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Editorial

Welcome to the final issue of the sixth volume of the *Journal of Cetacean Research and Management*. This has been another good year for the Journal. A total of 34 papers have been published involving some 120 authors from 24 countries (including from Europe, Africa, Asia, Australasia, North America and South America). I am particularly pleased at the wide geographic spread and range of disciplines included. The published papers once again serve to illustrate that the *Journal* is fulfilling its aim of improving conservation science in general and in particular the world. An author and keyword index to Volume 6 appears at the end of this issue.

The present issue again covers a broad range of subjects, areas and species. One of the most endangered species of the great whales is the North Atlantic right whale (*Eubalaena glacialis*) – even the largest population, that in the western North Atlantic, numbers only about 300 animals (see *Journal of Cetacean Research and Management* (special issue 2)). Any human induced mortality threatens the survival of this population. In order to mitigate the direct threats (largely ship strikes and entanglement in fishing gear), it is important to try and understand the cause of death in any carcases found. This is the subject of the paper by Moore *et al.* A related species, the bowhead whale is the subject of a paper on feeding ecology which provides fascinating new information on the nature and extent of feeding during the spring and autumn migrations.

For the effective management of any population, it is important to understand its abundance. This volume includes two papers presenting abundance estimates obtained from individual identification mark-recapture analyses (humpback whales off Brazil, Freitas *et al.*; Irrawaddy dolphins, Kreb). Similar data are used to examine site fidelity in the marine tucuxi (Azevedo *et al.*). Linetransect surveys are perhaps the most common way of estimating cetacean abundance. Proper interpretation of those, particularly when looking at long-term studies requires a good understanding of relevant covariates. This is the subject of a paper by Murase *et al.*

Related to the interpretation of abundance data is the question of distribution and stock structure. De March *et al.* discuss an integrative approach to addressing stock structure in white whales using contaminant profiles and molecular genetics. With respect to distribution, Moore *et al.* report on the most northerly record of Gervais' beaked whale while Scheidat *et al.* examine the summer distribution of harbour porpoises in the German North Sea and the Baltic. This is extremely important given the critical status of that species in the Baltic Sea. Harbour porpoises from the same regions are the subject of a paper examining the birth period by Hasselmeier *et al.*

Incidental capture of cetaceans in fishing gear is one of the most important threats to their conservation. Documentation and mitigation of this threat is a frequent subject of papers to the *Journal*. This issue includes a paper by Burdett and McFee on bottlenose dolphins taken by the Atlantic blue crab fishery in South Carolina, USA.

The quality of any Journal is a reflection of the quality and dedication of its reviewers. I would like to thank publicly here all those scientists who dedicate a considerable period of time to offering constructive and valuable criticism and advice on submitted manuscripts. This not only ensures the high quality of published papers but also serves to improve the quality of cetacean management science throughout the world. An updated list of referees can be found on the journal website (*http://www.iwcoffice.org/ Publications/reviewers.htm*).

G.P. DONOVAN Editor

Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970-2002)¹

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ABSTRACT

Fifty-four right whale mortalities have been reported from between Florida, USA and the Canadian Maritimes from 1970 to 2002. Thirty of those animals were examined: 18 adults and juveniles, and 12 calves. Morphometric data are presented such that prediction of body weight is possible if the age, or one or more measurements are known. Calves grew approximately linearly in their first year. Total length and fluke width increased asymptotically to a plateau with age, weight increased linearly with age, weight and snout to blowhole distance increased exponentially with total length, whereas total length was linearly related to fluke width and flipper length. Among the adults and juveniles examined in this study, human interaction appeared to be a major cause of mortality, where in 14/18 necropsies, trauma was a significant finding. In 10/14 of these, the cause of the trauma was presumed to be vessel collision. Entanglement in fishing gear accounted for the remaining four cases. Trauma was also present in 4/12 calves. In the majority of calf mortalities (8/12) the cause of death was not determined. Sharp ship trauma included propeller lacerations inducing multiple, deep lacerations that often incised vital organs including the brain, spinal cord, major airways, vessels and musculature. Blunt ship trauma resulted in major internal bruising and fractures often without any obvious external damage. In at least two cases fatal gear entanglements were extremely protracted: where the entanglements took at least 100 and 163 days respectively to be finally lethal. The sum of these findings show two major needs: (1) that extinction avoidance management strategies focused on reducing trauma to right whales from ship collisions and fishing gear entanglement are highly appropriate and need to be continued and; (2) that as mitigation measures continue to be introduced into shipping and fishing industry practices, there is a strong effort to maximise the diagnostic quality of post-mortem examination of right whale mortalities, to ensure an optimal understanding of resultant trends.

KEYWORDS: MORPHOMETRICS; CONSERVATION; STRANDINGS; RIGHT WHALE; NORTH ATLANTIC; SHIPSTRIKE; INCIDENTAL MORTALITY

INTRODUCTION

Coastal North Atlantic right whale (Eubalaena glacialis) habitat in the western North Atlantic ranges from the southeastern US coast for calving, to New England and Canada for feeding, although whether there is a specific site for major breeding activity is unclear (Winn et al., 1986). The estimated population size has remained at 300-350 for the period 1980-1998 (Kraus et al., 2001). These authors cited significant anthropogenic mortality and diminishing reproductive rates for failure of the population to grow. The low viability of this population and the finding that it is probably declining (Caswell et al., 1999) is concerning (e.g. IWC, 2001a; b). This decline in productivity is in contrast to a 7% net growth rate for southern right whales (Payne et al., 1990; Best et al., 2001). The reproductive rate for North Atlantic right whales is half that of southern right whales (Knowlton et al., 1994; Best et al., 2001; Kraus et al., 2001) although the exact cause of the decline in North Atlantic right whale reproduction is not known.

The mortality rate for North Atlantic right whales is double that of southern right whales (Kraus, 1990; Best *et al.*, 2001). Collisions with vessels and entanglement in fishing gear are major contributors to the increased mortality rate of adults (Kraus, 1990; Knowlton and Kraus, 2001). Calf mortalities have been more difficult to assign a specific cause of death.

This review summarises data from necropsies of 30/54 confirmed western North Atlantic right whale mortalities from 1970 to 2002. It is notable that had those 54 mortalities not occurred the population would be 20% larger today. This review allows us to assess the quality of data collected, to examine natural history measurements, and suggest possible lines of investigation that might allow better interpretation of data gathered from past cases and lead to better examination techniques and interpretation of future cases. It will also focus attention on particular etiologic agents that may be potentially significant in the reproductive failure of this population.

METHODS

Reports for 54 mortalities during the period between 1970 and 2002 are available in the New England Aquarium data archive (Appendix Table 1; Knowlton and Kraus, 2001). These reports vary in detail from date and location only, to full history, morphometrics and necropsy reports with supporting histopathology and other follow-up investigations. At least partial necropsy data were available for 30 of these cases: 12 calves (<9.2m total length; Best and Rüther, 1992) and 18 juveniles and adults. Data were tabulated to summarise significant gross and histological

¹ This review is dedicated to the memory of David St Aubin: amongst many other things the prosector of Staccato, Eg # 1014, one of the most complete necropsies reported here.

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findings, key morphometrics, carcass condition and presumed cause of death, as well as disposition of bones, voucher materials and other samples. Statements in the reports concerning carcass decomposition condition were normalised to a standard scale (Geraci and Lounsbury, 1993) where: 2=fresh; 3=decomposed; 4=severely decomposed. Attention was given to availability of samples that could contribute to a retrospective analysis of reproductive function and pathology. Many of the data and conclusions were taken from the necropsy reports as submitted. These reports are also summarised in the text, where appropriate.

During necropsies, identification photographs were taken of most carcasses for comparison to the right whale catalogue archived at the New England Aquarium (Hamilton and Martin, 1999). This catalogue collates and matches all photographs of right whales taken at sea by research groups that contribute to the Right Whale Consortium. Photographs at necropsy are matched to archived images to compare head callosity patterns and other distinguishing marks such as scars and mutilations. The catalogue details time, place and associated individuals for all recorded sightings, giving a detailed history of the life of each animal. For animals first identified in the catalogue as a calf, an age in years was included in the data and for those not first identified as a calf, a minimum age was listed. The cases that involve chronic fishing gear entanglement have often been previously managed by the Atlantic Large Whale Disentanglement Network, where routine updates on disentanglement attempts are logged by the Center for Coastal Studies, Provincetown MA (http://www. coastalstudies.org/).

In a few necropsy cases, the weight of the carcass was determined. This was done by either placing the entire carcass on a flatbed truck and taking it to a local weigh station (truck weighed with carcass and then without carcass to calculate weight of carcass), or using a vessel travel lift as the whale was hauled out of the water (weight sensors are usually present on these devices), or by weighing each load of flesh and bones of the dismantled carcass at a weigh station before taken to the burial site; 6.8% was added to the weight to account for fluid loss for those carcasses that were weighed by this latter method (McLellan et al., 2002). Length and weight measurements were compared to minimum ages to develop curves for predicting weight and age from length. Length data for calves were also reviewed to determine the mean length at or near birth. When necropsies were performed and where a thorough search for gonads was conducted the success at finding gonads is reported.

Morphometric data were plotted and regressed using *Statistica*.

RESULTS

Not all carcasses come ashore or can be examined in detail. As far as it is possible to determine from the available data, necropsies were conducted on 3/9 animals in 1970-79, 5/15 in 1980-89, 17/21 in 1990-99, and 4/10 in 2000-02. Carcass decomposition condition averaged 3.4 (moderate to severely decomposed). Body weight was determined in 10 cases, and ranged from calves at 1,000kg to adults up to 52,640kg. There are 19 partial or complete skeletons archived at a variety of museums. Soft tissue archives were deposited for 18 individuals at various institutions, but the current state and availability of these materials has not been established in all cases.

Table 1 shows the 18 adults and juveniles, and 12 calves for which there are necropsy reports. In 14 cases the presumed cause of death was stated to be, or likely to be, vessel collision. Four deaths were presumed to be caused by gear entanglement. In 12 cases, no cause was given.

Table 2 shows available blubber thickness measurements, and Appendix Table 2 shows available morphometric measurements. Girth data were at times available, and have been included where the animal was not thought to be significantly bloated or deflated. Table 3 shows weight records of total and individual organ weights for a neonate.

Fig. 1a shows the relationship between Julian Day of stranding and calf total length. Fig. 1b shows the logarithmic relationship between age and total length. Fig. 1c shows the linear relationship between age and body weight for a limited subset for which weight and age were available (n=8). Fig. 1d shows the exponential relationship between length and weight. Fig. 1e shows the linear relationship between total length and fluke width. Fig. 1f shows the exponential relationship between snout to blowhole length against total length. Fig. 1g shows age against fluke width and Fig. 1h, total length against flipper length. Trauma from collisions of right whales with ships is shown both externally (Fig. 2) and internally (Fig. 3). Fig. 4 shows fishing gear entanglement, Fig. 5 shows summary sketches of two entanglements and Fig. 6 shows lesions in the integument of one case.

Case reports (for which greater details are available than summarised in Table 1)

NEAq 1504

This animal was found floating and retrieved off Cape Cod. It was examined on 4 August 1986. Four cuts, 250-300cm in length, ran cranially from a point 60cm cranial to the flukes on the left lateral aspect, through blubber and muscle into the abdominal cavity. The cuts were spaced at approximately 30cm intervals. The most caudal incision penetrated to the spine and possibly through a vertebra.

MH-89-424-Eg

This calf live stranded on Cumberland Island, GA on 3 January 1989 with foetal folds still visible. It was frozen and trucked to Boston for a full necropsy in March 1989. There were no obvious signs of injury. It did have significant oedema that was not described in detail, but a full forensic examination was not conducted, so the cause of death was undetermined beyond a perinatal death. Detailed organ weights for this animal are given in Table 3.

NEAq 1907

This animal was last seen alive two weeks before washing ashore on 12 March 1991. It was a two year old in poor body condition. Net and line were wrapped tightly around the tail stock for at least eight months, with apparent restriction of movement. Several meters of 6mm line had embedded up to 5cm in to the tail stock, with scar tissue overgrowing the embedded line. Blood flow was not affected. An inflamed area 50cm in diameter was observed caudal to the blowhole. Severe and massive comminuted fractures in the right maxillary and frontal bones extended in to the cranial vault (Fig. 3c). Blood clots were observed around the fractures and in adjacent tissues. Haemorrhage was also observed under the periosteum in the pterygoid sinus area. Dermal discolouration above this area revealed the impact point. Mud was found in gullet and vagina suggesting the whale

Summary of post-mortem findings for right whales that died in the NW Atlantic between 1970 and 2002.

(Dashes = no data).

Year	ID number(s)	Sex	Age (y)	Tissue quality (0-4)	Presumed cause of death
1975	USNM 504257	М	-	4	Undetermined
1976	JGM 165/ USNM 504343	М	0	3	Possible collision
1979	JGM 415/ 504886	Μ	3	-	Vessel collision
1981	HNN 893	М	0	-	Undetermined
1983	MME00084/ NEAq 1128	Μ	2	-	Vessel collision
1986	MH86142 Eg	F	-	2	Vessel collision
1989	MH89424 Eg	Μ	0	2	Live stranded/probable perinatal
1991	RKB-1420/ MH91762Eg/ NEAq 1907	F	2	3	Vessel collision
1992	NEAq 1223	F	Min 12	3	Vessel collision
1993	RKB-1424	Μ	0	2	Vessel collision
1993	RKB-1425	F	0	4	Undetermined
1995	NEAq 2366	Μ	2.5	-	Entanglement
1995	NEAq 2250	Μ	Min 4	4	Probable vessel collision
1996	RKB-1429/ NEAq 1623	Μ	Min 12	3	Vessel collision
1996	MH96441Eg/ NEAq 2220. Satellite tagged	Μ	Min 5	4	Vessel collision or septicaemia
1996	Jan 02 96 calf	F	0	4	Undetermined
1996	RKB-1430	F	0	4	Undetermined
1996	GA96II2201	Μ	0	-	Undetermined
1997	NEAq 2450	F	Min 4	3	Vessel collision
1997	RKB-1449	Μ	0	3	Undetermined
1998	WJW 001/ NEAq 1333/ NCSM 8287	Μ	Min 21	4	Undetermined
1998	RKB-1451	F	0	3	Undetermined
1999	NEAq 1014	F	Min 28	3	Vessel collision
1999	NEAq 2030	F	Min 10	4	Entanglement
2001	NEAq 1238	Μ	Min 19	4	Entanglement
2001	RKB-1452 VMSM 2001 1021	Μ	0	3	Vessel collision
2001	NY-2680-2001	F	0	3	Vessel collision
2002	VMSM 20021097	F	-	-	Undetermined
2002	WAM 577 Eg	F	-	4	Undetermined
2002	NEAq 3107	F	1	3	Entanglement

Table 2 Axillary blubber + skin thickness (cm). * = blubber only.

Case	Sex	Age	Dorsal	Lateral	Ventral
NEAq 3107	F	1	11	27	-
NY-2680-2001	F	0	13	14	17
RKB-1452	М	0	11	11	-
NEAq 1238	М	Min 19	10.5*	-	-
NEAq 1623	М	Min 12	15	17	20
NEAq 2030	F	Min 10	15*	15*	-
NEAq 1014	F	Min 28	13	13.5	-
NEAq 2450	F	Min 4	13.3	-	-
RKB 1449 calf	М	0	3.7	5	4.8
NEAq 2220	Μ	Min 5	-	-	16.5
504343	М	-	11.3	10.5	12
504886	М	3	13	15	14
HNN 893 calf	М	0	3	5	5
NEAq 1504	F	-	17	17	17
RKB 1420	F	2	8	8	10
NEAq 1223	F	Min 12	14.5	16.2	21.6
NEAq 2250	М	Min 4	12.5	-	-
Jan 02 96 calf	F	0	2.75*	3*	3.5*
RKB 1430 calf	F	0	5	-	-

was forced into the bottom. Diagnosis was vessel collision impact. The debilitation from entanglement could have compromised the whale's ability to avoid vessel traffic.

NEAq 1223 – Delilah

The animal was seen with her first calf in the Bay of Fundy on 5 September 1992, when she was photographed thrashing violently, after which she became motionless and was then determined to be dead on close approach. The calf survived. The carcass floated ashore on Grand Manan on 9 September. Three possible bruises were then photographed: on the chest ventrally between the flippers; one meter cranial to the genital slit; and a large area 80cm in diameter 250cm caudal to the insertion of the left flipper. A necropsy was undertaken on September 13 and 14. Large amounts of blood were found in the thorax and abdomen suggestive of internal haemorrhaging. Several dark red masses about 10cm in diameter, of a putty-like consistency, soluble in formalin, were thought to represent 'cooked' clotted blood. Samples from these were positive for occult blood. A few of the same were also in the thoracic cavity. Microscopic examination at 400x of smears revealed abundant terminal sporulating bacilliary bacteria. The left lung appeared normal. Other solid visceral organs were badly autolysed. Mammary glands were full of milk. The gastrointestinal tract was largely intact, with some gastric fluid and scant faeces in the lumen. A complete dissection revealed no broken bones. Lung, intestine and skeletal muscle were examined histologically. All were very decomposed. The intestinal serosa were covered in a strongly acidophilic material suggestive of autolysed blood. The internal bleeding along with the surface bruising was assumed to have been caused by severe blunt trauma.

RKB 1424

This calf was run over off the Florida coast by a twin screw 25m vessel travelling at 15 knots on 5 January 1993. It was observed bleeding severely at the surface for 45 minutes before the crew lost sight of it. It was relocated, towed ashore and necropsied five days later. Two distinct and separate propeller laceration series were observed (Fig. 2a).



Fig. 1. Relationships between age, weight and length parameters in North Atlantic right whales examined at necropsy in the period 1970 to 2002. Animals less than 9.2 m were assumed to be calves in their first year. (a) Julian day of stranding of calves vs. total length; (b) Age vs. total length; (c) Age vs. body weight; (d) Total length vs. weight; (e) Total length vs. fluke width; (f) Total length vs. snout to blowhole distance; (g) Age vs. fluke width and (h) Total length vs. anterior length of flipper.

Table 3Total and some organ weights for MH-89-424-Eg.

Item	Weight (kg)	Dimension (cm)	% of total weight
Total whole weight:	861.84		100
Testis R	0.136	15.3 x 4.6 x 2.5	0.02
Testis L	0.128	14 x 4.2 x 4	0.01
Epididymis R	0.105		0.01
Epididymis L	0.71		0.08
Vas deferens	0.256		0.03
Prostate	0.351		0.04
Heart	7.9		0.92
Lung L	5.178		0.60
Liver	14.29		1.66
Spleen	0.216		0.03
Kidney R	3.14		0.36
Kidney L	2.97		0.34
Stomach	3.7		0.43
Intestine	22.9	3,100	2.66
Pancreas	1.06		0.12
Adrenal R	0.015		0.00
Adrenal L	0.021		0.00
Thymus R	0.42		0.05
Thymus L	0.49		0.06
Skull	21.26	106L x 59W	2.47
Humerus R	1.64		0.19
Flukes	17.35		2.01
Thyroid L	0.0685		0.01
Epaxial muscle	26.942		3.13
Hypaxial muscle	11.98		1.39
Transversus	1.95		0.23
Diaphragm	3.904		0.45
Rectus abdominus	0.8		0.09
Iliocostalis	4.114		0.48
External oblique	2.1		0.24
Internal oblique	2.07		0.24
Pectoralis	0.659		0.08
Seratus	0.226		0.03
Levator ani'	0.789		0.09
Intercostalis	2.875		0.33
Post cranial skeleton	102.22		11.86
(incl. ribs & scapulas)			
Blubber	181.3656		21.04
Tongue	46.9476		5.45

Vertebrae: 7 cervical, 14 thoracic, 11 lumbar, 23 caudal, 12 chevron. There was significant edema, so weight data should be interpreted with caution. In addition to body fluid loss, some organs and/or tissues were not weighed as parts. Brain was liquid.

The first extended from the dorsal peduncle to just caudal to the cranium, while the second entered the ventral left flank and ran down the ventral throat to the head. The blade marks travelled from the tail to the head. The viscera were autolysed and severely macerated. A patent ductus arteriosus was present with a 1.5cm internal diameter. Severe massive acute fractures affected the left frontal bone in to the cranium, the left humerus, radius and the proximal tip of one rib. A large contusion with clotted blood was evident dorsally caudal to the cranium. The diagnosis was severe massive acute trauma with fractures and associated haemorrhage, as caused and witnessed by the vessel.

RKB 1425

This calf was observed floating dead on 18 January 1993 off the Florida coast. A necropsy was conducted on 19 January. It was severely decomposed and had severe post-mortem shark predation. Nutritional state appeared to be good. Most of the viscera were missing, although some meconium was present in the distal colon. A patent ductus arteriosus was observed with a 1cm diameter. The intact lungs were heavy (a)



(c)



Fig. 2. External trauma from collisions of right whales with ships. Orientation is shown by a long arrow pointing cranially, and a short arrow dorsally. (a) Multiple lacerations in a right whale calf induced by a large ship propeller. Case: RKB 1424. Photographer: Robert Bonde. (b) 12 propeller cuts from the right mid-rostrum, over the dorsal midline to the left-lateral at mid-thoracic. Box show area of dissected detail in Figure 3e. Case: NY-2680-2001 Photographer William McLellan. (c) Sternal bruise (arrows) overlying blubber hemorrhage and fractured transverse processes. Such external evidence of major internal trauma is rare in right whales. Case: NEAq 1014. Photographer: New England Aquarium.

and saturated with blood. Diffuse haemorrhage was observed in the coronary groove of the heart. The diagnosis was perinatal death.

NEAq 2366

This animal came ashore in Rhode Island and was examined on 17 July 1995. It was entangled in 1cm diameter lobster line, with one piece through the mouth at the tongue base, and 6 to 8 lines wrapped tightly around the right flipper insertion, embedded several cm into the distal end of the radius (see Fig. 4a-c). The animal had been entangled for at least one and a half years. The soft tissues overlying the lesion in the radius had a complex pattern of diffuse patchy ossification. These changes were lost in the museum preparation, except for those evident in the image, adherent to the periosteum. The testes were weighed, measured and fixed in formalin: left – weight 1,003g, length 22.5cm, width 12cm, circumference 35.5cm, and right - weight 800g, length 22.5cm, width 11.5cm and circumference 29cm. Many other samples were also taken. No necropsy or histology report can be located.

NEAq 2250

This animal was towed ashore on 20 October 1995. The whale appeared to have been dead about two weeks. It was last seen in good health when satellite tagged on 8 October. Logistics precluded a full necropsy. The animal was deflated with a large area of missing skin, blubber and muscle dorsally, with the spine separated from surrounding muscle and partially protruding. The satellite tag never functioned, nor was it found. The tag insertion point was recorded to have been in the region missing from the dorsum. The wound started 3.6m caudal to the blowholes, and ran caudal for 4.6m. It is unclear if the wound was induced by a propeller, and if it were, whether the wound preceded death. The blubber directly caudal to the blowhole was dark red. Samples of dorsal blubber that were frozen, had little of the usual structural integrity on thawing. Ventral blubber retained its structure under the same treatment. Bacteriological and histological study of dorsal blubber for evidence of septicaemia, in terms of vasculitis and inflammation proved negative, albeit with severe autolysis noted. Blubber samples also tested negative for bacterial endotoxin, using the Limulus Amebocyte Lysate test. At least four vertebral epiphyseal plates were fractured on the ventral surface, with others fractured on the dorsolateral aspect. It was assumed that these fractures were induced by ship strike. Given the good condition of the animal two weeks prior to the discovery of the carcass, an ante-mortem ship strike was assumed to be the most parsimonious cause of death.

Jan 02 1996

This calf was discovered on 2 January 1996 stranded in Florida. It died at least four days prior to being frozen. It was necropsied nine days after discovery. The umbilicus had a 5cm diameter ragged orifice, through which intestinal loops herniated. The baleen was missing, and sand had been driven into the orifices. The only bone fractures were two ribs, thought to be post-mortem. Yellowish waxy deposits were found in the muscle cranial of the peduncle, in the pleural space and elsewhere. Kidney, heart, stomach, intestines and reproductive tract appeared normal. The thymus weighed 1.04kg. No histological samples were taken. Umbilical vessels were patent, with no evidence of infection. The ductus arteriosus was patent with a 15mm diameter. The foramen ovale was occluding with five, 4-6mm circular openings still patent. The major abnormality was the herniation of the intestine at the umbilicus. It was debatable as to whether this was a sign of ante-mortem herniation, or as a result of post-mortem bloating. In the absence of any other changes, it was assumed that the animal died from a congenital umbilical defect.

NEAq 1623 – Lindsay

This animal was found floating dead on 30 January 1996 off the coast of Georgia. It was towed ashore and necropsied the next day. Overall the animal looked fat and healthy. There was no external evidence of any trauma. Most of the viscera were cranial to the liver. The gastrointestinal tract was largely empty of contents. Kidneys and lungs were autolysed but unremarkable. Testes were absent. A 2×1.5 m area of blubber and underlying musculature just dorsal to the left flipper was infused with blood. This area overlay a region of acute bone damage. Severe massive comminuted fractures affected the occipital, basioccipital and parietal bones, penetrating fully through these massive bones into the brain cavity. Clotted blood infused the musculature overlaying these fractures. Both ear bone complexes suffered extreme multiple fractures suggesting intense mechanical force. Samples of these areas were taken in formalin. Left ribs 2 and 3 and the caudal tip of the left scapula were also fractured. It was concluded that the animal had suffered massive blunt trauma from a moving vessel and died approximately five days prior to examination.

RKB 1430

This calf was observed off the Georgia coast on 19 February 1996, was towed ashore and necropsied at Gainesville Veterinary School, FL on 20 February. It was in good physical condition with no external abnormalities. Milky fluid was found in the oesophagus and stomach, and mustard yellow colonic contents were also observed. The viscera were autolysed, with a reddened intestinal serosa. Samples of the severely oedematous lungs floated, but marginally. The autolysed right ovary measured 20 imes 10 imes3cm. Some cranial bones were disarticulated along fissure lines, but it was unclear if this was pre- or post-mortem. Histologically the left eye showed chronic, active perivasculitis, the lung, ovary, heart, skeletal muscle, retrobulbar tissue and left optic nerve were unremarkable. The animal was assumed to have died two to three days prior to examination of an undetermined cause.

GA96II2201

This calf was found floating off the Georgia coast, towed ashore and examined on 24 February 1996. There was substantial post-mortem shark scavenging, including the blowhole and ventral abdomen areas. There were no other external marks. The stomach contained a watery fluid, while most of the small intestine was missing. The remaining distal 2m of colon contained meconium. The testes measured 14cm in length and 4cm in diameter. The heart had a small amount of pericardial fluid. The lungs had a prominent sub-capsular oedematous serosanguinous exudate: a sample floated in water. Haemorrhage and loose blood clots were observed caudal to the left orbit. There was no evidence of skeletal trauma. Histology showed multifocal alveolar oedema and congestion in the lung, with multifocal patchy atelectasis and haemorrhage also present, suggestive of acute agonal cardiovascular collapse. Heart, eyes and skin were all unremarkable histologically. The unilateral retrobulbar haemorrhage suggested a unilateral traumatic event, but with the absence of external ocular trauma the changes were inconsistent with a concussion event. Ears showed no fracture or structural disruption. Both middle ears contained mesenchymal webs with associated soft tissue. Postnatal persistence of these in humans is often associated with respiratory, middle ear and mastoid disease. The diagnosis remained open.

NEAq 2220

This animal washed up on the beach as a deflated 'blubber bag' containing dissociated bones on 9 March 1997. Remarkably, the epidermis was still adherent to the dermis. One of its vertebrae was found 100m down the beach. Surf and tide precluded adequate anchoring. 8mm polypropylene line ran through the mouth and then over the body to the tail, where there was a single tagged lobster trap, that had been set as part of a string of 20 on 14 November 1996 in the Bay of Fundy, Canada. The string was noted missing in mid-December. The animal was last sighted alive at a satellite tagging attempt on 3 October 1996. The tag had failed to penetrate, but the tag anchor was assumed to have remained in the whale. The polypropylene line had incised the oral



Fig. 3. Internal trauma from collisions of right whales with ships. Orientation is shown by a long arrow pointing cranially, and a short arrow dorsally. (a) Fractured right mandible. 1: lip dermis overlying fractured mandible. 2: Distal and 3: Proximal part of fractured mandible. A 15 cm mandibular fragment was found free in the oral cavity. Case: NEAq 2450. Photographer: Christopher Slay. (b) Fractured right mandible of case in Fig. 2c. Oval overlies fracture site. 1: lip dermis overlying fractures mandible. Case: NEAq 1014. Photographer: New England Aquarium. (c) Cleaned skull of a right whale that sustained a heavy blow to the right side of the head. Fractures in the right maxillary and frontal bones that entered the brain are evident. Case: NEAq 1907. Photographer Robert Bonde. (d) Incised blubber/ muscle interface on the right flank of thorax/abdomen, showing gross evidence of hemorrhage and oedema on the muscle surface. The carcass lay on its left side. The blubber sheet (1) has been partially reflected from the underlying muscle (2). Arrows show the base of the incision at the sub-dermal sheath. Case: NEAq 2450. Photographer: Michael Moore. (e) Multiple propeller cuts through the skull of a juvenile right whale shown in Fig. 2b. The series of cuts (long white arrows) completely bisected the right blowhole, severed the right premaxilla and maxilla, penetrated into the braincase and cleaved the right orbit from the rest of the skull as the trauma proceeded from cranial to caudal across the skull. Short black arrow: baleen. Short white arrow: left orbit. Case: NY-2680-2001. Photographer: William McLellan.

rete, scarred the upper and lower lips, damaged the baleen, and scarred the peduncle and fluke leading edges with scars showing at least two lines wound around the peduncle in opposite directions. Blubber condition was good. A 326cm sagital slice through the blubber on the left of, but parallel to the dorsal midline ran from the peduncle cranially. The depth of penetration below the blubber was not determined, as the skeletal muscle was mostly absent, following liquifaction. The cranial end of the cut ended in three parallel propeller type cuts at a 30-degree angle to the major cut, at 20cm spacings. A healed penetration wound was found dorsal to the right axilla. A tract in the fascial plane between the blubber and muscle, containing a purulent exudate, ran from this abscessed area up towards the blowhole. Histology and microbiology of this area was unremarkable. No internal organs remained. A fracture of the left palatine bone adjacent to the left occipital condyle was observed to protrude from the roof of the mouth. The



Fig. 4. Fishing gear entanglement of right whales – external and internal trauma. Orientation is shown by a long arrow pointing cranially, and a short arrow dorsally. (a) Multiple wraps of 1cm diameter line around the right flipper. View from caudal, animal lying on back. Case: NEAq 2366. Photographer: Amy Knowlton. (b) The same flipper as in 4a after the rope was removed at necropsy. The leading edge of the flipper was deeply incised. View from cranial. Case: NEAq 2366. Photographer: Philip Hamilton. (c) Medial aspect of right radius: rope induced erosion, and adjacent periosteal proliferation in the leading edge of the distal third of cleaned right radius from the specimen shown in 4a and b. Skeleton at Museum of Comparative Zoology, Harvard University, Cambridge MA MCZ 62052. Case: NEAq 2366. Photographer: Michael Moore. (d) Rope wrapped around the right flipper of a right whale that struggled acutely and apparently died as a result of entanglement in what was probably a Danish Seine. Image taken looking down on the antero-ventral aspect of the flipper. Case: NEAq 1238. Photographer: Amy Knowlton. (e) Ventral aspect of peduncle of an animal that was chronically entangled with a single loop of line. The line was removed, but the animal subsequently floated ashore dead. Case: 3107. Photographer: Peter Brown. (f) Loss of dorsal post-blowhole blubber sheet induced by a single polypropylene line slowly cutting in dorsally between both axillae during the period May to October 1999. Case: NEAq 2030. Photographer: Lisa Conger. (g) Right side of the case shown in 4f. Part of head and flipper still in the water. Rope is knotted around the right axilla. The line incising the dorsal blubber is evident at left. Case: NEAq 2030. Photographer: Lisa Conger.





Fig. 5. Sketches of fatal entanglements. Artist: Scott Landry. Sketch made at necropsy (a) or two months prior (b and c). (a) Case: NEAq 1238. Dorsal view, see Fig. 4d; (b) Case: NEAq 2030. Dorsal view, see Fig. 4 f and g; (c) Case: NEAq 2030. Left lateral view.

advanced state of decomposition precluded determination if the ship strike was pre- or post-mortem, although given that dead right whales usually float on their side, a dorsal propeller cut is likely to be pre-mortem. There was also speculation that the healed penetrating wound may have induced a septicaemia. The gear entanglement was assumed to be insufficiently severe to cause the death, especially as the good blubber condition gave no indication of debilitation. The diagnosis remained open.

RKB-1449

This calf stranded dead on 9 January 1997 at Flagler Beach, FL, with evidence of bruising on the tongue and underlying muscle. The lungs were inflated, foetal skin folds remained along the flank of the peduncle, callosities and cyamids were absent, umbilical vessels were open, baleen plates were short (*ca* 5cm), and physical condition was good. The stomach was empty and meconium was present in the intestine. Liver and kidney were autolysed. The heart was normal. Histology revealed widespread autolysis with abundant alveolar and interstitial proteinaceous fluid in the lung, and focally extensive haemorrhage in the tongue. The animal was assessed as a neonate, with death at or close to parturition, that was possibly associated with dystokia, given the lingual bruising.

NEAq 2450

This animal was found floating dead on 19 August 1997 in the Bay of Fundy; it was towed ashore for necropsy on the next day. It appeared to be in good body condition. It had an open comminuted fracture of the right mandible 1/3 the length of the bone from the temporomandibular joint, with a 15cm section lying free in the oral cavity (Fig. 3a). The



Fig. 6. Surface lesions of case shown in Figs 2c and 3b. Case NEAq 1014. (a) Lingual ulcerations. Scale bar = 5cm. Photographer: New England Aquarium; (b) Dermal papillomatous ulcer. Scale bar = 2cm. Photographer: Moira Brown.

fracture surface varied from ragged to smooth, suggesting some chronicity, with a creamy exudate at the fracture site. Clots were found in adjacent severed blood vessels, with haemorrhage in the adjacent lip and gingiva. Several loose bone fragments were found ventral and caudal to the right middle/inner ear complex. Both ear bone complexes were frozen and scanned later using a spiral CT protocol at 140kV and 206mA. Foci of demineralisation most probably caused by a traumatic event, but possibly a degenerative disease were observed. Histology suggested these to be antemortem. An extensive area of haematoma and oedema was observed in the blubber-muscle interface on the left lateral. from the cranial thorax to the genital slit region, with red tinged fluid and torn underlying muscle (Fig. 3d). The muscle tears extended to the underlying vertebrae. This lesion measured 6 \times 1m in width a depth of 3-5cm. Histology failed to confirm if this was an ante-mortem traumatic lesion. The kidneys contained 3cm diameter calcified masses, which were found to contain nematodes of unknown species on histological examination. A ruptured diaphragm was found, with intestinal loops and hepatic lobes in the thoracic cavity. Diaphragmatic muscle adjacent to the left body wall had a diffuse area of haemorrhage which underlay the area of bruising described above. Other than the aortic arch and some lung tissue, little else remained of the viscera. The cervix, uterus and mesosalpinx were not decomposed, but the ovaries were not found in

spite of an intense search. Diagnoses were mandibular fracture at some time prior to death, probable massive blunt trauma to the left side and parasitic nephritis. It is interesting to note that there was an anecdotal report of a right whale behaving oddly in the shipping channels for the two days prior to discovery of the carcass, which would concur with the finding of some remodelling in the jaw fracture, suggesting the animal survived for some days after a major traumatic event. The skeleton was taken to the Nova Scotia Museum of Natural History in Halifax, NS. Once the skull had been cleaned (04/2003), it became apparent that the premaxilla, maxilla, vomer and nasals were all damaged. The nature of the fractures appeared to be pre-mortem (A. Hebda, pers. comm.). This finding corroborates the diagnosis made after necropsy of death due to vessel collision.

RKB 1451

This calf was found floating off the Georgia coast, towed ashore and examined at the Gainesville FL Veterinary School on 11 January 1998. No cyamids were present. It was in good body condition and had moderate to severe contusions in the musculature surrounding the left flipper and along the spinous processes. The abdominal cavity contained several litres of serosanguineous fluid. Bruising was also present at the base of the tongue and several areas around the cranium. The serosae of the stomach and intestines were dark purple. The stomach was empty except for a small piece of membrane, identified histologically as amnion. The liver was congested and dark purple. The pericardium contained about a litre of dark red watery fluid. The pleural cavity contained several litres of dark red watery fluid. A lung sample did not float in water. The following organ weights were recorded in kg: lungs 38, left ovary 0.25, right ovary 0.2565, brain 1.25, right kidney 7.4, left kidney 6.9, heart 16 and spleen 0.7. The intestines were 35.3m long. No broken bones were observed. Histology of heart and kidney was unremarkable. Lung, liver and kidneys were totally autolysed. The diagnosis was perinatal stillborn, with possible delivery complication, given the bruising observed. The absence of cyamids concurs with the assumption that the animal had not suckled.

NEAq 1014 – Staccato

This animal was seen alive in Cape Cod Bay on 15 April 1999 and found dead on 20 April and towed ashore. On the 15 April she was observed with her mouth open just below the surface, in aggregates of pteropods and copepods, suggestive of normal feeding activity. When the animal was examined by a diver prior to towing ashore, blood was observed to be pooling along the lower, right jaw. Multiple papillomatous lesions were found on the body surface, especially along the caudal peduncle, up to 8cm in diameter, with a whitish, mottled, proliferative centre often raised above the skin surface (Fig. 6b). On a cut section a firm well-demarcated nodule of connective tissue was found in the underlying dermis. Histology showed vacuolation and hydropic degeneration of keratinocytes, ulceration, papilliform proliferation, loss of pigment, and perivascular infiltration of acute and chronic inflammatory cells. No viral inclusions were observed. A sternal patch of haemorrhage was observed in the epidermis (Fig. 2c) extending into underlying blubber, along with a granulating abrasion on the left pectoral flipper. Good blubber quality and thickness were observed. Oedema was present in the ventral thoracic fascia from right axilla to mid-abdomen. A fracture was observed in the right mandible (Fig. 3b), 1m from the

temporomandibular joint, with haemorrhage and oedema overlying the fracture site. A thin layer of regenerating cartilage was observed histologically on the exposed fracture surface, suggesting the fracture was at least seven days pre-mortem. The right transverse processes of the last two thoracic and first three lumbar vertebral transverse processes were also fractured. Oedema and haemorrhage were observed in the right axillary and right hypaxial musculature overlying the above transverse process fractures sites. Extensive multi-focal ulceration of the glossal mucosa was observed (Fig. 6a): histology showed full thickness loss of the epithelium. Autolysis prevented adequate gross or histological analysis of the viscera. A dark pasty faecal material was observed in the distal 3-4m of the intestine, red blood cells were observed here microscopically. Diagnoses were: traumatic injury sustained on the right side fracturing the mandible, lingual ulcerations, epidermal papillomatosis and ulceration, haemorrhagic colitis, and suspected septicaemia precipitated by trauma and complicated by chronic illness. The precipitating traumatic event was assumed to be a ship strike. A conference abstract was published on this case (De Guise and St Aubin, 1999).

NEAq 2030

This animal was first sighted entangled on 10 May 1999 on Cultivator Shoals, on the western edge of Georges Bank. It had three wraps of 7/16th inch diameter polypropylene line and gillnet across its back which was tight but not incising. The animal was then sighted in the Bay of Fundy on 2 September. Subsequently two wraps were cut by the disentanglement team, but a third remained deeply embedded across the back, tightly stretched between the two axillae. The last sighting in the Bay of Fundy on 13 September showed the dorsal line to have incised to the base of the blubber. It was found floating dead on 20 October, 5 miles east of Cape May, NJ. Both flippers were incised at the leading edge by the lines into the bone to a depth of 13cm by one wrap on the left and 18cm by two wraps on the right (Fig. 4g). There were knotted tangles at each flipper leading to a single embedded line dorsally and two tight lines under the ventral surface. Tangled line and monofilament gillnet trailed from the left flipper. By this time the dorsal line had embedded in to the musculature, and 1.4m of muscle tissue along the dorsal midline was exposed (Fig. 4f). As the cut moved laterally the gap tapered until closing at the flippers. There was evidence of shark bites at the wound edge. As the animal was hauled up the beach the left scapula partially fell away from the animal. The lines were under extreme tension and snapped back when cut. No histology samples were taken. The medial aspect of the right scapula was described as having proliferative bony change. This was not evident in photographs of the scapula after cleaning. Blubber thickness was low: 11 to 15cm, except in the dorsal keel cranial to the tail, suggesting an emaciated condition. Internally there was no evidence of traumatic skeletal damage or haemorrhage in soft tissue. Internal organs were autolysed, no samples were taken for histology. Skin and blubber were frozen. The diagnosis was massive traumatic injury induced by entanglement in fishing gear with resultant starvation. A sketch of the entanglement is shown in Fig. 5b.

NEAq 1333 – Delta

This animal was examined on the beach in North Carolina on 8 October 1998. There was no skin or baleen remaining and the carcass had been heavily shark scavenged. The premaxilla and maxilla at mid-rostrum were fractured. Additional old healed fractures were found in the vomer. There was no evidence of bruising in the blubber. Fractured neural spines were found between vertebrae T8 and T17, with the trauma increasing in depth caudally. The shoulder and rib/transverse process joint capsules were heavily ossified. Viscera were absent, with the exception of large vessels and rings of bronchial cartilage. An experimental protocol from the Armed Forces Institute of Pathology (AFIP) was conducted on this specimen. It was designed to determine if there was evidence of anti- or post-mortem tissue reaction from the bones of severely decomposed large whales that were potentially killed from ship strike. Histological examination found no evidence of a vital tissue reaction within the marrow spaces, periosteum or trabeculae of the examined sections of bone, suggesting that the fractures at this site occurred after the animal's death. Cause of death was undetermined.

NEAq 1238

This animal was examined on the beach in the Magdelene Islands, Canada from 4-6 November 2001. It was heavily wound up in approximately 200m of 22mm diameter synthetic three-strand line that passed the right corner of the mouth, between two baleen plates, across the tongue, and exited by the left corner of the mouth, to go under the left flipper, across the chest to the right flipper, circling the right axilla three times and trailing off (Figs 4d and 5a). Each strand of the rope carried a lead filament. A second piece of line appeared to pass through the baleen with a frayed end that exited the mouth at the middle of the right lip. The exact relationship of this line to the rest was obscured by the use of some of the lines to secure the carcass at the initial beaching. At that time, before the necropsy examination, 30m of line was removed that was trailing from the flukes. This line was of a similar size, but different manufacture. A deep rope abrasion was evident around the tailstock, despite the absence of skin. There was also an abrasion on the ventral surface of the left fluke from the leading edge at the insertion to the caudal notch. At the initial beaching a further three wraps were also observed on the peduncle. The majority of fisheries specialists who examined the gear believed the ropes were from a Danish Seine system, although one suggested that it was offshore crab pot line. The depth of the rope-induced wounds was assumed to have arisen from trauma that could only have been induced prior to death, suggesting the animal had struggled in more of the seine gear than was present at the necropsy. Before the animal could be examined internally it was rolled up the beach using an excavator bucket as a lever at the thoracic region. Sub-dermal bruising was observed in the peduncle region beneath the rope burns described above. Blubber was in good condition. Testes and all other internal organs except tongue and aortic arch were fully autolysed. Vertebral epiphyses were fused. No broken bones were observed, except those damaged during carcass manipulation on the beach. It was concluded that the animal had struggled in the entangling gear, although the actual cause of death was unclear, but likely to reflect severe entanglement.

RKB-1452

This animal was examined on the beach in Chincoteague, VA on 19 March 2001; it was in good general nutrition condition, with ample body fat. Five large propeller slashes were observed at 50cm spacing along the dorsal peduncle, penetrating up to 70cm into hemorrhagic tissue. Detailed measurements of the wounds were recorded. Two of the wounds penetrated the abdominal cavity. The muscle mass appeared ischaemic, suggesting heavy blood loss. Viscera were fully autolysed with the exception of the terminal large intestine. Several of the lumbar vertebrae and epiphyses directly beneath the external propeller lacerations were fractured, and the associated epaxial muscle was hemorrhagic, as observed grossly and histologically. The cuts suggested that the vessel travelled from right caudal to left cranial. The strike had to be pre-mortem as dead whales tend to float on their sides after death. It appeared the animal had its head down to dive at the time of the strike. The diagnosis was that the animal died after massive trauma from a propeller of at least 165cm in diameter.

NY-2680-2001

This animal was found floating off the coast of Long Island and towed to a pier in New York harbour on 19 June 2001. It had 12 propeller cuts from the mid-rostrum, over the dorsal midline to the left-lateral at mid-thorax (Fig. 2b). Epaxial muscle had ruptured through the middle 4-5 wounds in the incision series. Slice 3 cut through the blowhole, maxilla and premaxilla. Four went through the sagital crest. The remaining cuts were in the thoracic region. A number of left ribs and the heart were found dorsal to the transverse processes of the thoracic vertebrae. Haemorrhage was evident at the wound sites and throughout the fascia. Viscera were largely autolysed. The vagina and caudal uterus were present. The diagnosis was vessel strike with 12 propeller gashes along the left side of the animal.

NEAq 3107

First sighted entangled on 6 July 2002, this animal washed up dead in heavy surf on Nantucket Island on 14 October 2002. A single loop of 3/8" polypropylene three-strand line was removed by a disentanglement team from its peduncle five weeks prior to beaching. The entanglement lasted at least seven weeks. The disentanglement followed attachment of a satellite tag buoy to the entangling line to enable relocation of the case. The animal was observed by an aerial survey to be alive, but 'somewhat thin' two weeks prior to beaching. On the beach it was observed to have a substantial post cranial dorsal dip in the lateral profile, typical of an emaciated right whale (Pettis et al., 2004). Extreme surf conditions precluded examination before most of the soft tissues and bones were macerated and extruded via the oral cavity from within the blubber coat, however examination of the peduncle laceration revealed 15 and 19cm cuts respectively in the left and right lateral aspects, and 5cm ventrally (Fig. 4e). Tendons were intact, but two ventral 8mm internal diameter medial caudal veins (which are thick walled) appeared to have been severed and walled off. The dorsal blubber coat was incised from blowhole to tail. The blubber was found to be thinnest caudal to the blowhole, reflecting the emaciation described above. Death was assumed to have resulted from complications arising from the chronic entanglement. Blubber samples were retained. Unremarkable histology was taken of one of the walled off veins.

DISCUSSION

The major finding of these incomplete reports is that the primary cause of death in adults and juveniles appears to be human induced trauma from ship collisions (14/30) and fishing gear entanglement (4/30). Thus, of the 443 animals catalogued in the period 1976-2002 (Kraus *et al.*, 2001;

Right Whale Consortium Database. contact aknowlton@neaq.org) plus 16 dead neonates that were never catalogued, a minimum of 3% (14/459) of the population were killed by ships. It is important to note that ship struck whales may come to shore or be sighted more easily than whales dying from gear entanglement or debilitation. Both the latter cases are more likely to sink if feeding has been precluded for a significant time prior to death, resulting in a significant loss of the low density body lipids, making the carcass negatively buoyant. Furthermore, whereas shipping density decreases rapidly with distance from shore, much of the heavier fixed fishing gear is on the offshore half of the continental shelf, reducing the likelihood that rapidly fatal entanglements will be identified, as such cases once dead are likely to go further offshore with the prevailing offshore wind and currents in much of the North American Eastern seaboard. In spite of the majority of adult and juvenile cases receiving a diagnosis, the conclusions are based on an incomplete dataset given the limitations of the material. An even less complete understanding of the causes of death is evident for the neonatal cases. Necropsy reports used various descriptors, such as 'peri-natal' death, or 'stillbirth'. These conclusions are highly valid, given the recorded size class, lung inflation, presence of meconium in the gastrointestinal tract, and carcass recovery location in the calving ground. But there was no diagnostic conclusion as to etiology in any case. In three cases there were contusions thought to reflect dystokia. It is possible that these cases are all expressions of the expected mortality associated with parturition in any wild mammal population, but equally it is possible that these cases represent other etiologies. It is thus important to analyse any available material and future cases with the concern in mind that these neonatal mortalities may have one or more common underlying causes.

Many of the case reports summarised here raise more questions than they give answers. The enormity of the problem facing an objective analysis from necropsy of the causes underlying right whale mortality is eloquently summarised by the opening narrative of the internal examination of NEAq Catalogue #1907 (Buoy Girl): 'A violent eruption occurred on opening the abdominal cavity. Several meters of intestine and liver were expelled'. On another occasion on 17 October 1990 where a very large male right whale was examined in Maine; the body was on one island and the head on another. In addition to these obvious practical barriers to a complete gross necropsy, none of the necropsies for which histopathological sampling was conducted had tissues available from a full suite of organs. The complex physical, legal and political logistics of this kind of case usually add up to inevitable delays. Autolysis always compromised or destroyed many of the tissues. Eye, aorta and lung seem in general to be the least affected by autolysis. We are thus limited here to a very incomplete dataset, but one which has substantially improved for some more recent mortalities in terms of reducing the time delay between discovery of the animal and necropsy, completeness of the necropsy examination, and the utilisation of diagnostic histopathology and laboratory analysis.

The need to retrieve and fully examine and sample carcasses as rapidly as possible is obvious, given the rapid autolysis that occurs in these extremely well insulated animals. Unfortunately, the material and the working conditions rarely afford the opportunity to fulfil such a protocol in its entirety. Abdominal autolysis occurs rapidly. Given the importance of analysis of the reproductive tract in helping to understand reproductive failure the abdomen should be opened as soon as the animal is in place for a necropsy. This will allow a search for the gonads as soon as practical, minimising the extent of autolysis. It should be noted that is seems probable that autolysis was the likely cause for the absence of gonads in Eg 2450. A major disappointment in this case series is the frequent absence of gonads. Two reasons could account for this: (1) the right whale ovary and testis is very susceptible to liquefaction and autolysis post-mortem; or (2) there is a significant proportion of the population that is agonadal. The latter would seem to be highly unlikely, but a number of experienced anatomists have been surprised by the absence of these organs in specific cases. To standardise postmortem observations on right whales, a necropsy protocol has been developed (McLellan et al., 2004).

The numerical data shown in Fig. 1 provide a useful starting point for the management objectives needed for entangled and otherwise injured right whales. In particular, knowledge of length, fluke width, snout to blowhole distance and age will give an indication of likely body weight. This will allow calculations for possible drug doses, logistic planning for necropsies, and mechanical engineering input for fishing gear entanglement mitigation studies. The general shape of the length to weight graphs is strongly reminiscent of those shown for fin and sei whales taken by Icelandic whaling operations (Lockyer and Waters, 1986).

Blubber thickness measurements should be regarded with significant caution. The following affect their accuracy: (1) the orientation of the animal in relation to where the measurement was taken - if the measurement was made close to the ground, there will be many tons of whale compressing that portion of blubber; (2) whether the measurement is taken from an extracted sample, from the resulting hole in the animal, or from an incised blanket piece, the act of incising the fibroelastic blubber system in itself imparts new stresses and releases others, so that it is not possible to obtain an absolute blubber thickness measurement; (3) when blubber is peeled off an animal the hypodermis tears variably, leading to varying thicknesses left on the animal. The records rarely give the necessary details to allow unbiased comparisons between different data series.

There are two cases reported here with diffuse soft tissue ossification in the area around where rope chronically incised into bone (#'s 2030 and 2366). Both lesions were largely or totally lost during museum preparation. Thus, this lesion type should be carefully sampled in future cases.

Data in Table 5 allow an approximation of the proportion of the total weight contributed by individual organs and muscle groups to a neonate.

In summary, this review has shown that gross observations at necropsy have given a good case series of the trauma associated with vessel collisions and gear entanglement. In contrast, the more subtle processes underlying the causes of neonatal mortalities require greater focus on laboratory diagnostic procedures that may elucidate the underlying cause and effect. For all right whale mortalities, a more rapid necropsy response is needed. Finally, each death must be viewed as an opportunity to: (1) test a variety of methods to better assess the health and reproductive status of this species; and (2) provide the federal and state managers of this species the necessary information to assess whether strategies to mitigate human impacts are successful. There are no obvious trends of improvement evident in this dataset.

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Case #	Field number(s)	Date of Exam.	Location found	Sex	Initial state	Necropsy	Primary observer	Disposition of skeleton	Disposition of other samples
1	-	Jan 26 1970	Neptune Beach FL	F	Live on beach	Ν	D. and M. Caldwell	-	-
2	-	Fall 1971	Atlantic Beach, NY	-	-	Ν	-	-	-
3	_	Ian 20 1972	Freeport TX		Tail severed	Ν	_	-	-
4	USNM 500860	Jan 12 1974	Edisto Island,	М	-	N	-	Skull to USNM	-
5	USNM 504257	May 13 1975	Monomoy	М	-	Y	J. Mead,	Skull to	Blubber to
6	MH-75-044-Eg JGM 165/ USNM 504343	Apr 15 1976	Island, MA Duck Hbr.,	М	Floating off Race Pt.	Y	J. Mead,	USNM Skull to	NEAq -
7	MH-76-056-Eg SEAN1226	Nov 05 1976	Wellfleet, MA 32km SE of	-	then beached. Floating, lost. Cuts	Ν	SIMNH -	USNM -	-
8	IGM 415/ 504886	Mar 25 1979	Portland ME Wainscott	м	and slashes on back Tail severed	v	I Mead	Skull to	_
0	MH-76-026Eg	Dec 11 1070	Long I., NY	90	Strondad dood	N	SIMNH D. Janking	SIMNH Tawad aut ta	
9	S-Eg-42	Dec 11 1979	Beach, FL	Υ Γ	Stranded dead	IN	Marineland	sea	-
10	HNN 893	Dec 30 1981	St Simons Isl., GA	М	Stranded dead	Y	H. Neuhauser	· _	-
11	JEH 1063	Feb 20 1982	Ossabaw Island, GA	F	Stranded dead	Ν	R. Bonde, USGS	Natural History Museum of Los Angeles County (LA 054763)	None
12	-	Apr 19 1982	SW Georges Bank	F	Floating	Ν	T. Joyce WHOI	-	-
13	MME00084/ NEAq 1128/ MMSC 83-003	Feb 2 1983	Isl. Bch., State Pk., NJ	М	Tail severed	Y	-	-	-
14	MH-86-142-Eg/ NEAa1504	Aug 07 1986	17nm ENE Race Pt_MA	F	Prop slashes: floating	Y	G. Early, NEAg	Callosity to USNM	NEAq
15	-	May 22 1987	42° 17'N, 70° 27'W (MA)		Floating	Ν	M. Weinrich, Cet Res Unit	-	-
16	-	Jul 09 1987	Cobble Bch., Seaforth NS	М	Several gashes in back	Ν	-	Buried on site	-
17	-	Jan 17 1988	Melbourne Bch FI	М	-	Y?	D. Odell, Sea World FI	Sea World of	-
18	-	Mar 15 1988	Portan Pnsl., Newfoundland	-	Stranded dead	Ν	J. Lien, Memorial II	-	-
19	-	Nov 17 1988	Bay of Fundy	-	Drowned in lobster	Ν	L. Murison, Grand Manan	Discarded at	-
20	MH89-424-Eg	Jan 03 1989	Cumberland	М	Alive on beach. Dead	Y	N.E.Aq.	MCZ 61280, Harvard	-
21		Ian 26 1080	Ormond		Decomposed	v	т	11al varu	
21		Jan 20 1909	Beach, FL		Decomposed	1	Lowenstein- Whaley		
22	S89Eg22/ NEAq 1219	Sep 08 1989	St Augustine,	F	Beached: decomposed	Ν	D. Odell	-	-
23	S-89-Eg-23	Sep 08 1989	Nr, St Augustine, FL (6 mi from Eg-22)	-	Stranded dead	-	-	-	-
24	-	Oct 17 1990	Head Hbr.	М	Stranded dead	Ν	P. Stevick,	-	-
25	RKB-1420/ MH-91-762- Eg/ NEAq 1907	Mar 12 1991	Fernandina Bch., FL	F	Stranded dead	Y	R. Bonde, USGS 1	Bone and baleer FL Mus. Nat Hist Gainesville, FL	l -
26	NEAq 1223	Sep 05 1992	Nr. Bulkhead, Bay of Fundy	F	Death photographed at sea	Y	S. Kraus, NEAq	New Brunswick Mus.	-
27	RKB-1424	Jan 10 1993	Off St Augustine, FL	М	Hit by USCG Jan 05	Y	R. Bonde, USGS	Held at necropsy site.	-
28	RKB-1425	Jan 19 1993	Off Plyalinda Bch. FL	F	Floating dead	Y	R. Bonde, USGS	-	-
29	-	Dec 06 1993	15 nm E of Cape Charles, VA	-	Floating dead, lost	Ν	K. Cute, Manomet	-	-
30	GM-94-01	Jul 13 1994	So. Cove, Kent Island	М	Stranded dead	Ν	GM?	-	-

Appendix Table 1 Summary of right whale mortalities on file at New England Aquarium 1970-2002. Dash = no data.

Appendix Table 1 cont.

Case #	Field number(s)	Date of Exam.	Location found	Sex	Initial state	Necropsy	Primary observer	Disposition of skeleton	Disposition of other samples
31	NEAq 2250	Oct 20 1995	Long Island, NS	М	Stranded dead	Partial	P. Hamilton, NEAg	Left on beach	-
32	NEAq 2366	July 17 1995	Middletown, RI	М	Dead	Y	1	MCZ 62052	-
33	Jan 02 96 calf	Jan 11 1996	Atlantic Beach, FL	F	Stranded dead Jan 02, frozen and trucked to Boston	Y	G. Early, NEAq	Skull to MCZ	-
34	EGNE9603WBB	Feb 08 1996	22 nm E of Jacksonville Bch., FL	F	Floating dead, lost	Ν	W. Brooks, Fl DEP	-	-
35	RKB-1429/ NEAq 1623	Feb 01 1996	10 nm E of Sapelo Isl., GA	М	Floating dead	Y	R. Bonde, USGS	U. GA Mus. Nat. Hist.	-
36	RKB-1430	Feb 20 1996	20nm E of S end of Cum- berland I., GA	F	Floating dead Feb 19	Y	R. Bonde, USGS	Skull retained at FL Vet Sch.	-
37	GA96II2201	Feb 24 1996	-	М	-	Y	S. Wright, FL Mar. Res. Inst	-	-
38	MH-96-441-Eg/ NEAq 2220	Mar 11 1996	Newcomb Hollow Bch, Wellfleet, MA	М	Stranded dead	Y	G. Early, NEAq	North-Eastern U.	-
39	RKB-1449	Jan 09 1997	Flagler Beach, FL	М	Stranded dead	Y	R. Bonde, USGS	Skull and baleer to Fl Mus. Nat. His.	1 -
40	NEAq 2450	Aug 20 1997	Flour Cove, Long Isl. NS	F	Floating dead	Y	W. McLellan, UNC Wilm.	Nova Scotia Museum	-
41	RKB-1451	Jan 11 1998	30 nm E of St. Simmons I, GA	F	Floating dead	Y	R. Bonde, USGS	Not retained	-
42	WJW 001/ NEAq 1333/ NCSM 8287	Oct 8 1998	VA/NC State line	М	Stranded dead	Y	W. McLellan, UNC Wilm.	NC State Museum	-
43	MH-99-601-Eg/ NEAq1014	April 21 1999	Duck Hbr. Wellfleet, MA	F	Floating dead	Y	D. StAubin, Mystic Aq.	U. Mass. Amherst	-
44	CCSN99-143, NEAq 2030	Oct 21 1999	Cape May, NJ	F	Floating dead	Y	D. StAubin, Mystic Aq.	Paleontological Research Inst., Ithaca, NY	-
45	EGNEFL0103CTT	Feb 13 2001	Flagler Beach	Μ	Stranded dead	Ν	J. Hain, Assoc. Sci. of Woods Hole	-	-
46	RKB 1452 VMSM2001 1021	Mar 17 2001	Assateague Island, VA	М	Stranded dead	Y	R. Bonde, USGS	-	-
47	NY-2680-2001	June 19 2001	Jones Beach Inlet, Long Island, NY	F	Floating dead	Y	W. McLellan, UNCW	Buried	-
48	-	July 1 2001	St Theresa's, Newfoundland	М	Stranded dead	Ν	W. Ledwell, MUN	MUN - partial	-
49	Eg 1238	Nov 04 2001	Magdalen Isl., QE, Canada	М	Stranded dead	Y	P.Y. D'Aoust, AVC	Royal Ontario Museum	-
50	NEA130602	Jun 10 2002	93 mi. E of Provincetown MA	М	Floating dead	Ν	H. Pettis, NEAq	-	-
51	02-EGL-34	Aug 22 2002	23 mi. off Ocean City, MD	F	Floating dead	Ν	C. Driscoll MD DNR	-	-
52	VMSM 20021097	Sep 25 2002	See Note 1	F	Floating dead	Ν	M. Swingle	-	-
53	WAM 577 Eg	Sep 14 2002	See Note 2	F	Stranded dead	Ν	W. McLellan, UNCW	Scattered on beach	-
54	NEAq 3107 MH 02 726 Eg	Oct 12 2002	Nantucket, MA	F	Stranded dead	Y	M. Moore, WHOI	11 ribs only, WHOI	-

AFIP: Armed Forces Institute of Pathology; AVC: Atlantic Veterinary College, PEI Canada; CCS: Center for Coastal Studies; MCZ: Museum of Comparative Zoology, Harvard University; MD DNR: State of Maryland Dept. Natural Resources; MUN: Memorial U., Newfoundland; NEAq: New England Aquarium - (MH #'s); USNM: United States National Museum, Smithsonian Institution; UNCW: University of North Carolina, Wilmington; USGS: United States Geological Survey; VMSM: Virginia Marine Science Museum (now Virginia Aquarium and Marine Science Center). Note 1: Probably the same carcass as sighted 20mi. E Chincoteague VA on Sept 3 2002. Examined at False Cape State Park, VA. Note 2: Probably the same carcass as sighted by US Navy 93 mi. SSE Ocean City MD Sept 6 2002. Examined at Pea Island National Wildlife Reserve,

Note 2: Probably the same carcass as sighted by US Navy 93 mi. SSE Ocean City MD Sept 6 2002. Examined at Pea Island National Wildlife Reserve, NC.

						I	Distance	e from snoi	ıt, in cn	1, to:									
	Total lenoth	Age			Angle of		Blow-	Anterior nectoral	Imbi	Genital		Fluke	Max flinner f	Cranial inner edge	Caudal flinner edøe	Axillarv	Max	Anal	
Field number(s)	(cm)	ð (S	Sex	Weight (kg)	mouth	Eye	hole	insertion	licus sl	lit centre	Anus	width	width	length	length	girth	girth	girth Baleen count	
USNM 504257 JM455	1,030		Σ		235	234	192	275	,			325	92	150	142		•	- 185 (?+10-20) left	I I
JGM 165/ USNM 504343	760	ı	Σ	ı	140	133	130	168	380	430	551	272	83	135	75	524	550	360 213 left	
JGM 415/ 504886	1,100 (E)	ю	Σ	ı	197	192	190	,	505	586	753	ŀ	85	178	148	642	700	440 212 left; 220 right	
HNN 893	479	0	Σ	·	ı	76	71	117	240	258	312	138	48	88	75	262	274	180 207 left; 205 right	
JEH 1063	457	0	ſ.	I	ı	89	79	114	236	295	315	145	33	71	43	ï	')	
MH86-142-Eg/ NEAq1504	1,090	ī	ш	I	230	249	231	295	ı	770	770	388	105	180	ı	828	'		
MH89-424-Eg	412	0	Σ	1,227 W	69	75	58	88	195	217	270	106	39	72	09	224	226	148 190 right	
RKB-1420/ MH91762Eg/ NEAq 1907	1,005	7	щ	15-20,000 E	ı	253	187	264	510	699	681	ı	·	ı	ı	520	544	196 247 left; 220 right	
NEAq 1223	1,360	Min 12	ſщ	29,700 (less	300	318	270	328	663	862	922	452	124	230	215	920	880	- 009	
				baleen) W															
RKB-1425	473 (E)	0	ĹŦ			,	,			300	317	,		ı	ı	,	'	1	
GM-94-01	1,155	ī	Σ	·	299	306	228	342	ı	640	790	328	ı	ı	ı	ī	ı	1	
NEAg 2250	1,266	Min 4	Σ	·	235	272	244	320	ı	732	881	438	111	213	140	706	748	1	
NEAg 2366	1,030	2.5	Σ	9,055 W	200	232	170	ı	1	494 (E)	580 (E)	357	87	157	145	·	•		
Jan 02 96 calf	478	0	ſщ	1,151 S	90	105	80	140	ı	310 (E)	,	137	45	89	50	,	260	200 -	
RKB-1429/ NEAq 1623	1,415	Min 12	Σ	ı	337	337		383	ı	780	1,050	464	132	230	230	,			
RKB-1430	513	0	ſĿ,		101	95	81	109	240	328	538	167	48	101	85	332	342	230 235 left; 238 right	
MH96441Eg/ NEAq 2220	1,270	Min 5	Σ	ı	250	270		330	ı	720	875	440	105	215	ı	Ţ			
RKB-1449	417	0	Σ	909 E	LL	70	57	85	202	222	280	133	40	75	62	260	262	150 225 left	
NEAq 2450	1,259	Min 4	ĹŦ		278	268	261	332	ı	834	878	443	109	197		814	824	524 225 left; 217 right	
RKB-1451	455	0	ĹŦ.,	1,130 W	ı	,	ŀ		ı	ı	,	145	44	82	68	,	265	- 187	
WJW 001/NCSM 8287/ NEAq 1333	1,460	Min 21	Σ	ı	ı	,	310	ı	ı	ı	ı		144	232	202	Ţ	,		
MH99601Eg/ NEAq1014	1,370	Min 28	ĹŦ.,	52,640 S	309	319	314	383	ı	942	973	543	135	226	ı	930	1	610 210 left; 212 right	
CCSN99-143, NEAq 2030	1,350	Min 10	ĹŦ	14,785 S	320	310	220	360	ī	860	940	440	110	190		ī	1	 163 left; 159 right 	
RKB-1452	771	0	Σ		128	129	106	ī		ı	,	263	ł	125	85	ī	ı		
NY-2680-2001	910	0	ĹŦ.,	11,045 W	165	142	140	427	ı	555	596	320	90	173	128	ī	680	460 -	
Eg 1238	1,455	Min 19	Μ		·	360	ı	·	- 810) (anterior	1,064	526	130	198	220	1	,		
										end)									
WAM 577 Eg	1,200 (E)	'	ſĽ,		,		ı		,		,	ı	,	,		'	•		
NEAq 3107; MH 02 726 Eg	1,100	-	ſ		245	255	240	230	ı		ı	394	,		ı	,	'		

Appendix Table 2

Morphometric data from dead right whales. All distances in cm. W = Whole weight; S = Sum of parts + 6.8%; E = Estimated weight. Dashes = no data.

Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses

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ABSTRACT

This study examined feeding of bowhead whales (*Balaena mysticetus*) taken by Alaska Natives at Barrow (western Beaufort Sea), Nuiqsut (central Alaskan Beaufort Sea) and Kaktovik (eastern Alaskan Beaufort Sea) during 1969-2000. The objectives were to: (1) identify the proportion of harvested whales that had been feeding; and (2) describe the diet based on stomach contents. Data used were field records for 242 whales whose stomachs were examined and laboratory analysis of samples from 123 animals. There were no significant differences in the proportions of animals that had been feeding during the autumn at Kaktovik (83%) and Barrow (75%), or in sub-adults (78%) versus adults (73%). Copepods occurred significantly more frequently in animals from Kaktovik, while euphausiids and hyperiid amphipods occurred more frequently at Barrow. During the autumn, the percent copepods by volume was greater in animals taken at Kaktovik than at Barrow, while the percent euphausiids by volume was greater in whales taken at Barrow. At Barrow, a larger proportion of animals was feeding in the autumn (76%) than the spring (34%), and copepods occurred more often in the spring. Examination of five whales taken at Nuiqsut in the autumn suggests a feeding pattern similar to that seen at Kaktovik. There were no significant differences in diets of males versus females or of sub-adults versus adults. It is concluded that in the autumn, bowheads feed regularly in the eastern, central and western Alaskan Beaufort Sea, and that feeding during the spring migration is more common than previously thought.

KEYWORDS: BOWHEAD WHALE; ARCTIC; NORTH AMERICA; FEEDING; FOOD/PREY; FEEDING GROUNDS; EUPHAUSIIDS; COPEPODS

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is the only baleen whale that spends its entire life in cold northern waters. In Alaska, bowhead whales migrate in spring from their Bering Sea wintering grounds to the Beaufort Sea. The return migration generally occurs during the late summer and autumn. The whales travel from their eastern Beaufort Sea summering grounds, westward along the coast, and into the Chukchi Sea (Fraker and Bockstoce, 1980; Moore and Reeves, 1993). At least some of them travel southwest to the northeast coast of the Chukotsk Peninsula in autumn before returning to the Bering Sea for the winter.

Examination of the stomach contents of bowhead whales harvested by Alaska Natives provides an opportunity to study their diet. Bowhead whales are harvested by hunters from three communities along the Alaskan coast of the Beaufort Sea (Fig. 1) and access varies regionally (Stoker and Krupnik, 1993). Due to whale movement patterns and ice conditions, Inupiat subsistence whalers from the community of Kaktovik, in the eastern Alaskan Beaufort Sea, hunt only during the autumn, mainly in September and early October. The same is true of whalers from Nuiqsut, in the central Alaskan Beaufort Sea, who hunt from Cross Island. However, whalers from Barrow, in the western Alaskan Beaufort Sea, have access to bowhead whales during both the spring (April-June) and autumn (September-October) migrations.

Since 1976, stomach contents samples from bowhead whales have been collected by personnel from the North Slope Borough Department of Wildlife Management (NSB-DWM), the Alaska Department of Fish and Game (ADF&G) and the National Marine Fisheries Service (NMFS). Diet data from 30 bowhead whales harvested in the Alaskan Beaufort Sea from 1976-1988 were reported by Lowry *et al.* (1978), Lowry and Burns (1980), Lowry and

Frost (1984), Carroll *et al.* (1987) and Lowry (1993). Planktonic crustaceans, especially copepods and euphausiids, were the most important food items found in those studies.

Results of those scientific studies, combined with traditional knowledge of Inupiat subsistence whalers, suggested that the Alaskan Beaufort Sea was an important feeding area for bowhead whales. Concerns about plans to lease the eastern Alaskan Beaufort Sea for oil and gas exploration led the US Minerals Management Service to fund a study to assess the importance of that region for



Fig. 1. Map of Alaska and the Beaufort Sea showing the three coastal whaling locations in the Beaufort Sea area: Barrow, Cross Island and Kaktovik.

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bowhead whale feeding. The report from that 1985-1986 study concluded that feeding in the eastern Alaskan Beaufort Sea region was not significant to the annual nutrition of bowheads (Richardson, 1987), but the design of and conclusions from that study were criticised by the North Slope Borough Science Advisory Committee (1987). Partly to resolve that controversy, a multidisciplinary study entitled 'Bowhead whale feeding in the eastern Alaskan Beaufort Sea' was conducted during 1997-2000 (Richardson and Thomson, 2002). As part of that study stomach contents samples were collected from bowheads harvested at Kaktovik; field records and previously-unanalysed stomach contents samples from other bowheads taken in the Beaufort Sea were also acquired and analysed (made available by the NSB-DWM and other sources). The objectives of this study were to: (1) evaluate the frequency of bowhead whale feeding in this region by examining the field records and stomach contents samples from harvested whales; and (2) to quantify the composition of the diet of bowhead whales in the Alaskan Beaufort Sea based on analysis of stomach contents from harvested whales.

METHODS

Field records and feeding status

Bowhead whales harvested in the Beaufort Sea by Alaskan native subsistence whalers during 1969-2000 were classified as either 'feeding', 'not feeding' or 'uncertain' based on descriptive field records and laboratory data on stomach contents. If field records indicated that a substantial amount (i.e. at least 10 items or 1 litre) of prey was present in the stomach, the whale was classified as feeding. If field records indicated that the stomach was empty, the whale was classified as not feeding. If field records recorded the presence of only a small amount of prey (i.e. less than 10 items or less than 1 litre), or that food was present but no quantity was indicated, the feeding status of the whale was recorded as uncertain. For some whales field records did not provide any information about stomach contents, but collected samples were available for laboratory analysis. In those instances, a whale was classified as feeding if the sample contained 10 or more identifiable prey items, not feeding if there were no identifiable prey items, and uncertain if the sample contained fewer than 10 prey items. Items such as algae, feathers and pebbles were not considered to be food items. Data were grouped by harvest location and harvest season. The proportions of feeding whales from different harvest locations and seasons were compared using chi-square tests. Whales with feeding status classified as uncertain were not included in these comparisons.

Collection and analysis of stomach contents samples

A biologist was stationed in Kaktovik to sample bowhead whales taken during September 1997, 1998, 1999 and 2000. The stomach of each whale landed was examined as soon as possible, usually within a few hours after the animal was brought to shore. An estimate was made of the total stomach contents volume and a sample of contents was collected from the forestomach, when possible. Stomach contents samples were kept frozen until examined in the laboratory.

Additional stomach contents samples were provided from bowhead whales harvested at Barrow and Kaktovik during 1986-2000, and by Nuiqsut hunters based at Cross Island in 1999-2000. Those samples were either preserved in 70% isopropyl alcohol, 10% buffered formalin, or were frozen.

In the laboratory, samples were gently rinsed in freshwater on a 1.0mm screen with a 0.42mm screen layered underneath. Prey items were sorted macroscopically into major taxonomic groups, examined microscopically, and identified to the lowest taxonomic level possible by the authors and species taxonomy experts at the University of Alaska. Voucher specimens of prey items were stored in 70% isopropyl alcohol. The water displacement volume of sorted prey items was measured to the nearest 0.1ml in graduated cylinders. Volumes were recorded as measured with no correction for state of digestion. These methods were similar to those used in the collection and analysis of bowhead whale stomach contents in previous years (e.g. Lowry and Frost, 1984).

Stomach contents data analyses

Data were entered into an electronic database that also contained all previously existing data on stomach contents of bowhead whales harvested in Alaska. Prey data from individual whales were grouped into major prey types (e.g. copepod, euphausiid, etc.), and comparisons were carried out for whales harvested in autumn at Kaktovik versus autumn at Barrow, for whales harvested at Barrow in spring versus autumn, for males versus females, and for whales <13m versus \geq 13m in length. The division into size categories was based on the length at which bowhead whales reach sexual maturity, which is approximately 13m (Koski *et al.*, 1993).

Bowhead whale prey data were analysed in two ways. First, when a group of whales included at least five animals, the frequency of occurrence of major prey types was calculated as the number of samples containing that prey divided by the total number of samples examined. Then, the frequencies of all prey types consumed were compared using 2×2 contingency tables with an experiment wise error rate of $\alpha = 0.05$ using Bonferroni's procedure (Neter et al., 1990). All whale stomachs for which ≥ 10 prey items were enumerated were used in the frequency of occurrence analysis. Second, principal components analysis with varimax rotation (Johnson and Wichern, 1982) was used to define diet indices, and multiple regression analysis was then applied to those indices to test for possible simultaneous effects of the following covariates on diet: location, season, whale sex, whale length and collection year. Principal components analysis was applied to data on the rank order of prey importance in each individual bowhead stomach, considering 16 identified prey groups (Appendix 1). For each prey group, importance was defined as the ratio of the volumetric contribution of that prey type to the total volume of the sample examined. Therefore, only specimens with quantitative data on prey composition were used in this analysis. For each stomach used in the analysis, principal component scores after varimax rotation ('dietary indices') were computed for the three principal components that explained the greatest amount of variance in the dataset. Those dietary indices were then used as the dependent variables in multiple regression analyses to assess relationships between the covariates and diet. Type 3 sums of squares were used to compute p values for the significance of each covariate. Type 3 sums of squares for each covariate were computed by including all other covariates in the model before computing that covariate's sum of squares.

RESULTS

Data and specimen collection

Field records were obtained from 444 bowheads harvested in the Beaufort Sea during 1969-2000, of which 242 had their stomachs examined. Thirteen bowheads were harvested during the 1997-2000 whaling seasons at Kaktovik, and stomach contents samples were collected from 12 of them. Additional samples not described in previous papers were obtained from 73 bowheads harvested during 1986-2000 at Barrow (69), Kaktovik (1) and Cross Island (3). Further details on whales and stomach samples examined are given in Lowry and Sheffield (2002).

Feeding status and diets

Of 32 bowhead whales sampled or examined at Kaktovik during the autumn harvest (1979-2000), 24 were considered to have been feeding, 5 were categorised as not feeding while the feeding status of 3 was uncertain. Stomach contents samples were available from 21 whales; at least 46 prey taxa were identified in the samples (Appendix 1). Copepods occurred in all 21 samples, and euphausiids, amphipods (both gammarid and hyperiid) and mysids each occurred in more than half (Table 1). Copepods were the dominant prey by volume in 62% of the 21 samples with volumetric data; euphausiids were dominant in 24% (Fig. 2). The most commonly eaten species of copepods were *Calanus hyperboreus* and *C. glacialis*. The most commonly eaten euphausiid was *Thysanoessa raschii* (Table 2).

Of 5 bowheads sampled or examined at Cross Island during the autumn harvest (1987-2000), 4 were considered to have been feeding and 1 was not feeding. At least 9 prey taxa occurred in the 3 stomach contents samples examined (Appendix 1). Copepods occurred in all 3 samples; gammarid amphipods, hyperiid amphipods and decapods each occurred in 2; and euphausiids and cumaceans each occurred in 1 (Table 1). Only one of the samples from Cross Island was in suitable condition for sorting and volumetric analysis; it contained >99% copepods. *C. hyperboreus* occurred in all 3 Cross Island stomach samples, and *C. glacialis* occurred in 2 (Table 2).

Table 1

Percent frequency of occurrence of major prey types identified from bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomach contents samples examined).

Prey type	Kaktovik autumn (<i>n</i> =21)	Cross Island autumn (<i>n</i> =3)	Barrow autumn (<i>n</i> =69)	Barrow spring (<i>n</i> =30)
Copepod	100	100	20	80
Euphausiid	62	33	94	93
Gammarid amphipod	81	67	55	23
Hyperiid amphipod	67	67	28	33
Mysid	57	0	49	20
Fish	48	0	26	3
Decapod	52	67	29	7
Isopod	24	0	19	0
Cumacean	24	33	13	3

Of 105 bowhead whales sampled or examined at Barrow during the autumn harvest (1976-2000), 77 were considered to have been feeding, 26 were categorised as not feeding while the feeding status of 2 was uncertain. Stomach contents samples were available from 69 whales, and at least 54 prey taxa were identified in the samples (Appendix 1). Number of identified occurrences of copepod and euphausiid species in stomach contents samples from bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomach contents samples examined).

Table 2

Prey species	Kaktovik autumn (n=21)	Cross Island autumn (n=3)	Barrow autumn (<i>n</i> =69)	Barrow spring (<i>n</i> =30)
Copepod				
Calanus cristatus	-	-	-	2
C. finmarchicus	1	-	-	-
C. glacialis	10	2	8	20
C. hyperboreus	15	3	4	5
Chiridius obtusifrons	1	-	-	2
Derjuginia tolli	1	-	-	-
Euchaeta glacialis	2	1	1	4
Heterorhabdus sp.	2	-	-	-
Limnocalanus grimaldi	3	-	-	-
Metridea lucens	2	-	-	-
M. longa	4	-	-	4
Pseudocalanus sp.	4	-	-	1
Euphausiid				
Thysanoessa inermis	2	-	7	8
T. raschii	6	-	26	14



Euphausiid □ Copepod ■ Amphipod ■ Mysid □ Other

Fig. 2. Percent prey by volume for 21 individual bowhead whales harvested in the eastern Alaskan Beaufort Sea near Kaktovik, Alaska, during the autumn (1979-2000).

Euphausiids were the main prey item, occurring in 94% of the samples; copepods occurred in 20% (Table 1). Euphausiids were the dominant prey by volume in 88% of the 64 samples with volumetric data whereas copepods were dominant in only 5% (Fig. 3). The predominant species of euphausiid eaten was *T. raschii*; *C. glacialis* and *C. hyperboreus* were the most commonly eaten copepods (Table 2).

Of 99 bowhead whales sampled or examined at Barrow during the spring harvest (1969-2000), 31 were considered to have been feeding, 60 were categorised as not feeding while the feeding status of 8 was uncertain. Stomach contents samples were available from 30 whales, and at least 40 prey taxa were identified in the samples (Appendix 1). Euphausiids occurred in 93% of the samples and copepods in 80% (Table 1). Euphausiids were the dominant prey by volume in 63% of the 28 samples with volumetric data and copepods were dominant in 27% (Fig. 4). Copepods were the dominant item in 6 of 11 whales taken in 1977-1988 but only 1 of 17 taken in 1993-1998. *T. raschii* was the most commonly eaten species of euphausiid, and *C. glacialis* was the most commonly eaten copepod (Table 2).

Comparisons of diets between sexes, sizes, regions and seasons

There was no significant difference in the proportion of bowhead whales feeding in the autumn at Kaktovik and Barrow (Table 3; $\chi^2=0.69$; df=1; p>0.1). For whales harvested near Barrow, a larger proportion was feeding in

the autumn than in the spring ($\chi^2=35.77$; df=1; p<0.001). The proportions of whales <13m and ≥13m long that were feeding were virtually identical for all seasons and locations (Table 3), and for all samples combined there was no significant difference (91/160 versus 42/67; $\chi^2=0.52$; df=1; p>0.1).

There were significant differences in the frequency of occurrence of prey types between bowhead whales harvested in autumn at Kaktovik and Barrow (Table 1); copepods occurred more often in whales harvested near



Fig. 3. Percent prey by volume for 64 individual bowhead whales harvested in the western Alaskan Beaufort Sea near Barrow during the autumn (1976-2000).



Fig. 4. Percent prey by volume for 28 individual bowhead whales harvested in the western Alaskan Beaufort Sea near Barrow during the spring (1977-98).

Kaktovik (χ^2 =43.04; df=1; *p*<0.001), whereas euphausiids (χ^2 =10.61; df=1, *p*<0.005) and hyperiid amphipods (χ^2 =12.39; df=1; *p*<0.001) occurred more often in whales harvested near Barrow.

Bowhead whales harvested at Barrow showed seasonal differences in the frequency of occurrence of prey types (Table 1), with copepods occurring significantly more often in whales harvested in the spring ($\chi^2=31.52$; df=1; p<0.001). Euphausiids occurred with similar frequency in autumn and spring ($\chi^2=0.01$; df=1; p>0.1).

Within each location and season there were no significant differences in the frequency of occurrence of prey types in male and female bowhead whales (Bonferonni-adjusted χ^2 tests; p>0.1). Likewise, there were no significant differences in whales <13m and \geq 13m long (p>0.05), although during autumn at Barrow mysids and fish occurred with a marginally greater (0.05) frequency in whales <13m long. When all samples were considered in aggregate (Table 4), the frequency of occurrence of prey types was virtually identical in males and females (<math>p>0.1 for all tests). There were some small differences between length classes, with copepods, mysids, fishes, and isopods occurring more frequently in small whales, but the differences were not statistically significant (p>0.1 for all tests).

Table 3

Percentages of bowhead whales taken in the Alaskan Beaufort Sea (1969-2000) that were categorised as feeding, by location, season and length class. Numbers in parentheses are total sample sizes. Whales of uncertain feeding status were not included in calculations.

	Length <13m	$Length \ge \!\! 13m$	All lengths
Kaktovik autumn	85 (20)	78 (9)	83 (29)
Cross Island autumn	100 (2)	67 (3)	80 (5)
Barrow autmun	75 (67)	75 (36)	75 (103)
Combined autumn	78 (89)	75 (48)	77 (137)
Barrow spring	34 (71)	32 (19)	34 (91)

Table 4

Percent frequency of occurrence of major prey types identified in bowhead whales taken in the Alaskan Beaufort Sea (1969-2000) separated by sex and size (n = the number of stomach contents samples examined).

Prey type	Males (<i>n</i> =61)	Females (<i>n</i> =58)	Length <13m (<i>n</i> =83)	Length $\geq 13m$ (n=36)
Copepod	49	50	55	36
Euphausiid	87	88	88	86
Gammarid amphipod	49	55	53	50
Hyperiid amphipod	39	33	35	39
Mysid	43	45	51	28
Fish	23	26	30	11
Decapod	28	28	27	31
Isopod	15	16	18	8
Cumacean	10	16	12	14

In the principal components analysis, the three most important 'dietary indices' accounted for 48.9% of the variance in the ranked volumetric data on prey. Multiple regression analysis was applied, in turn, to each of these three indices to determine whether that measure of diet differed with location, season, whale length, or whale sex. All three dietary indices showed a significant effect of season, while location was significant for one index (Table 5). There was no evidence for effects of sex, length class, or year on diet ($p \ge 0.1$ in all cases). The index that showed a difference for both location and season (Factor 1) was one that strongly contrasted the ranking of copepods and euphausiids in the diet.

Estimates of the volume of stomach contents were available for 46 bowhead whales harvested at Kaktovik and Barrow. The estimates are imprecise and often given as ranges, and are therefore not suitable for rigorous analysis. However, a summary of those observations (Table 6) shows that at both Kaktovik and Barrow autumn stomachs frequently contained 20 litres or more, and sometimes had over 100 litres of contents. In the latter case, stomachs were often described as 'full' in field records. Estimated contents volumes at Barrow in the spring were generally lower and never exceeded 60 litres.

Table 5

P values from multiple regression analyses testing for differences in three indices of bowhead whale diet according to location, season, whale sex and length class and year. Diet indices ('factors') are based on a principal components analysis of the rank order of volumetric importance of major prey types identified in 123 bowhead whale stomachs from the Alaskan Beaufort Sea.

Variable	Factor 1	Factor 2	Factor 3
Location	< 0.01	0.16	0.22
Season	< 0.01	< 0.01	0.01
Sex	0.52	0.92	0.62
Length class	0.33	0.19	0.23
Year	0.06	0.60	0.10
% variance in diet			
explained by this factor:	18.0	15.4	15.5

Table 6

Estimates of volume of stomach contents in bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomachs for which contents volume was estimated).

Estimated contents volume	Kaktovik autumn (<i>n</i> =18)	Barrow autumn (<i>n</i> =16)	Barrow spring (n=14)
% with ≥ 20 litres	39	56	29
% with ≥ 100 litres	11	31	0
Range (litres)	2-150	1-189	1-60

DISCUSSION

Prior to this study, our understanding of the diet composition of bowhead whales in the Alaskan Beaufort Sea was based on samples collected from 30 animals (Lowry, 1993). As a result of this project, quantitative diet data based on laboratory analysis of stomach samples are now available for a total of 123 animals. The frequency of feeding and types of food that were eaten are now reasonably well described for whales taken in the eastern Alaskan Beaufort Sea (Kaktovik) in autumn and the western Beaufort Sea (Barrow) during both autumn and spring. This paper also describes the first diet samples collected from bowhead whales in the central Alaskan Beaufort Sea (Cross Island).

Previous studies (Lowry and Burns, 1980; Lowry and Frost, 1984; Lowry, 1993) have shown that bowhead whales taken in the Alaskan Beaufort Sea during the autumn commonly have food in their stomachs. Using field records and laboratory results this study concluded that 105 bowhead whales taken in the Alaskan Beaufort Sea during September-October had been feeding and 32 had not (Table 3). The estimate of 77% overall frequency of feeding in autumn bowheads is likely to be an underestimate for several reasons. For some of the whales that were recorded as not feeding, stomachs could not be examined until many hours after the initial strike during which time contents could have been completely digested. The three Kaktovik whales assigned uncertain feeding status each had small amounts of prey in their stomachs. In addition, some stomach contents samples were received in such poor condition (e.g. filled with congealed blood) that locating and identifying prey was difficult or impossible.

Copepods and euphausiids were the main bowhead whale prey items in the eastern Alaskan Beaufort Sea near Kaktovik, which agrees with previously presented results for this area (Lowry and Burns, 1980; Lowry and Frost, 1984; Lowry, 1993). Of the two groups, copepods were the most important as they were present in every stomach sample and were essentially the only item in 12 of the 21 samples. However, euphausiids were also an important prey item and dominated the contents of five whale stomachs. Other crustaceans and fishes also were eaten, but they generally were minor components of samples that consisted mostly of copepods or euphausiids.

In the western Beaufort Sea near Barrow, bowhead whale diet during September-October was dominated by euphausiids, which made up almost the entire contents of 54 of the 64 samples examined. These results confirm the importance of euphausiids in the autumn diet of bowhead whales in this region, a conclusion that had previously been based on samples from only five stomachs (Lowry, 1993). Copepods were the predominant prey in 3 stomachs and mysids in 4. Interestingly, the only whales with copepods dominant were taken on the same day in 1998, and 2 of the 4 with mysids dominant were taken on the same day in 1997. This may be indicative of temporal/spatial patches of prey that are found and exploited by the whales.

Regional differences in diets of autumn-harvested bowheads may be explained by regional differences in prey availability. Copepods are known to dominate the zooplankton of the Canadian Beaufort Sea and eastern Alaskan Beaufort Sea and euphausiids are not considered abundant there (Bradstreet and Fissel, 1986; Griffiths and Thomson, 2002). In that region, bowhead whales often occur at locations where copepods dominate the biomass (Griffiths and Buchanan, 1982; Griffiths *et al.*, 2002). In contrast, euphausiids have been found in substantial quantities in the western Beaufort Sea, where copepods were less abundant (Griffiths *et al.*, 1987).

Previous studies (Lowry and Frost, 1984; Carroll et al., 1987; Lowry, 1993) concluded that bowhead whales fed only occasionally while migrating northward along the west coast of Alaska in spring. This study estimated the overall frequency of feeding at Barrow during spring at 34%. This frequency was significantly less than at either Barrow or Kaktovik in the autumn, and estimated quantities of contents in the stomach were considerably smaller. Fourteen of 28 spring samples were comprised almost entirely of euphausiids and 6 had nearly all copepods, but several contained mixtures of different crustacean groups. Copepods occurred significantly more often in whales that fed near Barrow in spring than in autumn. This difference could be partly due to the locations where whales are taken as spring hunting occurs in the Chukchi Sea to the west of Point Barrow whereas autumn whales are taken in the Beaufort Sea mostly to the north and east of the Point (J.C. George, unpubl. data). There are essentially no data available on zooplankton distributions in this region during spring. In contrast with previous studies that found that copepods were the dominant prey of bowhead whales taken during the spring migration in 1980-88 (Carroll et al., 1987; Lowry, 1993), this study suggests that euphausiids overall have been the more important prey in the western Beaufort Sea in spring as well as autumn. It appears that there may have been a change in the spring diet of bowheads in this area, with euphausiids being more important in the 1990s than in pre-1990s samples (Fig. 4). It is unknown whether this apparent change in diet is due to changes in oceanic conditions that may have altered abundance patterns of copepods or euphausiids, differences in specific locations where whales were harvested or where they were feeding, or some other factor.

The frequencies of occurrence of various prey types in stomachs of male and female bowhead whales were nearly identical, and indications of slight age/size effects on diet were not statistically significant. Lowry (1993) examined size-related differences in diet based on samples from 32 bowhead whales and concluded there was a slightly greater tendency for benthic taxa to occur in whales <10.5m long. The analysis here of a larger number of samples also suggests slight differences in the diet of small (<13m) versus larger (\geq 13 m) whales. Prey groups such as mysids, fish and isopods that occurred relatively infrequently in larger whales were found more commonly in small whales, but those differences were small and not statistically significant. If real, the differences may reflect size-related differences in feeding abilities (probably as a function of baleen length) or in feeding areas, as has been suggested for bowhead whales in the eastern Canadian Arctic (Finley, 2001).

It is difficult to use bowhead stomach contents data to estimate the overall diet composition for a location/season for a number of reasons. Those include variation in the state of digestion of samples, the wide range in the volumes of collected samples, and the frequent lack of data on total volume of stomach contents. Nonetheless, preliminary estimates of diet composition based on the data shown in Figs 2, 3 and 4 were calculated using two methods: (1) averaging the percent volumes of contents for each prey type found in individual whales; and (2) calculating the percent of times that a prey type was the dominant component of a stomach contents sample. The two methods produced remarkably consistent estimates (Table 7), in agreement with the patterns of regional and seasonal importance of copepods and euphausiids described above.

There are other sources of information on feeding of bowhead whales in the Beaufort Sea. One is the traditional knowledge of local subsistence whalers. While much of the Inupiat knowledge on bowhead whale feeding has not been recorded in written form, personal observations of the authors and other sources show that hunters are quite aware that bowhead whales feed in certain parts of the Alaskan Beaufort Sea. Whalers at Kaktovik have described feeding areas in the eastern Alaskan Beaufort Sea (Galginaitis and Koski, 2002), and at Barrow they have long known about autumn feeding areas and tend to focus their hunting activities in those areas (Minerals Management Service, 1997). Hunters are also aware of the types of behaviours whales exhibit when feeding, and have described weight gain of bowheads over the summer feeding season and a seasonal change in the taste of the muscle (Puiguitkaat, 1981). Another source is sightings and behavioural observations made during aerial surveys and systematic behavioural studies. Sightings of feeding bowhead whales, when accumulated over many late summer/autumn seasons, have been widely distributed across the Alaskan Beaufort Sea (Ljungblad et al., 1986; Miller et al., 2002; Treacy, 2002), and in the eastern Alaskan Beaufort Sea feeding is the most commonly observed activity (Würsig *et al.*, 2002). Such observations support the conclusions of this paper. Information on feeding also comes from the analysis of stable isotope ratios in bowhead whale tissues. Such studies by Schell et al. (1989) and Hobson and Schell (1998)

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Estimates of bowhead whale diet composition in the Alaskan Beaufort Sea (1969-2000) based on: (1) averaging the percent composition by volume in individual stomach contents samples; and (2) the percent of times a prey type was the dominant component of stomach contents samples (n = the number of stomach contents samples that were suitable for volumetric analysis).

	Kaktovik	(<i>n</i> =21)	Barrow autumn (<i>n</i> =64) Barr		Barrow sp	row spring (<i>n</i> =28)	
	Mean % volume	% times dominant	Mean % volume	% times dominant	Mean % volume	% times dominant	
Copepod	61	62	5	5	28	27	
Euphausiid	22	24	84	88	61	63	
Amphipod	5	5	1	0	4	4	
Mysid	6	5	6	6	1	0	
Other	6	5	4	1	5	7	

concluded that in terms of total annual nutrition, the eastern and central Beaufort Sea is a relatively unimportant feeding ground for bowhead whales, especially for adult animals. However, Hoekstra *et al.* (2002), also using isotopic methods, concluded that the Beaufort Sea is an important feeding area for bowhead whales of all sizes. The direct evidence of feeding presented in this paper more closely agrees with the conclusions of Hoekstra *et al.* (2002).

CONCLUSIONS

Results of this study change our previous understanding of the feeding ecology of bowhead whales in two important ways. First, bowhead whales feed regularly in the nearshore waters of the eastern, central and western Alaskan Beaufort Sea during September-October. With food found in more than three-quarters of the animals examined, this entire region should be considered an integral part of the summerautumn feeding range of bowhead whales. Results of stomach contents analysis, aerial observations, and traditional knowledge suggest that reference to the passage of bowhead whales through this region as a 'westward autumn migration' is misleading. At the least, it is a very incomplete description of their activities in the region. In fact, a major activity of bowhead whales in the Alaskan Beaufort Sea during autumn is feeding, with whales moving west when prey are not available in sufficient numbers (Griffiths et al., 2002), or when the whales choose not to feed, or when they combine feeding with simultaneous westward travel (Würsig et al., 2002). Second, feeding near Barrow during the spring migration is not just occasional, but rather a relatively common event as evidenced by the fact that approximately a third of the animals sampled there had been feeding. However, the amount of food in the stomachs tends to be lower in spring than in autumn.

The conclusions drawn from this study appear to contradict those of Richardson (1987, p.485) who concluded that 'Food resources consumed in the Eastern Alaskan Beaufort Sea do not contribute significantly to the annual energy needs of the Western Arctic bowhead stock'. However, examination of stomach contents only showed whether or not bowhead whales had fed and what prey were eaten, and it does not directly address the relative significance of feeding in various regions. Nonetheless, for the conservation of these whales and their habitats it seems inappropriate to dismiss areas where the majority of animals show evidence of having fed as being unimportant to their nutrition. This unresolved issue remains important in the evaluation of possible cumulative effects of oil and gas development on bowhead whales, and additional studies are warranted (National Research Council, 2003).

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Appendix 1 Prey and other items consumed by bowhead whales harvested in the Alaskan Beaufort Sea (1969-2000). Locations and seasons where whales were harvested are indicated after each taxon

1. Cnidaria		Copepoda (cont.)		Gammarid amphipods (cont.)		Gammarid amphipods (co	ont.)	Decapoda (cont.)	
Scyphozoa	BS, BF	Euchaeta sp.	BS, K	Acanthostepheia behringiensis	BF, K	Onissimus nanseni	K	Sabinea septemcarinata	BF, K
2. Annelida		Euchaeta glacialis	BS, BF, K, C	Acanthostepheia incarinata	K	Podoceridae	BF	Sclerocrangon sp.	BF
Polychaeta	BF	Heterorhabdus sp.	K	Acanthostephia malmgreni	BF	Pontoporeia femorata	BF	Sclerocrangon boreas	BF
Mollusca		Limnocalanus grimaldii	К	Aceroides latipes	K	Protomedeia sp.	BF	Decapod zoea	BF, K, C
3. Gastropoda	K	Metridea sp.	BS, K	Anonyx sp.	BS, BF, K, C	Rhacotropis sp.	BS, BF, K	15. Echinodermata	
Limacina helicina	BS	Metridea lucens	K	Anonyx nugax	BS	Rozinante fragilis	BF, K	Ophiuroidea	BS
Margarites sp.	BS	Metridea longa	BS, K	Ampelisca macrocephala	BF	Weyprechtia sp.	BF, K, C	16. Vertebrata	BF, K
Natica sp.	BS	Pseudocalanus sp.	BS, K	Apherusa glacialis	K	Weyprechtia heuglini	BF, K	Ammodytes sp.	BF
Natica clausa	BS	8. Mysidacea	BS, BF, K	Arrhis sp.	BF	Weyprechtia pinguis	BF, K	Agonidae	BF
Neptunea sp.	BS	<i>Mysis</i> sp.	BF, K	Atylus carinatus	BF, K	12. Hyperiid amphipods	BS, BF, K	Gadidae	C
4. Bivalvia	BF	Mysis litoralis	BS, BF, K	Boeckosimus affinis	BF	Hyperia sp.	BS, K	Boreogadus sp	BF
Astarte sp.	BS	Mysis occulata	BF, K	Boeckosimus krassini	BF	Hyperia galba	BS, K	Boreogadus saida	BS, K
Liocyma fluctuosa	BS	Neomysis sp.	BS, BF	Boeckosimus litoralis	K	Hyperia medusarum	BS, K	Cottidae	BF
Nuculana sp.	BS	Neomysis rayii	BS, BF	Byblis sp.	BS, BF	Hyperoche medusarum	BS	Icelinus sp.	BF
Tellinidae	BS	9. Cumacea	K, C	Erichthonius sp.	BS	Parathemisto sp.	BS	Lepidopsetta bilinicata	BF
Yoldia sp.	BS, BF	Brachydiastylis resima	BS	Eusirus cuspidatus	BS, BF	Parathemisto abyssorum	BS, K, C	Lycodes sp.	BF
5. Chelicerata		Diastylis sp.	BF, K	Gammarus sp.	BS, BF, K	Parathemisto libellula	BF, K, C	Myxocephalus sp.	BF
Pycnogonidae	K	Diastylis dalli	K	Gammarus zaddachi	BF	13. Euphausiacea	BS, BF, K, C	Myxocephalus quadricornis	K
Crustacea		Diastylis galbra	K	Gammaracanthus sp.	BF	Thysanoessa sp.	BS, BF, K	Pleuronectidae	BF
6. Ostracoda	BS	Diastylis sulcata	BF	Gammaracanthus loricatus	BF, K	Thysanoessa inermis	BS, BF, K	Pungitius pungitius	K
7. Copepoda	BS, BF, K, C	Leuconidae	BF	<i>Harpinia</i> sp.	BS	Thysanoessa raschii	BS, BF, K	Stichaeidae	BF
Aetideidae	BF	Leucon sp.	BF	Lysianassidae	BF, K	14. Decapoda	BF, K, C	Zoarcidae	BF
Calanus sp.	BS, BF, K	Leucon nasica	BS	<i>Melita</i> sp.	BF	Crangonidae	K	17. Phaeophyceae	
Calanus cristatus	BS	10. Isopoda	К	Melita quadrispinosa	BF	Argis sp.	BS, BF	Plant material	BF
Calanus finmarchicus	K	Munnopsis sp.	К	Monoculodes sp.	BF, K	Eualus sp.	BS, BF	18. Other	
Calanus glacialis	BS, BF, K, C	Saduria sp.	BF, K	Monoculodes zervoni	BF	Eualus gaimardi	BF, K	Baleen	BS, BF, K, C
Calanus hyperboreus	BS, BF, K, C	Saduria entomon	BF, K	Oedicerotidae	BF	Heptacarpus sp.	BF	Bird feathers	BF, K
Chiridius obtusifrons	BS, K	Amphipoda	BS, K, C	Onissimus sp.	BF, K	Hippolytidae	BF	Plastic sheeting	BF, K
Derjuginia tolli	K	11. Gammarid amphipods	BS, BF, K, C	Onissimus glacialis	K	Pandalus goniurus	K	Wood	BF, K
Euchaetidae	K	Acanthostepheia sp.	BS, BF, K	Onissimus litoralis	K	Sabinea sp	BF	Sediments	BS, BF, K

Abundance of humpback whales on the Abrolhos Bank wintering ground, Brazil

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ABSTRACT

Abundance estimates are presented for the humpback whales wintering off Brazil which 'visit' a surveyed area off Abrolhos Bank and display fluke-exposing behaviour. The study is based on photo-identification data collected between 1996 and 2000. Chapman-corrected Petersen estimates for all pairs of data result in estimates from 1,948 individuals up to 3,001 with coefficients of variation around 0.25. A more elaborate closed population multiple-recapture maximum-likelihood estimate is 2,393 with 95% profile-likelihood confidence interval (CI=1,924, 3,060). Replacing the closed-population assumption with a population allowed to grow (or decrease) according to some constant rate over the study period, the maximum-likelihood estimate of population size for the year 2000 becomes 3,871 (CI=2,795, 5,542) associated to an estimated annual growth rate of 31% over the study period and in the surveyed area. Although the inclusion of the growth rate results in a less restrictive assumption about population size, it is unclear at this time how to interpret it since the population around the Abrolhos Bank is some (unknown) fraction of whales wintering off Brazil. Alternatively, a fit of Whitehead's model allowing for emigration and re-immigration gives an estimate of about 3,000 whales (CI=2,500, 3,650).

KEYWORDS: ABUNDANCE ESTIMATE; ATLANTIC OCEAN; BREEDING GROUND; HUMPBACK WHALE; PHOTO-ID; SOUTH AMERICA

INTRODUCTION

The use of a catalogue of photo-identified whales and markrecapture models to estimate cetacean abundance is well known (e.g. see review Hammond *et al.*, 1990) particularly for humpback whales (e.g. Katona and Beard, 1990; Smith *et al.*, 1999).

Although over 200 humpback whales have been individually identified in the Southern Hemisphere, relatively few studies have attempted to use the information to estimate abundance by capture-recapture models (Baker, 1995). The International Whaling Commission's Scientific Committee began a major assessment of the status of Southern Hemisphere humpback whales in 2000 (IWC, 2001). Humpback whales wintering off the Brazilian coast are considered part of the western South Atlantic breeding stock (breeding stock 'A') but there are no estimates for the total abundance of that breeding stock or any information on recent trends (e.g. see summary in IWC, 2004).

The humpback whales found on the breeding ground of Abrolhos Bank (off the southernmost coast of Bahia state, Brazil) have been studied since 1988. Work on obtaining population estimates based on the photo-identification of individual animals began in 1995. A photographic catalogue of 982 individually identified whales assembled over 11 years of surveys in the area provides the most complete record of sightings of humpback whales off the Brazilian coast. Preliminary assessment of the population abundance for 1996 using within-year resightings in a continuous time non-parametric closed population model (Bethlem, 1998) resulted in a confidence interval of 237, 1,519. An empirical-Bayes approach applied to within-year resightings in 1995 resulted in a 90% credibility interval of 1,379, 1,887 (Kinas and Bethlem, 1998). On the Abrolhos Bank the distribution of this population has also been studied in relation to bathymetry, proximity to land and water turbidity (Martins et al., 2001; Freitas et al., 2001). Recent aerial surveys over the whole of Abrolhos Bank (including areas never surveyed before) provide complementary information about habitat use patterns, distribution and abundance (Andriolo *et al.*, 2002).

This analysis is based on photo-identification data collected over the five years 1996-2000 and provides abundance estimates of the fraction of humpback whales wintering off Brazil which 'visit' the surveyed area off Abrolhos Bank and display fluke-exposing behaviour.

METHODS

Survey area and photographic identification

The surveyed area is located off the northern portion of the Abrolhos Bank (16°40'S-19°30'S; 37°25'W-39°45'W). The region (Fig. 1) is an extension of the Brazilian continental shelf that rarely exceeds depths of 40m and reaches a maximum distance from shore of approximately 245km. The bank (average depth = ca 30m) is formed by coral reefs, some of them rising above the sea level in the low tide, mud and calcareous algae bottoms. Five small volcanic islands form the Abrolhos archipelago, located 30 n.miles offshore. The average annual sea surface temperature ranges from 22° to 27°C (winter from 22°-24°C) (IBAMA/FUNATURA, 1991). These features are typically associated with breeding grounds for humpback whales (Baker et al., 1995; Clapham and Mead, 1999). Abrolhos Bank is considered the most important breeding and calving ground for the species in the western South Atlantic (Martins et al., 2001). The whales use the area during the austral winter, between July and November each year (Siciliano, 1997).

Humpback whales were individually identified by the pigmentation patterns of the ventral flukes (Katona and Whitehead, 1981). Calf photographs were excluded from the analysis, since their fluke pigmentation patterns can change considerably in short periods of time (Carlson *et al.*,

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Fig. 1. Map showing Abrolhos Bank and the survey area.

1990) which would be characterised as loss of marks. Photographs were taken using Nikon 35mm power winder cameras with 200 or 300mm lenses. Colour negative and slide films (100, 200 and 400 ASA) were used.

Data analysis and statistical models

Photographs in the catalogue were selected according to image quality (focus, glare, angle) regardless of recognition pattern of the flukes (i.e. the presence of distinctive scars or pigmentation that would improve one's ability to re-identify the animal; Mizroch *et al.*, 1990). This is essential in order to decrease the recapture heterogeneity and the likelihood of flukes not being recognised on recovery (Hammond, 1986; Friday *et al.*, 2001; Stevick *et al.*, 2001). Only the quality-screened photographs were compared within and across years to determine the total number of identified whales (marks) and the number of resightings (recaptures).

Within any year, sampling without replacement was used because multiple recaptures of whales may not be independent. This will also reduce heterogeneity in capture probabilities among whales as a source of bias in abundance estimates (Seber, 1982; Otis *et al.*, 1978; Hammond, 1986; Hammond *et al.*, 1990).

Four abundance estimation models are used. First, the Chapman-modified Petersen estimator (Hammond, 1986) is applied to all pairs of consecutive seasons. The model assumes: (1) a closed population; (2) a constant probability of capture among animals; and (3) neither loss nor misclassification of marks (Seber, 1982). The estimated abundance (\tilde{N}) is calculated as follows:

$$\tilde{N} = \frac{(n_1 + 1)(n_2 + 2)}{m + 1} - 1 \tag{1}$$

where n_i is the number of (distinct) whales photo-identified in season *i* (*i*=1, 2) and *m* the number of whales seen in both seasons. The estimated standard error (SE) of \tilde{N} is:

$$SE = \sqrt{\frac{(n_1+1)(n_2+1)(n_1-m)(n_2-m)}{(m+1)^2(m+2)}}$$
(2)

Given five seasons of data, four different estimates of \tilde{N} (and SE) are obtained.

A second model estimates the population size N by using all data simultaneously in a multiple-recapture model. Changes to previously listed assumptions are as follows: (1) population is closed to recruitment and immigration but death and emigration are allowed if they affect marked and unmarked animals equally (Gazey and Staley, 1986); (2) the probability of capture at any given season is equal to the proportion of marked whales in the population at the time. This corresponds to a M_t-type model (Otis *et al.*, 1978), constrained to a non-decreasing sequence of capture probabilities.

Since sampling without replacement is used, the hypergeometric model applies. Therefore, the likelihood function is:

$$L(N) = \prod_{i=2}^{s} \frac{\binom{M_i}{m_i} \binom{N - M_i}{n_i - m_i}}{\binom{N}{n_i}}$$
(3)

where *s* is the number of seasons, n_i the number of whales identified in season *i*, m_i the number of whales identified in season *i* that had already been 'marked' in some previous season and M_i the total number of (distinct) whales that have been marked before the *i*-th season. Notice that $M_{s+1}=M_s + n_s-m_s$ is the total number of distinct whales identified during the study and determines a lower bound for *N* provided there were neither deaths nor emigration among marked whales during the study period.

A third model drops the assumption of population closeness and replaces it with: (*i*') an open population with constant growth rate. The population size N_i in any given year *i*, is related to the population size N_{i-1} in a previous year by:

$$N_i = N_{i-1}e^r \tag{4}$$

Parameter r indicates the population growth rate over the period. Although r can be positive, zero or negative – indicating a growing, constant or declining population, respectively – it is assumed to be constant over the study period. The value e^r denotes the annual rate of change in population size.

For convenience $N=N_s$ is defined as the population size in the wintering season of year 2000. Hence, by rearranging equation (4), population sizes for all previous years can be defined as a function of N:

$$N_i = N \cdot e^{-(s-i)r} \tag{4a}$$

for seasons i=1, ..., s-1. The likelihood function for model 3 is an extension of equation (3) resulting in:

$$L(N,r) = \prod_{i=2}^{s} \frac{\binom{M_i}{m_i}\binom{N_i - M_i}{n_i - m_i}}{\binom{N_i}{n_i}}$$
(5)

subject to the restrictions $N_i \ge M_{i+1}$ for i=1 to s and with N_i given by equation (4a).

Finally, the fourth model was taken from Whitehead (1990) and includes the possibility for animals to emigrate and later re-immigrate into the study area. The emigration and re-immigration rates (λ and μ , respectively) are estimated together with population size *N*. The overall population is assumed to be reasonably constant over the period.

For all models except the first, the maximum-likelihood estimates are calculated by evaluating the likelihood functions for a large number of points and determining its maximum on the grid. Confidence interval or twodimensional confidence regions were determined through the method of profile likelihood (Buckland et al., 1993). If R(N)=L(N)/L(N) and $R(N,r)=L(N,r)/L(N, \hat{r})$ denote the relative likelihood functions for equations (3) and (5) respectively, and if R_n is the normal approximation of R, then $-2\log(R_n)$ has a chi-square distribution with p degrees of freedom (where p is the number of parameters in the model). Let $\chi^2(\alpha)$ be the 100(1- α) percentile of a chi-square distribution with p degrees of freedom. The collection of points that satisfy $-2\log(R) \le \chi^2(\alpha)$ will be used to build the 100(1- α)% profile likelihood confidence set. For *p*=1, the smallest and the largest values in the selected collection define the confidence interval. For p=2, a scatter plot of the selected points defines the approximate shape of the joint confidence region. Marginal confidence intervals can be obtained as before. Similar criteria were used to analyse estimates obtained with Whitehead's model.

RESULTS

The data collected during the years 1996 to 2000 (after selection for photographic quality) were compared between seasons to obtain information on recaptures (Table 1). The survey effort (in number of searching hours per year) has been stable over the study period (Table 2).

Pairwise abundance estimates for the Abrolhos Bank using the Chapman-modified Petersen estimates resulted in a population size between 1,848 (for 1996-1997) and 3,001 (for 1998-1999) with CV ranging from 0.246 (1997-1998) to 0.310 (1996-1997) (Table 3).

Table 1

Number of humpback whales identified at Abrolhos Bank in different seasons (years) and re-identifications for pairwise comparisons between seasons.

	No identified		Re-identifi	cation year	
Year	[newly]	1997	1998	1999	2000
1996	101 [101]	7	15	7	6
1997	143 [136]	*	12	13	6
1998	216 [193]	*	*	11	11
1999	164 [137]	*	*	*	12
2000	218 [188]	*	*	*	*

Table 2	
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Vessel effort in hours per month for surveys between 1996-2000.

Year	Jul.	Aug.	Sept.	Oct.	Nov.	Total
1996	70.25	98.91	83.16	70.91	81.58	404.81
1997	106.75	138.83	80.41	96.5	105.08	527.57
1998	101.25	128	115.6	64.38	37.66	446.89
1999	82.58	83.08	72.33	107.91	64.83	410.73
2000	73.58	122.16	95.16	81.83	102.5	475.23

Table 3

Chapman-modified Petersen pairwise abundance estimates, standard errors and 95% confidence intervals (all numbers were rounded to nearest integer).

Pair of seasons	N	SE	95% CI
1996 – 1997	1,848	573	725-2,971
1997 - 1998	2,414	595	1,247-3,581
1998 - 1999 1999 - 2000	3,001 2,791	693	1,478-4,524 1,433-4,150

The abundance estimate obtained with the multiplerecapture, closed population model 2, for the period from 1996 to 2000 (s=5) resulted in the maximum-likelihood estimate of 2,393 whales. The relative likelihood function (Fig. 2) is used to define the 95% confidence interval given in Table 4. The multiple-recapture, open population, twoparameter model 3, estimates a population size of 3,871 whales for the 2000 winter season and a growth rate r=0.267over the period 1996 to 2000. The approximate 95% confidence region of the maximum-likelihood estimate for (N, r) is delimited by the plotted points which represent a projection of $R(N,r) \ge \exp(\chi^2/2)$ onto the N x r space (Fig. 3). This interval displays a marked positive correlation between these parameters. It also makes clear why the marginal confidence interval (Table 4) is so wide. Although the estimate of r is not precise, ranging (marginally) from 0.028 to 0.400, it clearly suggests a growing population (r > 0).

Whitehead's three-parameter model (N, λ, μ) , was fitted to a three-dimensional grid of 8,100 points ranging from 1,000 to 5,000 for *N* and between 0 and 1 for λ and μ . A likelihood ratio test showed that the hypothesis $\mu=0$ is not rejected $(\chi^2_{(1)}=0.045; p=0.832)$; a second likelihood ratio test to check if $\lambda=0$ (given that $\mu=0$) is not rejected either $(\chi^2_{(1)}=1.34; p=0.247)$. With both rates set to zero, Whitehead's model reduces to the Schnabel model of a closed population being randomly sampled. The maximumlikelihood estimate of *N* resulted in 3,000 whales (Table 4).



Fig. 2. Relative likelihood function for population size *N* of humpback whales at Abrolhos Bank according to assumption of a constant population size (model 2).



Fig. 3. Scatter plot representing the approximate 95% profile likelihood confidence region of the maximum-likelihood estimate for (N,r) in model 3. (Includes all pairs (N,r) with $-2 \log R(N,r) \le 5.9915$).

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Maximum-likelihood abundance estimates for three population models: the closed population hypergeometric model (HG); an open population hypergeometric model with constant intrinsic growth rate r (HG+r) and Whitehead's model allowing for emigration and re-immigration. Years 1996-2000.

Model	Ν	95% CI
HG (model 2)	2,393	1,924-3,060 ^b
HG + r (model 3)	3,871 ^a	2,795-5,542 ^b
Whitehead	3,000	2,500-3,650 ^b

^aMaximum-likelihood estimate for year 2000. ^bProfile likelihood confidence intervals.

DISCUSSION

All models considered in this analysis assume that the probability of photo-identifying a whale is constant within a season. As it stands, this assumption is hardly ever satisfied for at least three reasons.

First, the behaviour of adequately exposing the tail to facilitate a photographic record will depend on sex, age and group composition (Perkins *et al.*, 1984; Hammond, 1990; Friday *et al.*, 2001). For instance, animals which execute the 'tail up' behaviour (consisting of tail exposition for minutes, even hours – Morete *et al.*, 2003) will have an increased probability of being photo-identified, while other groups like resting mothers and calves rarely expose the tail in fluke-up dives. The effect of this variability could only be reduced by some kind of stratification into sub-groups of similar behaviour (Hammond, 1986). However, the information needed to stratify properly is not available and sample sizes within strata will be small.

Second, the surveyed region represents only a fraction of the home range for the whales using the Abrolhos Bank wintering ground. Photographic data collected opportunistically in 1997 and 1999 and during vessel surveys in 2000 off Salvador (approximately 550km north of the Abrolhos Archipelago) resulted in 15 photo-identified individuals. Three matches of whales previously sighted on the Abrolhos Bank were found among them, indicating that Abrolhos' humpbacks use other areas off Brazil as well. This suggests that in different cruises different animals might be available for marking. Furthermore, within-season resightings might not be independent as a given whale can stay in the region for the period of the cruise and be sighted more than once. The heterogeneity in photo-identification probability induced by both phenomena will be reduced if the whole season is taken as a single (without replacement) sampling event. Finally, by considering all photoidentifications over the whole season without replacement, effectively means we have been using a yearly 'mean probability of capture' for each whale and we would therefore expect lower variability.

Third, whales with significant tail pigmentation patterns are easier to photo-identify than animals with poor recognition quality patterns, although this problem is greatly reduced by first selecting only high quality photographs (Hammond, 1986; Friday *et al.*, 2001; Stevick *et al.*, 2001).

The Chapman-corrected Petersen abundance estimates calculated for all possible combinations of seasons were included to provide a direct comparison to similar results presented elsewhere for other wintering seasons for humpbacks (Baker *et al.*, 1992; Rosenbaum *et al.*, 2000). Calculated coefficients of variation are reasonable (around 0.25), and abundance estimates suggest an increasing time trend.

More precise abundance estimates are obtained when simultaneously using all data as part of a multiple-recapture experiment. This was possible to achieve with models 2 to 4. In closed population model 2, the associated 95% profile-likelihood confidence interval (1,924-3,060) does not cover the Petersen estimates for 1996-97. Calculating the identification frequencies of individual whales across the five years and confronting them with expected frequencies calculated for a zero-truncated Poisson distribution (Caughley, 1977) resulted in a significant departure ($\chi^2_{[1]}$ =76.445, *p*=0.0111) between both sequences (Table 5). According to Caughley, this difference could be caused by heterogeneity in captures or by changes in population size. The consequences of each of these two possibilities are examined below.

To check for the effect of heterogeneity, the data were fitted with program CAPTURE (Otis *et al.*, 1978). The model selection index and resulting estimates are summarised in Table 6. The inclusion of heterogeneity only (model M_h) causes the estimate of *N* to be low. The most realistic model from a biological standpoint (model M_{th}) results in estimates which are closest to those obtained by open model 3 (model HG+r in Table 4).

Table 5Observed and expected frequencies of observation for 755 humpback
whales photo-identified between 1996 and 2000
 $(\chi^2_{[1]} = 76.445; p = 0.0111).$

		Identificat	ion frequer	ncy (seasons	5)
	1	2	3	4	5
Observed	681	63	9	2	0
Expected ^a	674.2	74.9	5.5	0.3	0.0

^aCalculated from the zero-truncated Poisson distribution.

Table 6
Model selection and maximum-likelihood abundance estimates obtained
with program CAPTURE. Years 1996 to 2000.

Model (index)	M _h (1.0)	M _{th} (0.83)	M ₀ (0.74)	M _t (0.01)
<i>N</i>	2,040	4,107	2,770	3,031
95% СІ	(1,921; 2,171)	(3,196; 5,358)	(2,509; 3,874)	(2,536; 3,688)

Alternatively, if we assume that we have dealt with considering sampling heterogeneity by without replacement, we can focus attention on the second possible cause: the population growth over the period. Model 2 was modified in order to include a second parameter, the growth rate r. By giving up some precision in the estimate of population size, some insight was gained into the rate of population change between 1996 and 2000. The analysis suggests an annual growth rate of about 31% (er=1.31) over the period – biologically implausible. The interpretation of ris difficult, however, until a better understanding of the whale distribution in the area is available. Since the surveyed area is only a fraction of the wintering ground off Brazil, the estimated population growth rate might include some change in behaviour pattern in favour of this sub-area without any substantial change in population size in area A. However, regardless of the interpretation of r, we believe that its inclusion in model 3, allows for a better estimate of population size in year 2000.

The positive correlation observed in the 95% profilelikelihood confidence region for (N, r) reveals an important aspect of the uncertainty in estimating the parameters of model 3. The interval allows for relatively small population sizes associated to small growth rates or alternatively large growth rates and associated large population size in year 2000. However, the location of the confidence region away from r=0 suggests that the number of whales using Abrolhos during the reproductive season has been growing between 1996 and 2000.

Finally, the use of Whitehead's model allowed us to explore the possibility of measuring emigration and reimmigration rates to the Abrolhos Bank over the years. The statistical tests suggest that these rates are negligible and the fitted model (Table 4) reduces to a closed population model M_t . In fact, a comparison with the estimate obtained in CAPTURE (Table 6) confirms this. The small observed differences are caused by rounding errors due to a somewhat coarse grid.

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Bycatch of bottlenose dolphins in South Carolina, USA, and an evaluation of the Atlantic blue crab fishery categorisation

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ABSTRACT

In the USA, commercial fisheries that interact with marine mammals are categorised according to the number of incidental takes of marine mammals relative to the defined Potential Biological Removal (PBR) for the population. Three categories exist for such commercial fisheries: Category I, II and III, each varying in the degree of regulation. Fishery categorisation is based on a five-year running average of the number of incidental entanglements in that fishery and is published annually in the Federal Register. The Atlantic blue crab (*Callinectes sapidus*) fishery is one of South Carolina's largest commercial fisheries in terms of volume and value and was recently re-categorised as a Category II fishery, resulting in heightened regulation. The Atlantic blue crab fishery exists in known areas of bottlenose dolphin (*Tursiops truncatus*) habitat; therefore, interaction between the two is probable. This study uses historical marine mammal stranding data and on-board investigations of the blue crab fishery in South Carolina to investigate the degree of fishery and dolphin interaction. Analysis of historical strandings showed that approximately 24% of the 42 entanglement cases in South Carolina from 1992-2003 resulted from the blue crab fishery. In nine of the 12 years examined, bottlenose dolphin mortality rates were found to be greater than or equal to 10% of the South Carolina Management Unit's PBR, which is significant according to the US Marine Mammal Protection Act's (MMPA) definitions for the Atlantic Coastal Stock of bottlenose dolphins. In addition, results from this study showed that the average number of bottlenose dolphin defines a Category II fishery. Thus, entanglement data from South Carolina from 1992-2003 support the re-categorisation of the blue crab fishery and the introduction of heightened regulations under the MMPA.

KEYWORDS: BOTTLENOSE DOLPHIN; FISHERIES; INCIDENTAL CATCHES; CONSERVATION; MANAGEMENT PROCEDURE

INTRODUCTION

Marine mammals and fisheries often utilise overlapping areas; therefore, interaction between the two is likely. Fisheries present a significant mortality threat to marine mammals, as they may be incidentally taken or killed in fishing gear, or their habitat may be damaged as a result of fishing practices (Beddington et al., 1985; Perrin et al., 1994; Fertl and Leatherwood, 1997; Read and Murray, 2000). Incidental entanglements of marine mammals in fishing gear might occur if the animals are distracted, manipulate fishing gear, behave carelessly during social interactions, or by mere accident (Fertl and Leatherwood, 1997; Anderson et al., 1998). A primary goal of the US Marine Mammal Protection Act (MMPA) of 1972 and its 1994 Amendments was to reduce the incidental mortality and serious injury of marine mammals that result from fishing practices. To do so, fisheries managers and marine mammal conservationists must quantify the interaction between the two.

General management framework

The MMPA of 1972 was originally designed to prevent the depletion of marine mammal stocks as a result of anthropogenic factors. In addition, the Act was written to stimulate efforts to replenish stocks that were already considered in danger of extinction, and increase research to obtain more ecological information on marine mammals. Amendments were passed in 1994 to create a management scheme that was more focused on the human-caused mortality of marine mammals, termed bycatch (16 U.S.C. 1361 Sec. 2, 118)¹.

¹ 16 U.S.C. 1361 et seq. United States Congress. Marine Mammal Protection Act (MMPA) of 1972 As Amended.

According to these amendments, commercial fisheries that incidentally take marine mammals are listed in the Federal Register as Category I, II or III. Each category is associated with a different degree of incidental mortality, and is therefore coupled with varying degrees of regulation. The categorisation is based on the number of marine mammals in a given stock that are annually taken, relative to the stock's Potential Biological Removal (PBR). PBR defines the number of individuals that can be taken per year from a stock, by human activities, in order to maintain or reach the stock's optimum sustainable population (OSP) (Barlow et al., 1995). OSP describes the population size that maximises reproductive potential within the constraints of the habitat's carrying capacity. The goal of these regulations is to eventually reduce the incidental mortality rate of marine mammals in these fisheries to 'insignificant levels, approaching a zero mortality rate goal' (ZMRG). Mortality rates are considered insignificant when they equal less than 10% of a stock's PBR. ZMRG is not a defined number, rather a goal to encourage fisheries to reduce their incidental mortality levels in order to reach OSP (16 U.S.C. 1361 Sec. $2, 3, 118)^{1}$.

Categorisation of commercial fisheries

The categorisation of fisheries is published annually in the Federal Register for a 90-day comment period, and reexamined annually based on new available data for each fishery listed in these categories (16 U.S.C. 1361 Sec. 117, 118 (c)(1))¹. Category I fisheries frequently interact with marine mammals, or remove 50% or more of a stock's PBR. Category II fisheries, or fisheries that occasionally take marine mammals, include those that collectively remove more than 10%, or individually take 1-50% of a marine mammal stock's PBR. Fisheries that rarely interact with marine mammals, Category III fisheries, are collectively
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responsible for the removal of 10% percent or less of a stock's PBR, or 1% or less in a single fishery (16 U.S.C. 1361 Sec. 118)¹. For Category I and II fisheries that incidentally take marine mammals beyond the stock's PBR, a take reduction plan is instituted. The short-term goal of a take reduction plan is to reduce the occurrence of incidental takes to a level below the PBR, ideally within six months after implementation. Ultimately, these plans outline the steps necessary to bring incidental take rates to levels approaching ZMRG (16 U.S.C. 1361 Sec. 118)¹.

Stranding analysis

Estimates of fishery-related mortality depend primarily on reporting by fishers, the National Marine Fisheries Service (NMFS) Marine Mammal Observer Program, and investigation of strandings. Sources of marine mammal mortality can sometimes be explained by evidence from necropsies of stranded animals (Cox et al., 1998; Friedlaender et al., 2001). External evidence of fishery entanglement often includes attached fishing gear, rope indentations on the epidermis, lacerated appendages, amputated appendages and net hatch marks on the epidermis (Cox et al., 1998; Read and Murray, 2000; Friedlaender et al., 2001; McFee and Hopkins-Murphy, 2002). Internally, entangled animals have been documented as having froth in the lungs and bronchi, stomachs full of fish remains and haemorrhaging below the skin at wound locations (Read and Murray, 2000).

Bottlenose dolphins in South Carolina

The population dynamics of bottlenose dolphins in South Carolina are not well documented, other than residence patterns in a river system located in the Charleston area (Zolman, 2002). Historically, bottlenose dolphins occurring in South Carolina were grouped as part of the Western North Atlantic Coastal Stock with a hypothesised habitat ranging from central Florida to New York (Scott et al., 1988). However, recent genetic, stable isotope, telemetry and photo-identification studies have indicated a complex mixture of stocks, and the Western North Atlantic stock has been divided into seven management units (Waring et al., 2002). Abundance estimates for each management unit were calculated from aerial survey data obtained in the winter and summer of 2002. Based on preliminary studies by Garrison et al. (2003), the abundance of dolphins occurring in the South Carolina management unit is approximately 2.300.

The categorisation of commercial fisheries is relative to an individual stock's PBR. For the South Carolina management unit, the PBR is set at 20 individual bottlenose dolphins (Palka, 2003). According to the categorisation scheme, Category I fisheries take at least 10 bottlenose dolphins each year incidental to fishing practices, whereas Category II fisheries collectively take at least 2.0 dolphins per year, or individually take 0.2 to 10 dolphins per year. Fisheries in South Carolina that are placed in the Category III listing, collectively take less than 2.0 dolphins, or individually take 0.2 dolphins or less per year.

Blue crab fishery in South Carolina

The blue crab fishery operates year-round, and is one of the largest commercial fisheries in South Carolina and the USA (Johnson *et al.*, 1998; Whitaker *et al.*, 1998). In South Carolina, the fishery typically ranks first in terms of weight landed and second in value (Whitaker *et al.*, 1998). The commonly used crab pot is a baited, two-foot cubed cage with four funnels through which crabs enter. Crab pots rest

on the waterway's bottom and are connected to a buoy on the water's surface by a braided, sinking line, varying in length depending on the depth of placement. Although this fishery is year-round, the predominant fishing months in South Carolina estuarine waters are August to November (NMFS, 2003).

The goal of this study was to verify the categorisation of the Atlantic blue crab fishery, relative to marine mammal mortality, based on historic and current stranding data from South Carolina. Evidence from strandings and interviews with commercial crab fishers were used to validate the reclassification and quantify the interaction between bottlenose dolphins and the Atlantic blue crab fishery in South Carolina. This study provides an example of how the integration of stranding and interview data can be used to evaluate and verify management approaches designed to reduce the incidental mortality of marine mammals in commercial fisheries.

METHODS

General stranding record analysis

Analysis of historical stranding data began by sorting through the catalogued Marine Mammal Stranding Level A Data Report Forms (OMB No. 0648-0178) for all bottlenose dolphins suspected of fishery interaction in South Carolina. Pathology reports from the United States Armed Forces Institute of Pathology (USAFIP), and photo-documentation were also obtained for each of the suspected entanglement cases. Data obtained from the stranding, necropsy and pathology reports included stranding location and date, gross body condition, stranding event description, internal conditions and pathological signs of other sources of death. These data were compiled into summary tables and compared with entanglement evidence from 'confirmed' crab pot interactions to predict possible mortality sources. For this study, only animals with indications of fishery interaction such as rope abrasions, lacerated appendages, puncture wounds, net marks or internal pathologies associated with an acute death were considered in the analysis.

Photographs of each entanglement case were examined to note the location of the wounds along the dolphin's body, as well as wound patterns and dimensions. The widths of wounds in historical stranding records and photographs were noted and compared to a simulated wound study in which samples of rope varying in diameter were used to make impressions on the peduncle and dorsal fin of deceased dolphins in the laboratory. Samples of rope utilised by various fisheries were rubbed in a back and forth motion across the leading edge of the peduncle and dorsal fin in order to obtain an impression width associated with different diameters. The resulting widths were measured and recorded for each rope diameter, and then compared to the widths of wounds discovered on the entanglement cases.

Fisheries may be ruled out as potential entanglement sources based on the timing and location of fishing effort (Cox *et al.*, 1998). Temporal trends in total strandings and entanglements were identified on a yearly, monthly and seasonal basis. Months were divided into four seasons according to McFee and Hopkins-Murphy (2002) to observe trends during different times of the year. In addition, the geographic coordinate data from the stranding reports were used to view the spatial distribution of the fishery interaction cases in South Carolina.

Classification of fishery entanglement cases

A classification scheme was developed for the fishery entanglement cases based on the likelihood that the interaction was due to the blue crab fishery. The five classes included: (1) confirmed; (2) unconfirmed, probable; (3) unconfirmed, possible; (4) cannot be determined (CBD); and (5) other fishery. Stranded dolphins were classified as 'confirmed' (class 1) only if they were seen entangled in crab pot gear, or washed ashore with crab pot gear attached to the body. Dolphins with indications of rope marks on the body were typically placed into either the 'probable' or 'possible' category. The 'probable' entanglement cases (class 2) were distinguished from the 'possible' cases (class 3) based on the location of the entanglement wounds, the dimensions and patterns of entanglement wounds, internal body conditions and the geographic location of the entanglement cases. Dolphins placed in the 'CBD' category (class 4) had indications of fishery interaction such as net marks or lacerations, but because of decomposition or scavenging, the fishery that may have been responsible for the entanglement could not be determined. The 'other fishery' category (class 5) was created for entangled animals that had markings unrepresentative of the gear used by crab fishers, such as monofilament line and nets.

Table 1 outlines the criteria used to place animals in their respective categories, and Figure 1 depicts a flow chart that diagrams the steps used to classify the entanglements as 'confirmed', 'other fishery', 'probable' or 'possible'. Since the seasonality and location of commercial fisheries may fluctuate throughout the year, these parameters were also examined in relation to stranding events during the study period (see Fig. 2). Cox *et al.* (1998) noted that differences in fishing location and season relative to stranding date and location might narrow potential entanglement sources.

Fishery survey

A survey of blue crab fishers was conducted to gain fishers' perceptions of the degree of interaction between bottlenose dolphins and the blue crab fishery, as well as to determine if similar types of interaction seen in Florida's Indian River Lagoon (Noke and Odell, 2002) occur in South Carolina. Ten fishers, representing seven water bodies, were surveyed for this project. During these surveys, fishing practices and location, as well as the spatial overlap of the fishery and bottlenose dolphin habitat was noted during on-board interviews.

The names of commercially licensed blue crab fishers were obtained using guides, snowball sampling and convenience sampling techniques (Berg, 1989). Initial informants, or guides, provided contact information for other crab fishers in the Charleston area, thus snowballing the sampling list. In addition, local seafood stores and boat landings were visited to obtain further contact information for local crab fishers. Most interviews occurred during fishing trips, but due to the unavailability of many crab fishers, a few were conducted by telephone. Semi-standardised interviews, or guided discussions, were conducted aboard fishing vessels, while specific survey questions were used for standardised telephone interviews (Berg, 1989). In several cases, the telephone interviews resulted in an offer to accompany the fisher during fishing trips.

Data obtained from the interviews were examined with content analysis, a technique to objectively identify data in text (Berg, 1989), to observe trends in fishing effort and gear, rate of crab pot loss and degree of interaction with bottlenose dolphins during fishing trips. Given that the crab fishers were not chosen at random and included a small sample size (n=10), statistical analysis of the results from interviews was not conducted.

RESULTS

Historic stranding analysis

From 1992-2003, a total of 440 bottlenose dolphin strandings were recorded in South Carolina. Of these 440 stranding events, the number of yearly strandings ranged from 28 in both 1992 and 2002, to 68 in 2001. The mean number of total strandings per year over the study period was 36.7 (SD \pm 13.0). Over the 11-year period, most strandings occurred in the month of July (*n*=50), whereas the fewest strandings occurred in January and October (*n*=21). Seasonally, most bottlenose dolphin strandings in South Carolina occurred during spring (*n*=141), and the fewest in winter (*n*=89).

Approximately 10% (n=42) of the 440 bottlenose dolphin strandings showed evidence of fishery entanglement, as previously described. The number of fishery entanglements per year ranged from one (0.2% of total strandings) in 1994 and 2001, to 10 (2.3% of total strandings) in 1997. The mean number of entanglements each year between 1992 and 2003 was 3.5 (SD±2.5). The greatest number of entanglements (n=8, 19% of total entanglements) over the study period occurred in August, and fewest (n=1, 2.4% of total entanglements) in January and November. Most of the entanglements in South Carolina occurred during the summer (n=17, 40% of total) and the fewest entanglements occurred during autumn (n=5, 12% of total).

For the simulated wound study, the diameters of rope used for the tension tests ranged from 3/16 of an inch to 0.5 of an inch, with resulting wound widths ranging from 0.35cm to 1.60cm (Table 2). By knowing the widths of wounds seen on stranded carcasses, this study may help determine the diameter of rope by which the dolphin was entangled.

Table 1

Criteria used for classification of entanglements according to interaction with the blue crab fishery in South Carolina (1992-2003).

Classification	Criteria
Confirmed crab pot interaction	Stranded with gear, reported sighting with gear, freed from gear.
Unconfirmed, probable	Wounds and body condition very similar to confirmed cases (i.e. rope abrasions, stomach full of fish remains, robust
	body condition, froth in lungs and bronchi).
Unconfirmed, possible	Wounds and body condition similar to confirmed cases. Wounds may have resulted from other fishing practices and may
	not be characteristic of crab fishing gear (i.e. puncture wounds, lacerations, rope marks that may be post-mortem).
Cannot be determined (CBD),	Interaction with the crab fishery could not be determined. Animals showed signs of fishery interaction but carcass was
mutilation	too heavily mutilated or appendages were lost, preventing complete wound analysis.
Other fishery	Interaction with a fishery other than the crab fishery. Dolphins stranded with gear attached or showed evidence of
	entanglement not congruent with crab fishing gear (i.e. net hatch marks along body, monofilament lacerations).



Fig. 1. Flow chart showing the classification process to distinguish 'confirmed', 'probable', 'possible' and 'other fishery' entanglements.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Number of entanglements	1	3	4	3	9	3	5	8	4	2	1	2
Classification	1 probable	1 confirmed 1 possible 1 other	1 confirmed 1 probable 1 possible 1 CBD	1 confirmed 1 probable 1 possible	2 confirmed 3 possible 1 CBD	1 possible 2 CBD	1 confirmed 1 probable 3 possible	2 confirmed 4 probable 2 other	1 confirmed 3 other	1 confirmed 1 CBD	1 CBD	1 other 1 CBD
Shrimp trawl												
Shrimp channel												
Shrimp bait												
Crab commercial												
Crab recreational												
Shad – Winyah Bay												
Shad – Santee River												
Shad – Charleston Harbor												
Shad – Edisto River												
Shad-Ashepoo River												
Shad-Combahee River												
Shad-Savannah River												
Shad-ocean												

Fig. 2. Entanglements according to month and the seasonality of major commercial fisheries in South Carolina. Shaded regions are months in which fishing season operates.

 Table 2

 Rope diameter, location of applied tension, and wound width for each rope sample.

Rope diameter (in) and braiding style	Location of tension	Wound width (cm)	Average width
3/16 - solid	Peduncle	0.35	0.35
1/4 - diamond	Peduncle	0.4	
1/4 - solid	Peduncle	0.8	
1/4 - solid	Peduncle	0.75	
1/4 - loose hollow	Peduncle	0.8	
1/4 - loose hollow	Dorsal fin	0.75	0.7
9/32 - diamond	Peduncle	0.5	0.5
5/16 - diamond	Peduncle	0.6	
5/16 - solid	Peduncle	0.8	
5/16 - solid	Peduncle	0.95	
5/16 - double	Peduncle	1	
5/16 - pot warp	Dorsal fin	1	0.87
3/8 - solid	Peduncle	1.2	
3/8 - twisted	Peduncle	1.1	
3/8 - twisted	Peduncle	1.1	
3/8 - hollow	Peduncle	0.9	1.075
7/16 - double	Peduncle	1.2	
7/16 - double	Peduncle	1.25	1.225
1/2 - solid	Peduncle	1.6	
1/2 - twisted	Peduncle	1.3	1.45

Classification of bottlenose dolphin strandings

The 'confirmed' blue crab fishery entanglements constituted 23.8% (n=10) of total known entanglements since 1992 (Fig. 3). These dolphins were observed with gear attached to the body, or were freed from blue crab fishing gear. Generally, these animals were robust and healthy, and showed internal evidence of fishery interaction such as a stomach full of fish remains and foam in the lungs and bronchi, indicating asphyxiation. Stomachs full of fish remains may indicate fishery interaction as some theories suggest that marine mammals may actively forage in the presence of fishing gear or follow fisheries as they feed on discarded bait and manipulate gear to obtain food (Fertl and Leatherwood, 1997; Noke and Odell, 2002). In addition, the 'confirmed' cases often had approximately 1cm wide, haemorrhagic rope wounds located around the base of the flukes and occasionally on other parts of the body (Figs 4 and 5).



Fig. 3. Status of bottlenose dolphins entangled in the Atlantic blue crab fishery in South Carolina (1992-2003).

The 'probable' cases included 19% (n=8) of the total, and showed evidence of entanglement very similar to the 'confirmed' cases such as wound location pattern (e.g. around the base of the flukes), as well as a robust body, full stomach and foam in the lungs. However, because the animals did not have physical evidence of interaction with a crab pot (e.g. stranded with gear), these cases were considered probable crab pot entanglements.

Ten of the entanglements (23.8% of total) since 1992 were classified as 'possible' blue crab fishery interactions. These animals had evidence of entanglement similar to the 'confirmed' cases, but the entanglement indications could have resulted from other fisheries. Evidence of entanglement for the 'possible' cases included puncture wounds, lacerations and rope wounds that may have been post-mortem.

For the seven animals (16.7% of total entanglements) placed in the 'CBD' category, interaction with the blue crab fishery could not be determined. These animals had indications of human interaction, such as rope or net markings and amputated appendages, but often the carcass was too heavily decomposed for proper wound analysis.



Fig. 4. Rope wounds for confirmed crab pot interaction (SC9731).



Fig. 5. Rope wounds on flukes of a confirmed crab pot entanglement (MMES2003089SC).

Bottlenose dolphins that were entangled in a fishery other than the blue crab fishery constituted 16.7% (*n*=7) of total entanglements. Evidence of entanglement for bottlenose

dolphins grouped in this category included the attachment of fishing gear uncommon to the blue crab fishery, or external evidence incongruent with the 'confirmed' cases such as net hatch marks along the body or monofilament lacerations.

Table 3 summarises the reasons for the classification of each entanglement, and details the sex, length and location of the entanglement cases. According to the archived data, approximately 43% of the 42 entanglements in South Carolina from 1992-2003 were definitely or probably due to the blue crab fishery.

Fishery survey results

A total of 46.6 hours was spent in the field from May 2002 to February 2003. Ten different blue crab fishers were interviewed for this study aboard fishing vessels and via telephone, representing seven different water bodies. Twelve fishing trips were taken, and four telephone interviews were conducted.

The crab fishers surveyed typically place 50-190 pots in their fishing areas at one time. Several fishers mentioned that the numbers of pots set at a given time fluctuates with weather parameters and catch rate, as does the frequency with which they check their pots. Regulations require that crab fishers check their pots every five days (South Carolina Department of Natural Resources (SCDNR), 2001); therefore, pot replenishment ranges from once a week to every day. These crab fishers generally used two different rope diameters (1/4 of an inch and 5/16 of an inch) and fishing lines ranging from 30-85ft in length. Fishing line occurs in a variety of braiding styles; however, the crab fishers interviewed typically used diamond, solid and double braid. Menhaden (Brevoortia tyrannus) is the primary bait used in the fishery, and gear modifications to improve fishing efficacy included different coloured wire on parts of the pot, and heavy irons on the bottom of pots to prevent them from moving with currents.

The crab fishers reported an annual pot loss of as few as 20 pots to as many as 200. Reasons commonly given for such loss included theft, fast currents associated with spring tides, and boat traffic that cuts off buoys. Suggestions to reduce pot loss included stricter law enforcement of crab pot theft and vandalism, reducing competition among crab fishers, and decreased boat traffic in areas outside the main channels of waterways.

Dolphins were seen on 11 of 12 fishing trips, and group size ranged from one to four. The behaviour of dolphins during fishing operations included mill, close approach and travel (Irvine *et al.*, 1981; Noke and Odell, 2002). During fishing trips conducted for this study, the close approach behaviour was seen only once.

The types of interaction between bottlenose dolphins and the blue crab fishery that have been documented by Noke and Odell (2002) in the Indian River Lagoon were not reported by fishers in the Charleston area. An indication of dolphin interaction with the crab fishery in Florida included pots that were missing both bait and crabs (Noke and Odell, 2002). The crab fishers in this study stated that pots are sometimes retrieved absent of bait and crabs; however, they feel that the likely cause is theft by humans rather than dolphin interaction. While most crab fishers regularly see dolphins during fishing practices (75-100% of the time), they did not indicate that dolphins impede fishing progress or vice versa. Most of the fishers interviewed stated that dolphins occasionally approach the fishing vessel begging for food, and several admitted to feeding dolphins despite the prospect of a fine. Two of the crab fishers interviewed

Table 3

Classification, location, date, sex and length of bottlenose dolphin fishery interaction cases in South Carolina (1992-2003).

Field No.	Date	Location	Sex	Length	Classification	Criteria for classification
SC9202	6-Feb-92	Beaufort Co.	-	-	Confirmed	Crab pot line and buoy around flukes.
SC9206	12-Mar-92	Charleston Co.	-	-	CBD	Poor body condition; knife slice marks along body.
SC9212	20-May-92	Charleston Co.	-	242	Confirmed	Crab pot rope and float wrapped around tail.
SC9215	25-May-92	Beaufort Co.	-	218	Possible	Flukes entangled in yellow rope; line marks on peduncle.
SC9326	8-Jul-93	Beaufort Co.	F	227	Possible	Puncture wound between flippers; haemorrhagic lung.
SC9337	17-Nov-93	Horry Co.	F	210	CBD	81cm mid-ventral slit; puncture wounds.
SC9408	16-Mar-94	Beaufort Co.	F	230	Possible	Puncture wound; clean cut fish in esophagus; stomach mostly full.
SC9503	7-Feb-95	Horry Co.	F	250	Other	Parallel lacerations on flipper; haemorrhagic lung.
SC9509	5-Apr-95	Charleston Co.	М	264	Probable	3cm wide line marks on peduncle and edges of flukes; full stomach;
						haemorrhagic lungs.
SC9608	14-Mar-96	Beaufort Co.	Μ	145	Probable	Line marks at base of flukes and epidermis rubbed off; haemorrhagic lungs.
SC9611	8-Apr-96	Colleton Co.	F	265	Possible	Rope marks at base of flukes; internal data unavailable.
SC9628	18-Jun-96	Colleton Co.	Μ	262	CBD	Poor body condition; flukes amputated; full stomach.
SC9631	28-Aug-96	Colleton Co.	Μ	166	Probable	Rope marks on tail; full stomach.
-	16-Sep-96	Beaufort Co.	-	-	Confirmed	Dolphin disentangled from crab pot.
SC9636	22-Sep-96	Georgetown Co.	Μ	149	Other	Dolphin stranded entangled in gillnet.
SC9725	18-May-97	Charleston Co.	F	111	Possible	Tooth rake or net marks on dorsal fin; line marks on peduncle; haemorrhagic
						lungs; full stomach.
SC9726	1-Jun-97	Charleston Co.	Μ	145	Possible	Line marks on side of body; full stomach.
SC9730	23-Jun-97	Beaufort Co.	-	225	CBD	Poor body condition; flukes amputated; heavily scavenged.
SC9731	2-Jul-97	Charleston Co.	М	192	Confirmed	Dolphin retrieved from crab pot; rope marks (1.5cm wide) at base of peduncle; haemorrhagic lung; full stomach; good body condition
SC9732	4-In1-97	Colleton Co	м	211	Probable	Rone marks around hase of flukes and peduncle
SC9733	9-Jul-97	Beaufort Co	F	122	Possible	Rope marks at base of penducle (maybe post-mortem): empty stomach
SC9734	2-Aug-97	Charleston Co	-	-	Confirmed	Dolphin released from crab not
SC9735	10-Aug-97	Charleston Co.	F	238	Probable	Good body condition: rope marks (1cm wide) around peduncle and flukes:
505700	10 1148 57			200		haemorrhagic lungs; full stomach.
SC9737	24-Aug-97	Colleton Co.	М	263	Probable	Rope marks (1cm wide) round peduncle; haemorrhagic lungs; partially full stomach.
SC9759	11-Dec-97	Georgetown Co.	Μ	195	CBD	Decapitated; dorsal fin and half of fluke cleanly cut off.
SC9804	13-Jan-98	Charleston Co.	F	176	Probable	Line marks (1cm wide) on flukes, peduncles; haemorrhagic lungs; full
						stomach.
SC9826	28-May-98	Charleston Co.	Μ	248	Possible	Line marks on side of body; left fluke cleanly cut off; haemorrhagic lungs.
SC9835	4-Jul-98	Charleston Co.	Μ	221	Possible	Line marks near flipper and around body; haemorrhagic lung; full stomach.
SC9846	2-Sep-98	Charleston Co.	-	-	Other	Net marks covering body.
-	27-Mar-99	Charleston Co.	-	-	Confirmed	Dolphin disentangled from crab pot.
SC9913	21-Apr-99	Beaufort Co.	F	243	Confirmed	Dolphin found dead entangled in crab pot; line marks (0.99-1.0cm wide) at
						base of flukes; haemorrhagic lungs.
SC9916	13-May-99	Charleston Co.	Μ	200	CBD	Peduncle cut off posterior to anal slit.
SC0006	25-Feb-00	Charleston Co.	F	203	Possible	Braided rope around rostrum; haemorrhagic lung.
SC0045	28-Sep-00	Beaufort Co.	F	239	Other	Hook found at base of tongue and monofilament line was wrapped around
	16.0 + 00					goosebeak.
-	16-Oct-00	Charleston Co.	-	-	Confirmed	Dolphin released from two crab pots.
SC0165	22-Oct-01	Deautort Co.	IVI E	180+	CBD	ran and right hipper cut off.
SC0223	22-Aug-02	Berkeley Co.	F E	201	Other	Dolphin entangled in trammel net.
SC0224	23-Aug-02	Beautort Co.	r F	152	Other	Dolphin entangled in lazy line of shrimp boat.
SC0230	11-Dec-02	Charleston Co.	1 M	229	Other	Net impressions on dorsal fin, fluke, and flipper.
SC0314	3-may-03	Charleston Co.	M	~250	Confirmed	Dolphin disentangled from crab pot.
SC0322	1/-Aug-03	Charleston Co.	IVI M	1/3	Drohabla	Line marks on flyles (0 for wide) and densel wides of flyles (1 for)
500525	21-Aug-03	Charleston Co.	IVI	201	FIODADIE	Line marks on nuke (0.00m whee) and dorsal ridge of nuke (1.40m).

reported that dolphins had been entangled in their gear in the past; however, the animals were freed from fishing gear and subsequently swam away.

DISCUSSION

The use of stranding data to predict mortality

Stranding data provide critical information about the causes of marine mammal mortality. Investigation of stranded marine mammals may reveal indications of fishery interaction such as rope abrasions and net marks, or evidence of other types of human interaction such as boat strike wounds or dismemberment (Cox *et al.*, 1998; Read and Murray, 2000; Friedlaender *et al.*, 2001; McFee and Hopkins-Murphy, 2002). Necropsies of stranded animals may provide additional evidence of asphyxiation consistent with entanglement, such as froth in the lungs, or may provide pathological evidence of alternative sources of mortality such as disease. Stranding data, however, underestimate total mortality. Not every animal that dies reaches shore, and not every animal that strands is discovered. In addition, incidental mortality in fisheries may be further underestimated because not every marine mammal that interacts with a fishery strands, and not every fishery-related stranding shows definitive evidence of entanglement (Cox *et al.*, 1998). The conclusions derived from this study, therefore, are based solely on available stranding data, and likely represent an underestimate of fishery-related mortality of bottlenose dolphins in South Carolina.

Classification

Stranding data showed that approximately 43% (*n*=18) of the bottlenose dolphin entanglements in South Carolina from 1992-2003 were either 'confirmed' or 'probable' crab pot entanglements, indicating that the blue crab fishery is a substantial source of mortality for bottlenose dolphins in South Carolina.

The classification of the 'confirmed' cases depended on physical evidence of interaction with the blue crab fishery. Five bottlenose dolphins (50% of all 'confirmed' cases) stranded with crab fishing gear attached to the carcass, including crab pot line and a buoy. Other animals in this category were either sighted with blue crab fishing gear attached to the body, or were freed from gear. In May 2003, a bottlenose dolphin was successfully disentangled from a crab pot line in an estuary near Morris Island, South Carolina (32°44'064N, 79°53'378W). The dolphin was entangled around the flukes, where the line was wrapped tightly three to four times. Continuing to breathe, the dolphin was held at the water's surface by the taut fishing line, and the animal's disposition was calm. In August 2003, this dolphin was captured during a capture-release project, and the dolphin seemed to be healthy, with healed entanglement wounds. The dimensions of the healed wounds from this previously entangled dolphin were compatible with the 'confirmed' cases documented by historic stranding reports. Crab pot line was wrapped around the base of the flukes, leaving wounds that were approximately 1cm in width. The rope was approximately 5/16 of an inch in diameter, corresponding with the fishery survey data. The wounds on this dolphin emphasised the importance of the simulated wound study. Different diameters of rope will leave wound impressions of varying widths; therefore, it is possible to measure the width of wounds on entangled animals and associate them with a particular rope diameter. The data obtained from the live entanglement reinforced the criteria that were used to classify the historic entanglement cases.

Distinguishing between the 'probable' and 'possible' cases was less obvious. The pictures, stranding reports and necropsy notes for the 'confirmed' cases were used as models for the placement of the other entanglement cases in their respective categories. In addition, the fisher interview data revealed that two diameters of rope are primarily used in the fishery, so knowing the widths of wounds that are created by these ropes may help to further distinguish between 'probable' and 'possible' entanglement cases. For example, one dolphin was classified as a 'probable' entanglement because of 1cm wide rope marks around the base of the peduncle and flukes, foam in the bronchi, a stomach full of fish and shrimp, and sub-dermal haemorrhaging at the site of the wound. These were indications of entanglement that were present in several of the 'confirmed' cases; however, it could not be classified as 'confirmed' because the gear was not attached to the animal.

Entanglements were categorised as 'possible' when the evidence of entanglement could have resulted from interaction with a fishery other than the blue crab fishery, or if the animal had wounds that may have occurred postmortem. For example, one dolphin had a puncture wound and a partially severed pectoral flipper that could have resulted from contact with blue crab fishing gear, but could also be due to the gear of other fisheries. Another example of an animal placed in the 'possible' category had wounds that appeared to be post-mortem, as the rope marks could have resulted from line used to transport the animal for proper stranding response.

In many cases it appeared that there was an overlap of criteria used to classify the entanglement cases. There may have been animals placed in the 'probable' category that had similar entanglement evidence as the 'possible' cases; however, classification relied on a suite of criteria such as stomach content analysis, wound dimensions and locations, and internal indications of an acute death. The flow chart (Fig. 1) that was developed during the course of this study aided in determining 'probable' versus 'possible' victims of crab pot entanglement.

Fisheries may be ruled out as potential entanglement sources if the stranding occurred in a location that is not utilised by a particular fishery, or during a time that is not in season for that fishery. Generally, the confirmed entanglements occurred throughout the year, in the southern portion of the state, and often in the upper reaches of the estuaries. The blue crab fishery operates year-round and most crab pots are placed in estuarine areas. During peak times of entanglement (May, July and August), only the blue crab and the shrimp fishery are highly active (Fig. 2). Other large fisheries, such as the coastal ocean shad fishery, appear to have minimal impact on local dolphin populations (McFee et al., 1996), but were considered in the classification. The shad fishery occurs between January and April, whereas the shrimp fishery occurs during the months from May through December. Even though an entanglement may occur during active fishing times, the location of the entanglement may be in an inactive fishing area. The 'probable' entanglements were examined in relation to the location and timing of the shad and shrimp fisheries. For example, three 'probable' entanglements occurred during active shad fishing times; however, only one case could possibly be a result of interaction with the fishery because of the stranding location. There were four 'probable' entanglements during the active shrimp trawl season; however, more data on the location of trawling activities are required before entanglements due to the shrimp fishery can concluded. The classification of 'probable' be entanglements is supported when the strandings occurred in areas that are not occupied by these other fisheries, and during times outside of the fishing seasons. Based on these results, location and seasonality may be contributing factors that would place an entanglement in the 'probable' rather than 'possible' category.

Fishery survey

When questioned on their perceptions of the interaction between their own fishery and bottlenose dolphins, crab fishers indicated that the interaction was minimal and not damaging to either group. Most fishers commented that they see dolphins almost every day, but that the dolphins and the fishery are independent of each other. Several crab fishers stated that sea turtles pose a greater risk to the fishery and fishing gear than dolphins.

Observations in the Charleston area did not provide evidence that bottlenose dolphins interact with the blue crab fishery as reported in Florida. According to Noke and Odell (2002), indicators of crab pot interaction in Florida included a close approach of a dolphin to the fishing vessel, a bait well door that had been pried open and the actual observation of dolphins manipulating pots. Of these indicators, the only one observed in this study was the close approach behaviour. Although several crab fishers commented that dolphins regularly approach their boat to beg for food, this behaviour was seen only once during fishing trips. The dolphin followed the boat closely while the fisher checked the crab pots, begging at the side of the boat where the pots were retrieved and replenished. Occasionally, the crab fisher reinforced the close approach behaviour by offering food.

Little is known about the mechanism of entanglement. Studies by Fertl and Leatherwood (1997) suggested that marine mammals become entangled in fishing gear because they actively feed near fishing operations and the dolphins in Florida actively manipulate crab pots to retrieve bait (Noke and Odell, 2002); however, this does not appear to be the case with the blue crab fishery in South Carolina. According to the fishers interviewed for this study, bottlenose dolphins in South Carolina are attracted to fishing vessels and regularly beg for food, but have not been observed 'tipping' crab pots.

Management issues

Recently, PBR for the South Carolina management unit was changed from 24 to 20 (Palka, 2003). Insignificant levels are approximated at less than 10% of PBR (Barlow *et al.*, 1995); therefore, insignificant mortality and serious injury for the South Carolina management unit would be less than 2 dolphins per year. Based on results from this study, there would be only 2 years (1994 and 2001) where incidental mortality and serious injury levels would be considered insignificant according to the MMPA.

In South Carolina, fisheries are classified as Category I if incidental take rates equal or exceed 10 bottlenose dolphins per year. Although there were 10 entanglements in 1997, the mortalities cannot be attributed to a single fishery. Based on this analysis of historical stranding data, there has not been a fishery that would qualify for a Category I listing in South Carolina.

The Atlantic blue crab fishery was recently re-categorised as a Category II fishery, which means that the number of entanglements in the South Carolina blue crab fishery must range from 0.2 to 10 dolphins annually. Based on the 'confirmed' blue crab fishery entanglements and the new PBR for the South Carolina management unit, the blue crab fishery has exceeded 1% of PBR for six of the 12 years studied. PBR is reviewed every eight years, resulting in a PBR of 20 for the South Carolina management unit until 2011. The categorisation of fisheries is based on a five-year running average of the number of entanglements in particular fisheries. In order for the blue crab fishery to be removed from a Category II classification, there must be a five-year average of entanglements that does not exceed 0.2 dolphins based on the PBR of 20. According to the results from this study in South Carolina, the five-year average (1999-2003) of bottlenose dolphin entanglements in the blue crab fishery is 0.6 per year, exceeding the threshold classification as a Category II fishery.

Recommendations

Accurate stranding records as well as comprehensive and clear photographic evidence of entanglements are essential in classification. Stranding reports and photographs must be accurate and detailed to provide sufficient criteria for classification. In this study, external evidence of entanglement was not always clearly photographed or documented with a scale for measurement, and the descriptions of wounds on the stranding reports were not consistently specific enough to classify an entanglement. In the future, stranding response personnel should have sufficient training that will ensure descriptive stranding reports and illustrative photographs.

Interviews aboard vessels are critical in obtaining accurate data on incidental mortality because underreporting by fishers is suspected (Lopez *et al.*, 2003). Not all fishers report incidental takes of marine mammals during fishing practices. Fishers may be unaware of the time limit to report incidental takes, or they may be apprehensive to report an entanglement for fear of heightened regulation or individual reprimand. Public outreach should be improved to assure fishers that there are no legal ramifications for reporting, unless fishing illegally at the time. Fishers must also be convinced that reporting incidental mortality will not lead to a negative image of the fishery (Lopez *et al.*, 2003) or heightened regulations under the MMPA. Greater educational efforts should be made to clarify the penalties for neglecting to report an entanglement, as well as emphasise the importance of fishery-dependent data to estimate incidental marine mammal mortality in commercial fisheries.

Stranding data alone cannot accurately account for the degree of marine mammal interaction with fisheries. Trained observers aboard fishing vessels provide a quantitative estimate of the bycatch rates in large-scale fisheries (Cox et al., 1998); however, for smaller fisheries, increased observer coverage may not necessarily provide more accurate mortality and interaction data. Observations aboard blue crab fishing vessels in the Indian River Lagoon were beneficial to document and describe the interaction with bottlenose dolphins, as they were seen manipulating crab pots there during fishing operations (Noke and Odell, 2002). In South Carolina, however, observer coverage may not be as beneficial because dolphins have not been observed tipping crab pots to steal bait. Data from the interviews with crab fishers indicate that there is minimal interaction between bottlenose dolphins and the fishery during fishing practices. The only clear indication that dolphins interact with the fishery is evidence from stranding events. In addition, the large number of commercial licenses that are issued annually, lengthy fishing season, and fluidity of the fishery may decrease the efficacy of observer coverage.

The PBR for the South Carolina management unit (20) has been calculated according to the best available data; however, this estimate may include both estuarine and coastal dolphins (Garrison, 2002). Management problems may arise for fisheries that exist in coastal areas but not in estuarine areas, and vice versa. As a result, fisheries that are not actually responsible for the incidental mortality of bottlenose dolphins may be subject to unnecessary regulations because bottlenose dolphins are combined into one management unit. Combining coastal and estuarine units may also provide an overestimate for PBR, further increasing regulatory difficulties. Because more data on residency patterns, genetic variability and behavioural differences among dolphins in South Carolina are needed before these animals can be divided into coastal and estuarine stocks, increased effort in photo-identification and genetic biopsies should be encouraged.

CONCLUSIONS

As methods to survey and identify marine mammal populations improve (i.e. aerial surveys, biopsies, photoidentification), abundance estimates improve also. The PBR for individual marine mammal populations is determined by the status of the stock, as is the categorisation of commercial fisheries that interact with marine mammals. As efforts to measure and estimate marine mammal populations continue to progress, management schemes to prevent the depletion of such populations become more effective.

The Atlantic blue crab fishery was re-categorised as a Category II fishery as a result of an increase in the number of entanglements documented by strandings data (W. McFee, pers. comm., 2003). According to the entanglement data for South Carolina from 1992-2003 (n=42), the blue crab fishery has taken bottlenose dolphins incidental to fishing practices at a rate that classifies their interaction as 'occasional' under the MMPA. The number of incidental

takes of bottlenose dolphins in the blue crab fishery is not insignificant and is not progressing toward ZMRG; therefore, the Category II classification is justified.

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The combined use of organochlorine contaminant profiles and molecular genetics for stock discrimination of white whales (*Delphinapterus leucas*) hunted in three communities on southeast Baffin Island

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ABSTRACT

Putative stock differences in white whales (*Delphinapterus leucas*) landed by hunters between 1992 and 1996 from the southeast Baffin Island communities of Kimmirut (KI), Iqaluit (IQ) and Pangnirtung (PA) were examined using organochlorine contaminant (OC) profiles of 124 whales, the molecular genetics of 270 whales and both types of data from 97 whales. OC concentrations were generally lower in whales hunted in PA than those hunted in KI and IQ, and many OCs were lower in KI than IQ. In canonical discriminant function (CDA) using 13 OC predictor variables (10 OC groups, mirex, octachlorostyrene and endosulfan), the first canonical function accounted for 77% of the variance and separated whales from PA with those from IQ and KI; the second canonical function separated whales from KI with those from IQ. A previous study of the molecular genetics of white whales showed that whales hunted in the three communities were significantly differentiated on the basis of haplotype and/or microsatellite allele frequencies (de March *et al.*, 2002).

When the results of two studies were combined, many whales were slightly more strongly associated with a particular source hunting community than they were in the component studies. Using *a posteriori* crossvalidation probabilities in an analysis with variables from both studies, 72% of white whales were correctly crossvalidated to their source hunting community; 82.5% from PA; 56.5% from IQ; and 58.8% from KI. The highest misclassification rates were KI to IQ (23.5%), IQ to KI and IQ to PA (21.7% in both cases) and the lowest rates were PA to KI (3.5%), PA to IQ (14.0%) and KI to PA (17.6%). This pattern of assignments was not significantly different from those in the genetics or contaminants studies alone. However, the crossvalidation probabilities to the most likely source communities were approximately 20% larger in the combined analysis than in the component studies. Canonical scores in the combined analysis were more strongly correlated with variables from the OC Study than with variables from PA also had a strong PA genetics signature. Whales from IQ were identifiable only by their OC signatures. Both a strong KI genetics and OC signature described approximately half of whales from KI. We believe that at least three stocks were sampled from the three communities.

Some whales in PA were very distinct, confirming previous beliefs that a separate stock occurs in Cumberland Sound. Whales hunted in IQ and KI differed to a lesser degree, and may be from stocks subject to a gradient or from a mixture of stocks. Some whales from PA are more likely to have genotypes and OC signatures that are also found in IQ and KI than the reverse. It is possible that summering areas of the stocks that were identified in KI and IQ are not consistent from year to year or across generations.

The main problems in combining results for individuals used in several studies, particularly when there are many measurements for relatively few individuals, is to find a limited number of relevant predictor variables that can be used in the combined analysis, while avoiding both overparameterisation and results blurred by meaningless variables.

KEYWORDS: GENETICS; ORGANOCHLORINES; DISTRIBUTION; MIGRATION; ARCTIC; NORTH AMERICA

INTRODUCTION

The southeast Baffin white whale (*Delphinapterus leucas*) stock was once defined as the whales summering near southeast Baffin Island and caught by hunters from Pangnirtung (hunted in Cumberland Sound), Iqaluit (formerly Frobisher Bay, hunted in Frobisher Bay) and Kimmirut (formerly Lake Harbour, hunted on the southeast coast of Baffin Island) (Sergeant and Brodie, 1975; Richard and Orr, 1986; Richard, 1991; Bodaly *et al.*, 1992) (Fig. 1). It is now believed that several stocks are hunted in this area although the stock boundaries are not clear. It is important to understand whether or not southeast Baffin (SEB) communities hunt the same stocks of white whales so that appropriate management decisions can be made.

In Kimmirut (KI), white whales are hunted mainly during the spring and autumn migrations. It is hypothesised that they are whales originating from Hudson Bay summer aggregations, and that they overwinter in the Hudson Strait and its open waters. Hunters from KI believe they hunt a 'local' stock in spring and summer, and migrating animals in the autumn, the same animals that migrated past Coral Harbour one week earlier (P. Richard, pers. comm.). Thus some white whales that are hunted from KI may also be hunted in summering areas in Hudson Bay and northern Québec (Reeves and Mitchell, 1989; Richard *et al.*, 1990).

The stock identity of white whales from Iqaluit (IQ) is unclear. Unlike in KI, whales are hunted in Frobisher Bay all summer, whenever they become available. It is possible that these whales are the remnants of a reduced summering stock (G. Williams, pers. comm.) or they may be summer wanderers from northern Québec or from offshore areas.

There is considerable evidence supporting the hypothesis that at least some white whales hunted in Cumberland Sound are a separate stock. Hunters from IQ and KI have always believed that they do not hunt the same white whales as Pangnirtung hunters because of differences in migration times and adult sizes (Southeast Baffin Beluga Review Committee (SEBBRC), 1991; Planning Committee for the Co-management of Southeast Baffin Beluga, 1994; Department of Fisheries and Oceans (DFO), 2002). In fact, hunters from PA report that there are three different white whale groups that come into Cumberland Sound that can be distinguished by their appearance, size, health, taste, texture of maktaq and behaviour (Kilabuk, 1998). White whales hunted from PA and IQ are on average larger at a given age



Fig. 1. Study area.

than those from KI (de March, unpublished data). In addition, recent radio-tagging work by Richard (pers. comm.; Department of Fisheries and Oceans (DFO), 2002) showed that Cumberland Sound white whales stay in the northeast sector of Cumberland Sound in the winter. The white whales that congregate near the Ranger River at Clearwater Fiord on Cumberland Sound were listed 'endangered' by COSEWIC in 1989 (Campbell, 1989) after considerable declines in this area. With this and genetics evidence (see below), quotas were lifted for IQ and KI in 1999, whilst the quota was maintained for PA (Richard, 1991). Since that time, attempts have been made to obtain more information on all SEB stocks.

Genetic results support ecological knowledge about whales hunted in SEB communities. De March et al. (2002) examined a maternally-inherited d-loop mitochondrial DNA (mtDNA) sequence of 324 nucleotides with 22 variable positions and 15 nuclear microsatellite loci in white whales from the three SEB communities and from several high Arctic locations. Twenty of 55 haplotypes found in North America were found in SEB. On the basis of mtDNA haplotypes, white whales hunted in KI were not significantly differentiated from those hunted in IQ (lesser F_{st} , p=0.44), but whales from both IQ and KI were significantly differentiated from those hunted in PA (lesser F_{st} , both p<0.00) (de March *et al.*, 2002). Whales from PA had more uncommon and unique haplotypes than those from IQ and KI. Several haplotypes from PA whales occurred only in the North American western Arctic, while those from KI and IQ mostly resembled those from western and northern Hudson Bay (de March and Postma, 2003). In addition, whales hunted in the three SEB communities were significantly differentiated from each other on the basis of allele frequencies at 15 microsatellite loci. Whales from PA differed strongly from those from KI (p<0.00), and whales from IQ did not differ from those from KI or PA (both p=0.01, not significant at a table-wide level) (de March et

al., 2002). In a dendrogram using microsatellite loci, whales from the three communities clustered on one branch that was distant from other high Arctic locations (de March *et al.*, 2002). In another comparison involving samples from KI, northern Québec and Hudson Bay locations, KI samples most resembled those from northern Québec (de March and Postma, 2003). There were also temporal differences among years within communities for both types of loci, though these were smaller than differences among the three locations (de March *et al.*, 2002). This observation also supports the hypothesis that several stocks exist, even if not strongly delineated.

Organochlorine contaminants have been used to determine stock affiliations of whales in univariate and multivariate analyses (Aguilar, 1987; Aguilar et al., 1993; Stern et al., 1994; Krahn et al., 1999; Innes et al., 2002). Different patterns of organochlorine contaminant (OC) concentrations in marine mammals are caused by differences in feeding. They may thus reflect a number of factors including: different prey species or proportions of these in the diet; the trophic status of prey species; feeding patterns in summering and wintering areas and/or on migration routes; differential feeding behaviour of different social groups etc. An analysis of eastern North American white whales using OC data showed that there were strong differences in OC concentrations among samples from Greenland, Grise Fiord, PA, KI and several Hudson Bay locations (Innes et al., 2002). This study showed significant differences in OC concentrations between whales hunted in the SEB communities of PA and KI (n=7 whales from PA, n=15 from KI). Of 64 OCs used in the study, 33 were significantly different (p < 0.05) between PA and KI samples, and concentrations were higher in KI than in PA samples for 24/33 OCs. Differences were not as large as differences across larger geographic distances. Ten of 15 white whales from KI and 5 of 7 from PA were crossvalidated to their source hunting community in canonical discriminant function analysis (CDA). The remaining 7/22 from PA and KI were crossvalidated to the Belcher Islands (southern Hudson Bay). None were misclassified to hunting locations in Greenland or Grise Fiord in the Canadian High Arctic (Innes et al., 2002).

It is generally assumed that the results of more than one type of study using the same subjects will yield more information about stock differences than one study alone (Donovan, 1991; IWC, 2002). For this study, both genetics information and OC data were available from many white whales, thus providing the opportunity to investigate the SEB stock question further.

METHODS

Samples

Lower jaws, blubber and skin samples were obtained from white whales caught by hunters from Kimmirut (KI), Iqaluit (IQ) and Pangnirtung (PA) between 1982 and 1996 (Table 1). Blubber samples were frozen and stored at -20° C until organochlorine contaminant (OC) analyses were undertaken in 1995. The ages of the whales sampled were determined by counting annuli on sagital thin sections of the second or fifth tooth, whichever had the least wear (Perrin and Myrick, 1980; Goren *et al.*, 1987; Wainwright and Walker, 1988; Brodie *et al.*, 1990). White whales ≤ 2 years of age were not used in the OC analyses. Laboratory sex determinations were conducted using the methods described in Bérubé and Palsbøll (1996).

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 Table 1

 Locations, years and numbers of samples. A total of 297 white whales (270 from the genetics study and 124 from the OC study with 97 overlapping) were sampled.

Location and year	n genetics study	Sex ratio F:M	n OC study	Sex ratio F:M	Mean age F	Mean age M	<i>n</i> joint study
Pangnirtung (PA)							
1982	10	1:9	6	0:6		8.3	6
1985	2	0:2					
1986	20	5:18	20	4:16	3.5	5.8	20
1991	10	4:06					
1992	20	7:14	20	7:13	14.8	12.3	17
1993, 1994	26	13:19					
1995	17	9:8	17	9:8	6.6	13.7	14
1996	17	10:11					
Location total	122		63				57
Igaluit (IO)							
1984, 1989	21	7:15					
1992	18	9:9	12	6:6	6.7	4.8	12
1993, 1994	31	3:21					
1996	13	4:7	12	2:10	5.5	6.3	11
Location total	83		24				23
Kimmirut (KI)							
1992	22	11:11	28	13:15	10.7	9.3	17
1993, 1994	31	19:14					
1995	8	3:6	6	2:4	4.5	17.0	0
1996	4	1:3	3	1:2	7.5	5.8	0
Location total	65		37				17
	270		124				97

Genetic analyses

The whales used in the genetic analyses (Table 1) were the same 270 whales described in de March *et al.* (2002) that had both haplotype and microsatellite data. Of these, 97 whales were also used in the OC study. An mtDNA sequence of 324 nucleotides found near the beginning of the d-loop and 15 microsatellite loci were examined (de March *et al.*, 2002).

For the study presented here, probabilities were calculated of every individual's genotype, treated as an unknown, occurring in different sample populations. This was done to produce summary descriptions for all individuals that could be used in the analysis of both studies combined. For this calculation, population allele frequencies of '0' were reset to 0.5, as Waser and Strobeck (1998) suggest, to ensure that individuals with unique alleles or haplotypes would have positive probabilities of occurring in all populations. Individual whales were then 'assigned' to a most likely sample population of origin on the basis of this probability (Waser and Strobeck, 1998; Paetkau et al., 1995). The probabilities of an individual's genotype occurring in different populations were standardised to add up to 1 by applying Baye's formula, and these assignment probabilities were used in the CDA analysis combining the two studies. Assignment calculations were done using inhouse software using Visual Basic.

Genetic diversities in whales hunted in the three communities, not previously described, were calculated as 'rarefied' values of $D_l = 1 - \Sigma_u (p_{lu})^2$ for haplotypes and as $D = 1 - \Sigma_l \Sigma_u (p_{lu})^2/m$ for microsatellites, where p_{lu} is the frequency of the *u*th allele at the l-th locus, and *m* is the number of loci (Weir, 1996). The 'rarefied' values, which were calculated with 1,000 sub-samples without replacement of 15 white whales (Hurlbert, 1971), are not expected to be correlated with sample size.

Chemical analysis

A total of 124 samples from the three communities were extracted and analysed in random batches so that observed differences between sampling sites could not be attributed to any systematic analytical variation. All laboratory analyses were performed using the same methodology, instrumentation and analyst over a period of two years. Other quality assurance measures included the analysis of standard reference materials (NIST cod liver oil 1588) and duplicated analysis of every 12th sample. The duplicate results were satisfactory, and results were averaged for the duplicated analyses.

Determinations of OCs in white whale blubber tissues followed the procedures described by Stern et al. (1994). Blubber samples were partially thawed and 2g was combined with anhydrous Na₂SO₄ (heated at 600°C for 16 hours prior to use). The mixture was then extracted twice with hexane in a small (50ml) ball mill, with the hexane decanted between extractions. Surrogate recovery standards of PCB30 and octachloronaphthalene (OCN) were added prior to extraction. Extractable lipids were determined gravimetrically on a fraction (1/10) of the extract. A portion of the extract equivalent to approximately 100mg lipid was separated into three fractions of increasing polarity on Florisil (8g; 1.2 % v/w water deactivated). The first fraction was eluted with hexane and contained PCBs, DDE, transnonachlor and mirex; the second fraction was eluted with hexane:DCM (85:15) and contained HCHs, most chlorinated bornanes, chlordanes and most DDTs. Some chlorobornanes, most notably T2 (Parlar no. 26), were partially eluted with hexane. The third fraction, containing dieldrin and heptachlor epoxide, was eluted with a 1:1 mixture of hexane:DCM. After addition of aldrin as a volume corrector, each fraction was analysed for OCs by capillary gas chromatography (GC) with ⁶³Ni electron capture detection (ECD) by means of an automated Varian 3400 GC (Varian Instruments, Palo Alto, CA). Samples were injected on a 60mm \times 0.25mm i.d. DB-5 column (film thickness= $0.25\mu m$). H₂ was used as the carrier gas (2mL/min) and N₂ as the make-up gas (40mL/min). A total of 103 PCB congeners (including co-eluting congeners) and 40 OC pesticides were quantified by using external standard mixtures (Ultra Scientific, North Kingstown, RI).

Recoveries of the surrogates, PCB30 and OCN were uniformly greater than 90% and no corrections were made for recoveries. One hundred and thirty-three (OC) compounds, some co-eluded, were quantified. Of these, 88 had consistent non-zero values and were kept for statistical analyses. All data are in ug/g or ppb in wet blubber weight (approximately 80% lipid).

OC data were statistically corrected for covariates before they were used in multivariate analyses, as suggested by Tabachnick and Fidell (2001). Specifically, the model:

$$log (concentration) = a_s \times sex + b \times age + c_s \times sex \times age + d \times location$$
(1)

in which *sex* (= M or F) and *location* (= IQ, KI or PA) are class variables; *age*, a continuous variable describing age in years; *a_s* the sex effect; *d_l* the location effect; *b* the coefficient describing the effect of *age*; and *c_s* coefficient of the *sex*×*age* effect for each sex, was first used to describe every OC and OC group using the general linear models procedure (PROC GLM) in SAS Inst. Inc. (1989). When OC groups such as Σ DDT or Σ 7-CB were used, component concentrations were summed before using the logarithmic transformation. Raw logged values for each OC were then adjusted for covariates with coefficients from Equation (1) as follows assuming an age of 10 years and male sex:

$$log(concentration)_{adjusted} = log(concentration)_{observed} -a_s \times sex - b \times age -c_s \times sex \times age$$
(2)

Because of the covariate correction, results for CDA are not expected to correlate with age or sex. The values and partial probabilities (Type III error) of the four effects above and of the three contrasts comparing locations pairwise (Iqaluit *versus* Pangnirung = IQ – PA), (KI – PA) and (IQ – KI), were also calculated.

All statistical analyses of OC data, for 124 individuals in the OC Study and for the 97 used in both studies, were undertaken using various linear models programs available in SAS (Statistical Analysis System, SAS Inst. Inc., 1989). OC concentration patterns among sampling locations were described using Canonical Discriminant Analysis (CDA) with the PROC DISCRIM and PROC STEPDISC procedures (SAS Inst. Inc., 1989). The probabilities of population memberships were obtained by 'crossvalidating' all individuals (Option CROSSLIST in PROC DISCRIM in SAS Inst. Inc., 1989). In crossvalidation, the individual to be tested is removed from the data, the canonical functions are calculated without this individual, and then the individual is placed with the functions from the reduced dataset (Lachenbruch and Mickey, 1968).

In view of concerns about overparameterisation and lack of power (Tabachnick and Fidell, 2001; also see Discussion), we performed the presented CDA with a limited number of predictor variables. The 13 predictor variables were: Σ DDT (o,p'- and p,p'-DDT); Σ DDE; Σ DDD; Σ HCH; Σ CHL; Σ 4-CB (tetrachlorobiphenyls); Σ 5-CB; Σ 6-CB; Σ 7-CB; Σ 8-CB; mirex; endosulfar; and octachlorostyrene (Table 2). This number was considered to be few enough to avoid overparameterisation with the smallest sample size of 17 for KI. The results of stepwise CDA with these 13 predictor variables and stepwise CDA using all 88 OCs were also examined.

Statistical methods for combining results of two studies

Ninety-seven individual whales' probabilities of being identified as originating from KI, IQ or PA, in both the Genetics and the OC Study were used as predictor variables in the CDA of results from both studies (the Joint Study).

The term 'Genetics Placement Probability' (GenPP) will be used to describe the probabilities of assignment to each of three source communities in the Genetics Study and 'Organochlorine Contaminants Placement Probability' (OCPP), to describe the crossvalidation probabilities to communities in the OC Study. The term 'Joint Placement Probability' (JointPP) will be used to describe the three probabilities of assignment derived from CDA in the Joint Study.

All assignment probabilities (GenPPs and OCPPs), and crossproducts of these probabilities for 97 whales were examined using CDA (PROC DISCRIM, SAS, Statistical Analysis System, SAS Inst. Inc., 1989). Although this produces 21 predictor variables, only 10 are linearly independent. The CDA produced three JointPPs for each of 97 individuals, one to each source community. Individuals were then crossvalidated to a community on the basis of this probability (Option CROSSLIST in PROC DISCRIM in SAS Inst. Inc., 1989).

RESULTS

Molecular genetics

Actual probabilities of assignments to the source hunting communities in the genetics study can be identified in Fig. 2. Of 270 white whales in the genetics study, 74 of 122 (61%) from PA, 42 of 83 (51%) from IQ and 31 of 65 (48%) from KI were assigned to their source hunting community (Table 3). Misassignments were primarily between KI and IQ (31% both ways). Misassignments between PA and either IQ or KI were lower, ranging from 18-22%. Patterns of assignments and misassignments were not significantly different between these 270 whales and the subset of 97 used in both studies (comparison of columns 1 and 3 in Table 3, Chi Squared=10.22, p=0.2498, 8 df). In the study with 97 whales, individuals hunted in PA had a higher probability of being assigned to their source community than individuals from KI or IQ (column 3b, Table 3).

In whales from PA, 6.3 ± 1.2 (mean \pm SD of rarified values) haplotypes/15 whales was observed, while 5.0 ± 1.1 IQ and 4.1 ± 0.9 in KI. Actual numbers of haplotypes observed were 13, 9 and 7. Rarefied haplotype diversities for 15 individuals were 0.713 ± 0.09 for PA, 0.594 ± 0.11 for IQ and 0.527 ± 0.11 for KI. The number of microsatellite loci and microsatellite diversity did not differ notably in the three communities. The rarefied numbers of alleles for PA, IQ and KI were 80.0 ± 3.4 , 82.2 ± 5.0 and 80.4 ± 3.4 respectively, while diversities were 0.645 ± 0.01 , 0.648 ± 0.02 and 0.648 ± 0.02 .

OC Contaminants

The R^2 values for univariate OC analyses of covariance (Equation 1) were consistently higher with log-transformed than with untransformed data (Mean $r^2=0.336$ versus mean $r^2=0.303$). The sex \times age interaction was significant at $p \leq 0.05$ for 67/88 OCs, while age was in 20/88 and sex in 0/88. The coefficient of the sex \times age interaction was positive for all OCs, and the age coefficient was always smaller in magnitude and usually negative.

Among 88 OCs examined, 72 had significant location effects at $p \leq 0.05$. Significant probabilities ranged from 4.73 $\times 10^{-2}$ for PCB28 to 3.48×10^{-12} for PCB187 (Table 2). When table-wide statistical criteria were applied as a sequential von Bonferroni test (Rice, 1989), yielding a minimum significance level of p=0.0004 for a table-wide $\alpha=0.05$, 52% (46/88) of OCs still had significant location

Table 2

Statistics for selected organochlorine contaminants (OC) for white whales hunted in three communities on southeast Baffin Island. Mean concentrations and CVs are from corrected values from Equation (2). Other descriptions are from Equation (1), and include R^2 values, significance of covariates at $p \le 0.05$ indicated as a 'y', significance of overall location effects and of contrasts comparing OC concentrations from the three communities pairwise. Sign of contrasts are designated by + or -, and contrasts not significant at $p \le 0.05$ are bracketted. 'Trend' represents order of mean concentrations in white whales from the three communities.

Contaminant											Contrast		
or contaminant group	Mean ng/g Kimmirut	CV (%)	Mean ng/g Iqaluit	CV (%)	Mean ng/g Pangnirtung	CVE (%)	Equation [1] R ²	Covariates significant?	Probability of stock effects	IQ-KI	KI-PA	IQ-PA	- Trend
Congener and iso	mer groups												
∑3-ČB	100.68	35	91.36	27	84.91	34	0.368	У	3.56E-02	(-)	+	(+)	KI>IQ>PA
∑4-CB	611.51	35	701.63	40	506.65	37	0.388	У	1.99E-03	(+)	+	+	IQ>KI>PA
∑5-CB	1510.76	39	1639.22	30	1088.58	35	0.479	У	8.44E-07	(+)	+	+	IQ>KI>PA
∑6-CB	1905.37	41	2408.73	40	1403.26	36	0.475	У	9.85E-08	+	+	+	IQ>KI>PA
∑7-CB	681.04	38	839.61	37	460.74	36	0.506	У	1.77E-10	+	+	+	IQ>KI>PA
∑8-CB	54.15	37	75.11	41	48.57	39	0.331	У	1.72E-04	+	(+)	+	IQ>KI>PA
PCB05 (2-CB)	209.37	63	136.33	43	142.12	60	0.179		3.77E-03	-	+	(+)	KI>IQ>PA
PCB207 (9-CB)	4.67	55	5.88	50	4.00	79	0.210		4.13E-03	(+)	+	+	IQ>KI>PA
\sum PCB (all above)	5074.76	36	5882.73	35	3738.87	33	0.481	У	2.67E-07	(+)	+	+	IQ>KI>PA
∑DDT	2724.42	37	3051.93	42	1913.31	41	0.423	у	3.15E-05	(+)	+	+	IQ>KI>PA
∑DDE	826.87	35	868.38	34	655.75	38	0.417	У	5.39E-04	(+)	+	+	IQ>KI>PA
∑DDE	2449.99	44	2735.58	59	1847.96	39	0.360	у	4.08E-03	(+)	+	+	IQ>KI>PA
\sum DDs (all above)	6018.89	35	6662.16	43	4414.75	36	0.432	У	2.36E-06	(+)	+	+	IQ>KI>PA
ΣCHL	2322.73	33	2195.95	33	1739.30	34	0.407	у	2.27E-04	(-)	+	+	KI>IQ>PA
∑CBz	532.62	45	570.52	45	424.47	41	0.364	У	1.30E-02	(+)	+	+	IQ>KI>PA
∑HCH	281.58	31	243.40	32	229.83	36	0.281	У	1.37E-02	(-)	+	(+)	KI>IQ>PA
∑CHB	10,472.81	31	10,479.83	34	9119.43	31	0.390	У	7.62E-02	(-)	+	(+)	KI>IQ>PA
Endosulfan	14.06	95	17.18	56	8.78	74	0.255		1.81E-06	(+)	+	+	IQ>KI>PA
Octachlorostyrene	3.63	68	6.31	57	4.04	53	0.285		1.67E-03	+	(-)	+	IQ>KI>PA
Mirex	14.23	39	15.82	49	8.81	59	0.367		1.23E-08	(+)	+	+	IQ>KI>PA
Dieldrin	573.73	33	646.21	48	528.10	38	0.308	У	2.64E-01	(+)	(+)	(+)	IQ>KI>PA
Individual OCs of	finterest												
PCB187	195.84	45	267.37	37	119.18	54	0.498	У	3.48E-12	+	+	+	IQ>KI>PA
PCB193	25.67	51	22.59	30	13.40	57	0.435	У	1.19E-10	(-)	+	+	KI>IQ>PA
PCB132	81.50	47	120.71	48	57.39	45	0.460	У	1.32E-09	+	+	+	IQ>KI>PA
PCB185	10.38	44	12.66	36	6.82	45	0.434	у	2.39E-09	(+)	+	+	IQ>KI>PA
PCB136	42.14	51	31.45	38	21.74	46	0.373	У	8.09E-09	(-)	+	+	KI>IQ>PA
o,p'-DDD	202.62	47	247.80	47	196.99	48	0.373	У	9.74E-09	(+)	(+)	+	IQ>KI>PA
o,p'-DDT	1379.95	44	1572.48	43	819.49	41	0.452	У	9.96E-09	(+)	+	+	IQ>KI>PA
β-НСН	74.42	40	62.67	34	43.01	39	0.387		1.32E-08	(-)	+	+	KI>IQ>PA



Fig. 2. Probabilities of assignment to three communities based on the Genetic Study and the OC study. The community to which each whale was assigned, based on the crossvalidation probability obtained from CDA combining the results of the two studies is given in the key.

effects. There were significant differences ($p \le 0.0004$) among all three locations for the following 10 OCs: PCB42; PCB87; PCB153; PCB132; PCB105; PCB138; PCB187; PCB201/157; PCB180; and PCB196/203. Also, at $p \le 0.0004$, concentrations of 34% (30/88) of OCs differed significantly between PA and KI, 39% (34/88) between PA and IQ and 16% (14/88) between KI and IQ. The most common trend in mean OC concentrations was IQ \ge KI >PA (Table 2). Covariates were not significant at $p \le 0.05$ for three OCs that had location effects significant at $p \le 0.0004$:

	Ger	netics	C	DC	G	enetics		OC		Joint	
	Ali	l data	All	data		What	ales us	sed in both s	tudies		
Column	(1)		(2)		(3)	(3b)	(4)	(4b)	(5)	(5b)	
Direction of pla	acement										
PA to PA	74	61%	46	73%	36	(0.846)	42	(0.822)	47	(0.922)	82.5%
PA to IQ	26	21%	10	16%	15	(0.672)	6	(0.795)	8	(0.850)	14.0%
PA to KI	22	18%	7	11%	6	(0.651)	9	(0.628)	2	(0.785)	3.5%
Total n PA	122	100%	63	100%	57		57		57		100%
IQ to PA	15	18%	3	13%	6	(0.636)	3	(0.662)	5	(0.781)	21.7%
IQ to IQ	42	51%	13	54%	10	(0.721)	13	(0.850)	13	(0.848)	56.5%
IQ to KI	26	31%	8	33%	7	(0.718)	7	(0.739)	5	(0.847)	21.7%
Total n IQ	83	100%	24	100%	23		23		23		100%
KI to PA	14	22%	3	8%	1	(0.622)	0		3	(0.748)	17.6%
KI to IQ	20	31%	10	27%	5	(0.727)	4	(0.535)	4	(0.772)	23.5%
KI to KI	31	48%	24	65%	11	(0.762)	13	(0.753)	10	(0.869)	58.8%
Total <i>n</i> KI	65	100%	37	100%	17		17		17		100%
Total n	270		124		97		97		97		

 Table 3

 Placement patterns and assignment probabilities (in brackets) in genetics, OC and joint studies.

 PA = Pangnirtung, IQ = Iqaluit and KI = Kimmirut.

endosulfan, β -HCH and mirex. There were significant covariate effects but not significant location effects in 10 OCs: dieldrin; PCB17; PCB31; PCB52; PCB91; PCB83; PCB179; PCB200; o,p'-DDD; and Σ CHB (p>0.05).

All 15 OC groups had location effects significant at $p \leq 0.05$, however only seven groups were significant at $p \leq 0.006$, the minimum significance level for table-wide comparisons among 15 groups (Table 2). The probability of location effects was highest for Σ 7-CB (p=1.77 × 10⁻¹⁰) and lowest for Σ 3-CB (p=0.0356).

In the CDA, the first discriminant function with the described 13 predictor variables accounted for 77% of the variance (Fig. 3). The first function mainly separated white whales from PA from the other two locations. The scores for the function were significantly correlated with 99 of 103 possible predictor variables ($p \le 0.05$, 88 OCs and 15 OC groups in Table 2), most strongly with Σ 7-CB (r=0.764), PCB185 (r=0.754), PCB187 (r=0.740), PCB180 (r=0.719), mirex (r=0.712), all IQ>KI>PA and PCB193 (r=0.748, KI=IQ>PA). The second canonical function mainly separated white whales from KI and those from IQ (Fig. 3). The scores were significantly correlated with 55 of 103 predictor variables, the highest correlations with octachlorostyrene (r=0.626, IQ>PA>KI), PCB194 (r=0.512) and PCB199 (r=0.437), both IQ>KI=PA, C3 (a chlordane isomer) (r=-0.410, KI \ge IQ \ge PA), and PCB105 (r=0.406, IQ>KI>PA). Mean concentrations of OCs were significantly $(p \leq 0.05)$ higher in IQ than in KI in 16 OCs and 3 OC groups (26-CB, 27-CB, 28-CB). Mean OC concentrations were significantly higher in KI than in IQ in only 3 OCs: PCB05 (2-CB), PCB45 (4-CB), y-HCH and in none of the OC groups (Table 2).

In stepwise CDA of the same 13 predictor variables, the following were chosen in order at $p \leq 0.05$: $\Sigma7$ -CB; Σ DDD; octachlorostyrene; mirex; endosulfan; Σ CHL and $\Sigma6$ -CB; and the remaining 6 OCs were not significant. The first 7 OC groups chosen had slightly different patterns of significant differences from each other among communities (Table 2). Pairwise plots of the OCs that were chosen by the stepwise CDA suggests that the major OC differences among communities may be best described as OC ratios, for example the Σ DDD/ $\Sigma7$ -CB ratio (Fig. 4). In stepwise CDA

of all 88 predictor variables, PCB187, o,p'-DDD and PCB136 were the first three predictor variables chosen, suggesting similar ratios.

Of 124 whales in the OC study, 67% (83/124) were correctly crossvalidated to their source hunting community (46/63=73% from PA, 13/24=54% IQ and 24/37=65% KI) (Table 3). As in the genetics study, whales from KI and IQ were often misassigned to each other (33% and 27%), while misassignment percentages between whales from PA and whales from IQ or KI were lower, ranging from 8-16%. Individuals that were misassigned had intermediate canonical scores (Fig. 3). Patterns of assignments and misassignments were not significantly different between the 124 whales and the subset of 97 used in both studies (comparisons of columns 2 and 4 in Table 3, Chi Squared = 7.148, p=0.5207, 8 df).



Fig. 3. Canonical Score $1 \times$ Canonical Score 2 from CDA of OC data from 124 white whales. The key identifies both the source hunting community and the community to which the individual was assigned.



Fig. 4. Σ DDD versus Σ 7-CB (ng/g) in 124 white whales.

Joint study

Comparisons of assignments

Mean probabilities of assignment to the source communities in the OC study were similar to those in the genetics study (columns 3a versus 3b, Table 3). In general, a few more individuals were placed to their source hunting community in the OC study, with the difference slightly stronger when the whole sample populations rather than the sub-sample of 97 individuals was considered (percentages from columns 1-4, Table 3). However, assignment percentages to the source hunting community were not significantly different between the two studies (Chi-square tests comparing columns 1-4, Table 3).

Nevertheless, individuals' assignments were not the same in both studies. The GenPPs and the OCPPs to the source hunting community were correlated for white whales from PA (r=0.347, n=57, p=0.0083), and not for whales from KI or IQ (r<0.12 and p>0.6, both locations) (slopes, Fig. 2). Fisher's Exact Test (Kendall and Stuart, 1967, pp.580-585) applied to whales from each source, comparing assignment of individuals to 3 source communities in the OC study \times 3 source communities in the genetics study, elucidated details of assignment differences. Patterns of individual assignment in the two studies were independent for whales from both IQ and KI (p=1.00, both cases). Assignment patterns were not independent for whales from PA (p=0.0465). In this comparison, there was more than an expected number of PA whales placed to PA on the basis of both genetics and OCs.

Joint assignments in genetics and OC studies combined

The first discriminant function using assignment probabilities as predictor variables in the CDA in the Joint Study accounted for 80.7% of the variance. The first score was strongly correlated with the OCPP for PA, and weakly with OCPP for IQ and GenPP for KI ($p \leq 0.05$). The second score was significantly correlated with the OCPP and squared values of the OCPP for all three communities.

In crossvalidations using JointPPs, 46 of 57 (80.7%) white whales from PA, 14/23 (60.9%) from IQ and 11/17 (64.7%) from KI were assigned to their source hunting community (Fig. 2; column 5, Table 3). As in both the genetics and OC studies, the highest percentages of

misassignments were between whales from KI and IQ (23.5 and 30.4%), and percentages of misassignments between PA and the other communities were lower, between 3.5% and 15.8%. Assignment patterns determined from JointPPs did not differ significantly from assignment probabilities in either component study (column 5 versus columns 1 to 4, Table 3, Fisher's Exact Test, p>0.05 all cases).

The crossvalidation probabilities from this CDA were slightly larger than those in component studies (Fig. 5, columns 6 and 7 versus 8, Table 3). Groups of assigned and misassigned whales could not be related to sampling years, season, sex or age.



Fig. 5. Assignment probabilities in the Joint Study versus mean of assignment probabilities to the same communities in the Genetics and OC studies. The key also describes which one of the two probabilities used to calculate the mean was larger.

DISCUSSION

Component studies

The assignment probabilities and percentages of misassignments calculated from genetics data among whales from the three communities are weakly correlated with genetic distances demonstrated in the previous study of de March et al. (2002). The highest percentages of misassignment were between KI and IQ, which had the smallest genetic distances between them, while the lowest percentages of misassignments were between KI and PA, which had the largest. In addition, rates of assignment to the source community were related to the presence of uncommon haplotypes, this in turn related to the genetic diversity. Whales from PA, which had a high diversity due to several unique and uncommon haplotypes, were most identifiable. Whales from KI had a low haplotype diversity, but had two haplotypes otherwise associated only with Foxe Basin samples (de March and Postma, 2003).

OC concentration values are similar to those previously observed in white whales from the Arctic (Muir *et al.*, 1992; Stern *et al.*, 1994; de March *et al.*, 1998; Krahn *et al.*, 1999). Results described here also support the patterns described by Innes *et al.* (2002) in that concentrations of most OCs were higher in KI than in PA. The patterns in covariate coefficients show that there is a higher rate of OC uptake in adult males than in females for most of the OCs examined, as expected, since females transfer OCs to their young.

Univariate and multivariate differences among concentrations of OCs and OC groups in whale whales hunted in KI, IQ and PA, support the hypothesis that some whales hunted in the three SEB communities are from different stocks. The first canonical function in the analysis of OC data strongly separated whales hunted in PA from those hunted in IQ and KI. It is possible that the Cumberland Sound food web is 'cleaner' than that of whales hunted from the other two communities. The second discriminant function was dominated by OCs of which concentrations in whales from IQ were significantly different than those from KI, most often IQ>KI. Particularly, OCs that are characteristic of animals that feed higher in the food chain, namely 6-, 7- and 8- chlorinated PCBs had higher mean concentrations in whales from IQ. It is possible that whales from IQ feed in an 'Atlantic' food web that differs from the Cumberland Sound and Hudson Bay food webs. There are no reasons to believe that the sources of OCs for whales from IQ are local. A small number of OCs, namely PCB05 (2-CB), PCB45 (4-CB), γ-HCH, ΣCHB, ΣHCH and ΣCHL had higher concentrations in KI whales than in IQ whales, and even lower concentrations in PA whales. Some of these OCs have lower fat solubilities than the higher chlorinated PCBs ($K_{ow}s = 3$ to 4 versus $K_{ow}s > 6$), and are metabolised faster. Most of these whales from KI were hunted in the autumn; thus this difference may reflect unknown aspects of recent feeding of KI whales, presumably in the summering areas in Hudson Bay or Foxe Basin.

OC differences among whales hunted from the three communities can be interpreted as differences in OC ratios as well as in concentrations. This manuscript demonstrated the $\Sigma DDD/\Sigma7$ -CB ratio (Fig. 4). DDD is a microbial degradation product most often found in sediments, and $\Sigma7$ -CB indicate a high food web level. The ratio is highest in whales from PA than in whales from KI and IQ, suggesting that whales from PA are feeding lower in the food web, perhaps on benthic fish or fish that feed on benthos. The ratio is smallest for whales from KI even though concentrations of both ΣDDD and $\Sigma7$ -CB are notably higher in KI than in PA. In view of the poor knowledge about feeding in these whales, it is difficult to interpret these ratios.

Combined results

Analysis of genetics and OC data jointly gave slightly stronger evidence for stock differences than in the component studies because some whales, particularly those from PA, had both OC and genetics signatures that associated them with the same hunting community. The degree of stock discrimination was only slightly more convincing in the joint analysis than in the component analyses. The CDA showed that OC data were more important for describing stock differences than the genetics data. Whales hunted in PA and IQ are identifiable mainly by their contaminant signature, although a notable fraction of whales from PA also had a strong PA genetics signature. Approximately half of whales hunted in KI had both a strong OC and genetics signature for KI.

In general, patterns of assignments among whales hunted in SEB communities suggest the possibility that the stock of whales hunted in KI and IQ might also be hunted in PA, but that a stock hunted in PA is not hunted in the other two communities. These results are consistent with the hunters' belief that more than one group of whales comes into Cumberland Sound (Kilabuk, 1998). In this study, 8 of 10 misassigned whales from PA were placed to IQ, with an average assignment probability 0.850. Cumberland Sound is a considerably more productive area than Frobisher Bay and it would be attractive to white whales.

Hunters in Kimmirut also believe they hunt two groups of whales. Of 35 whales hunted in KI for which dates were available, 11 were hunted before August and 24 after August. However, whales hunted in the two seasons showed no differences in assignment patterns.

Whales from KI and IQ are discriminated from each other in the Joint Study to the same extent as in the component studies. In view of this result, it must be considered that most individuals from KI and IQ are members of stocks subject to gradients. It is also possible that more than two stocks are hunted in these two communities, and this blurred results in this study. The similarities between these two hunted groups are difficult to explain in view of the fact that the summering locations are widely separated. A partial explanation may be that wintering areas and mating areas overlap. If this were true, it would still be possible to observe haplotype differences between the two areas, and this was not the case. Another explanation may be that the stocks of whales hunted in KI and IQ do not utilise the same summering areas their entire life, or that summering areas will change with time or with generations. It has even been suggested that some whales travelling toward Hudson Strait in the spring are diverted north by the land they encounter (P. Richard, pers. comm.). These whales then enter Frobisher Bay and some possibly parts of Cumberland Sound.

In conclusion, we believe that members of at least three different stocks are sampled in the three SEB communities. However, these stocks may overlap in geographic ranges, and the stock hunted in KI and IQ have similar genetic chacteristics. These results support management decisions that have been made.

Statistical considerations in combining results of different types of studies

When the results of different studies using the same subjects are combined, a measure of the covariance between responses in the two studies is desirable to reduce or quantify the residual error. If this covariance cannot be estimated, final conclusions can be based only on averages or on results weighted by the perceived importance of component studies. For this reason, multivariate statistics using results from all component studies, which take into account the covariance among responses from both studies, are a desirable method for analysing results.

'Responses' measured for the same test subjects in component studies can consist of raw data (OC concentrations, allelic information) to responses derived from the raw data (scores, probabilities, distances). A multivariate analysis which combines both OC and genetics raw data would require an underlying model with both continuous variables for the OC data and nested class variables (for alleles within loci) for the genetics data. Desirable output would consist of the comparison of linear combinations of OC data and also comparisons of variance components for the genetics data. At the present time, software for such an analysis is not available as a unit. Even if such an analysis were carried out, a model with many predictor variables might be overparameterised (see below). Thus the decision here to use summary responses from individual studies, was attractive in view of computationally difficult alternatives.

Before a researcher can consider combining the results, options in analysis of component studies must first be addressed. Studies with relatively few animals and many measurements, as both component studies are in this case, can be analysed by a diversity of numerical techniques which have different underlying hypotheses and which are known to have different biases. These biases can interact in a combined analysis. For example, if methods for describing both types of data are biased toward individuals' resembling other individuals from their source population, then the results of the different studies are more likely to be similar. For example, if whales from PA that had unique alleles also had a strong PA contaminants profile, we could be more confident in concluding that these alleles characterise whales from PA. Thus, the use of several types of data for scoring the same individuals can form a feedback loop in which the results of one study lead to that evaluation of numerical methods in the other. Of course, this feedback process is more likely to occur if some true stock differences exist and some predictor variables are both highly relevant and precise.

With respect to appropriate predictor variables in studies of OC contaminants, the use of many OCs must be carefully considered. Although a large number of OCs can be measured with a high degree of accuracy, the use of multivariate statistics and a large number of variables can yield results which are not representative of true differences among sampled populations ('overparameterised models' in Tabachnick and Fidell, 2001). Overparameterisation may be first noticed in multivariate data analyses when an unexpectedly high degree of discrimination among populations is obtained. This overparameterisation seems to disappear when individuals are crossvalidated (Lachenbruch and Mickey, 1968). However, in spite of the more plausible result after crossvalidation, Tabachnick and Fidell (2001) believe there may still be a lack of power. In other words, the number of individuals that are crossvalidated to their true source may not have improved. To avoid this, Tabachnick and Fidell (2001) recommend that the sample size of the smallest test group should 'notably' exceed the number of predictor variables. This is one reason why OC groups rather than individual OCs were used in these analyses.

Predictor variables can also be chosen to optimise discrimination among populations. Although 'stepwise selection' techniques can be informative for exploratory work, chosen predictor variables may describe differences that do not reflect true population differences (Tabachnick and Fidell, 2001). If there are many predictor variables, and particularly if experimental errors are associated with them, stepwise selection methods will find a combination of predictors that discriminate populations 'too' well.

With respect to molecular genetics studies similar problems can occur if AMOVA (Analysis of Molecular Variance; Excoffier *et al.*, 1992) and other common techniques for genetic analyses are used to analyse many loci, especially if some are 'meaningless'. Allele frequencies may have been used in an appropriate canonical CDA for the joint study with a nested structure for alleles within loci; however, this would have added 16 more predictor variables (loci) to the analysis.

For the genetics study, we chose to use assignment probabilities as summary statistics and predictor variables for the Joint CDA. One of the most important considerations in using assignments is that they are responsive to rare and uncommon alleles. We substituted 0.5 for all '0' allele frequencies within populations before assigning individuals, as suggested by Waser and Strobeck (1998). If this substituted frequency is set to '0' or a smaller value, then more or all individuals with unique or rare alleles cannot be assigned, or are assigned to their source hunting population because of the unique allele. If this value is higher, then more individuals would be assigned to populations with common alleles. The analysis is thus also dependenet of sample size, since a rare allele will have a higher frequency in a small population than in a large one. Thus different choices in the assignment methods would have yielded slightly different assignments in the genetics study, and this would have been passed into the larger analysis.

In conclusion, other summary statistics for component studies and therefore predictor variables for the joint study could have been chosen. The balance between choosing a predictor variable that might discriminate 'too' well due to chance and predictor variables that blur results because they are meaningless must be considered.

Assignment probabilities are one method of scoring or describing individuals. However, actual assignments cannot be considered to represent degrees of mixing. All 'assignment' methods, based on genetics or OC data, do not take into account that: (1) different distinct stocks should be at Hardy-Weinberg (breeding) equilibrium, thus some genotypes in each stock will resemble individuals in another stock more than in their own; and (2) if there are normal distributions of OC concentrations within each stock, then some individuals in each stock will resemble individuals in another stock more than in their own. Because of this, some individuals will be assigned to hunting sources other than the source community. Future methods, in genetics studies, OC studies, and combined studies, should concentrate on separating overlapping similarity distributions.

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ABSTRACT

Current plans to utilise German offshore waters as sites for windmill parks as well as ongoing investigation of potential areas to implement Natura 2000 have led to an increased research effort on local marine mammal populations. The aim of this study was to determine the spatial distribution of harbour porpoises in the German part of the North Sea and Baltic Sea. Aerial surveys were conducted from May to August 2002 using standard line-transect methodology. A total of 21 days of aerial surveying covered 8,072km tracks on effort; 4,908km were conducted in conditions of good visibility. A total of 785 harbour porpoises (488 sightings) were seen; 597 animals (427 sightings) were detected in conditions of good visibility. The study area was divided into a grid of 3 minute latitude by 6 minute longitude squares. Porpoise relative abundance and distribution were estimated as the number of animals per km on effort in each square. The results showed that in the North Sea, the highest number of porpoises per km was observed in the northeastern part of the surveyed area, close to the Danish border and in the area of Amrum Outerbank. In the Baltic Sea, the highest relative abundance of porpoises was seen in the Pomeranian Bight between the island of Rügen and the Polish border. Pod size in the Baltic was larger than in the North Sea. The aerial surveys were continued in 2003 in order to collect more information on temporal and spatial distribution of harbour porpoise and its intra and inter-annual variability in German waters. These data will serve as a baseline for management decisions.

KEYWORDS: HARBOUR PORPOISE; DISTRIBUTION; SURVEY-AERIAL; INDEX OF ABUNDANCE; CONSERVATION; BALTIC SEA; NORTH SEA

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is protected by a variety of national and international agreements. This includes Appendix II of the Convention on Migratory Species (CMS; www.cms.int), the Habitat Directive of the Commission (www.europa.eu.int/comm/ European environment/nature) as well as the Red List of Endangered Species (www.redlist.org) of Germany, which is currently under revision.

A focus of recent attention has been the endangered status of harbour porpoises and the management of marine mammals in general in the German part of the North Sea and Baltic Sea. This has been fuelled by the necessity to propose areas of offshore German waters, which need to be incorporated into Natura 2000 (www.europa.eu.int/comm/ environment/nature). Potential sites for windmill parks off the German coast and plans for the establishment of the first park ('Butendiek') have recently been accepted by the German government. The ongoing search for additional sites and future construction campaigns may interfere with marine mammals and risk habitat degradation.

Few data exist on the distribution of harbour porpoises in German waters. Current information for the German North and Baltic Seas is mostly based on results of the SCANS survey of 1994 (Hammond et al., 2002). However, the coverage during SCANS left out some areas of the German EEZ (exclusive economic zone), such as the region east of the island of Rügen close to the Polish border in the Baltic, and some parts of the Eastern Friesian Islands between the estuary of the river Elbe and the Dutch border in the North Sea. However, strandings data submitted to the IWC on an annual basis since 1990 suggest that harbour porpoises regularly occur in these areas, albeit in small numbers (e.g. see www.iwcoffice.org/commission/sci_com/scprogress. htm). Heide-Jørgensen et al. (1993) and Sonntag et al. (1999) surveyed some parts of the German North and Baltic Seas, but the areas were too small to draw conclusions about the general distribution of porpoises. In this paper results of aerial surveys conducted from May to August 2002 in all German waters are presented.

MATERIALS AND METHODS

Study area

The study area included the German EEZ in the North Sea and the Baltic Sea, as well as the 12 n.mile zone in front of the coastline (Fig. 1). The area was extended into Danish waters in the Baltic and the Danish Isles were chosen as a northern boundary of the study area (Fig. 1). The study area in the North Sea was divided into four different regions (A to D). The Baltic was separated into three blocks (E to G). Regions were separated according to differences in bathymetry and maximum endurance of the survey plane. One region (block) was typically surveyed within one day (between 3 to 9 flying hours). Consideration was also given to the putative stock boundary at the Darss and Limhamn Ridges, separating the central Baltic stock from the Kattegat-Belt Sea-Western Baltic stock (Koschinski, 2002).

Survey design and data acquisition

The surveys were conducted from May to August 2002 following standard line-transect methodology for aerial surveys (Hiby and Hammond, 1989; Buckland et al., 1993). A total of 8,190km of tracklines were conducted on effort following a parallel track design for a high-winged twinengine aircraft (Partenavia) flying at an altitude of 182m (600ft) and a speed of 167-186km/hr (90-100kts). The direction of tracks was north-south in areas D-G, and eastwest in areas A-C to follow gradients of depth (Fig. 1). Some smaller regions within the blocks A, C and D in the North Sea as well as F and G in the Baltic received a higher

Summer distribution of harbour porpoise (*Phocoena phocoena*)

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Fig. 1. Study areas and transect lines of the aerial surveys in the Baltic and the North Sea. The dashed line in the Baltic indicates the German EEZ (Exclusive Economic Zone). The main islands are marked as: S-Sylt, F-Fehmarn and R-Rügen.

survey effort. These regions are likely to host windmill parks in the future or are potential or designated Natura 2000 areas.

Data collection was based on the VOR software designed by Lex Hiby and Phil Lovell and described in Hammond et al. (1995). Every four seconds, the aircraft position was recorded automatically onto a laptop computer connected to a GPS. Additionally, the position was stored whenever a sighting was made. Sea state (Beaufort scale), glare, observer positions, turbidity (judged visually: 0 = clearwater with several meters of visibility to 2 = very turbid water with no visibility under the surface) and cloud cover (parts of eight) were entered at the beginning of each transect and whenever environmental conditions changed. Additionally the observers used all above parameters to subjectively decide on the sightability of a harbour porpoise. The scale for these 'subjective' conditions ranged from G for good, over M for moderate, P for poor and X for conditions too bad to survey. All observers on board discussed the visibility during each flight and agreed on one condition. The observer team (consisting of six observers) did not change over the study period, and therefore the resulting conditions can be considered consistent for this team of observers. Sightings data were acquired by two observers located at each bubble window of the aircraft. These windows enabled the observers to look straight down onto the survey track. Data were entered into the computer by the recorder located in the co-pilot's position. Sightings data included species, group size, presence of calves, behaviour, swimming direction, cue, reaction to the survey plane, position (at surface or under water) and clinometer angle measured from the aircraft to the porpoise group when it passed abeam of the aircraft.

Data analysis

Data collected from sightings were summarised every four seconds, which corresponds to a distance flown of about 200m. For each of these four second intervals the exact distance flown was determined. Using the number of animals seen, the relative density of animals per km survey was calculated for each interval.

Only data obtained in conditions considered 'good' by the observers were used for the distribution analysis. This category did not include sightings obtained in sea state of more than 2 or turbidity of more than 1. Observations collected in the region of the 'Entenschnabel' (furthest out in the North Sea, see Fig. 1) have not been included. Conditions encountered in this region were only moderate during the one flight conducted there.

Geographic cells, measuring 3 minutes latitude by 6 minutes longitude, were defined throughout the study area in order to obtain information on distribution and relative abundance of harbour porpoises. This was computed as sighting rates (animals/km) for each cell. The data were analysed using GIS software (ArcView). Empty cells were those cells where no effort (under good conditions) was conducted. All maps are shown in UTM (Universal Transverse Mercator).

RESULTS

Survey effort

Environmental conditions varied between survey days and sometimes during a single flight. Table 1 shows the survey effort covered under different environmental conditions, sea state and turbidity.

Table 1 Environmental conditions during aerial surveys from May to August 2002.

Conditions	% Effort	Sea state	% Effort	Turbidity	% Effort
Good Moderate Poor	23.9 36.6 39.5	0 1 2 3	9.4 38.0 34.3 17.4	0 1 2 3	19.0 67.3 13.5 0.2
		4	0.9		

Regions A and E received substantially less coverage in terms of survey effort than planned (Table 2). Region A (Entenschnabel) was only covered once during moderate conditions. Region E (Kiel Bight) could not be covered to the extent intended due to military activities in that area during weekdays.

Sighting rates in good conditions were always higher than in the data collected in moderate and poor conditions. This difference was significant when comparing all regions (Mann-Whitney U-Test, p<0.05, two-tailed). An example from region F demonstrates how dependable sighting rates were on weather conditions where a substantially increased effort (1,030km versus 572km) under less favourable sighting conditions only led to an increase in sighting rate from 0.002 to 0.017 (Table 2). When comparing animals per km from regions A through G in good conditions versus moderate and poor conditions the difference was not significant.

Pod size was consistently larger when comparing sightings data obtained under moderate and poor conditions than pod sizes obtained from sightings data made only in good conditions (Table 2). When testing this difference (U-Test, two-tailed) the resulting p value is less than 0.1. Maximum pod size of porpoises in the North Sea and Baltic Sea was 5 and 10 respectively. Mean pod size was 1.30 in the North Sea and 2.16 in the Baltic under good conditions (Table 2). In the North Sea, almost 78% of the sightings were of individual porpoises compared to only 57% in the Baltic (Fig. 2).

Fig. 3 shows all the tracklines flown on effort during the aerial survey in the German North Sea as well as the number of sighted porpoises and their pod sizes. A higher number of tracks was flown in areas C and D (Fig. 3).

Fig. 4 shows all the tracklines flown in the Baltic and the sightings of harbour porpoises. In the Baltic a larger number of tracks was flown around the island of Fehmarn (Area F) and in the Kadet fairway (Area F) as well as in the area Rügen/Pomeranian Bight (Area G). Larger pod sizes of up to 10 animals were only seen in the eastern part of the Baltic. This area includes the Oderbank, a shallow bank (about 8m deep) in the centre of the Pomeranian Bight (Fig. 4).

The study area was separated into 3 minute latitude by 6 minute longitude grids (about 3 n.miles \times 3.5 n.miles). For each cell the number of porpoises per km survey effort collected in good visibility was calculated. A dash indicates those cells in which no sightings were made. No dash or circle shows that no survey effort in good conditions was made in that part of the area (Figs 5 and 6). In the North Sea, the highest number of animals per km was seen in Area C. In the Baltic, the highest encounter rate was in Area G, east of the island of Rügen.



North Sea DBaltic Sea



DISCUSSION

Survey methodology

The sightability of cetaceans during surveys is influenced directly by environmental parameters (Buckland *et al.*, 1993). During shipboard surveys, an increase in Beaufort Sea state conditions led to a decrease in sighting rates of harbour porpoises (e.g. Palka, 1996; Teilmann, 2003). Similarly, during aerial surveys for white whales (*Delphinapterus leucas*), deMaster *et al.* (2000) showed that an increase in sea state also led to a reduction in the sighting rate. When surveying from a plane, animals are also sighted in the water column and therefore the sea state as well as the turbidity of the water affects the number of porpoises detected. Gunnlaugsson *et al.* (1988) also found an apparent relationship for sightings rate of harbour porpoises from

Table 2

Survey effort, sighting rates (animals and sightings per km) and group sizes in the North Sea and the Baltic study area (May to August 2002). Data are provided for total survey effort, survey effort in moderate (M) and poor (P) conditions and for survey effort in good (G) conditions only.

		North	Sea surv	ey regio	ns		Baltic S	ea survey	regions	
	A	В	С	D	All North Sea regions	Е	F	G	All Baltic regions	Summary total survey
Area size (km ²)	3,903	11,650	13,668	11,824	41,045	4,696	7,248	10,990	22,934	63,979
Effort km all conditions	144	647	2,991	1,804	5,586	382	1,030	1,075	2,486	8,073
Sightings per km all conditions	0.014	0.045	0.124	0.018	0.078	0.013	0.011	0.034	0.021	0.061
Mean group size all conditions	2.50	1.28	1.46	2.61	1.54	1.80	1.27	2.49	2.17	1.61
No. of animals per km all conditions	0.035	0.057	0.181	0.048	0.12	0.024	0.014	0.086	0.046	0.097
Effort kilometre in M and P	144	275	1,190	672	2,281	-	458	426	883	3,165
Sightings per km in M and P	0.014	0.004	0.040	0.012	0.026	-	0.002	0.002	0.002	0.019
Mean group size in M and P	2.50	3.00	2.75	5.38	3.10	-	1	4	2.5	3.08
No. of animals per km in $M + P$	0.035	0.011	0.111	0.064	0.080	-	0.002	0.009	0.006	0.059
Effort km in G	-	372	1,801	1,132	3,305	382	572	649	1,603	4,908
Sightings per km in G	-	0.075	0.179	0.022	0.114	0.013	0.017	0.055	0.032	0.087
Mean group size in G	-	1.21	1.27	1.72	1.30	1.80	1.30	2.44	2.16	1.40
No. of animals per km in G	-	0.091	0.228	0.038	0.147	0.024	0.023	0.136	0.069	0.122



Fig. 3. All tracklines flown on effort from May to August 2002 in the German North Sea and number of porpoises in each sighting.



Fig. 4. All tracklines flown from May to August 2002 in the Baltic and number of porpoises in each sighting.

aerial surveys with cloud cover. When using line-transect distance sampling, the effective strip width changes with environmental conditions and therefore densities can be calculated even if conditions change from good to moderate. However, when using sighting rate, the comparison between detection rates observed during different environmental conditions can lead to misinterpretation of the observed patterns of distribution. Data in this paper reiterated that the



Fig. 5. Distribution of harbour porpoises in the German part of the North Sea (May to August 2002). Each circle or dash represents a cell of 3' latitude by 6' longitude (3 n.miles \times 3.5 n.miles). For each cell the number of porpoises per km survey is shown. Only data obtained in good survey conditions are shown.



Fig. 6. Distribution of harbour porpoises in the Baltic Sea study area (May to August 2002). Each circle or dash represents a cell of 3' latitude by 6' longitude. For each cell the number of porpoises per km survey are shown. Only data obtained in good survey conditions is shown.

sighting rate, both for animals per km and sightings per km, decreased noticeably when all flights on effort (including those under deteriorating weather conditions) were included in the analysis. Mean pod size also increased when all flights were taken into consideration. This indicates that the probability of seeing single animals or small groups decreases with deteriorating weather conditions compared to larger groups. Due to the difficulty in sighting porpoises when the water is very turbid, certain areas (such as the river estuaries of Elbe and Weser) will probably always have worse sighting conditions than others. When surveys are conducted, e.g. for environmental impact studies, it is crucial that sighting conditions are described in detail. This is especially true if the data are compared to other studies conducted on the same or other temporal and/or spatial scales. In the following discussion only the results from the surveys conducted in good conditions are used.

North Sea

Highest aggregations of harbour porpoises were observed in the northern part of the German EEZ and close to the Danish border (Area C). This area also includes the German cetacean sanctuary off the island of Sylt. In the remainder of the study area harbour porpoises were more evenly distributed and no particular aggregations were found. The sighting rates of 0.18 sightings per km in Area C were substantially higher than those obtained during two preceding surveys in the same region in 1992 (0.06 sightings per km; Heide-Jørgensen et al., 1993) and 1994 (0.05 and 0.04 sightings per km; Hammond et al., 2002) using the same aircraft type and methodology. The higher sighting rate here can in part be due to the fact that the survey covered several months. May is the beginning of the mating and breeding season when harbour porpoises might be more gregarious than at other times of the year (Read and Hohn, 1995). It is also possible that these aggregations were caused by food availability. Swarm fish, such as herring or sprat, might have been present in the area. Other potential prey species were sand eels (Ammodytes marinus), which often burrow in the seabed from October to early April and are important to many marine predators (Wright and Begg, 1997). During April and May they emerge from the seabed to feed in the water column (Evans, 1990). At this time they aggregate in the water column and are available to predators. Analyses of stomach contents of porpoises from the German North Sea (1992/1993) showed that 37% of the fish found in the stomachs (by weight) were sand eel. Dab (Limanda limanda) and common sole (Solea vulgaris) made up 38%, and whiting (Merlangius merlangus) and cod (Gadus morhua) 15.1% of prey (Benke et al., 1998). If aggregations of harbour porpoises occur due to prey concentrating in certain areas, they would most likely occur in spring. Similarly, if aggregations occur due to reproductive behaviour we would expect to observe this in May and June when calving and mating occur (Read, 1990; Sørensen and Kinze, 1994). However, most previous aerial and ship surveys in this area took place in July and August and therefore might have observed a more even distribution over a large area.

Mean group sizes of 1.27 porpoises in Area C and 1.72 in Area D were comparable to those found during the SCANS survey with a mean pod size of 1.45 in area Y and 1.62 in area L (Hammond *et al.*, 2002). Heide-Jørgensen *et al.* (1993) surveyed only a small part of Area C directly off the island of Sylt in 1992 and found a lower mean group size of 1.03 porpoises. Again, seasonal changes in behaviour during the spring and summer months might be responsible for changing group sizes but little is known about temporal changes of group sizes in the North Sea.

Baltic Sea

In the Baltic Sea, harbour porpoises were only seen in Kiel Bight, around the island of Fehmarn (Fig. 4) and east of Rügen. Sighting rates in the Baltic were lowest in the two western areas: the Kiel and Mecklenburg Bight (E and F), with 0.013 and 0.017 sightings per km survey effort. During the SCANS survey the sighting rate in area X (south of the

islands of Fyn and Lolland, covering the Area E from this study) was 0.008 sightings per km (Hammond *et al.*, 2002) and during the survey flights conducted by Heide-Jørgensen *et al.* (1993) 0.004 sightings per km were recorded. For the Kiel and Mecklenburg Bight the mean group size was 1.8 and 1.3 animals respectively. Comparable values of 1.5 were found during the SCANS survey (Hammond *et al.*, 2002). Heide-Jørgensen *et al.* (1993) recorded a lower mean group size of 1.13 porpoises in 1992.

An unexpected observation was made during flights between the island of Rügen and the Polish border (Area G, Fig. 1) in May and July 2002. The highest sighting rates for the Baltic Sea, highest maximum pod size (10 porpoises) and the highest number of porpoises per sampling unit (4 seconds survey) for both the Baltic and North Sea were found in this area (Fig. 6). However, the subsequent flights in August, September and December 2002 in the same area did not locate a single porpoise. This demonstrated a dramatic change in seasonal density of porpoises between the island of Rügen and the Polish border.

The population east of the Darss and Limhamn Ridges is considered a different population from the rest of the Baltic/Belt Sea (Tiedemann et al., 1996; Börjesson and Berggren, 1997; Huggenberger et al., 2002). Both ASCOBANS and the IWC have underlined the precarious situation of this stock (IWC, 2003). With the exception of our observations during flights in May and August, sighting rates are extremely low. Two cruises of the IFAW sailing boat Song of the Whale between Darss ridge and the Bay of Gdansk in Poland in July/August 2001 and 2002 have revealed only single sightings or acoustic detections in the area (Gillespie et al., 2003). In 1995 the stock was estimated to be 599 animals (CV=0.57). Recent observations in Puck Bay (inner Bay of Gdansk) found very few animals (Berggren, pers. comm.). Bycatches of harbour porpoises in Puck Bay are on average 2.2 a year (a total of 22 animals from 1990-1999) and occur mostly in the winter months (Kuklik and Skóra, 2003).

The most likely explanation for the observed aggregation of porpoises in the Pomeranian Bight in May and July (2002) seems to be the availability of food. Large aggregations of up to several hundred harbour porpoises have been observed in other areas of the world, probably related to good feeding grounds (Rae, 1965). If prey is only available for a short period of time, as are for example spawning shoals of herring or sprat, these aggregations might be difficult to encounter using widely spaced transects. In addition, the aggregations were on the Oderbank, an area east of the island of Rügen on the border between Poland and Germany. It is characterised by shallow waters of around 8m depth. Most ship surveys avoid such shallow areas. The Swedish aerial surveys from 2002 included the area east of Rügen but were conducted in July and August, therefore possibly missing an event that only lasted a few months. Another scenario is that porpoises from the Belt Sea followed their prey into the area of the Pomeranian Bight. The presence of swarm fish such as herring could also explain the relatively large group sizes. In contrast to the German North Sea, herring are available in the Baltic year-round. Stomach analyses of harbour porpoises from the German coast of the Baltic showed that 22.8% of the fish found (by weight) was herring, 52.7% goby (Pomatoschistus spec.) and 14.8% cod (Benke et al., 1998). However, these results should be viewed with some caution because they were integrated over whole years and areas and may therefore mask seasonal and geographical variation in the diet.

The aerial surveys in German waters over the course of the 2002 summer yielded new information on distribution of porpoises that was in some ways unexpected. The main results were large aggregations and high densities of porpoises found in Area C in the North Sea and in Area G in the Baltic Sea. Information on abundance, distribution and stock identity at a greater scale are necessary to put the observations from this study into a broader management context.

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Stranding patterns of harbour porpoises (*Phocoena phocoena*) in the German North and Baltic Seas: when does the birth period occur?

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ABSTRACT

Stranded harbour porpoises were analysed to investigate differences in stranding patterns along the North and Baltic Sea coasts of Schleswig-Holstein, Germany. A total of 1,015 stranded or bycaught harbour porpoises were recorded between 1990-2000. Most of the stranded animals were found during the summer months: in the North Sea, the peak occurred in the months of June and July, whereas in the Baltic most of the porpoises were found in July and August. Strandings of mature females (>3.9 years) and young animals (<1 year) were positively correlated during the summer months. No significant correlation between mature males and young porpoises nor between mature males and females was observed. By using a non-parametric procedure, a birth period for the North Sea population between 6 June and 16 July was calculated, with 27 June as the mean date of birth. In the Kiel Bight population, births were assumed to take place one month later than in the North Sea.

KEYWORDS: HARBOUR PORPOISE; STRANDINGS; REPRODUCTION; EUROPE; INCIDENTAL CATCHES; PARTURITION; AGE AT SEXUAL MATURITY

INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is the cetacean found stranded most on German coasts as well as those of England, The Netherlands and Denmark (Kinze, 1990b; Hammond *et al.*, 1995; Benke *et al.*, 1998; Addink and Smeenk, 1999). Sometimes called the common porpoise, it is a small cetacean species inhabiting coastal waters of the Northern Hemisphere (Nowak, 1991; Jefferson *et al.*, 1993).

In the 1995 review of North Atlantic harbour porpoises (Donovan and Bjørge, 1995) by the IWC Scientific Committee, in the absence of firm biological data the boundaries of the North and Baltic Seas were defined by geographical divisions. In the Baltic Sea, the Darss and the Limhamn underwater ridges were defined as the boundaries between the Baltic and the inner Danish and German waters. The North Sea coasts of Denmark, Germany and The Netherlands were divided into three 'stock' areas derived largely from the 1994 SCANS (Small Cetacean Abundance in the North Sea) surveys (Hammond et al., 1995). In the German North Sea and Western Baltic waters, a further subdivision into local populations has been suggested by Tiedemann et al. (1996), who carried out DNA analysis of porpoises from the coasts of Schleswig-Holstein. They found that the Baltic Sea was inhabited by harbour porpoises several thousand years ago and that genetic exchange has been very limited between the two Seas. Thus, the animals of the North and Baltic Seas of Schleswig-Holstein can be considered as two different sub-populations.

The life history and reproductive cycle of harbour porpoises is relatively poorly understood. Generally, only rough estimates have been made to determine a birth (calving) period for harbour porpoises in the North (June-August) and Baltic (July/August) Seas (Fisher and Harrison, 1970; Kinze, 1990b; Lockyer, 1999; Lockyer and Kinze, 1999), although see Sørensen and Kinze (1994). In the present paper, German strandings data collected over 11 years have been analysed to investigate whether distinct stranding patterns exist and whether it is possible to calculate the birth periods of the local harbour porpoise populations in the North and Baltic Seas.

METHODS

In the North Sea, the sampling area included the mainland coast from the Danish border down to the Elbe River estuary, as well as all the islands in the Wadden Sea of Schleswig-Holstein. The area of the Baltic Sea referred to in this paper includes the mainland coast from the Danish border in the north down to Mecklenburg-Western Pomerania, as well as the island of Fehmarn (Fig. 1).



Fig. 1. Map of the study area: Federal State of Schleswig-Holstein, Germany.

Since 1990, the Federal State of Schleswig-Holstein and the Federal Ministries of Environment, Research and Technology, Germany, have financed a strandings network

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in order to perform research on stranded cetaceans along the coasts of the North and Baltic Seas. In addition to opportunistic reports, seal hunters, rangers and employees of environmental conservation authorities have patrolled the beaches and sandbanks regularly throughout the year since the last seal epidemic, to either take in the stranded animals or to give notice about a live stranding. Therefore, relatively constant observer effort can be assumed.

This paper considers data from 1990-2000, during which time 1,015 porpoises were recorded as either stranded or bycaught. In total, 106 bycatches were recorded, 20 caught in the North Sea and 86 in the Baltic. Some of the Baltic bycatches were reported directly by fishermen and some from post-mortem examination. For the North Sea, bycatches were only identified during dissection. Animals were classified by decomposition state and a total of 282 animals (147 >1 year and 135 <1 year) considered in states of either advanced decomposition or mummification, or of unknown state, were discarded from this study. An exception was made for animals >2 years where sex and the approximate age could be determined. Two females of unknown origin were also not included.

Before dissection, most animals were temporarily stored in a container at -20° C. Dissections were performed according to the procedures described in Siebert *et al.* (2001). From 1990-1993, age determination was performed by H. Kremer (Kremer, 1987). From 1994, age was determined by C. Lockyer by examining the zonation and Growth Layer Groups (GLGs) of the teeth as described in Lockyer (1995). Only a limited number of animals were aged for the period 1999-2000 and these years have thus been excluded from the study.

Four age categories of harbour porpoises were distinguished:

- Neonates: based on the lengths of the largest foetus (81.5cm) and smallest born animal (64.5cm). All porpoises between these values were considered neonates.
- (2) Calves: animals which were calculated to be younger than 1 year and larger than 85cm.
- (3) Juveniles: animals which were older than 1 year but not yet mature.
- (4) Sexually mature: animals older than 3.9 years.

Bandomir *et al.* (1998) reported that in the German North Sea, female porpoises become sexually mature at a mean age of 4.58 years and males between 2 and 5 years. For Danish waters, Sørensen and Kinze (1994) reported average ages of sexual maturity for females to be 3.64 years and for males 2.93 years. It is not appropriate to review the nature of those studies here but for the purposes of the present paper, sexual maturity has been assumed to be four years.

The data were analysed to determine whether there was any significant difference between the numbers of strandings of male and female harbour porpoises and to investigate potential correlations between the numbers of stranded animals <1 year old and sexually mature females and males.

From the dates the animals were located (not necessarily the date of death) and lengths of stranded harbour porpoises <1 year from the North Sea, a non-parametric approach was used to estimate the birth period. Neonates from the North Sea population were classified into 1cm length categories, ranging from 65-85cm. The 'mean' date of birth around which to estimate the birth period was taken as the most frequent median date for each (cumulative) length class (e.g. see Table 1).

In order to estimate the birth period, a number of assumptions are made: (1) it follows a normal distribution; (2) neonates are found shortly after birth; (3) the sample of stranded/bycaught animals is representative of the whole population.

Given these assumptions, the complete sample (260 neonates and calves) was compared with the 'mean' date of birth (animals found on the 'mean' date were divided equally amongst those found before and after the 'mean' date) to estimate an approximate mean deviation. This value was used to estimate the standard deviation (SD) of the birth dates; 95.4% of the values of a normally distributed variable lie within ± 2 SD of the mean (e.g. Lorentz, 1996). Sample size considerations (only 33 calves) precluded use of this method for the Baltic Sea.

A Pearson-Correlation-Matrix (see Zar, 1999) was used to examine whether a correlation between the number of sexually mature females or males (\geq 4 years; Bandomir *et al.*, 1998) and young animals (<1 year) exists during the summer months (June, July, August). Due to lack of data from the Baltic Sea and from the years 1999 and 2000 for both areas, only the North Sea data for the period 1990-1998 were examined.

RESULTS

The annual number of harbour porpoises found along the North and Baltic Seas of Schleswig-Holstein was about 100 with considerable annual variation (mean=98.5; SD=24). The numbers show no trend with time over the study period (Fig. 2), for the North Sea (r_s =0.326, p=0.301) or for the Western Baltic (r_s =0.380, p=0.224; Spearman rank correlation). There was also no significant difference in the sexes of the stranded animals (t=-0.474, p=0.645 for the North Sea; t=-0.080, p=0.938 for the Baltic; t-test for paired samples).

Although porpoises are found stranded year-round, most animals are found during the summer months. In the North Sea, the highest numbers are found in June, July and August



Fig. 2. Stranded and bycaught harbour porpoises along the coasts of the North (N) and Baltic (B) Seas of Schleswig-Holstein differentiated by sea and sex (1990-2000; m = male, f = female).

(Fig. 3), whereas in the Baltic the peak is about 1 month later, i.e. July, August and September (Fig. 4). In June and July, the strandings were dominated by young harbour porpoises (<1 year) in the North Sea (Fig. 3); in the Baltic most of the young animals were found in August (Fig. 4).

Table 1 shows the length classes for North Sea animals <1 year, the cumulative numbers and the median 'finding' date. As one might expect, as the length of animals increased, the median date generally became later. However, for the 70 neonates found in the length classes from 72-78cm, the median date was the same, 27 June (Fig. 5). The 'mean' date of birth for North Sea animals was thus assumed to be 27 June. The SD of the birth dates was about 40 days (or 5.7 weeks) around 27 June. Thus from our data, it is estimated that 95.4% of the births in the North Sea occur between 6 June and 16 July.

Using the data in Table 2 the Pearson-Correlation analysis (Table 3) revealed a significant correlation between the strandings of sexually mature females and animals <1 year (r=0.686) in the summer months (June, July, August in the North Sea). However, there was no correlation between males and young animals (r=0.145), or between adult males and females (r=0.238). Mature males stranded along the North Sea coast show a slight peak in August but are in general equally distributed over the year. Mature females however display a distinct peak in the summer months.

DISCUSSION

There are a number of possible explanations for the varying annual numbers of harbour porpoises found from 1990 to 2000 (Fig. 2) given the relatively constant effort. As is



Fig. 3. Total number of stranded harbour porpoises and animals <1 year from the North Sea coast of Schleswig-Holstein (1990-2000).



Fig. 4. Total number of stranded harbour porpoises and animals <1 year from the Baltic Sea coast of Schleswig-Holstein (1990-2000).

Table 1

Cumulative number of harbour porpoises (<1 year) of the different length classes and the respective median location date from the North Sea (1990-1998). The bold figures emphasise the most frequent median date and the respective length classes and number of animals found.

Length classes (cm)	Cumulative number	Median location date
65	10	26 June
66	15	25 June
67	22	26 June
68	30	26 June
69	36	27 June
70	41	25 June
71	49	25 June
72	57	27 June
73	73	27 June
74	81	27 June
75	93	27 June
76	104	27 June
77	111	27 June
78	127	27 June
79	138	28 June
80	146	28 June
81	151	30 June
82	154	30 June
83	161	01 July
84	168	01 July
85	177	02 July



Fig. 5. Median of the location dates of young harbour porpoises (<1 year) for the different length classes of the Schleswig-Holstein North Sea coast (1990-1998). The lighter dots emphasise the most frequent median location date for each length class.

Table 2
Number of animals (<1 year), sexually mature females and males
(>3.9 years) found in the summer months (June, July, August)
from the North Sea (1990-1998)

Year	Number of animals of <1 year	Mature females	Mature males
1990	6	7	3
1991	11	7	13
1992	24	6	6
1993	50	12	4
1994	40	7	6
1995	28	10	5
1996	30	7	6
1997	14	3	2
1998	46	10	12

Table 3

Pearson-Correlation-Matrix of animals (<1 year), sexually mature females and males (>3.9 years) found in the summer months (June, July, August) from the North Sea (1990-1998).

Female 1.000 <1 year 0.686 1.000 Male 0.238 0.145 1.000		Female (>3.9 y)	<1 year	Male (>3.9 y)
	Female <1 year Male	1.000 0.686 0.238	1.000 0.145	1.000

always the case with strandings data, it is not easy to ascertain whether the data are representative of the true population(s). One explanation of course is that they reflect actual changes in mortality by year while another is that they reflect varying weather and water conditions (see Polacheck et al., 1995). The truth is probably some combination of these. In 1998, for example, a total of 158 strandings were reported (146 on the North Sea coasts and 12 in the Baltic). In the summer of that year, landward westerly winds prevailed on the North Sea coast of Schleswig-Holstein, which would have increased the likelihood of dead animals being washed ashore. In 1997 however, only 53 strandings were reported. The temperatures that summer were mostly warm, with easterly winds predominating. The high water temperature would have accelerated the decomposition of the animals and, in addition, the easterly wind would have kept the carcasses off the shore.

Most of the animals died in the summer months (Figs 3 and 4) i.e. during the birth period. A correlation between the strandings of sexually mature females (>3.9 years) and young harbour porpoises (<1 year) during the summer was found. There is no reported geographical segregation by sex for porpoises in the North Sea but there are few data to deny or confirm this. Recent aerial surveys have sighted mothercalf pairs as far out as the 'Doggerbank' halfway between Germany and England (M. Scheidat, pers. comm.). This, alongside the fact that there is no equivalent peak in mature males, infers that the period around parturition may pose an increased risk for the mother as well as the calf. However, of the 53 sexually mature females from the North Sea found during the summer and dissected, some 32% were either lactating, pregnant or both. This contrasts with pregnancy rates of over 0.85 found for other areas in the western North Atlantic (e.g. see Polacheck et al., 1995; Read and Hohn, 1995) but is similar to those found off California (Hohn and Brownell, 1990). Other studies of (marine) mammals have shown that the mortality rate of adult females is highest during the birth period and (for both sexes) within the first vear of life (e.g. Caughley, 1966; Siler, 1979).

By contrast to the North Sea, on the northeast coast of the USA, more harbour porpoises are found stranded during the winter months than during the summer (Polacheck *et al.*, 1995). The different findings between the east coast of the USA and Schleswig-Holstein may reflect different weather conditions, currents and/or, most likely population structure and migration.

At present, there is no clear picture of the population structure and movements of North Sea harbour porpoises. Further genetic analyses are required to clarify population structure, including obtaining sufficient samples from Danish, Dutch, British and German North Sea waters (R. Tiedemann, pers. comm.). There are suggestions of seasonal offshore/inshore movements of harbour porpoises in a number of areas (e.g. Evans, 1990; Kinze, 1990a; Verwey, 1975) as well as migrations, including differential migrations by sex (Teilmann *et al.*, 2004). A better understanding of these aspects of harbour porpoise ecology in the region is required to fully understand the strandings data and how representative they are of the total population(s).

The findings in this paper represent the first comprehensive attempt to examine the birth period for harbour porpoises apart from the study of Sørensen and Kinze (1994) who calculated a mean birth date for harbour porpoises in Danish waters as 30 June, a little later than our estimate of 27 June. However, their data may have included animals from more than one population as it included animals from the Baltic, the Belt, Kattegat/Skagerrak and the North Seas. The importance of only considering samples from a single population is illustrated by the fact that birth periods and birth rates of harbour porpoises may vary considerably by population and over time (e.g. see Read and Hohn, 1995; Hohn and Brownell, 1990). In our area, for example, Tiedemann et al. (1996) regard the harbour porpoises in the German North and Baltic Seas as different (sub-) populations, based on DNA analysis.

The results of this work emphasise the continuing need for collection of biological data and the value of data from strandings in order to analyse the status of harbour porpoise populations (including for example to examine further the suggestion that there may possibly have been a recent decline in fertility).

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A note on site fidelity of marine tucuxis (*Sotalia fluviatilis*) in Guanabara Bay, southeastern Brazil

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ABSTRACT

Since 1995, photo-identification techniques have been used to study the marine tucuxis (*Sotalia fluviatilis*) found in Guanabara Bay (22°50'S, 43°10'W), southeastern Brazil. The bay is surrounded by a metropolitan complex and is the most degraded area of this species' distribution. From May 1995 to June 2003, 47 photo-identification boat surveys were conducted in the bay. Sixty-nine individuals were identified and catalogued. The results indicate that individual tucuxis have high site fidelity in Guanabara Bay. On average, dolphins were seen for 4.5 consecutive years, with a range of 1 to 8 years. Additionally, calves have remained in the area beyond sexual maturity. Guanabara Bay provides food and breeding grounds for this dolphin population, despite its high degree of degradation. The fact that such a small dolphin population, composed of resident individuals, depends on such a degraded area may pose serious problems for its conservation.

KEYWORDS: TUCUXI; SITE FIDELITY; PHOTO-ID; SOUTH AMERICA; SOUTH ATLANTIC; SURVEY-VESSEL

INTRODUCTION

The marine tucuxi (*Sotalia fluviatilis*) occurs exclusively in the western Atlantic coastal waters of South and Central America, from southern Brazil ($27^{\circ}35$ 'S, $48^{\circ}34$ 'W) to Nicaragua ($14^{\circ}35$ 'N, $83^{\circ}14$ 'W), with possible records from Honduras ($15^{\circ}58$ 'N, $79^{\circ}54$ 'W) (Flores, 2002). This small delphinid inhabits shallow waters and is often found yearround in bays and estuaries (Da Silva and Best, 1996). Due to its nearshore distribution, the marine tucuxi may be vulnerable to the effects of human activities such as habitat loss, chemical pollution, noise and bycatch. Despite these possible threats, there is little information on the ecology, biology and abundance of this species; it is listed as 'Data Deficient' by IUCN – the World Conservation Union (Reeves *et al.*, 2003).

Individual identification can be an effective approach for collecting detailed data on population parameters for many free-ranging cetaceans (e.g. Hammond *et al.*, 1990; Wells and Scott, 1990). Recently, this approach has been used to provide the first observations into site fidelity and calving intervals (e.g. Flores, 1999; Pizzorno, 1999; Santos *et al.*, 2001) for marine tucuxi, mainly in south and southeastern Brazil.

Since 1995, photo-identification techniques have been used to study marine tucuxi found in Guanabara Bay, southeastern Brazil. Recent studies showed that the bay is used daily by this species and calves are found year-round (Geise, 1989; Pizzorno, 1999). Approximately 70 individuals use the Bay (Pizzorno, 1999; Azevedo *et al.*, 2003a), seen most commonly in groups of 6-15 individuals, although they can form aggregations of up to 50 dolphins (Azevedo, 2000; Azevedo *et al.*, 2003b). However, little is known of the ecology of the species in this region.

Guanabara Bay is surrounded by a metropolitan complex and the habitat has been degraded by *inter alia* overfishing, harbour activities, inputs of metals and organochlorines (Amador, 1997; Perin *et al.*, 1997). The area is the second largest industrial concentration in Brazil, with 10,000 industries, the Rio de Janeiro Port Authority, 16 oil terminals, 12 shipyards, and two oil refineries (FEEMA, 1993). For these reasons Guanabara Bay represents the poorest habitat in the species' distribution (Lailson-Brito, 2000).

The present study was conducted from 1995-2003 to examine the site fidelity of marine tucuxis in Guanabara Bay, using photo-identification techniques.

MATERIALS AND METHODS

Guanabara Bay (22°50'S, 43°10'W) is located in Rio de Janeiro State, southeastern Brazil. The bay has a total area of 371km² and a total extension of 30km, with an entrance 1.8km wide (Fig. 1). Although the mean depth is only 5.7m, along the main channel, which follows the central S-N axis of the bay, depths reach an average of 20m (Costa, 1998). The bay possesses some features of an estuarine system. The freshwater contribution is derived from the 35 rivers that flow into the bay and from waste input (Mayr *et al.*, 1989).

From May 1995 to June 2003, 47 photo-identification surveys were conducted in Guanabara Bay. The effort was not equally distributed and the intervals between surveys ranged from 1-360 days (Table I). All surveys were carried out in Beaufort sea states <3, in small (4.5-6.6m) outboardpowered boats. Photographs were taken at close range (usually <10m). An auto-focus camera with a variablelength (70-300mm) lens was used. Most photographs were taken on ASA 400 colour and black-and-white film. Dorsal fin pictures were examined by negative projection. Nicks and notches along dorsal fins were the main features used to distinguish individual dolphins, but scars along dolphin bodies were used as auxiliary marks.

Photographs of individual dorsal fin marks were used to confirm each identification. Poor and intermediate quality photographs were rejected. From 9,690 photographs taken, about 30% were of good enough quality for individual recognition.

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In order to catalogue individuals, a tracing of each recognisable dorsal fin was made by projecting the negative onto a $8 \text{cm} \times 14 \text{cm}$ area of white paper (adapted from Defran *et al.*, 1990). When a visual match was located in the catalogue, the new dorsal fin photograph was projected onto the tracing of the potential match to confirm the resighting. Some dorsal fins attained new notches over the course of the study. In this case, a new tracing was made and the match was analysed by measuring the distance between the two largest notches and dividing that by the distance of the lower measured notch to the top of each dorsal fin (Defran *et al.*, 1990). The matches were always confirmed by at least two researchers.



Fig. 1. Map of Guanabara Bay (22°50'S, 43°10'W), southeastern Brazilian coast, where marine tucuxi photo-identification surveys were conducted between 1995 and 2003. The study area has a mean depth of 5.7m and a total area of 371km². The main channel is represented by isobaths of more than 10m.

Table 1 Marine tucuxi photo-identification effort in Guanabara Bay, southeastern Brazil (1995-2003).

Year	No. of surveys	Minimum number of days between surveys	Maximum number of days between surveys
1995	9	1	77
1996	4	20	140
1997	3	30	230
1998	6	35	138
1999	2	57	57
2000	6	1	295
2001	8	14	62
2002	2	20	20
2003	7	5	60
Total	47		

RESULTS

Sixty-nine individuals were identified and catalogued. Thirty-one of these dolphins (44.9%) were first photoidentified in 1995. About 55% (n=17) of the 31 animals identified in 1995 were seen during 2003 surveys. Only 17 (24.6%) of the 69 catalogued individuals were not seen during the 2003 surveys (Fig. 2). On average, dolphins were seen for 4.5 consecutive years, with a range of 1 to 8 years.

The percentage of re-photographed individuals in each year was high (Fig. 3) and was correlated with effort (Spearman test, n=8, rs=0.789; P=0.011). Sixty-five recognisable dolphins (94.2%) were resigned more than once and the 10 most frequently photographed animals were present in more than 50% of the surveys. Three dolphins were seen in at least 20 consecutive surveys and 11 others were present on more than 10 consecutive days.

A resighting index (RI) was calculated for each identified individual. This is the proportion of surveys subsequent to its first sighting during which the dolphin was identified:

$$\operatorname{RI} = (F_i / N)(n_i / N)$$

- where F_i = total number of sightings of an individual *i* after the first identification;
- n_i = total number of sightings of an individual *i*;
- N = total number of surveys from the first identification of individual *i*.

Resighting indices (Fig. 4) ranged from 0.0 to 0.89 (0.38 \pm 0.25) and 43 dolphins were photographed in one third of surveys after their first identification. The 10 most frequently photographed dolphins had resighting indices between 0.41 and 0.86.



Fig. 2. Summary of new identifications (●) and resightings (○) for marine tucuxis (*n*=69) in Guanabara Bay from 1995-2003.



Fig. 3. Percentage of all individuals photographed in a year that had been seen in previous years.



Fig. 4. Histogram of the resighting indices of marine tucuxis (*n*=69) in Guanabara Bay from 1995-2003.

DISCUSSION

The results indicate that marine tucuxis show high site fidelity in Guanabara Bay. Despite the long intervals between some surveys, a trend of residency was clearly identified. Most individuals had relatively high frequency of sightings and only a small number of individuals were not seen in the study area after their first identification. Additionally, most individual identifications were made in the first years of the study and many dolphins were seen for eight years.

Individuals resightings were high in each year, but the sampling effort was unevenly distributed and it was not possible to analyse individual year-round residence. However, a habitat use study was conducted from September 2002 to September 2003 and at least eight easily identifiable tucuxis (photo-identification tools not needed) were seen in all 21 surveys (A.F. Azevedo, unpublished data), which suggests that at least some dolphins are yearround residents in Guanabara Bay.

Site fidelity has already been documented in some coastal species of dolphin, such as Hector's dolphins, Cephalorhynchus hectori (e.g. Slooten et al., 1993) and bottlenose dolphins, Tursiops truncatus (e.g. Connor et al., 2000). For the tucuxi, two other studies concerning site fidelity also showed resident individuals. In North Bay, Santa Catarina, some marine tucuxis were observed for 4.8 years (Flores, 1999). At the Cananéia Estuary, individuals also have high residency patterns (Santos et al., 2001). These two areas, as well as Guanabara Bay, are relatively protected coastal waters, providing shelter from predators and abundant food (Santos et al., 2001). The level of site fidelity may be a function of prey availability. In areas where prey density is high, dolphins are not forced to range over long distances in search of food, resulting in a high level of site fidelity (Karczmarski, 1999).

Two calves photo-identified in 1995 were seen throughout the study. One of them has been seen with a calf since 2001, which indicates that tucuxi offspring remain in the area beyond sexual maturity. This pattern was reported for long-term resident bottlenose dolphins in western Florida (Scott *et al.*, 1990). In Guanabara Bay, other females (sex determined by consistent association with a calf or examination of collected carcasses) also have high resighting indices and short intervals between resightings. Guanabara Bay is also an important site for breeding in this species.

The marine tucuxi 'population' of Guanabara Bay is small (Pizzorno, 1999; Azevedo *et al.*, 2003b), in contrast to other near coastal sites where dolphin communities reach up to 200 individuals (Simao *et al.*, 2000). The high resighting indices suggest that these dolphins spend a considerable

amount of time within the bay. This site thus provides food and breeding habitat, despite being an area of high anthropogenic influence. However, the combination of a small resident dolphin population and a heavily degraded area may have serious implications for its conservation. Potential threats that require monitoring and possible mitigation include those related to chemical pollution (tucuxi from the Bay have high PCB and DDT concentrations in the blubber, comparable to some cetaceans which live in industrialised sites of the North Hemisphere; Lailson-Brito et al., 2003), intense vessel traffic (disturbance and strikes), and fishing activities (bycatches and overfishing). Such activities may have long-term effects and may operate cumulatively (Whitehead et al., 2000) and synergistically. Further research into abundance, biological parameters, habitat use and environmental disturbance is required to assess and monitor the status of these resident tucuxi dolphins.

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Abundance of freshwater Irrawaddy dolphins in the Mahakam River in East Kalimantan, Indonesia, based on mark-recapture analysis of photo-identified individuals

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ABSTRACT

From February 1999 to August 2002 *ca* 9,000km (840 hours) of search effort and 549 hours of observation on Irrawaddy dolphins (*Orcaella brevirostris*) were conducted by boat in the Mahakam River in East Kalimantan, Indonesia. An abundance estimate based on mark-recapture analysis of individuals photographed during separate surveys is presented here. Petersen and Jolly-Seber analysis methods were employed and compared along with earlier estimates derived from strip-transect analysis and direct counts. These comparisons serve to evaluate the biases of each method and assess the reliability of the abundance estimates. The feasibility of video-identification is also assessed. Total population size calculated by Petersen and Jolly-Seber mark-recapture analyses, was estimated to be 55 (95% CL=44-76; CV=6%) and 48 individuals (95% CL=33-63; CV=15%) respectively. Estimates based on strip-transect and direct count analysis for one sampling period, which was also included in the mark-recapture analysis, were within the confidence limits of the Jolly-Seber method, which are lower than the associated CVs. In addition, a high re-sight probability was calculated for both methods varying between 65% and 67%. Video images were considered a valuable, supplementary tool to still photography in the identification of individual dolphins in this study. For future monitoring of trends in abundance using mark/recapture analyses, a time interval is recommended between the two sampling periods that is short enough to minimise the introduction of errors due to gains and losses. Also, survey area coverage during photo-identification of event dolphin population.

KEYWORDS: ABUNDANCE ESTIMATE; CONSERVATION; MARK RECAPTURE; IRRAWADDY DOLPHIN; PHOTO-ID; ASIA

INTRODUCTION

Since 1970, photo-identification has proved to be a valuable tool in the assessment of population dynamics, social organisation, distribution and movement patterns for many species of cetaceans (e.g. Hammond et al., 1990; Whitehead et al., 2000). The technique involves collecting and cataloguing photographs of the dorsal fins, flukes and bodies of cetaceans with distinctive marks that allow for identification of individuals. However, the ease of getting good photo-identification results varies among species depending on uniqueness of the marks and behaviour of the species. Easily identifiable cetaceans with nearly complete photo-identification databases for certain populations include killer whales, Orcinus orca (Baird, 2000) and humpback whales, Megaptera novaeangliae (Clapham, 2000). For most other species, e.g. Indo-Pacific humpbacked dolphins, Sousa chinensis (Jefferson and Leatherwood, 1997; Jefferson, 2000); Pacific white-sided dolphins, Lagenorhynchus obliquidens (Morton, 2000) and northern bottlenose whales, Hyperoodon ampullatus (Gowans and Whitehead, 2001) only a proportion of the population can be reliably identified. Another factor limiting such studies is the elusive behaviour of some species. Photoidentification of Irrawaddy dolphins, commonly described as elusive (Lloze, 1973; Dhandapani, 1992; Kreb, 1999), requires greater effort, but was shown to be feasible for coastal populations in Australia (Parra and Corkeron, 2001). Freshwater populations of Irrawaddy dolphins that are known to occur in only three major river systems, i.e. the Mahakam River in Kalimantan, the Mekong River in Vietnam, Laos and Cambodia and the Ayeyarwady River in Myanmar (Burma) have been reported to be visually identifiable, but only an opportunistic photo-identification

effort had been undertaken until recently (Stacey, 1996; Smith *et al.*, 1997; Krebs, 1999). Since freshwater dolphin populations often live in a closed system with no exchange with coastal populations, photo-identification and subsequent mark-recapture analysis to determine total population size might be feasible. This study reports on photo-identification studies of a population of Irrawaddy dolphins in the Mahakam River, Indonesia and represents the first attempt to obtain a catalogue in which most individuals of an entire freshwater Irrawaddy dolphin population are identified.

The Irrawaddy dolphin is a facultative freshwater dolphin, occurring both in shallow coastal waters and large river systems in tropical South East Asia and sub-tropical India (Stacey and Arnold, 1999). Irrawaddy dolphins in Indonesia occur along several coastlines and in one river in East Kalimantan, the Mahakam, where they are commonly referred to as *pesut* (Kreb, 1999). The species has been fully protected by law in Indonesia since 1990 and is the adopted Kalimantan Province. symbol of East Their IUCN status was raised from 'Data Deficient' to 'Critically Endangered' based on data related to abundance collected from 1999 until 2000 (Hylton-Taylor, 2000; Kreb, 2002).

This study presents estimates of total population size based on photo-identification using different mark-recapture methods and compares these with earlier estimates of abundance from strip-transects and direct counts (Kreb, 2002). The feasibility of using digital video recordings as a tool to identify dolphins is also evaluated. This photoidentification study is part of a long-term conservation and research project begun in 1999 to provide a framework to protect the freshwater Irrawaddy dolphin population in the Mahakam River in East Kalimantan, Indonesia.

SURVEY METHODS

During the study period (February 1999 – August 2002), 12 surveys were conducted. Six extensive monitoring surveys (mean duration 20 days; standard deviation (SD) = 4 days) covered the entire range and six focussed surveys (mean duration 12 days; SD = 3 days) were conducted in areas of high dolphin density (Fig. 1). Extensive surveys were conducted with 12-16m long motorised vessels (between 12 and 21hp), travelling at an average speed of 10km hr⁻¹. The average observation time and photographic effort during the extensive monitoring surveys was one hour per sighting. The focussed surveys involved attempts to follow one group for an entire day, with daily alternation of groups and using a small, motorised canoe with a 5hp outboard engine. Photographic effort was spread out over the observation time (average duration 7 hours; range 1.5-13 hours).



Fig. 1. Study area.

Upon sighting, a group was approached to a minimum distance of 30m in order to take photographs and video images. Effort was made to take these photos from similar angles, i.e. perpendicularly to the dolphins' dorsal fin region. In addition, identification marks were recorded on datasheets. For each sighting, the duration, location, group behaviour, group size, group composition and environmental data were collected. Four age classes were defined: (1) 'neonates' – animals of less than 1/2 the average length of an adult, which spent all their time in close proximity to an adult and exhibited an awkward manner of swimming and surfacing; (2) 'calves' - animals between 1/2 and 3/4 the average length of an adult and which still spent most of their time in close proximity to an adult; (3) 'juveniles' - animals of 3/4 the average length of an adult and which swam independently; and (4) 'adults' - animals larger than an estimated 2m in length.

Photographs were taken using a *Canon* EOS 650 camera body with a *Sigma* 300mm/f4.0 lens, occasionally attaching a 1.4 teleconverter, effectively making it a 420mm/f5.6 lens. Manual focus was always used with shutter speeds of 1/250 to 1/1500 of a second. About 75% of the photo-id images were taken using slide films (*Sensia Fujichrome* 100 ISO) the rest using print films (*Fuji Superia* 200 ISO). Effort was made to photograph every individual within the group irrespective of whether they appeared to have distinct dorsal fin markings. Additionally, drawings of dorsal fins (made by aid of binoculars) were made by observers who did not take photographs. Dolphin age classes were also noted for each drawing. Direct observations and drawings were matched with a field photo-identification catalogue and assigned an existing or new identification code.

One field-assistant was assigned to the task of taking simultaneous video footage using a *Sony* VX 1000 digital camcorder with 10x optical and 20x digital zoom. In the majority of cases only the 10x optical zoom was employed to ensure better image quality. The auto-focus option was usually preferred since manual focusing proved more difficult with the camcorder than with the photo-camera.

Information on the number and occurrence of dead dolphins during the entire study period and in particular between the two sampling periods, was obtained through our own observations and from local, reliable reporters.

ANALYSIS

Photographs and slides were selected by aid of an 8x loupe for their good image quality (i.e. focus, glare, photographic angle, dorsal fin size coverage in image) and catalogued on the basis of identifiable features. Distinctive features noted included distinct fin shapes and notches, scars and cuts on the dorsal fin. Pigmentation patterns were only secondarily considered if they could be linked to a distinct fin shape. Pigment spots or areas do not occur symmetrically on both sides of the dorsal fin. In addition, it was found that pigmentation patterns on the bodies of dolphins and therefore likely also on dorsal fins, were not stable during the study period. Each photograph in the photoidentification catalogue corresponded to an identified individual and held information on the date, time and location at which the picture was taken as well as data on group size and composition. Photographs with distinctive features such as scars, cuts and humps on the dolphins' bodies were also selected, but catalogued under a separate identification code. Photographs with distinctive body features alone were only used for mark-recapture analysis if they could be linked to an individual, which was already identified based on its dorsal fin. Identifications that were obtained through direct observation and drawings were kept in a separate database to the photo-identified dolphins. These identifications were not used for the mark-recapture analysis.

For analysis of recorded video-images, each dorsal fin image was played in slow motion and paused. Again, only images of good photographic quality were selected. The selected images were then compared with individuals from the photo-identification catalogue, given an identification code and put into a video-identification catalogue together with related sightings data.

Two estimates of total population size (N) were calculated based on two different mark-recapture analysis methods. Only sampling periods with extensive area coverage were selected. The first estimate utilised the Petersen method for closed populations, involving one session of catching and marking and one recapture session and Bailey's modified estimator (Hammond, 1986) was applied for sampling with replacement (Equations 1.1-1.3).

Sample periods May/June 2000 and August 2001 were chosen because the photographic efforts (i.e. area coverage) were similar in those periods (Table 1).

The second method to estimate total abundance was the Jolly-Seber method for open populations, allowing for gains and losses within the sampling periods (Equations 2.1-2.4).

Table	1
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Photo-identification success rate and discovery rate of new individuals.

Year	Survey period	Survey area coverage	No. dolphin photographs	No. identified dorsal fins	No. different individuals (<i>n</i> _i)	No. of new individuals
1999	Feb/Mar	Е	25	3	2	2
	Apr/May	Е	25	7	5	5
	Oct	Е	49	28	16	13
2000	May/Jun	Е	206	90	33	21
	Aug	Ι	157	83	24	4
	Nov	Ι	65	23	16	1
2001	Jan/Feb	Е	175	82	29	6
	Jun/Jul	Ι	267	127	37	1
	Aug	Е	178	90	34	3
	Oct/Nov	Ι	89	36	23	1
2002	Apr	Ι	181	102	28	1
	Aug	Ι	82	54	23	1
Total	12 periods	_	1 499	728	-	50

E = extensive monitoring survey in entire dolphin distribution area; I = intensive monitoring survey in high dolphin density areas.

$$N = n_1 \frac{(n_2 + 1)}{(m_2 + 1)(1 - p)}$$
(Petersen method) (1.1)
$$CV(N) = N^{-1} \sqrt{\frac{n_1^2(n_2 + 1)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}} + \frac{\text{var}(1 - p)}{(1 - p)^2}$$
(1.2)

where:

 n_1 = number identified on the first occasion;

 n_2 = total number identified on the second occasion;

- m_2 = number of identified dolphins found on the second occasion;
- p = proportion of unidentifiable individuals.

$$N_{i} = \frac{M_{i}(n_{i}+1)}{(m_{i}+1)(1-p)} \text{(Jolly-Seber method)} \quad (2.1) \qquad M_{i} = \frac{m_{i}+(R_{i}+1)z_{i}}{(r_{i}+1)} \quad (2.2) \qquad \Phi_{i} = \frac{M_{i}+1}{(M_{i}-m_{i}+R_{i})} \quad (2.3)$$

$$CV(N_i) = \sqrt{x_i} \cdot \frac{\sqrt{\left(\frac{M_i - m_i + R_i + 1}{M_i + 1}\right)\left(\frac{1}{(r_i + 1)} - \frac{1}{(R_i + 1)}\right) + \frac{1}{m_i + 1} - \frac{1}{n_i + 1} + \frac{\operatorname{var}(1 - p)}{(1 - p)^2}}{\log_e N_i + 0.5 \log_e \left(\frac{0.5 - 3n_i}{8N_i}\right)}}$$
(2.4)

where:

- N_i = population size at the time of the *i*th sample;
- $\dot{M_i}$ = number of marked animals in the population when the *i*th sample is taken (excluding animals newly marked in the *i*th sample);
- n_i = total number of animals caught in the *i*th sample;
- R_i = number of animals that are released after the *i*th sample;
- m_i = number of animals in the *i*th sample that carry marks from previous captures;
- z_i = number of animals caught both before and after the *i*th sample but not in the *i*th sample itself;
- r_i = number of animals that were released from the *i*th and were subsequently recaptured;
- x_i = number of samples;
- $\dot{\Phi}_i$ = proportion of the population surviving from the *i*th to the (i + 1)th sampling occasion.

Capture histories of each identifiable individual are needed since the method requires both knowledge of the number of animals in each sample that were previously marked and information on the most recent previous sample in which each of them was last trapped. The number of marked individuals in four sampling periods, i.e. October 1999, May/June 2000, January/February 2001 and August 2001, with extensive area coverage, were higher than the minimum sample size of 10 marked individuals recommended to overcome the imprecision of abundance estimates (Sutherland, 1996). Prior to the calculation of an abundance estimate, a goodness-of-fit test was applied (Sutherland, 1996) to test if animals differed in captureprobabilities, which may cause a serious bias of the estimate. After testing, three sampling periods were chosen to be appropriate for abundance estimation (see results).

According to the Jolly-Seber method, no estimates of abundance can be calculated for the first and last sampling periods and thus only one estimate is derived from the second sampling period (Equation 2.1). For this last method, it was also possible to calculate the proportion of the population surviving (Φ) from the 1st to the 2nd sampling occasion (Equation 2.3).

A correction factor was applied to the population estimates from both methods to correct for the proportion (p) of dolphins that are not identifiable (Jefferson and Leatherwood, 1997). These were neonates and calves which could not be photographed effectively because their mothers protected them from the boat and from a good camera angle, and because calves often surface very suddenly (high arch dives). The averages of the proportion of neonates and calves encountered during two (Petersen) and three (Jolly-Seber) sampling periods are 10% and 8% respectively, which represent the proportion of unidentifiable dolphins (p).

For the Petersen method, binomial 95% confidence intervals were calculated for the fraction of marked individuals $(m_2+1) / (n_2+1)$, which were then applied to Equation 1.1 to obtain the 95% confidence limits for population size (Krebs, 1999). Jolly-Seber confidence limits were calculated using the formula provided by Manly (1971). Coefficients of variation were calculated for both methods according to the formulae in Equations 1.2 and 2.4. Estimated resighting probabilities for the Petersen estimator are given by m_2/n_2 and $p_2=m_2/n_1$ and for Jolly-Seber by n_i/N_i , in which N_i is (only here) the uncorrected abundance estimate for the proportion of identifiable dolphins.

Finally, maximum biases that may affect population size estimates for each method were calculated. A maximum bias using Petersen's method, which assumes no losses, was calculated by adding the number of dead dolphins (3) inbetween the two sampling periods, to the number of 'recaptured' animals during the second sampling period $(m_{2bias}=m_2+3)$. This number was also added to the total number caught on the second occasion $(n_{2bias}=n_2+3)$. When addressing this bias it is assumed that these dolphins would have been 'marked' during the first session and also assumes that they would have been 'recaptured' if they had not died.

A 'maximum' bias using the Jolly-Seber method can be obtained from the fact that one area was not surveyed during the second sampling period of the three sampling periods in total. This area, which is an area inbetween two rapids and known to be the home of a group of six dolphins, was surveyed only during the first and last sampling period. Two and three new individuals were marked during the first and last sampling period, respectively, without any recaptures. The largest deviation from the abundance estimate would apply for a situation in which it is assumed that this area would have been surveyed during the second sampling period, where four new individuals would be captured and marked and three of these would be recaptured during the third sampling period. This maximum deviation of the estimate is calculated following Equation 2 by adding three individuals to r_2 (number of marked dolphins in the 2nd sample, which were recaptured in the 3rd sample) and four individuals to n_2 and R_2 (total number caught and released in the 2^{nd} sample) Variable z_2 is not affected by the missing survey effort during the second sampling period because the individuals marked in that area were not similar during the first and last sampling period. This 'maximum' bias holds only if the following assumptions are true: neither of the two individuals marked during the first sampling period would be recaptured if the 'missed' area was surveyed during the second sampling period. Four individuals would be marked during the second sampling period so that $r_{2bias} = r_2 + 3$, $n_{2bias} = n_2 + 4$ and $R_{2bias} = R_2 + 4$. To assess the minimum annual birth rates the total number of newborns were counted during five separate surveys between November 2000 and November 2001, with an average gap of 2.5 months between surveys. Newborns were assumed to be different from those encountered in any earlier survey.

RESULTS

Estimates of abundance based on photo-identification mark-recapture analysis

During the entire study period from February 1999 until August 2002, a total of 2,074 photographs were taken during 83 days of which 1,499 (partially) portrayed dolphins and 558 (27%) completely failed, showing merely circles in the water (Table 1). Of the dolphin photographs, 753 photographs (50%) were selected for photo-identification because of good image quality. Some 728 photographs showed identifiable features on dorsal fins, sometimes in combination with other characteristic traits on the dolphins' bodies, producing an average of almost nine identifiable dorsal fin photographs per day. An additional 25 photographs only showed identifiable features on the dolphins' bodies. As such, a total of 59 individual dolphins were catalogued based on dorsal fin identification. Four individuals are shown in Fig. 2.

Within the four initially chosen sampling periods for the Jolly-Seber method, animals appeared to differ significantly in capture-probabilities (G=10.06; d.f.=2; P<0.01), meaning that the underlying assumptions (see discussion) of the method were violated. The bias was consequently rendered insignificant by only using sampling periods which include a high proportion (i.e. over 50%) of the population. Therefore, the October 1999 sampling period was removed from analysis, which included only 31% of the Petersen population estimate. Another *G*-test for the remaining periods revealed that this time no assumptions were violated (G=1.8; d.f.=1; P=0.17).

The number of dolphins identified by photograph for each sampling period (n_i) are presented in Table 1. For the Petersen method the number of dolphins that were identified in the first period (May/June 2000) and recaptured by photograph during the second period (m_2) (August 2001) is 22 individuals. For the Jolly-Seber method m_2 is 14 individuals (using periods May/June 2000 and January/February 2001). The estimated resighting probabilities for the Petersen method are either 65% or 67%; 66% for the Jolly-Seber method. The number of dolphins that were recaptured by photograph in the third sampling occasion (Jolly-Seber) and identified during earlier occasions (m_3) is 28 individuals, illustrating the high resighting probability over more than two sampling periods.

The estimate of total population size using the Petersen two-sample mark-recapture method was 55 individual dolphins (95% CL=44-76; CV=6%). Calculating a potential maximum bias due to loss of individuals between the sample periods, lowers the estimate to 54 individuals (95% CL=44-76; CV=10%), which is 2% lower than the population size estimate above. During the 3.5 year study period at least 17 dolphins have died but the specific dolphin identities were not available and thus could not be traced back to the photoidentification catalogue. An estimate of population size using the Jolly-Seber method arrives at 48 individual dolphins (95% CL=33-63; CV=15%). The proportion of the population surviving from the 1st to the 2nd sampling occasion is 66%. The reported number of dead dolphins between these two sampling periods is two individuals (4% of N_2). An estimate was also calculated including a maximum bias due to lack of survey effort during one of the sampling periods in one 'closed' area that is inhabited by a group of six dolphins. The corrected estimate is 53 individuals (95% CL=36-64; CV=19%), which is 10% greater than the unbiased population size estimate of 48.



Fig. 2. Left above = PM 2; Right above = PM 1; Left below = PM 8; Right below = PM 3.

Fig. 3 shows the cumulative number of new individuals identified in different survey periods in combination with photographic success in obtaining identifiable pictures of dorsal fins for each sub-period. The cumulative frequency curve begins to level off after the August 2001 survey period and during the next three survey periods only one individual was added each time (Table 1). Some 95% of the individuals of the photo-identification catalogue are identified in the period March 1999 until August 2001. After that date a plateau in the number of new identifications is more or less reached, with only a yearly 5% increase of new identifications (three individuals) of the total photoidentification catalogue. With an estimated annual birth rate of 10.5% of the total population, this yearly 5% increase is within this birth rate range and may therefore be attributed to possible neonates. It should however be noted that these



Fig. 3. Discovery rate of new individuals and number of identified dolphins per survey period in relation to the number of selected pictures.



Fig. 4. The number of re-sighted individuals during a number of survey periods, e.g. 14 individuals were re-sighted during four different survey periods.



Fig. 5. The number of re-sighted dolphins on photograph and video over a maximum of 21 days, e.g. 14 and 11 dolphins were re-sighted on photograph and video respectively during periods of 2 and 3 days.



Fig. 6. Example of a low quality photograph (small dorsal fin image), in which dolphin PM01 can still be identified over larger distances due to the distinctiveness of its mark. Dolphin PM01 was photographed during 21 different survey days, on 41 pictures and photographed here on 23 August 2000 (upper picture) and 2 July 2001 (lower picture).

neonates can be identified only when they are over one-year of age, since they are otherwise difficult to photograph. Thus, new identifications within any one year may include last year's neonates, i.e. one-year old calves. The plateau was not a result of low photographic effort, since the number of new individuals added to the catalogue is not correlated with the number of identifiable photographs (r=0.06; d.f.=10).

Some 98% of the identified dolphins were recaptured by photograph on at least two different days and 90% were recaptured during at least two different survey periods (Figs 4 and 5). Individual dolphins were recaptured on a mean of 7.0 different survey days (\pm SD=4.7) and 4.5 survey periods (\pm SD=2.4). Individual dolphins were recaptured on a maximum of 21 days and 10 survey periods (Fig. 6).

Feasibility of video-identification

Video recordings were made during seven different survey periods and 21 days. The total recording effort was 8.8 hours. Identifiable dorsal fins of surfacing dolphins were recorded on 79 video-images, from which 31 different individuals could be identified. On average, nine identification images per hour and four images per day recording were produced. Four individuals were identified based on body marks alone. Fifty-two percent of the individuals were encountered on more than one day (mean=2.1; \pm SD 1.4; range=1-5) (Fig. 5).

DISCUSSION

Estimates of abundance based on photo-identification mark-recapture analysis

Violated assumptions and biases

Two methods for analysing mark-recapture results of photoidentified dolphins were used in this study, the Petersen twosample method and the Jolly-Seber method. The former method was found to be appropriate to obtain an estimate of total population since during two of the 12 survey-periods photographic 'trapping' effort was equally spread over the entire dolphin distributional range. This ensured that all animals had the same probability of being identified (assumption 2, see below). Most other survey periods involved intensive monitoring surveys in only areas of high dolphin density. Also, one area in between two rapids was not surveyed during the other extensive monitoring surveys due to bad weather conditions. The second method (Jolly-Seber) was applied because it allows for gains and losses between sampling periods. The disadvantages of using these methods are that they rely on underlying assumptions, which, if violated, produce serious biases in the results. For the Petersen method, these assumptions are: (1) the population is closed; (2) all animals have the same probability of being caught; (3) marking does not affect the catchability of an animal; (4) the second sample is a simple random sample; (5) animals do not lose their marks; and (6) all marks are reported on recovery. For the Jolly-Seber method, assumptions 2 and 5 from Petersen are also applicable. Additionally it is assumed that: (7) every marked animal has the same probability of surviving from the *i*th to the (i+1)th sample; (8) every animal caught in the *i*th sample has the same probability of being returned to the population; (9) all samples are instantaneous (Hammond, 1986).

The first and second assumptions are violated in this study by the Petersen and Jolly-Seber methods, respectively, and the effects are discussed below. The first assumption of the Petersen method was violated as three dolphins (identity unknown) died and four dolphins were born between the sampling periods. Mortality is unlikely to have influenced n_2 (total number caught on the second occasion), since during each sampling period only 55-57% of the total photoidentification catalogue was captured on film. However, m_2 (number of 'marked' animals recaptured on the second occasion) may have been affected since the number of 'recaptured' animals was not equal (only 64-66%) to the total number of individuals caught on the first and second occasions. Therefore, these dead dolphins of unknown identity may not have been 'marked' on the first occasion or, if they were, had not been recaptured. However, the three dead dolphins may have produced a biased estimate and therefore a correction was calculated for this bias, which decreased the estimate at the most by two individuals. This bias only applies if we assume that these three dolphins were 'marked' on the first occasion and presumably would have been caught on the second occasion if they had not died. In that case, the abundance estimate would be 54 individuals, which is clearly within the confidence limits of the abundance estimate of 55 individuals as described in the Results section. This small difference may be a result of the fact that a high proportion of the estimated population was captured during each sampling period (65-67%). Catching over 50% of the population limits biases that may arise through violations of assumptions (Sutherland, 1996).

As for mortality, recruitment (dolphins born between two sampling periods) is unlikely to have influenced the overall number of dolphins caught on the second occasion (n_2) . Furthermore, neonates will not have influenced the number of 'marked' animals found on the second occasion (m_2) , since they were born after the first sampling period and were thus not recorded. Neonates and calves have a low chance of being identified since they surface very irregularly and briefly during their first few months and are hard to photograph as they swim very close to the mother. Consequently, neonates encountered during the first sampling period are unlikely to have been 'marked' and so did not affect any of the variables of the Petersen formula.

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Violations of the second assumption due to heterogeneity in catchability between dolphins and 'trap responses' were tested with a goodness-of-fit test for three sampling periods used within both analysis methods. This revealed no differences in capture probabilities except for the neonates and calves, for which a correction factor is applied to calculate abundance estimates (see analysis). This is in contrast to most other cetacean photo-identification studies in which unequal capture probabilities are often the case, due to variations in individual behaviour, such as wariness of boats or fluking behaviour, that affect the probability of obtaining good photographs (Whitehead et al., 2000). Capture probabilities are more likely to vary for bow-riding dolphins, whereas the dolphins in this study were all photographed some distance from the boat. Thus, boatshyness or attraction probably did not play a major role. Since photo-identification is in principal a non-invasive technique, any issues of trap responses are not relevant here. In spite of the fact that in theory dolphins had equal probabilities of being photographed, differences in distinctiveness of marks and in survey area may have caused capture probabilities (obtaining identifiable images) to vary among individuals and caused a bias of the population size estimate (Gowans and Whitehead, 2001). Although all photographs of good image quality yielded identifiable marks, photographs of lower quality (smaller images) were only identifiable for those individuals with very distinct marks (Fig. 6). Other markings needed to fill a significant part of the frame for identification and therefore more slides were discarded for use in connection with these features. Another bias in capture probability was related to differences in area coverage for each sampling period. However, the G-test result and the high percentage of resightings over different survey days and periods (95% and 90% of total identified individuals were re-sighted over two days and periods or more, respectively), indicate that the bias is not large, possibly due to the fact that a large part of the population was caught during both samples, as stated earlier. Nevertheless, a maximum bias was calculated that could affect the Jolly-Seber estimate for the difference in area coverage. This bias produced an estimate that only differed from three individuals from the Jolly-Seber estimate. Finally, dolphins in this study were only identified using natural marks, which would be stable over long sampling intervals (such as notches, cuts, scars and fin shapes) to prevent biases when marks are lost (such as pigmentation patterns) as suggested by Gowans and Whitehead (2001). Furthermore, other underlying assumptions of both methods did not seem problematic in this study.

The difference between the total number of dolphins identified (59) and the estimated total population size (N=48-55), may be explained by the fact that the first number was derived from a 3.5 year study period, during which 17 dolphins died. The total number of dolphins identified therefore does not represent an abundance estimate.

The proportion of the population surviving from the 1st to the 2nd sampling occasion was estimated to be 66% based on the Jolly-Seber equation, whereas the proportion surviving based on the reported number of dead dolphins between these two sampling periods is 96%. The difference may be explained by the fact that the probability of survival using the Jolly-Seber equation is determined by sampling the marked population only and variations in the size of this population may occur between two sampling periods for reasons other than mortality and emigration. For example, photographs are not always successful for all sightings within each sampling period due to the dolphins' group behaviour at that specific moment, which may vary through time for the same group. In this way, some groups may be missed from identification during one period but identified during another.

Identifiability

As stated above, from all photographs of good image quality of dorsal fins, individual dolphins could be identified. This agrees with a photo-identification study on coastal Irrawaddy dolphins in North Queensland, Australia, although juveniles were reported to lack any distinctive features that allow identification (Parra and Corkeron, 2001). In addition, as in the Australian study, no standardised identification measure (e.g. the Dorsal Fin Ratio; Defran et al., 1990) could be used to identify Irrawaddy dolphins in the Mahakam River, since fins lacked clearly distinct top and bottom points. Irrawaddy dolphins in this study and those of others could also be identified based on the variation of dorsal fin shapes (Stacey, 1996; Parra and Corkeron, 2001). With regard to possible false matches, only three dolphins with more uniform, smooth dorsal fin shapes were found (although not similar compared to each other). However, each of these dolphins was only re-sighted on 5, 7 and 11 different survey days, i.e. within one standard deviation of the mean number of days on which all dolphins were re-sighted (mean=7 days, SD=4.7). So, the probability that other dolphins were identified as one of these three is low and otherwise the number of sighting days for these dolphins would be expected to be higher. In addition, fins were still identifiable on the basis of overall shape, even though characteristic notches were missing.

With regards to identification of calves and juveniles, Irrawaddy dolphins in the Mahakam River had identifiable features on their dorsal fins. This stands in contrast to work by Parra and Corkeron (2001), who conducted a photoidentification study of coastal Irrawaddy dolphins in Australia and found that calves and juveniles had no distinctive features to allow identification. During each of the extensive sampling periods (covering entire dolphin distribution range), one group of animals consisting of some six juveniles without adults was encountered. Unfortunately, only drawings of dorsal fins, (made by aid of binoculars) and one photograph showing distinctive marks on the juvenile's body were taken for this group due to their elusive surfacing behaviour. Juveniles in mixed groups were on the other hand much less shy, in fact they often surfaced near the boat. Since no record was kept in the field of the dolphin age classes of each photograph, it is not possible to trace which identified dolphin is a juvenile and which is an adult on the basis of the picture alone. However, occasionally, when drawings were made during the study of several characteristic dorsal fins, age class was also noted and these included both juveniles and calves.

The high percentage of individuals that were re-sighted on more than one occasion (98% of 59 identified dolphins) is an indication of the closeness of the Mahakam dolphin population. Percentages of re-sightings were similar (97% and 100%) for resident populations of marine tucuxis, *Sotalia fluviatilis* in Southern Brazil and of 21 identified bottlenose dolphins, *Tursiops truncatus*, in the Stono River estuary in South Carolina (Flores, 1999; Zolman, 2002). Resightings of seasonally occurring groups are typically lower; varying percentages of 32%, 50% and 57% were found for 675 identified individual Pacific white-sided dolphins in the Broughton Archipelago, Canada, 35 identified Irrawaddy dolphins in Cleveland and Bowling Green Bay in North Queensland, Australia and 213 identified Indo-Pacific hump-backed dolphins in Hong Kong waters, respectively (Jefferson, 2000; Morton, 2000; Parra and Corkeron, 2001).

Comparison of different techniques to estimate population abundance

The estimates of population size based on two different methods are similar and each is within the confidence limits of the other (combined between 33 and 76). Although the Petersen estimate (N=55) is somewhat higher than the Jolly-Seber estimate (N=48), the CV is smaller for the first estimate (CV=6% and 15%). The latter estimate is close to the estimate derived from direct counts and strip-transects in May/June 2000 (N_{count} =35 and N_{strip} =43) by Kreb (2002), with both estimates within the confidence limits of the Jolly-Seber estimate. Because the low estimates calculated here represent the total population size of dolphins in the Mahakam, immediate conservation measures are required to reduce the high minimum mortality rate of 10.5% dolphins of total population per year. It also shows that intended livecaptures of dolphins for display in a local oceanarium should not be allowed for this small population.

In order to monitor future trends in abundance, photoidentification may be a valuable tool. However, to increase precision and prevent biases due to gains and losses of individuals it is recommended that photographs be taken during two extensive monitoring surveys in sequence covering the entire dolphin distribution range with a minimum time interval. Conclusively, since the results of the mark-recapture studies and direct count and striptransect studies are very similar, future surveys to monitor trends in abundance of the latter type are feasible, if one needs to be cost efficient. However, surveys in combination with photo-identification are preferable in order to obtain data on long-term social systems and migration patterns.

Feasibility of video-identification

The number of identifiable video-images per hour recording in this study (9 images hr⁻¹), was much lower than those recorded in the video-identification study of bottlenose dolphins in South Carolina (Zolman, 2002), which yielded 31 images per hour recording time. This may be a result of the fact that in the latter study only a video was used for identification of dolphins, which may increase the drive to make good quality recordings. Another reason is that it may be more difficult to record dorsal fins of Irrawaddy dolphins because of their shy and irregular surfacing pattern (Kreb, 1999). The number of identifiable video images per day (4) was much lower than for still photography (9) in this study.

Nevertheless, although the yield of identifiable images may be less than in other studies and in comparison to still photography, video-identification has some advantages as an additional tool. Firstly, in most cases the entire movement of the dolphin is visible during playback, including all the different angles from which a dorsal fin can be seen. This was particularly useful in cases when there were any doubts within the photo-identification catalogue about whether two assumedly different identified dorsal fins belonged in fact to one and the same individual. Although dorsal fin pictures were always attempted to be taken perpendicularly to the dolphin's body axis close to the dorsal fin region, small deviations from this angle could in some cases cause confusion in the identification. Secondly, this technique can link body characteristics to individuals, which are initially identified based on dorsal fins alone. Thirdly, for other purposes, such as study of social structure, video recordings make it possible to record the physical position of individual dolphins with regard to each other.

However, disadvantages in the use of a video camera were experienced in connection with the slow adjustment between wide-angle and zoom modes. Despite attempts to use a fixed zoom length and estimation of where the dolphins would surface, the poor manoeuvrability of the video camera in comparison with the photo-camera limited the quality of the results obtained. In addition, the quality of video images for which a digital zoom was used often did not allow accurate identification. Since the images were analysed by using the slow motion, or pause mode, the quality of still video images decreased significantly as a consequence, as did images recorded with the optical zoom.

No mark-recapture analyses were performed using video images, since the images were not recorded systematically throughout the study period. The quality of the still video images was found to be low in comparison with the photographs. Therefore, identifications were not directly based on the video images, but were first traced back to the photo-identification catalogue. However, overall videoidentification in combination with photo-identification appears to be useful for individual dolphin identification.

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A note on the most northerly record of Gervais' beaked whale from the western North Atlantic Ocean

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ABSTRACT

A juvenile male Gervais' beaked whale (*Mesoplodon europaeus*) was found dead in Barnstable Harbor, Cape Cod Bay, Massachusetts, USA. It apparently died from a septicaemia, possibly induced by a puncture wound of unknown origin. The previous most northerly stranding for this species in the western North Atlantic ocean was from New York State, USA.

KEYWORDS: BEAKED WHALE-GERVAIS'; NORTH ATLANTIC; STRANDINGS; MORPHOMETRICS; DISTRIBUTION; DISEASE

INTRODUCTION

Gervais' beaked whales (*Mesoplodon europaeus*), occur in tropical and warm-temperate waters of the Atlantic Ocean (Mead, 1989) and appear to be most concentrated in the western North Atlantic (Norman and Mead, 2001). This species is the most frequently stranded mesoplodont along the US Atlantic coast (Mead, 1989).

MATERIALS AND METHODS

A single cetacean was reported alive on riprap under a pier at the Sandwich Marina, Massachusetts, at 23:15 on 18 September 1997 and then again in Barnstable Harbor at Harbor Point Road at 15:30 on 19 September, where it was pushed back out by local residents. It was observed swimming erratically on that day. On 21 September 1997, a single Gervais' beaked whale was reported dead at Mill Creek, Barnstable Harbor, Cape Cod Bay at 41°42.7'N, 070°15.7'W, 10 miles ESE of the initial sighting. The animal was found dead in right lateral recumbency (Fig. 1). The sandy mud below the dorsal fin was mounded up around the fin margin suggesting that the animal had been struggling prior to death at that site. Personnel from the Woods Hole Oceanographic Institution (WHOI) and the New England Aquarium (NEA) performed a necropsy on the animal on 22 September in Woods Hole, including measurement of external features and a gross examination of its external and internal organs. All major organs except the brain were sampled for histology, and examined for histopathology at the Armed Forces Institute of Pathology, in Washington DC.

RESULTS

The animal was identified as Gervais' beaked whale morphologically (C. Potter, pers. comm.) and genetically (P. Rosel and B. McLeod, pers. comm.). Measurements of the animal are shown in Table 1. This male had a total straight length of 386cm and weighed 545.5kg. Colouration was dark grey to black over the dorsum, becoming lighter on the sides. The ventral surface was light grey to white. Overall, it appeared to be in relatively good body condition. Numerous superficial holes, scrapes and cuts were distributed over the body. No fishing gear or rope marks were found on the animal. Fig. 2 shows the left lateral view of the head. A ragged puncture wound measuring 8cm long and 1cm deep was observed dorsocaudal to the right eye with surrounding surface gouges (Fig. 3) and with underlying focal haemorrhage in the blubber and underlying muscle (Fig. 4). Patches of skin were also missing, along the direction of linear scratch marks. An erupting tooth whose apex was just visible on the right mandible 9.1cm from the anterior tip of the beak and 16cm from the angle of the jaw. An ulcer was observed on the tongue surface. The lungs were a uniform dark red in colour (Fig. 5). The heart and lungs weighed 18.652kg. Half of the post-cranial blubber weighed 57.933kg. The heart chambers appeared normal. The stomach and bladder were empty. All muscles and joints examined appeared normal.

Apparent parasitic nodules were observed at several sites in the blubber. Histopathologic examination revealed evidence of acute pulmonary congestion accompanied by alveolar and interstitial edema. Such changes are common, non-specific findings in stranded cetaceans. A focus of



Fig. 1. Gervais' beaked whale stranded at Mill Creek, Barnstable Harbor, MA, USA on 21 September 1997. Note the mud ridges below the dorsal fin suggesting a pre-mortem struggle at this site (arrow).

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Table 1 Morphometrics of stranded Gervais' beaked whale, MH-97-566-Me (= WHOI 97-246) (all measurements in centimetres).

Measurement		cm	% of total length
Snout to centre of blowhole		48	12.4
Snout to eye		46	11.9
Snout to angle of mouth		24	6.2
Snout to anterior insertion of flipper		82	21.2
Snout to centre of genital slit		261	67.6
Snout to anus		283	73.3
Snout to anterior end of dorsal fin		230	59.6
Snout to dorsal fin tip		256	66.3
Snout to midline caudal edge of fluke (no	386	100.0	
Flipper length		39	9.0
Flipper width		9	2.3
Fluke width		80	20.7
Fin height		17	4.4
Axillary girth		186	
Maximum girth (170cm from snout)		208	
Anal girth		128	
Blubber thickness (excluding skin)	Dorsal	Latera	al Ventral
Axilla	2.7	2.2	2.0
Maximum girth	3.0	2.2	2.0
Anal	6.6	1.5	2.5

granulomatous and eosinophilic inflammation that surrounded a small cavity was present in the blubber and was probably caused by a parasite. The glossal ulcer was associated with edema and hemorrhage; a subjacent blood vessel was occluded by a cluster of Gram-negative bacilli. No inflammatory cells were present. This lesion provided evidence of a peracute Gram-negative bacterial septicaemia, which was the likely cause of death. The puncture wound between the eye and the blowhole may have been the site of origin of the bacterial infection. Kidney, liver, adrenal, thymus, muscle, lymph node, four heart chambers, trachea, tongue, optic nerve, three stomach chambers, esophagus, skin and pericardium all appeared normal, as far as the degree of autolysis would allow assessment. Seminifeous tubules in the testis showed no oriented or polarised spermatogonia or indication of active spermatogenesis.



Fig. 2. Left lateral view of the head of the animal shown in Fig. 1.



Fig. 3. Puncture wound (short arrow) and surface scrapes dorsocaudal to the right eye (long arrow).



Fig. 4. Focal haemorrhage in blubber (short arrows) and muscle (long arrows) underlying the puncture wound shown in Fig. 3.



Fig. 5. Lungs and airways showing the dark red colour of the cut lung surface.

DISCUSSION

According to Mead (1989), four species of mesoplodonts are found off the east coast of the USA: Sowerby's beaked whale (*Mesoplodon bidens*); Blainville's beaked whale (*Mesoplodon densirostris*); Gervais' beaked whale and True's beaked whale (*Mesoplodon mirus*). Of these, Gervais' and Blainville's beaked whales appear to favour the more southerly warm temperate waters in the North Atlantic, sympatric in a large portion of their range (MacLeod, 2000). The stranded animal appeared to be a juvenile on the basis of its total length (Mead, 1984) and testicular immaturity. The stranding of this specimen provides the most northerly record of Gervais' beaked whale from the western North Atlantic. Previously the most northerly record was from New York State (Raven, 1937). It is interesting to note that Gervais' beaked whales are the predominant mesoplodont found beached on the US east coast, whereas Sowerby's beaked whales are the most common mesoplodont taken as bycatch in east coast fisheries (Waring *et al.*, 2002). The furthest south the species has been reported is Sao Vicente ($23^{\circ}58'S$; $46^{\circ}24'W$), Sao Paulo state, Brazil (de Oliveira Santos *et al.*, 2004).

The small holes observed were probably scavenger induced, but the scrape marks appear to have been inflicted prior to death, as the substrate upon which the animal apparently died was smooth sandy mud. The suspicion that the initial stranding occurred on marina riprap is pertinent here. Some but not all scrapes appeared to be tooth rake marks. The depth of the wound caudo-dorsal to the eye and the extent of the underlying bruising would suggest that it would be unlikely for the wound to have been self-inflicted on the beach. This wound could have been inflicted by a swordfish or by a harpoon used for tuna or swordfish. The lesion in the tongue was believed to provide strong evidence for a peracute Gram-negative bacterial septicaemia, which was probably the cause of death. The pulmonary congestion and oedema were assumed to be terminal changes. It is not unreasonable to suppose that the septicaemia was initiated by the puncture wound observed between the eye and the blowhole.

Histopathology samples from 26 organs, and the entire head, heart, lung, stomach and reproductive tract (except for the testes) along with 70 photographs of the stranding and necropsy were archived at WHOI, Wood's Hole, MA (MH-97-566-Me, 97-246). The postcranial skeleton was deposited at the Smithsonian Institution, Washington DC (USNM 572520). The skull will be deposited at the Smithsonian once examination is complete in Woods Hole.

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estimation parameters in the IWC/IDCR-SOWER surveys

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ABSTRACT

The effects of observed covariates (school size, sighting cue, latitude and sea state) on Antarctic minke whale abundance estimation parameters (effective search half-width, sighting forward distance and mean school size) were examined qualitatively. As the school size decreased, the effective search half-width and the sighting forward distance decreased. Most single and two animal schools were sighted by body, which was difficult in high sea states in comparison with those sighted by blow. Proportions of single and two animal schools increased as sighting latitude moved north. Small school sizes and bad weather conditions prevailed in the northern part of the survey area. As the survey area was extended to the north, the effects of small school size and bad weather conditions could be substantial in the third circumpolar survey. Observed covariates analysed in this paper should be incorporated into the estimation of effective search half-width and mean school size as covariates

KEWORDS: ABUNDANCE ESTIMATE; ANTARCTIC MINKE WHALE; g(0); ANTARCTIC; SOWER; SURVEY-VESSEL; TRENDS

INTRODUCTION

The International Whaling Commission (IWC) has conducted the Antarctic minke whale (Balaenoptera bonaerensis) abundance assessment cruises since 1978/79 in the Antarctic austral summer. The cruises began under the International Decade of Cetacean Research programme (IDCR, from 1978/79 to 1995/96) which then became the Southern Ocean Whale and Ecosystem Research programme (SOWER, from 1996/97 to present). Matsuoka et al. (2003) presented an extensive review of these cruises. At the time of writing, these cruises have covered almost three circumpolar surveys. Abundance estimates have been calculated using each circumpolar dataset: 1978/79-1983/84 (first circumpolar, CPI); 1984/85-1990/91 (second circumpolar, CPII); and 1991/92-present (third circumpolar, CPIII). Although the third circumpolar set is currently incomplete and the estimate is tentative, a noticeable abundance decline from the second (766,000) to the third (268,000) circumpolar surveys using the IWC standard abundance estimation method (Branch and Butterworth, 2001) has raised questions as to whether the decline is true or apparent. Several factors that might affect the apparent abundance change have been identified (IWC, 2002). Butterworth et al. (2001) analysed the effects of a number of these (proportion of like-minke whale sightings, change in area coverage, mean school size estimation methods, efficiency of sighting survey observer and change in survey timing) and concluded that the net effect of those factors increased the third to second survey abundance ratio from 35-40% to 65-75%. However, effects of the observed covariates (i.e. those that affect the detectability of cetaceans) on the Antarctic minke whale abundance estimation parameters were not fully examined. The effect of Beaufort sea state on estimated mean school size and the effective search half-width (ESW) have been shown for fin whales (Balaenoptera physalus) in the North Atlantic (Buckland et al., 1992). Similarly, the sighting rate of common minke whales (B. acutorostrata) decreased as sea state increased in Icelandic waters (Gunnlaugsson, 1991) and the school size of Antarctic minke whales affected the ESW in the 1987/88 Japanese feasibility study (Kasamatsu et al., 1990). Sea state has also been shown to affect the sighting rate of harbour porpoises (Phocoena phocoena) along the coasts of California, Oregon and Washington (Barlow, 1988) and in the Gulf of Maine (Palka, 1996). These results indicated that g(0) could be less than 1 in some circumstances but that the changes could also be a result of changes in detection functions. These covariates require further examination in the context of Antarctic minke whale abundance estimation using the IDCR/SOWER data. Although covariate adjustment methods (e.g. Ramsey et al., 1987; Schweder et al., 1997; Beavers and Ramsey, 1998) have been developed to account for the influence of observed covariates in line transect surveys, it is sensible to examine the effects of the individual factors in order to better understand how they affect the sightings of Antarctic minke whales in order to develop appropriate models.

The purpose of this qualitative analysis is to see if the observed covariates affect the ESW, the sighting forward (or radial) distance (f) and the mean school size (E(s)) which are important parameters in estimating Antarctic minke whale abundance. Although f is not directly used as a parameter to estimate the abundance in the standard methods (e.g. Branch and Butterworth, 2001), it is treated as a covariate in the detection function in the spatial hazard probability model (Schweder, 1999). Therefore it is also important to consider the effects of observed covariates on f. The observed covariates chosen were: school size, sighting cue, sighting latitude and sea state (Beaufort scale). The underlying hypothesis is that f, ESW and E(s) change along observed covariate gradients.

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MATERIALS AND METHODS

Data

General

Primary sightings data of Antarctic minke whales south of 60°S from 1985/86 to 1998/99 were used. Data stored in DESS Version 3.1 (Strindberg and Burt, 2000) were extracted for this analysis. The geographical distributions of minke whale sighting positions are shown in Figs 1-3.

Partition of second and third circumpolar surveys

To examine differences between the CPII and CPIII sets, data were pooled into each circumpolar set. Data from 1985/86-1990/91 and 1991/92-1998/99 were treated as CPII and CPIII, respectively. Since no independent observer mode (IO mode) surveying (see 'Survey mode' section for details) was conducted during CPI, it has not been included in this analysis.



Fig. 1. Primary sighting positions of Antarctic minke whales in CPII (black circle) and CPIII (grey circle).



Fig. 2. Primary sighting positions of Antarctic minke whales in CPII. Black circles: single animal schools; grey circles: schools of more than one animal.



Fig. 3. Primary sighting positions of Antarctic minke whales in CPIII. Black circles: single animal schools; grey circles: schools of more than one animal.

Antarctic minke whale species code Minke whale species codes listed in Branch and Butterworth (2001) were used.

Survey mode

To see the effect of closing mode and passing mode with IO mode, sighting records were pooled by each survey mode based on the effort codes as described by Branch and Butterworth (2001). In closing mode, two observers were stationed in the top barrel while no observer was stationed on the independent observation platform (IOP). Once a sighting was made, the ship approached the sighting to confirm species and school size. In IO mode, two observers was stationed in the top barrel while an observer was stationed on the IOP. No approach was made to the sightings. A detailed explanation of survey modes is given in Branch and Butterworth (2001).

Separation of South-North stratum

Data were separated into northern and southern strata to examine possible differences between them. Southern strata were set near the ice-edge while northern strata were set north of southern strata. In general, the northern stratum was noted as 'X'N, and the southern stratum was noted as 'X'S, (where 'X' is replaced by either 'E' (east) or 'W' (west)). However, there were some exceptions to the above rule as given below (abbreviations are given in Branch and Butterworth, 2001):

- (1) EM (1985/86) was treated as the southern stratum because it was the northern half of the Ross Sea.
- (2) WBAY and EBAY were treated as the southern stratum.
- (3) EM (1986/87) was treated as the northern stratum because the majority of it was the same as the northern part of CPIII (1996/97 and 1997/98).
- (4) BN (1988/89) was treated as the southern stratum because, in this case, the 'N' denoted the northern part of Prydz Bay.
- (5) ESBAY (1989/90) was treated as the southern stratum.
- (6) EN (1991/92) was treated as the southern stratum because it was half of the northern side in the Ross Sea.
- (7) PRYDZ (1989/90) was treated as the southern stratum.

Sighting angle, perpendicular distance and forward distance

'Estimated Perp Distance' and 'Recalculated Angle' recorded in DESS (Strindberg and Burt, 2000) were used. For the sightings width, 'Estimated Perp Distance' was used. 'Estimated Perp Distance' was calculated with bias corrected radial distances and angles. Values of 'Estimated Perp Distance' exceeding 1.5 n.miles were excluded. 'Recalculated Angle' was used for the forward distance calculation, but values above 90 degrees were excluded from the analysis. Angle bias was corrected in 'Recalculated Angle'. f was calculated from 'Recalculated Angle' and 'Estimated Perp Distance' using a trigonometric function. A definition of the sighting width and f is shown in Fig. 4.

School size

'Best estimated school size' values (i.e. estimated visually by the observers) recorded in DESS were used. Only confirmed school size data were used to estimate E(s)because estimates of school size using unconfirmed data may be negatively biased (Butterworth, 1988). To examine



Fig. 4. Definition of sighting radial distance (*r*), perpendicular distance (*w*) and search forward distance (*f*).

the effects of school size on f and ESW, confirmed 'Best estimated school size' results were separated into three groups (1, 2 and 3+ individuals).

Sighting cue

Eight sighting cue codes were used: 1=blow; 2=jump or splash; 3=animal (body); 4=slick or rings; 5=blow and animal simultaneously; 6=colour under water; 7=associated wildlife; 8=other. When all sightings data from CPII and CPIII were combined, proportions of sightings by blow, body and other cues were 54%, 28% and 18%, respectively. To estimate ESW and E(s), a minimum of 15 sightings in each stratified dataset was required, in accordance with the IWC standard abundance estimation procedure (e.g. Branch and Butterworth, 2001). If sighting cues were stratified for the estimation, the number of sightings for cues other than blow and body was smaller than the required samples in some stratified datasets because of the small sample size. Therefore, only sightings of blow and body were used in the analysis. Sighting cue was recorded at the time of first sighting.

Sea state (Beaufort scale)

The Beaufort scale was used to record sea state. In this analysis, Beaufort numbers were separated into three categories (0-2, 3 and 4+) as in Gunnlaugsson and Sigurjónsson (1990). Their categorisation was used to investigate the similarity of the observed covariates between the North Atlantic and Antarctic. Since sea state data were recorded only once per hour and not recorded at the time of sighting, the hourly weather records were used as the weather conditions at the time of sighting. Data recorded during the hour prior to the time of the sighting were used.

Latitudinal separation

Sighting and weather data were latitudinally separated into four groups of three degrees (60-62, 63-65, 66-68 and $69+^{\circ}S$) in order to provide a large enough sample size for each category.

Analysis

Data stratification

Data were stratified by circumpolar survey, by survey mode and by north-south stratum. Sample size in each stratified dataset was maintained at a minimum of 15 sightings in accordance with the IWC standard abundance estimation procedure (e.g. Branch and Butterworth, 2001). Each stratified dataset was given a unique name based on the following rule. Names of datasets used are shown below:

Circumpolar set – Survey mode – Stratum (South or North)

2-CL-N	2-IO-S	3-CL-S
2-IO-N	3-CL-N	3-IO-S
2-CL-S	3-IO-N	

These datasets were further stratified by school size, sighting cue and sea state. The latitudinal stratified dataset was not stratified into South or North strata because northsouth observed covariate differences were already taken into account with respect to latitudinal gradient.

Effective search half-width

The ESWs with school size, sighting cue, latitude and sea state gradients were estimated using a hazard-rate model with no adjustment term. Truncation distance was set at 1.5 n.miles. DISTANCE Version 3.5 (Thomas *et al.*, 1998) was used for the estimation. Z-tests as described in Buckland *et al.* (1993) were carried out to see whether there were statistically significant differences in the estimates along given gradients.

Sighting forward distance

No models which can estimate the effective search forward distance have yet been developed. For this reason, the median value was used to examine changes in f with school size, sighting cue latitude and sea state. As the distribution of f was skewed towards shorter distances and was highly variable (range of CV in each stratified group was 0.5–1.0), using the median instead of the mean was adequate. To test the difference among medians along given gradients, a multi-sampling median test (Zar, 1999) was applied. This test only reveals if all populations have the same median or not, therefore the existence of trends along environmental variables was qualitatively analysed graphically.

School size

Confirmed school size sighted during closing mode was used to estimate the mean school size following Branch and Butterworth (2001). Z-tests as described in Buckland *et al.* (1993) were carried out to see whether there were statistically significant differences in the estimates along given gradients.

RESULTS

Searching forward distance, ESW and E(s) by each observed covariate are shown in Appendix Tables 1-3, respectively.

Effect of school size

The median f increased as school size increased (Appendix Table 1(a), Fig. 5(a)). At least one of the median f values among three school size groups was statistically significant

at the 5% level when the median test was applied to four datasets (2-CL-N, 3-CL-N, 2-CL-S and 3-CL-S). Combined with graphical analysis, results of the median test suggested a decreasing trend in f as school size decreased from more than three individuals to one individual. There was no notable difference between CPII and CPIII. ESWs also decreased as school sizes decreased (Appendix Table 2(a), Fig. 5(b)). ESWs in CPIII were wider than those in CPII. The ESWs were statistically significant at 5% levels for the Z-test in all pairs, except between single and two animal schools in 2-CL-N.



Fig. 5. Changes in: (a) search forward distance (*f*) and (b) effective search half-width (ESW) with school size. Only confirmed school size data were used.

Effect of sighting cue

The median f values where the initial sighting cue was body were shorter than those for blow in all eight datasets (Appendix Table 1(b), Fig. 6(a)). The differences were statistically significant at 5% levels using the median test for all datasets. There was no significant difference between CPII and CPIII. The ESWs of sightings by body were also narrower than those of sightings by blow (Appendix Table





Fig. 6. Changes in: (a) search forward distance (*f*), (b) effective search half-width (ESW) and (c) mean school size (E(*s*)) with different initial sighting cues (blow and body).

2(b), Fig. 6(b)). The ESW in CPIII was wider than that of CPII. The E(s) values for sightings where the initial cue was body were smaller than those for blow (Appendix Table 3(a), Fig. 6(c)). E(s) values in CPIII were smaller than those in CPII. The proportions of single animals for which body was the initial cue were also higher (Fig. 7).

Effect of sighting latitude

The median f values decreased with decreasing latitude (Appendix Table 1(c)). The effects were large for 60-62°S in CPIII. Most of the f values for CPIII were less than for CPII. The ESWs were narrowest for 60-62°S except 3-IO (Appendix Table 2(c)). Mean school size decreased with decreasing latitude in CPIII (Appendix Table 3(b)). ESWs in CPIII were wider than those in CPII in most cases. Mean school sizes were lower for CPIII than CPII. Fig. 8 shows the school size composition by latitude. The proportion of single animal schools was higher in the northern latitudes in CPIII, while no apparent change in proportion was observed

in CPII. Proportions of sightings with body as the initial cue were higher in the northern latitudes in CPIII, whereas in CPII proportions with blow as the initial cue were high regardless of latitude (Fig. 9).

Effect of sea state (Beaufort scale)

No consistent trend in f values was observed along the sea state gradient when all school sizes were used in the estimation (Appendix Table 1(d)). However, decreasing trends with increasing sea state were observed in the 3-CL-N and 3-IO-N datasets, if only single animal schools were used (Appendix Table 1(e), Fig. 10(a)). At least one of the variables was statistically significant at the 5% level in each circumpolar dataset when the median test was applied. The ESWs also showed decreasing trends with increasing sea state in these two datasets (Appendix Table 2(e), Fig. 10(b)). ESWs in CPIII were wider than those in CPII in most of cases. E(s) values in CPIII were smaller than those in CPII.





Fig. 7. School sizes by sighting cue for (a) the northern stratum and (b) the southern stratum. Numbers in bars denote actual numbers of sighted schools.



□1 individual ■2 individuals ■3+ individuals

Fig. 8. Changes in school sizes along latitudinal gradients for (a) CPII and (b) CPIII. Numbers in bars denote actual numbers of sighted schools. Note that sightings in Area II accounted for 68% (77 out of 114) for 60-62°S in CPII.



Fig. 9. Changes in type of sighting cue along latitudinal gradients for (a) CPII and (b) CPIII.



Fig. 10. Changes in: (a) search forward distance (f) and (b) effective search half-width (ESW) with sea state for single animal schools.

DISCUSSION

Effect of school size

The survey effort in the northern strata during CPIII was 30-50% greater than for CPII because the survey area was extended to the north (Matsuoka et al., 2003). Proportions of smaller (1 and 2 animal) schools increased as the latitude moved to 60°S in CPIII. This concurs with JARPA data findings (Fujise et al., 1999) that small immature male Antarctic minke whales with small school sizes prevailed in the northern part of the survey area. For these small schools, the initial cue was usually the body as is also found with common minke whales in the North Atlantic¹ (e.g. Gunnlaugsson and Sigurjónsson, 1990). Such small schools are more difficult to see than large schools (with blow the initial cue); the sighting ranges (f and ESW) are greatly reduced. The median f values for single animals, pairs and 3+ schools were in the ranges of 0.47-0.74, 0.49-1.13 and 1.2-1.57 n.miles, respectively. The maximum blow interval of Antarctic minke whales was estimated at 7.33 minutes by Joyce (1982), within which time a survey vessel would steam around 1.4 n.miles. Since the f values for singles and pairs were less than 1.4 n.miles, some proportion of diving animals is likely to have been missed by observers. Longer diving durations of common minke whales in the North Atlantic (8.33 minutes, Øien et al., 1990; 13.43 minutes, Stockin et al., 2001) have been recorded and studies using telemetry show that some surfacings may be missed e.g. (Joyce et al., 1990) emphasising that the probability of missing animals cannot be ignored. Smaller f values may also result in shorter confirmation times (see 'like-minke consideration' below). Average Antarctic minke whale blow intervals for 1 animal, 2-5 animals, 6-20 animals and more than 20 animal schools within the sighting range of 0.25-0.5 n.miles were reported as 1.50, 0.43, 0.15 and 0.11 minutes, respectively by Joyce (1982). Given the difficulty in seeing animals that are not blowing visibly, the reported surfacing rates for small group sizes sighted by body would be even lower than the blow interval studies suggest. The surfacing rates of small groups, especially in the northern stratum, should thus be measured in future and interactions between

¹ In the North Atlantic, common minke whale blows are rarely visible.

surfacing rate and f should be examined using a surfacing based abundance estimation model such as that of Cooke (1997).

Effect of sighting latitude

Even though changes in the abundance estimation parameters by latitude elucidated the differences in northsouth observed covariates at the first attempt, there are some difficulties in interpreting the results because topographical heterogeneities along latitudinal lines (e.g. the extension of the Antarctic Peninsula) exist at the circumpolar level. Changes in the abundance estimation parameters by the distance from the ice-edge could be more informative since they may eliminate topographic variation effects.

'Like-minke' consideration

Even if schools of potential minke whales are sighted once, some proportion of them may not be resighted at all, if confirmation time is short (see above). As a result, those sightings will be recorded as 'like-minke' rather than minke.

Effect of sea state

Bad weather conditions generally prevailed in the northern stratum in CPIII as described in the recent cruise reports (e.g. Ensor *et al.*, 2001). The higher the sea state, the smaller the sighting range of single animal schools. Poor weather makes the sighting of small schools (which predominate in the north) even more difficult. This was confirmed in the North Atlantic where the sighting rate of minke whales decreased as sea state increased (Gunnlaugsson and Sigurjónsson, 1990).

Recommendations

General trends in f, ESW and E(s) along the observed covariate gradients were identified in the circumpolar datasets in this analysis. However, regional and temporal effects must be considered when corrections of g(0) are made. The observed covariates examined in this paper should be incorporated using covariate adjustment methods (e.g. Beavers and Ramsey, 1998; Ramsey *et al.*, 1987; Schweder *et al.*, 1997) to adjust for their influence in the IDCR-SOWER Antarctic minke whale abundance estimates. In addition, the effect of distance from the iceedge and the proportions of like-minke sightings should also be considered in future analyses.

In CPIII, mean school sizes were smaller than those in CPII in most cases, suggesting that g(0) in CPIII may be smaller than in CPII. If this effect is considered, the CPIII/CPII abundance ratio for closing mode would increase by some 15% assuming a strip half-width of 0.2 n.miles and g(0)=0.3 for single animal schools (Butterworth *et al.*, 2003). Wider ESW in CPIII may also be linked to E(s) changes. A change in school size between CPII and CPIII is a possibility, but it is difficult to tell whether the change is apparent or absolute. Possible causes of change such as modifications to the survey design and biotic and abiotic environmental factors should be considered further.

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Appendix Table 1

Medians of searching forward distances (*f*) by: school size; sighting cue; latitude; Beaufort number (include all school sizes); and Beaufort number (single animal schools only).

	2-CL-N				3-CL-N			2-CL-S			3-CL-S		
(a) School size (individual)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
1 2 3+	105 39 113	0.47 0.49 1.41	100.00 100.00 64.47	59 28 23	0.45 0.85 1.2	93.75 71.59 58.82	227 165 323	0.63 0.99 1.37	94.2 82.8 62.7	175 108 144	0.74 1.13 1.57	75.9 60.8 56.3	
		2-CI	L-N		3-CL-	N		2-IO-N			3-IO-N		
(b) Sighting cue	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
Blow Body	157 87	1.39 0.4	61.07 98.39	64 42	1.12 0.58	50.43 72.88	242 87	1.36 0.36	56.55 81.82	77 91	1.2 0.49	53.60 83.08	
(b) Sighting que		Z-CI Median	5 	n	J-CL-	-S CV		Z-10-5	CV	3-10-8			
(b) Signing cue	11 550		CV (5.10			57.00			50.04		1.20	51.66	
Blow	558 227	1.3 0.69	65.10 88.64	274 173	1.4 0.76	57.69 73.03	810 364	0.92	58.94 75.49	409 318	1.38 0.82	51.66 71.88	
		2-0	ĽL		3-CL	-		2-IO			3-IO		
(c) Latitude (degrees south)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
60-62 63-65 66-68 69+	135 477 212 405	0.89 1.06 0.98 1.07	84.62 77.31 78.07 74.62	47 173 252 188	0.58 0.92 1.04 1.24	88.46 72.73 71.17 66.42	196 441 520 666	0.96 1.03 1.02 1.23 2 IO N	67.89 72.41 70.09 66.91	83 331 448 284	0.68 1 1.08 1.05	75.61 69.44 65.83 65.22	
(d) Beaufort number (all school sizes)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
0-2 3 4+	72 101 126	1.05 0.76 0.88 2-CI	82.03 89.36 78.50 L-S	43 33 69	0.78 0.39 0.79 3-CL-	59.78 101.61 73.33	69 214 160	0.89 1.08 0.82 2-IO-S	70.19 74.02 71.43	59 92 72	0.99 0.72 0.64 3-IO-S	62.38 78.41 85.90	
(d) Beaufort number (all school sizes)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
0-2 3 4+	234 317 382	1.28 1.04 0.99 2-CI	68.09 81.40 72.81 N	215 146 158	1.14 1.15 1.08 3-CL-	72.31 65.04 69.49 N	532 369 486	1.28 1.04 1.03 2-IO-N	68.53 68.91 65.83	349 281 297	1.06 1.1 1 3-IO-N	63.48 63.20 69.83	
(e) Beaufort number (single animal school)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
0-2 3 4+	26 48 62	0.54 0.47 0.58 2-CI	86.59 97.30 93.67 2-S	26 21 41	0.89 0.29 0.61 3-CL-	51.49 105.13 84.93	45 126 105	0.76 0.98 0.98 2-IO-S	69.57 64.49 64.49	40 58 56	0.85 0.48 0.55 3-IO-S	61.62 88.00 85.29	
(e) Beaufort number (single animal school)	n	Median	CV	n	Median	CV	n	Median	CV	n	Median	CV	
0-2 3 4+	92 98 171	1.03 0.86 0.65	75.96 80.61 87.78	99 61 81	0.88 0.98 0.74	72.63 73.53 75.56	292 201 331	1.04 0.91 0.94	62.07 66.33 63.11	189 162 178	0.99 0.9 0.76	67.96 71.43 69.23	

Appendix Table 2

Effective search half-width (ESW) by: school size; sighting cue; latitude; Beaufort (include all school sizes); and Beaufort (single animal school only).

2-CL-N 3-CL-N 2-CL-S 3-CL-S ESW CV ESW CV CV CV (a) School size (individual) ESW ESW n n n n 105 0.30 17.15 59 0.28 21.60 227 0.36 9.21 175 0.42 11.93 1 2 28 0.45 108 0.80 11.95 0.12 140.53 0.88 7.81 165 13.60 39 144 3+ 113 0.59 17.67 23 1.14 6.20 323 0.57 9.58 0.83 18.80 2-CL-N 3-CL-N 2-IO-N 3-IO-N CV ESW ESW CV ESW CV(b) Sighting cue ESW CV n n n n 0.91 157 0.72 1.07 5.87 0.69 10.15 21.73 Blow 11.33 64 242 77 Body 87 0.23 21.66 42 0.36 18.25 87 0.33 11.81 91 0.45 14.30 3-CL-S 3-CL-S 2-IO-S 3-IO-S ESW CV ESW CVESW CVESW \mathbf{CV} (b) Sighting cue n n n n Blow 558 0.62 7.10 274 0.89 7.50 810 0.74 5.17 409 0.82 6.03 Body 227 0.40 8.71 173 0.48 12.95 364 0.41 12.12 318 0.53 8.99 3-CL 2-IO 3-IO 2-CL ESW ESW ESW ESW (c) Latitude (degrees south) CV $\mathbf{C}\mathbf{V}$ \mathbf{CV} \mathbf{CV} n n n n 60-62 47 10.15 10.31 135 0.30 20.72 0.38 30.63 196 0.45 83 0.81 63-65 477 0.49 7.94 173 0.59 13.16 441 0.53 9.22 331 0.64 9.60 66-68 13.38 252 0.52 0.64 448 0.54 212 0.36 10.35 520 6.80 13.43 69 +405 0.63 6.43 188 0.61 16.17 666 0.64 6.41 284 0.63 9.19 2-CL-N 3-CL-N 2-IO-N 3-IO-N ESW ESW ESW \mathbf{CV} (d) Beaufort number (all school sizes) ESW CVCVCVn n n n 0-2 72 0.47 43 0.61 18.54 69 0.48 21.49 59 0.90 12.30 21.76 101 0.29 77.91 0.49 92 0.51 3 28.7333 0.17214 11.48 22.62 72 4 +126 0.40 16.19 69 0.49 17.60 160 0.49 12.91 0.53 18.94 2-CL-S 3-CL-S 2-IO-S 3-IO-S ESW (d) Beaufort number (all school sizes) n ESW CV n ESW CVn ESW CV n CV0-2 234 0.55 10.69 215 0.65 10.28 532 0.72 7.86 349 0.66 8.42 281 317 0.46 8.86 15.66 369 0.64 9 29 9.99 3 146 0.65 0.61 4 +382 0.48 9.11 158 0.48 17.79 486 0.54 6.32 297 0.65 7.20 2-CL-N 3-CL-N 2-IO-N 3-IO-N (e) Beaufort number (single animal n ESW CV n ESW \mathbf{CV} n ESW \mathbf{CV} n ESW CV school) 0-2 26 0.45 26.89 26 0.57 17.56 45 0.46 24.79 40 0.87 17.20 3 48 0.32 22.53 21 0.25 36.82 126 0.51 11.70 58 0.47 18.73 4+ 62 0.33 20.52 41 0.30 25.96 105 0.49 15.67 56 0.41 26.52 2-CL-S 3-CL-S 2-IO-S 3-IO-S (e) Beaufort number (single animal ESW CVESW \mathbf{CV} ESW CVESW CVn n n n school) 0-2 92 0.46 14.43 99 0.50 14.19 292 0.55 11.98 189 0.66 12.23 3 98 0.52 10.94 61 0.64 13.16 201 0.55 12.27 162 0.62 8.79 4+ 171 0.39 12.10 0.32 0.53 6.53 178 0.55 81 20.36 331 9.12

Mean school size $(E(s))$ by sighting cue and latitude.													
	2-CL-N				3-CL-N			2-CL-S			3-CL-S		
(a) Sighting cue	n	E(<i>s</i>)	CV	n	E(<i>s</i>)	CV	n	E(s)	CV	n	E(s)	CV	
Blow Body	136 74	3.49 1.80 2-	9.50 8.24 CL	50 29	2.41 1.36 3-	8.73 8.65 ·CL	422 180	3.30 2.13	4.83 5.29	227 139	2.48 1.54	4.94 5.00	
(b) Latitude (degree south)	n	E(<i>s</i>)	CV	n	E(<i>s</i>)	CV							
60-62 63-65 66-68 69+	114 392 166 298	2.59 2.78 2.23 2.79	12.35 4.87 6.32 4.88	36 135 205 157	1.57 1.47 1.77 1.91	11.97 5.31 4.58 5.99							

Appendix Table 3 Mean school size (E(s)) by sighting cue and latitud

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