys using fixed-wing aircraft and distance sampling methodology have been extensively used to study distribution and to estimate abundance of mammals (e.g.

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Burnham *et al.*, 1980; Guenzel, 1986; 1994; Firchow *et al.*, 1990; Johnson *et al.*, 1991; Andriolo *et al.*, 2001; Secchi *et al.*, 2001). This technique (including correction for missed animals) can provide reliable estimates with associated confidence intervals relatively inexpensively even when animals are widely distributed. It is useful for studying humpback whales because they are found throughout a large area along the Brazilian coast.

The potential impact of increasing vessel traffic and shoreline development has brought about concern for the future of the Brazilian humpback whale population. The objective of the study presented here was to investigate humpback whale abundance in the Brazilian coastal breeding ground in order to provide baseline information for the development and monitoring of future conservation measures.

METHODS

Study area and survey design

Between 25 August and 2 September 2001, a fixed wing, flat window, aircraft (Mitsubishi Marquese) was used to survey transect lines along the north limit of Bahia State (12°10'S) down to the southern limit of Espírito Santo State (20°42'S). It was not possible to obtain a plane with bubble windows (which enable observers to search directly under the plane and on the trackline). The sighting survey was planned such that it took place at the yearly peak of humpback whale abundance off the Brazilian coast (Paiva and Grangeiro, 1965; Paiva and Grangeiro, 1970; Williamson, 1975).

The study area was divided into five independent blocks (A-E). The total area covered was 25,139.1 n.miles². Seventy-seven parallel transects were systematically designed 25km apart, covering the area from the coast to the 500m isobath (Fig. 1). The parallel design of the transects avoids sub- and over-sampling depending on the shape of the coast. However, in the north of the Bahia State (A block), the transects were designed in a zig-zag shape due to the shelf narrowness in order to better cover the area and to maximise flying effort. The total length on effort was 2,125.25 n.miles, subdivided by block as follows: (1) A block – 511.35 n.miles; (2) B block – 294.35 n.miles; (3) C block – 530.08 n.miles; (4) D block – 384.02 n.miles; and (5) E block – 405.47 n.miles. Survey design and flights were planned using the software *GPS Trackmaker 11.4*.

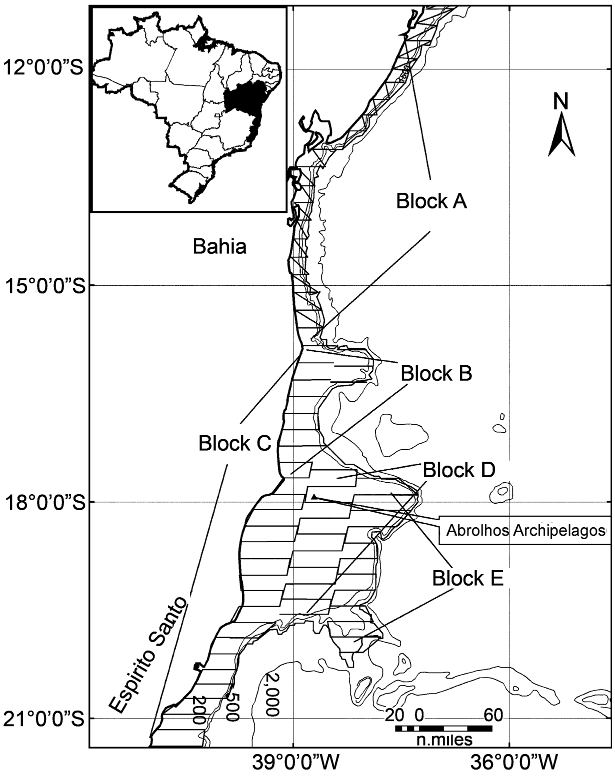

Fig. 1. Transects of aerial survey conducted along the Bahia and Espírito Santo States in late August and early September of 2001. The letters refer to areas used for analysis (Blocks A, B, C, D and E).

Survey protocol

Total time spent flying was 56hrs. The aircraft flew with a constant airspeed of 120kt at an altitude of 500ft (lower than normal for large whale surveys to enable sightings of small cetaceans as well). Flights occurred between 08:00hrs to 17:00hrs when conditions were suitable, i.e. Beaufort sea state 4 (they were usually 2-3) with a clear view of the sea surface (cloud cover ranged from 0-100%). Planning meetings and training sessions were held three days prior to the survey start. Five observers participated in each flight, three on effort and two resting. They rotated at approximately 30min intervals, which corresponded with the end of the transect. Search effort was suspended at the end of each line in order for the plane to circle, before beginning the next one. Species, group size and composition as well as general comments were recorded for each sighting. Two observers sat behind the data recorder, searching downwards and laterally through flat windows on each side of the aircraft. The observers used hand-held clinometers to record the declination angles (0° is at the horizon and 90° is directly below the aircraft) when the animal (or group) passed perpendicularly to the trackline. The sighting position was determined using Global Positioning System (GPS) and all major information was written down on a data sheet by the data recorder. All sightings were recorded following standard line-transect methodology (Burnham *et al.*, 1980; Buckland *et al.*, 1993).

Data analysis

Perpendicular distances were calculated using the aircraft's altitude and the declination angle to the sighting. The flat windows meant that animals could not be seen under the plane out to a declination angle of approximately 50°. A limit at 45° was imposed to assure data quality and this corresponds to a 152m offset on either side of the line. The blind spot distance from the measurements ($g(152)=1$) was subtracted and 3° bands were used, giving intervals corresponding to distances of 0, 11, 30, 49, 73, 100, 133, 173, 224, 289, 378, 506, 710, 1,085, 2,021 and 8,556m. Truncation was applied, discarding all observations beyond 4,000m.

Abundance was estimated in accordance with standard line-transect methodology (Burnham *et al.*, 1980; Buckland *et al.*, 1993). Data analysis was undertaken using the software *DISTANCE* (Laake *et al.*, 1993). Data were pooled across blocks to estimate the global detection function and the global expected group size. Various models were tested to the distances, including the uniform function with cosine and simple polynomial adjustments, half-normal function with cosine and the hazard rate function with cosine and simple polynomial adjustments. The model that best fitted the data was selected according to the Akaike Information Criterion (AIC) (Burnham and Anderson, 1992) as implemented by Laake *et al.* (1993). Abundance estimates were obtained by multiplying the density of whales (D) by the survey area (A). Variances of encounter rate (n/L) and group size were empirically estimated from the sample and variance of the probability density function [$\hat{f}(0)$] was calculated using maximum likelihood estimation.

Detection probability: *g*(0)

Line transect methods assume that all animals on the trackline will be seen. Since the detection probability on the trackline, $g(0)$, is not equal to 1 in aerial surveys the probability of detecting a humpback whale was estimated following the approach of Barlow *et al.* (1988):

$$\hat{g}(0) = \frac{s+t}{s+d}$$

where

s is the average time a humpback whale is at the surface;
d is the average time a humpback whale is submerged;
t is the time window during which the humpback whale is within the visual range of an observer.

The variance of $\hat{g}(0)$ was calculated by the delta method (Seber, 1982).

RESULTS

The total number of humpback whale sightings and individuals observed on effort and considered in the analyses are summarised in Table 1. Whales were not regularly found in the survey area. A concentration of groups is evident over the Abrolhos Bank (Fig. 2). The distribution and concentration of whales seems to be small in the northern portion of the study area and increases south of 18°S. Besides the humpback whales two southern right whales (*Eubalaena australis*), 14 unidentified large whales, 3 unidentified dolphins and 1 minke whale (*Balaenoptera sp.*) were seen.

Table 1

Number of groups and individuals registered in each block, and respective sighting rate considered in the analyses.

Block	Groups	Individuals	Calves	Area (n.miles^2)	Effort (n.miles)	Sighting rate
A	9	14	0	3,575.2	511.3	0.017
B	8	13	1	4,005.5	294.3	0.027
C	62	100	5	7,205.8	530.0	0.116
D	60	92	0	5,426.4	384.0	0.156
E	14	18	0	4,926.2	405.5	0.034
Total	153	237	6	25,139.1	2,125.3	0.074

Group size and composition

Group sizes of humpback whales ranged between 1-5 and mean group size was 1.52 (±0.07). Calves were observed only in six of the total humpback whale groups sighted (Table 1).

Abundance

The model that best fitted the perpendicular distance data was the hazard rate model, based on its minimum AIC value of 621.49. Fig. 3 presents the distributions of perpendicular distance and fitted detection function. Uncorrected abundance was estimated at 1,493 individuals (CV=0.21).

Detection probability – correction of *g*(0)

Solitary individuals accounted for 57% of sightings and the remaining 43% were of groups of two or more individuals. The detectability of groups will be higher than solitary animals. Twenty-seven groups of humpback whales (six solitary individuals and 21 cow-calf pairs) were consistently observed from a land base station at Santa Barbara island in the Abrolhos Archipelago, using continuous sampling methodology (Mann, 1999). The surface and dive times were calculated as proportions of the total observation time. When calculating the mean group size, solitary animals sightings were separated from group sightings and these values were used to calculate the final mean surface and dive times. Humpback whales were found to spend 66.46% of the time at the surface and 33.53% submerged. The time that an animals was visible from the aircraft's window (t), was estimated as 14.53sec (95% confidence interval (CI=±9.79). This measurement was directly made by recording the duration of visibility of any object at the surface of the sea. The estimate for $\hat{g}(0)$ as a correction factor was 0.67 (CI=±0.15). Table 2 presents the corrected analyses for each block and combined result, which increased the population size estimate to 2,229 individuals (CV=0.31).

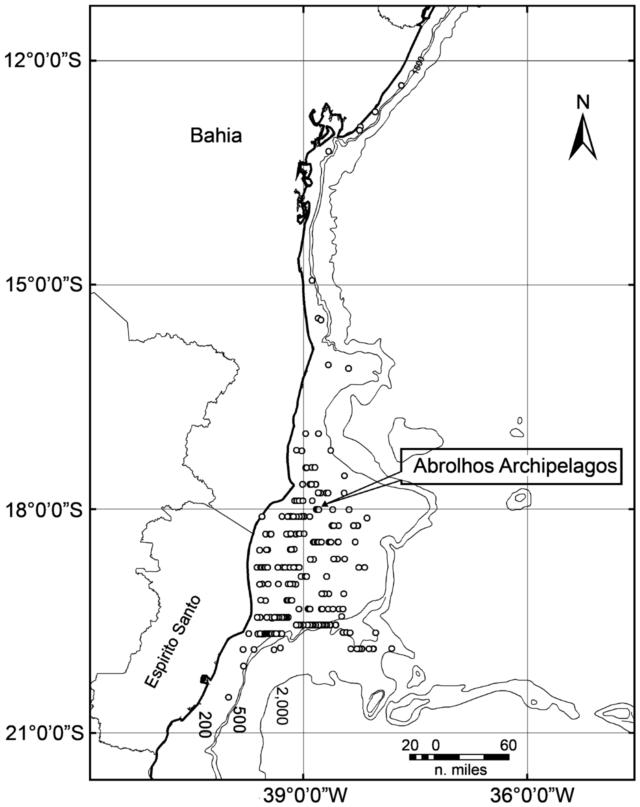

Fig. 2. Sightings recorded during the aerial survey of humpback whales at the Brazilian breeding ground. Isobaths are indicated in metres.

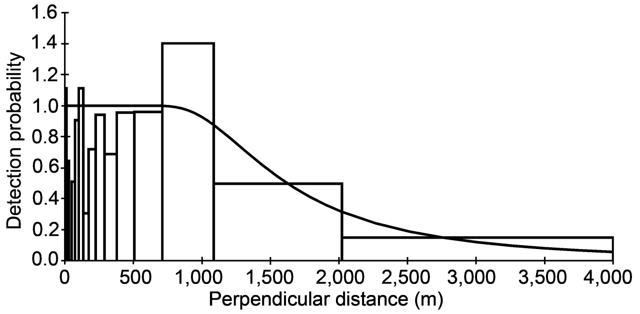

Fig. 3. Distribution of perpendicular distances and the fitted detection function.

Table 2

Parameters of estimated densities and population size of corrected data independently for each block and combining all blocks. (DS=density of clusters; D=density of animals; N=number of animals).

	Estimate	%CV	95% Confidence interval	
Block A				
DS	0.0129	31.51	0.0571	0.0295
D	0.0192	32.17	0.0846	0.0440
N	69	32.17	30	157
Block B				
DS	0.0200	9.68	0.0069	0.0581
D	0.0298	9.81	0.0102	0.0863
N	119	9.81	41	346
Block C				
DS	0.0863	18.15	0.0414	0.1799
D	0.1282	18.75	0.0614	0.2677
N	924	18.75	443	1,929
Block D				
DS	0.1153	10.03	0.0457	0.2907
D	0.1713	10.22	0.0679	0.4320
N	930	10.22	369	2,344
Block E				
DS	0.0254	11.63	0.0081	0.0799
D	0.0378	11.75	0.0120	0.1187
N	187	11.75	59	585
Combined estimates				
DS	0.0596	29.57	0.0322	0.11052
D	0.0886	31.31	0.0477	0.16455
N	2,229	31.31	1,201	4,137

DISCUSSION

The flat windows of the plane, coupled with the possible inexperience of some observers, will have affected the distribution of the detection probability. One alternative approach to help reduce problems associated with imprecise measurements is grouping perpendicular distance data (Buckland *et al.*, 1993). This strategy was applied to the data set presented here.

Distribution

This study has shown that humpback whales are not equally distributed throughout coastal waters as far north as 12°10'S at Bahia State, to the southern limit of Espírito Santo State (20°42'S), which is evident from the different results for each block (Table 1). The Abrolhos Bank is the preferred area (mainly blocks C and D) as it had the highest number of sightings for both individuals and groups. A low density area was observed approximately between the parallels 13°30'S-16°30'S. It is thought that the whales tend to concentrate near islands and coral reef systems, which was proposed by Clapham and Mead (1999).

The area covered previously has been recognised as a major calving/nursing area (Martins *et al.*, 2001), however, during this study few calves were observed. A possible explanation is poor calf visibility, caused by the flat window. Calves are probably only visible when looking straight down, as their profile out of the water and any blow would be less visible than for an adult, and as they swim close to their mother. An improvement for future studies would be to use a slower aircraft, adapted with bubble windows, which would permit downward observations.

Abundance

The total abundance of the humpback whale stock wintering off Brazil is unknown. The 1995 population was previously estimated at about 1,600 individuals (SD=155.16) in the Abrolhos Bank, using photo-identification data and an empirical Bayes closed mark recapture model (Kinas and Bethlem, 1998). Freitas *et al.* (2004) presented new estimates also based on photo-identification data, collected from 1996-2000. However, these photo-identification data were collected in a relatively limited area when compared to the known stock range. The present study provides an estimate for this previously studied area, which can be used for comparison.

In 2000, line transect methodology was employed in northeastern Brazil for the first time to estimate the abundance of humpback whales (Zerbini *et al.*, 2004). The vessel covered an adjacent area north of the area surveyed in the present study and abundance was estimated at 628 individuals (CV=0.311, 95% CI=366-1091). Given the low speed of the vessel, an assumption that $g(0)=1$ is more reasonable. However, there are other advantages of conducting aerial surveys, including the ability to cover large areas in a shorter period of time. This should allow a better picture of spatial distribution. The main drawback of the present aerial survey was the absence of bubble windows preventing searching directly below the plane. Missing animals close to the trackline is inevitable given the diving behaviour of cetaceans (this is known as availability bias) and the correction factor used here tries to account for this. Even though humpback whales are relatively conspicuous, perception bias (due to observers missing animals that were at the surface) may occur, even though observers swapped positions during flights and were trained in collecting this type of data.

We recognise that the data used to estimate the correction factor used here are not ideal for a number of reasons. However, we believe the approach we adopted can be considered conservative, i.e. will probably result in an underestimate of the population size. Considering that this is the first aerial survey for humpback whales in Brazil and noting other difficulties, primarily the lack of bubble windows, we believe that taking a conservative approach is most appropriate from a conservation perspective. The survey covered the area at a time when the population density was expected to be at its highest and our abundance estimate for the area covered is about 2,300 (CV=0.31). As noted earlier, a vessel survey had also been carried out to the north of our region (5° and 10°S) at a similar time of year (Zerbini *et al.*, 2004). However, without further information on possible annual changes in distribution it is not appropriate at this time to add together these two estimates.

Conservation

The results presented here suggest that aerial surveys employing distance sampling techniques can be used to monitor humpback whale populations over time. This methodology can be used to estimate parameters such as the population growth rate; consistent data collection not only allows analysis of annual variation but allows trends to be considered without the use of a correction factor, if this factor can be assumed to be constant over the monitoring period.

Despite the fact that the humpback whale population is recovering and reoccupying its historical areas, the population is still small when compared with that prior to the commencement of whaling (Findlay *et al.*, 2000; Findlay and Johnston, 2001; Johnston *et al.*, 2001; Zerbini *et al.*, 2004). Information on the current status and dynamics of the humpback whale population off the Brazilian coast using data such as those presented here can help in clarifying appropriate mitigation measures to anthropogenic threats where necessary (e.g. protected areas) and provide information that might contribute to the local economy (e.g. identification of new areas for regulated whalewatching).

ACKNOWLEDGEMENTS

The authors would like to thank the observers Bruno Lopes Bastos, Luciana P. Juliano, Gabriel Vianna, Leonardo Wedekin and the pilots César and Yshida. We are also grateful for the logistic support of Abrolhos Turismo, Iga Táxi Aéreo Ltd. This study was financially supported by Aracruz Celulose and Cia. de Navegação Norsul. The official sponsor of the Instituto Baleia Jubarte is Petrobras S.A. We would also like to thank Claudia Bethlem, who was responsible for the start of this co-operation. Finally, we are greatly indebted to the reviewers as their contributions significantly improved the manuscript.

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Date received: June 2005
Date accepted: July 2006

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