Three forms of killer whales (*Orcinus orca*) in Antarctic waters

ROBERT L. PITMAN* AND PAUL ENSOR+

Contact e-mail: Robert.Pitman@noaa.gov

ABSTRACT

This paper provides field descriptions and biological observations of three different forms of killer whale (*Orcinus orca*) that occur in Antarctica based on field observations and a review of available photographs. Identifications were based on the relative size and orientation of the white eyepatch and the presence or absence of a dorsal cape. Type A (presumably the nominate form) has a medium-sized eyepatch oriented parallel to the body axis, no dorsal cape, it occurs mainly off-shore in ice-free water, has a circumpolar distribution and apparently preys mainly upon Antarctic minke whales (*Balaenoptera bonaerensis*). Type B also has an eyepatch oriented parallel to the body axis, but the eyepatch is at least twice as large as in Type A, it has a dorsal cape, mainly inhabits inshore waters, regularly occurs in pack-ice, is distributed around the continent and is regularly sighted in the Antarctic Peninsula area. Although it may also prey upon Antarctic minke whales and possibly humpback whales (*Megaptera novaeangliae*), seals seem to be the most important prey item. Type C has a small, forward-slanted eyepatch, a dorsal cape, inhabits inshore waters and lives mainly in the pack-ice; it occurs mostly off East Antarctica, and to date it has been recorded feeding only on Antarctic toothfish (*Dissostichus mawsoni*). Type C appears to be referable to *Orcinus glacialis* as described by Berzin and Vladimirov (1983). Although similar ecological specialisations have been reported for sympatric killer whale populations in the Northeast Pacific (i.e. an inshore mammal-eater, an inshore fish-eater and an offshore form), the extent of morphological divergence, habitat segregation and, perhaps, reproductive isolation, appears to be more pronounced among Antarctic populations. Although under a Biological Species Concept these forms appear to warrant separate species status, it will be important to show that this interpretation is consistent with results of molecular genetic analyses and additional morphological studies.

KEYWORDS: KILLER WHALE; ANTARCTICA; COLOURATION; DISTRIBUTION; TAXONOMY

INTRODUCTION

Killer whales (*Orcinus orca*) are generally considered to constitute a single species with a cosmopolitan distribution in the world ocean (Rice, 1998). However, during the late 1970s, several different groups of researchers independently concluded that, based on differences in morphology, ecology and acoustic repertoire, there were recognisably different forms of killer whales in Antarctica.

Mikhalev *et al.* (1981) used catch data from killer whales taken opportunistically by the Soviet whaling fleet in Antarctica during 18 seasons between 1961/62 and 1978/79, and reported what they thought was sufficient evidence to describe a new species – *Orcinus nanus*. During the following season (1979-80), Soviet whalers specifically targeted killer whales in Antarctica and took 916 (Berzin and Vladimirov, 1983). Based on catch data from that season, Berzin and Vladimirov (1982; 1983) described another new species of killer whale – *Orcinus glacialis*. Although the purported new species in each case was described as a 'dwarf' form (*ca.* 1-1.5m smaller than the nominate form), it is not clear from the descriptions if they were describing the same or different species (Rice, 1998). For example, when fluke sizes of the new forms were compared to *O. orca*, *O. nanus* reportedly had relatively larger flukes (at least in females; Mikhalev *et al.*, 1981), while those of *O. glacialis* were 40% smaller (Berzin and Vladimirov, 1983).

There were some additional problems with the Antarctic killer whale descriptions. Mikhalev *et al.* (1981) provided few descriptive details and did not designate a holotype specimen, making *O. nanus* a *nomen nudum* (IWC, 1982). Berzin and Vladimirov (1983) provided much more descriptive detail and designated a holotype specimen and five paratypes for *O. glacialis*, but their specimens were deposited at the Pacific Research Institute of Fisheries and Oceanography, TINRO, Vladivostok, and apparently all of them have been subsequently discarded (R.L. Brownell, pers. comm.).

Berzin and Vladimirov (1983) cited a number of other biological and morphological features to support their claim for a separate species. According to them, *O. glacialis* lived in the pack-ice (at least during the summer) and fed mainly on fish, while the typical form (*O. orca*) foraged in ice-free waters and preyed mainly upon marine mammals, especially Antarctic minke whales (*Balaenoptera bonaerensis*). Although the nominate form was black and white, the smaller form was often yellowish, which the authors attributed to diatom infestation. Berzin and Vladimirov (1983) also described differences in skull morphology and relative appendage size, and reported that tooth size alone could reliably distinguish adults of the two species, with a tooth from *O. glacialis* being half as long and one quarter the mass of a comparable tooth from *O. orca*.

In the late 1970s, US researchers reported that killer whales inhabiting the pack-ice near McMurdo Sound in the Ross Sea had distinctive colour patterns and vocalisations (Jehl *et al.*, 1980; Thomas *et al.*, 1981; Awbrey *et al.*, 1982; Evans *et al.*, 1982). In addition to a yellowish colouration (also attributed to an 'algal concentration'), the McMurdo whales had a discernable dorsal cape and eyepatches of variable shape and size. Given that the Soviet scientists did not discuss size and shape of the eyepatch or mention the presence of a dorsal cape in their descriptions, and the American scientists did not examine any carcasses, it has not been possible to determine if the McMurdo whales might be the same as either of the species described in the Soviet papers.

More recently, Miyazaki (1992) reported 18 killer whale sightings made during a cetacean survey in the Ross Sea in 1980-81. Although based on estimated body length, dorsal

* *Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA.*
+ *Governors Bay, Lyttelton RD1, New Zealand.*

fin size and colouration (yellow versus white), he speculated that there might be several populations of killer whales in the Ross Sea, but expressed doubt about the validity of *Orcinus glacialis* as a separate species.

To date, the lack of specimen material, coupled with the inadequate descriptions, has left most cetologists skeptical of the evidence for more than one species of killer whale in Antarctica (IWC, 1982; Miyazaki, 1992; Rice, 1998; Dahlheim and Heyning, 1999). In a preliminary effort to clarify the taxonomic status of Antarctic killer whales, this study considers field observations and reviews literature and available photographs. Based on colour patterning, habitat selection and prey preferences, evidence indicates there are at least three field-identifiable forms of killer whales in Antarctica. This paper provides field descriptions of these forms, along with some biological observations and discusses their status relative to the two previously described killer whale species from Antarctica.

METHODS AND RESULTS

Published and unpublished photographs of killer whales from Antarctica (i.e. waters south of 60°S) were reviewed, and records of Antarctic-type killer whales north of 60°S were also compiled. The terminology used for colour pattern elements follows Perrin (1972) and Dahlheim and Heyning (1999).

Three distinct forms of killer whales were identified in Antarctica (Types A, B and C), based mainly on the size and shape of the eyepatch (Fig. 1). The presence of a dorsal cape (Figs 1c and 1f) was also important in identifying two of the types (B and C). Although other morphological characters, such as tooth size, may prove to be more useful for specimens in hand, the features discussed here are mainly relevant to field observers.

Descriptions

The typical form of *O. orca* in Antarctica is relatively large, black and white (rarely with a yellow tinge), and looks like the familiar killer whale seen worldwide (Type A: Figs 1a-b). It is apparently the largest of the Antarctic killer whales with reported lengths of up to 9.0m for males and 7.7m for females (Mikhalev *et al.*, 1981). It lacks a visible dorsal cape and the eyepatch is of medium size, generally oval, with the long axis roughly parallel to the body axis. Although numerous unpublished photos of Type A in

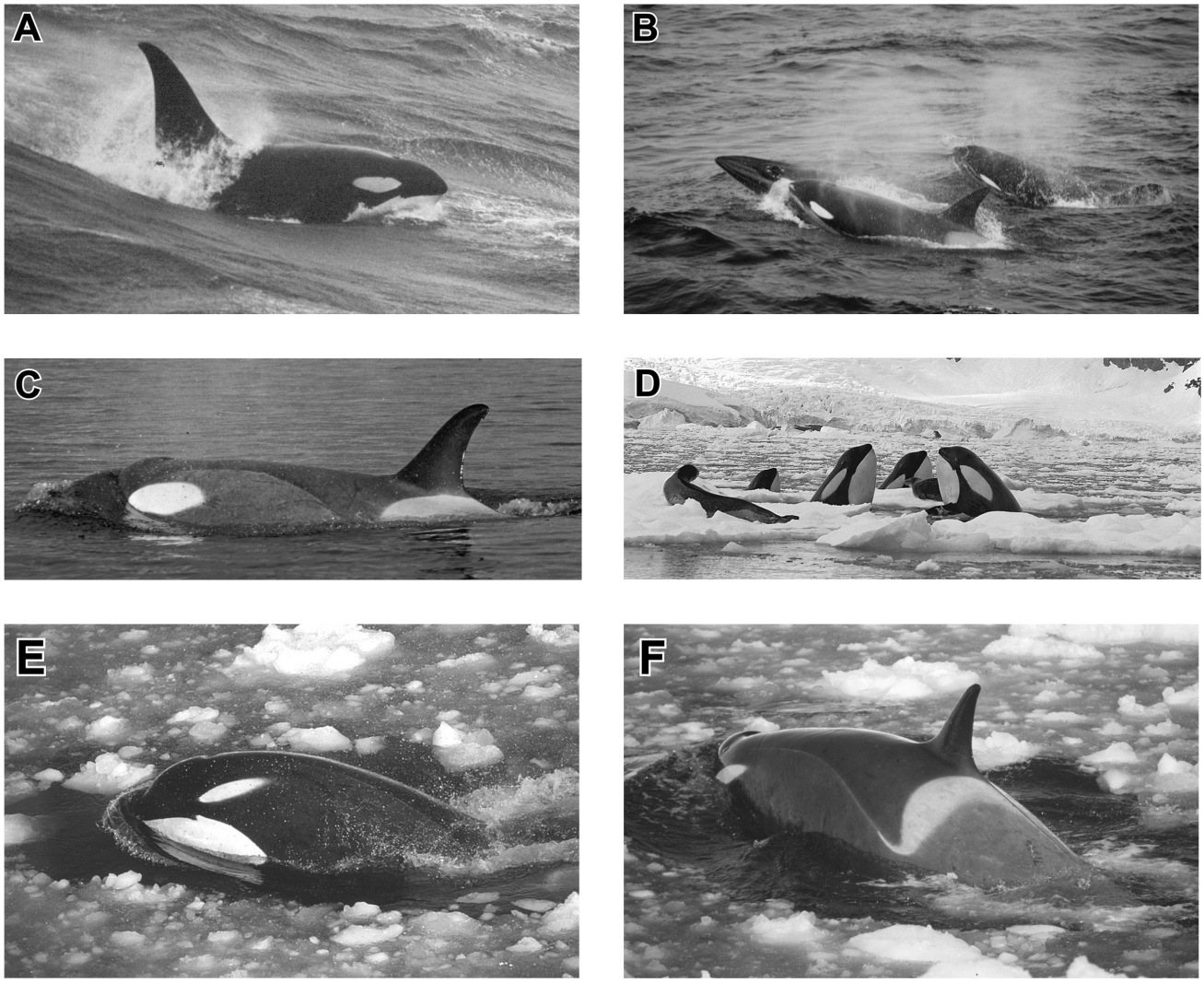

Fig. 1. Three forms of killer whales that occur in Antarctica (see text for description of Types): (a) Type A — showing medium-sized, horizontally-oriented eyepatch and no cape, K. Sekiguchi photo, 2 February 2002, 66°03'S, 150°01'E; (b) Type A — attacking an Antarctic minke whale, R. Rowlett photo, 13 January 1985, 65° 00'S, 117° 00'E; (c) Type B — showing large, horizontally-oriented eyepatch and cape, I. Visser photo, 23 December 2001, 64°54'S, 62°52'W; (d) Type B — spyhopping, next to a leopard seal (left), and a Weddell seal on ice floes, O. Carlsson photo, 14 January 2000, 64°14'S, 64°10'W; (e) Type C — showing small, slanted eyepatch, R. Pitman photo, 20 Jan 2002, 77°39'S, 165°54'E; (f) Type C — showing slanted eyepatch and cape, R. Pitman photo, 20 Jan 2002, 77°39'S, 165°54'E.

Antarctica were found (Table 1), the only published photographs of this type in Antarctic waters were found in Miyazaki (1992, pp.57-58, School No. 4).

The other two forms (Type B: Figs 1c-d; Type C: Figs 1e-f) both have dorsal capes that are visible when lighting conditions are favourable. They are two-toned-gray and white, instead of black and white, often with a strong yellow cast apparently due to a diatom film on the body. In both forms, a dark gray dorsal cape is set off against a medium-gray lateral field. At sea, the dorsal surface of Type A appears as black behind the saddle as it is in front of it, so that the dorsum usually appears all black with a pale saddle. In the caped forms, the paler lateral field merges over the back immediately behind the saddle, making that area noticeably lighter than in front of the saddle (e.g. Dahlheim and Heyning, 1999, p.288; Visser, 1999).

In both of the caped forms, the anterior end of the cape begins at the forward tip of the white eyepatch and arches well above the eyepatch as it passes posteriad (Type B: Fig. 1c; Type C: Fig. 1f). The cape is narrow forward, and widens mid-body as it dips down adjacent to the dorsal fin. Posterior to the dorsal fin, the cape sweeps upward and becomes confluent with the trailing edge of the saddle, so that the saddle appears to be derived from the cape (Fig. 1f). The lower part of the saddle projects forward as a thin taper, sometimes extending far forward as a narrow outline of the cape (Fig. 1f).

Although killer whales in Antarctica have often been reported to be yellowish (e.g. Evans *et al.*, 1982; Berzin and Vladimirov, 1983; Shiriahi, 2002), yellow colouration appears to occur only on the caped forms (Type B: Taylor, 1957; RLP, pers. obs.; Type C: Wu, 2002; RLP, pers. obs.). In addition to colouring the white areas yellow, a heavy concentration of diatoms will cause black areas to appear brown (Shiriahi, 2002; RLP, pers. obs.).

The two caped forms are readily distinguishable in the field. Type B has a very large, white eyepatch (at least twice as large as in Type A), oriented parallel to the body axis (Figs 1c-d). Type C has a much smaller eyepatch than Type B and it angles downward in the front (Figs 1e-f). A useful way to distinguish between the two caped forms is to imagine a line running through the long axis of the eyepatch and compare that to the horizontal black border that runs from the gape to the flipper. In Types A and B, the axis runs more or less parallel to the flipper-to-gape line, but in Type C, the forward end of the patch points down at a *ca*. 45° angle (see Evans *et al.*, 1982; Visser and Mäkeläinen, 2000).

Published photos of Type B killer whales can be found in Taylor (1957, Plate 1, Figs 3-4), Porter (1978, p.77), Smith *et al.* (1981), Bonner (1998, p.132), Miyazaki (1992, p.58, middle right and bottom right; p.59, bottom), Todd (1993, p.161, bottom left), Heimlich-Boran and Heimlich-Boran (1994, p.14), Miyashita *et al.* (1995, p.127), Rowell (1995, p.71), Monteath (1996, p.135), Carwardine *et al.* (1998, p.5), Dahlheim and Heyning (1999, p.288), Lanting *et al.* (1999, p.249), Visser (1999), Stone (2001, p.40) and Shirihai (2002, p.28).

Published photos of Type C killer whales can be found in Evans *et al.* (1982, Fig. 2), Payne and Crawford (1989, Plate 40, Fig. 4), Martin (1990, p.120), Gill and Thiele (1997), Carwardine *et al.* (1998, p.187), Lundgren and Carlsson (2001, pp.23-24), McGonigal and Woodworth (2001, p.273), Nybakken (2001, p.105), Shirihai (2002, pp.333, 336 and 462) and Wu (2002).

Specific data on body lengths of Type B and C animals are not available because it is not known which types were included in the Soviet catch data. It is clear however that at least one, and probably both of these are smaller than Type A killer whales. Mikhalev *et al.* (1981) reported that adult females of 'regular' killer whales (Type A) taken by Soviet whalers reached 7.5-7.8m, but '*Orcinus nanus*' females reached only 6.4-6.5m. Since the latter was taken in high latitudes of Area 1 in Antarctica (120°W-60°W), an area where we found Type B to be common but no Type C (see below), we suspect that Type B could be a dwarf form. Miyazaki (1992) also reported that individuals in their School No. 10-A (Type B) were smaller than individuals in School No. 4 (Type A), and adult males of the former had relatively smaller dorsal fins. The only other information on the relative size of Type B is from Visser (1999) who reported that individuals in a herd she observed in New Zealand were *larger* than the resident killer whales from that area. From our experience in the field, Type B appears smaller than Type A. Berzin and Vladimirov (1983) reported that male '*O. glacialis*' (probably Type C; see Discussion) averaged 112cm shorter than 'white' killer whales (Type A), and that females were 64cm shorter.

Distribution and Movements

Killer whales are known to occur throughout Antarctic waters (Kasamatsu and Joyce, 1995). However, because previous workers did not distinguish between the three forms described here, practically nothing is known about their relative distributions or movements. Possible exceptions to this come from Berzin and Vladimirov (1983), who reported that *O. glacialis* (probably Type C — see Discussion) was commonly encountered from at least 60°E to 141°40'E and might have a circumpolar distribution, and Visser (1999), who reported a 'possible Antarctic killer whale' sighting (Type B, see Table 1) from New Zealand.

It was possible to classify 101 sightings of Antarctic killer whales to type that had at least general location information and 96 that had specific coordinates (Table 1). Fig. 2 shows plots, by type and location, of all the identified sightings compiled (two additional sightings in Table 1, 1 Type B and 1 Type C, occurred north of 40°S and were not included in the plots). Type A killer whales (Fig. 2a, $n = 32$) were circumpolar in Antarctica. An apparent concentration of sightings just west of the Ross Sea is an artefact of a recent cruise there by PE after he was able to correctly identify killer whales to type. Type B (Fig. 2b, $n = 47$) also had a circumpolar distribution but appeared to be especially common in the Antarctic Peninsula area. The apparent concentration of Type B sightings there is due to the many photos available from the numerous cruise ships that regularly visit that area. Type C (Fig. 2c, $n = 17$) may also have a circumpolar distribution but as yet it has not been recorded in the Antarctic Peninsula area; most of the sightings were from East Antarctica, especially the Ross Sea.

There is also relatively little specific information on seasonal movements of these forms in Antarctic waters. Many killer whales apparently leave Antarctica during the austral winter and migrate to lower latitudes (Mikhalev *et al.*, 1981; Kasamatsu and Joyce, 1995), although there has been very little survey work conducted in the Antarctic in the austral winter (Gill and Thiele, 1997). Type A apparently migrates from lower latitudes to Antarctic waters during the austral summer in pursuit of its main prey, Antarctic minke whale, and then moves north again when the minke whales migrate in the autumn (Budylenko, 1981; Mikhalev *et al.*, 1981; Berzin and Vladimirov, 1983; Kasamatsu and Joyce, 1995). To date, there are no verified records of Type A killer whales overwintering in Antarctica.

Table 1

Sightings of three different types of killer whales in Antarctic and adjacent waters (see text for description of Types).

Type	Date	Location	Herd size	Source	Comments
A	16 Jan 1981	64° 33'S, 162° 06'E	14	Miyazaki (1992), p. 57-58, School No. 4	
A	3 Jan 1982	59° 33'S, 44° 10'W	14	R. Rowlett, photo	
A	14 Jan 1983	67° 40'S, 74° 33'W	35	R. Rowlett, photo	
A	23 Jan 1983	69° 03'S, 96° 31'W	?	Photo courtesy R. Reeves	
A	13 Jan 1985	65° 00'S, 117° 00'E	21	R. Rowlett, photo	Attacking a minke whale
A	6 Feb 1986	69° 40'S, 170° 40'W	12	R. Rowlett, photo	
A	5 Jan 1988	62° 34'S, 39° 23'E	18	R. Rowlett, photo	
A	5 Jan 1989	64° 21'S, 62° 38'W	?	F. Todd, photo	
A	27 Dec 1996	63° 16'S, 53° 53'W	15-20	K. Robertson, photo	
A	26 Jan 1998	60° 09'S, 45° 29'E	10	P. Ensor, photo	
A	21 Feb 1999	62° 56'S, 128° 57'E	21	P. Ensor, photo	
A	21 Feb 1999	63° 52'S, 124° 40'E	35?	K. Sekiguchi, video	5 'small, yellow' individuals reportedly in this scattered school
A	8 Feb 2001	71° 21'S, 175° 40'E	14	C. Olavarría, photo	
A	2 Feb 2002	66° 04'S, 150° 01'E	14	K. Sekiguchi, photo	2 groups of 7 animals each
A	26 Dec 2002	64° 12'S, 174° 03'E	10	P. Ensor, pers. obs.	
A	31 Dec 2002	67° 48'S, 178° 34'W	15	P. Ensor, pers. obs.	
A	31 Dec 2002	67° 45'S, 178° 30'W	18	P. Ensor, pers. obs.	
A	31 Dec 2002	67° 44'S, 178° 30'W	?	P. Ensor, pers. obs.	
A	31 Dec 2002	67° 40'S, 178° 27'W	12	P. Ensor, pers. obs.	
A	31 Dec 2002	67° 15'S, 177° 57'W	38	P. Ensor, pers. obs.	
A	6 Jan 2003	61° 23'S, 63° 16'W	5	R. Pitman, pers. obs.	
A	6 Jan 2003	63° 09'S, 61° 50'W	8	R. Pitman, pers. obs.	
A	16 Jan 2003	61° 29'S, 173° 26'W	5	K. Matsuoka, pers. comm.	
A	18 Jan 2003	60° 31'S, 171° 32'E	3	P. Ensor, pers. obs.	
A	24 Jan 2003	63° 18'S, 167° 20'E	8	P. Ensor, pers. obs.	
A	24 Jan 2003	63° 47'S, 167° 42'E	35	P. Ensor, pers. obs.	
A	29 Jan 2003	64° 20'S, 150° 23'E	10	S. Rankin, photo	
A	30 Jan 2003	64° 40'S, 63° 00'W	5	R. Pitman, pers. obs.	
A	12 Feb 2003	62° 10'S, 157° 39'E	3	K. Matsuoka, pers. comm.	
A	16 Feb 2003	67° 14'S, 160° 04'E	1	K. Matsuoka, pers. comm.	
A	16 Feb 2003	67° 40'S, 161° 56'E	9	F. Ugarte, photo	
A	3 Mar 2003	60° 58'S, 53° 46'W	6	R. Pitman, pers. obs.	
B	13-16 Aug 1955	63° 52'S, 58° 08'W	?	Taylor (1957), Plate 1, Figs 3-4	In a polynya in winter
B	Feb 1979	64° 54'S, 62° 52'W	?	D. Larsen, photos, courtesy I. Visser	
B	12 Nov 1979	64° 53'S, 62° 53'W	7	Smith *et al.* (1981)	Apparently took a crabeater seal off an ice floe
B	Jan 1981	51° 41'S, 57° 51'W	?	D. Larsen, photos, courtesy I. Visser	Falkland Islands
B	5 Jan 1981	65° 23'S, 137° 50'E	4	J. Joyce, photo	
B	25 Jan 1981	75° 46'S, 169° 07'E	min. 12	Miyazaki (1992)	
B	28 Jan 1981	63° 51'S, 53° 49'W	?	R. Rowlett, photo	
B	1 Feb 1981	75° 48'S, 168° 36'W	18	Miyazaki (1992), p. 59, bottom	
B	28 Dec 1981	64° 06'S, 54° 04'W	5	J. Joyce, photo	
B	9 Jan 1982	63° 14'S, 37° 23'W	20	R. Rowlett, photo	
B	31 Jan 1982	69° 36'S, 11° 00'W	6	R. Rowlett, photo	In pack-ice
B	Feb 1982	62° 10'S, 58° 24'W	?	F. Todd, photo	
B	15 Dec 1985	65° 12'S, 64° 08'W	4	Heimlich-Boran and Heimlich-Boran (1994), p. 14; M. Webber, pers. comm.	Spy-hopping in pack-ice
B	31 Jan 1987	69° 44'S, 03° 53'W	15	J. Joyce, photo	
B	15 Jan 1988	64° 58'S, 63° 30'W	22	M. Webber, photo	
B	24 Jan 1988	69° 12'S, 01° 54'E	8	K. Matsuoka, photo	
B	7 Jan 1989	63° 52'S, 86° 12'E	2	K. Matsuoka, photo	
B	23 Jan 1990	'off the Antarctic Peninsula'	?	Dahlheim and Heyning (1999), Fig. 3; J. Heyning, pers. comm.	
B	1992	64° 52'S, 62° 53'W	5	Rowell (1995), p.71	
B	?	64° 52'S, 62° 53'W	?	Monteath (1996), p. 135	
B	1 May 1997	35° 09'S, 174° 08'E	8	Visser (1999)	Bay of Islands, New Zealand
B	1 Jan 1999	63° 31'S, 56° 47'W	6	I. Visser, pers. comm.	
B	14 Jan 1999	64° 37'S, 54° 56'E	31	K. Matsuoka, photo	
B	14 Jan 2000	65° 14'S, 64° 10'W	7	O. Carlsson, photo	Spyhopping around a Weddell seal on an ice floe
B	5 Feb 2000	62° 55'S, 61° 42'W	10	R. Pitman, pers. obs.	Travelling alongside 8 Antarctic minke whales
B	11 Feb 2000	63° 41'S, 61° 36'W	5	R. Hucke-Gaete, photo	
B	Jan 2001	63° 18'S, 56° 40'W	10	T. Dennis, photo	
B	15 Feb 2001	63° 37'S, 56° 43'W	5	S. Todd, photo	Chased a crabeater seal that got away; then attacked(?) a Gentoo penguin
B	20 Feb 2001	72° 02'S, 170° 04'E	30	Stone (2001), p. 40 lower; C. Olavarría, pers. comm.	In pack-ice

cont.

Table 1 continued

B	2 Mar 2001	65° 07'S, 64° 02'W	?	M. Pope, video	In pack-ice; tipped a crabeater seal off an ice floe
B	23 Mar 2001	63° 26'S, 61° 12'W	8	Photos courtesy D. Thiele	Followed 3 humpback whales (2 adults; 1 calf)
B	5 April 2001	67° 15'S, 67° 29'W	30	Photos courtesy D. Thiele	
B	19 Dec 2001	74° 25'S, 176° 19'E	3	R. Pitman, pers. obs.	
B	22 Dec 2001	64° 41'S, 62° 38'W	15	I. Visser, photo	
B	23 Dec 2001	64° 54'S, 62° 52'W	12	I. Visser, photo	
B	Feb 2002	63° 35'S, 57° 20'W	12	T. Dennis, photo	In pack-ice
B	Feb/Mar 2002	64° 47'S, 63° 30'W	?	M. Pope, photo	
B	23 Feb 2002	62° 43'S, 59° 50'W	12 (+11?)	Shirihai (2002), p. 28; M. Jorgensen, pers. comm.	1, possibly 2 herds apparently attacking a lone humpback whale
B	29 Dec 2002	64° 41'S, 62° 58'W	15	R. Pitman, pers. obs.	Feeding on a southern elephant seal
B	6 Jan 2003	63° 47'S, 57° 18'W	7	R. Pitman, pers. obs.	
B	6 Jan 2003	64° 09'S, 56° 52'W	12	R. Pitman, pers. obs.	Spy-hopping among loose ice floes
B	6 Jan 2003	64° 18'S, 57° 00'W	6	R. Pitman, pers. obs.	
B	29 Jan 2003	63° 34'S, 56° 22'W	13	R. Pitman, pers. obs.	
B	8 Feb 2003	64° 45'S, 62° 58'W	15	M. Jorgensen, pers. comm.	Attacking humpback calf with cow
B	14 Feb 2003	65° 04'S, 63° 58'W	18	T. Pusser, pers. comm.	Harassing (attacking?) 4 humpback whales
B	16 Feb 2003	67° 20'S, 160° 20'E	5	F. Ugarte, photo	Travelling along pack-ice edge
B	19 Feb 2003	67° 06'S, 66° 34'W	9	R. Pitman, pers. obs.	
B	19 Feb 2003	67° 04'S, 66° 45'W	20	R. Pitman, pers. obs.	
C	Nov-Dec 1973	McMurdo, Ross Sea	?	F. Todd, photo	
C	1975-76	McMurdo Sound	?	Porter (1978)	
C	31 Dec 1980	66° 00'S, 147° 18'E	28	P. Best, photo	In 2 sub-groups
C	3 Jan 1981	66° 32'S, 140° 46'E	150	J. Joyce, photo	
C	6 Jan 1981	65° 04'S, 133° 32'E	50-60	Payne and Crawford (1989), plate 40, fig. 4; P. Best, pers. comm.	In 5 sub-groups; possibly attacking humpback whales
C	30 Jan 1981	73° 50'S, 179° 19'W	78	J. Joyce, photo	At ice-edge
C	2 Feb 1981	76° 18'S, 175° 10'W	13	R. Rowlett, photo	
C	10 Feb 1985	66° 54'S, 70° 28'E	45	R. Rowlett, photo	
C	Jan 1990	69° 37'S, 14° 45'E	?	S. Lundgren, photo	Attacked(?) photographer; see text
C	19-20 Jan 1991	Ross Island, Ross Sea	?	F. Todd, photo	
C	10 Aug 1995	65° 42'S, 139° 56'E	40+	Gill and Thiele (1997)	In pack-ice
C	19 Jan 1999	64° 45'S, 72° 45'E	16	K. Matsuoka, photo	
C	Jan 2000	Off Dry Valleys, Ross Sea	?	F. Todd, photo	
C	Jan 2001	ca 76° 00'S, 26° 34'W	?	British Antarctic Survey, photo	In a lead
C	24 Jan 2001	35° 58'S, 174° 40'E	35-40	I. Visser, photo	In New Zealand
C	23 Dec 2001	76° 05'S, 172° 24'E	55	R. Pitman, pers. obs.	
C	6 Jan 2002	77°38'S, 165°51'E	15-20	J. Cato, photo	In a lead
C	12 Jan 2002	77°36'S, 165°41'E	35	R. Pitman, pers. obs.	In pack-ice
C	16 Jan 2002	77°24'S, 165°01'E	10	R. Pitman, pers. obs.	In pack-ice
C	30 Jan 2002	66°05'S, 141°10'E	75	P. Olson, photo	
C	9 Feb 2002	65°58'S, 141°22'E	30	J. Cotton, photo	

The migratory status of Type B and C killer whales is currently unknown. They could be year-round residents because at least some of the prey that they are known to feed on (see below) are non-migratory. There is at least one winter record of Type B killer whales in Antarctica: Taylor (1957) reported 60 killer whales 'trapped' in a polynya off the Graham Land coast in August 1955 and his photos show at least three Type B whales (Taylor, 1957: Plate 1, figs 3-4; the whales shown in his fig. 7 are of indeterminate type). Two records were found of Type B killer whales north of Antarctic waters that may be indicative of migratory movements; these include a group photographed in the Falkland Islands in February 1979, and a group photographed off New Zealand in May 1997 (Table 1).

The only specific evidence of Type C killer whales overwintering in Antarctica comes from Gill and Thiele (1997), who reported a group of at least 40 killer whales well inside the sea ice, 100km north of the Adelie Land coast in August 1995; their accompanying photograph shows a pair of Type C whales. There is one, possibly two, records of this form occurring north of Antarctic waters: a mass stranding of 17 whales in New Zealand in May 1955 was possibly this type (Baker, 1983; see also Visser and Mäkeläinen, 2000) and a group photographed off New Zealand in January 2001 was clearly this type (Visser, pers. comm.; Table 1).

RLP saw a pair of killer whales (an adult male and a female or sub-adult) each with an obvious cape pattern at 28°31'S, 145°46'W, *ca*. 350km south of Tahiti on 2 March 2001. Although the type (i.e. B or C) could not be verified at the time, it seems likely that at least one of the caped forms ranges into the tropics.

In summary, all three killer whale types occur in Antarctica during the austral summer. Type A apparently migrates to lower latitudes during the winter and there is some indication that Type B could also be migratory. Type B and C whales, but not Type A, have been found wintering in the pack-ice. It may be that the caped forms, because they inhabit the pack-ice and polynyas during the summer, are more likely to become trapped in advancing winter ice and perhaps forced to overwinter, or it could be that either form is normally a year-round resident in Antarctica.

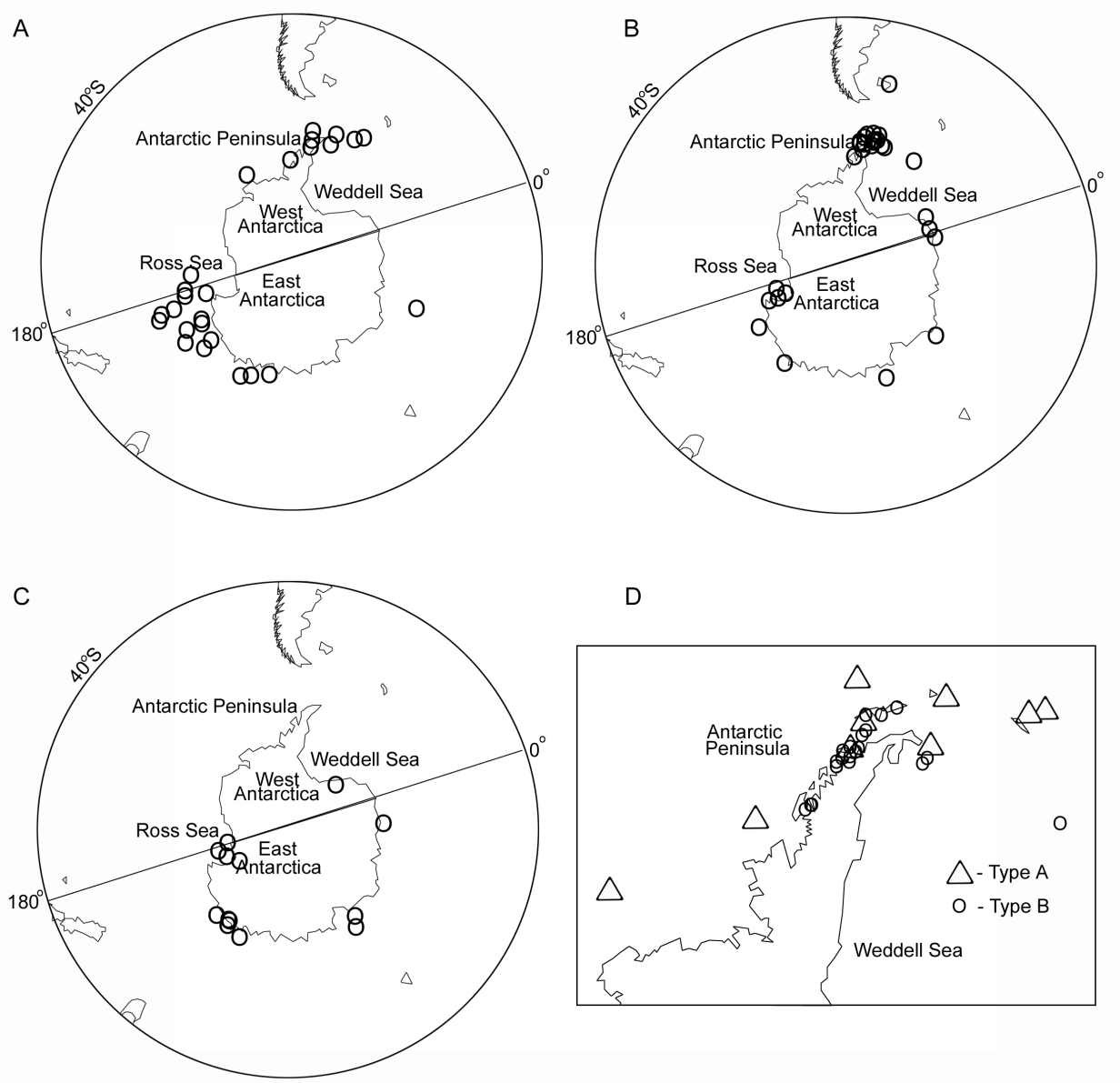

Fig. 2. Sighting locations of three forms of killer whales in Antarctica: (a) Type A; (b) Type B; (c) Type C; (d) Details of habitat preferences of types A and B in Antarctic Peninsula area (see text for description of Types).

Habitat

The observations indicate some clear habitat preferences among the three forms based on the amount of ice present. We found Type A only in open water, as did Berzin and Vladimirov (1983). Type B occasionally occurred in open water but was most often seen travelling among loose sea ice and regularly spyhopping next to individual floes, apparently looking for seals (see below). Fig. 2d shows a more detailed view of killer whale distribution around the Antarctic Peninsula and clearly indicates the preference of Type A for open water and Type B for nearshore habitat. Type C penetrated further into the ice than Type B and regularly occurred in dense pack-ice, along leads in fast ice and in polynyas. This form was often seen spyhopping also, but it appeared to be mostly interested in surveying for open water.

Biological observations

Group size

According to Berzin and Vladimirov (1983), the larger, offshore killer whale (presumably Type A) was usually found in groups of 10-15 animals, while groups of the ice-inhabiting form(s) ranged up to 150-200 animals. (Berzin and Vladimirov did not distinguish between B and C types but they were likely referring to Type C; see below). Ivashin (1981) put the school size of the smaller, yellow form as 'up to 150-300 whales'. Table 1 shows the data compiled on group sizes: Type A had an average group size of 13.6 individuals (range = 1-38; $n = 28$); Type B, 11.8 (range 2-31; $n = 37$) and Type C, 46.1 (range 10-150; $n = 14$).

Feeding

Specific information on prey preferences of Antarctic killer whales is relatively sparse but suggests that dietary specialisation occurs among the three forms, at least in Antarctic waters. Type A apparently feeds mainly on Antarctic minke whales (Berzin and Vladimirov, 1983; Fig. 1a; see also Yukhov *et al.*, 1975). Type B often spyhops among ice floes where seals are hauled out (Fig. 1d) and pinnipeds appear to be an important prey item (Table 1). This is supported by some observations that suggest that Type B killer whales have developed some sophisticated behaviours for taking seals off ice floes. Smith *et al.* (1981) reported on

the hunting behaviour of a pod of killer whales in the Peninsula area and their accompanying photo shows they were Type B. The whales were spyhopping among loose ice when they spotted a crabeater seal (*Lobodon carcinophagus*) on a floe. The whales moved 100m away, then charged at the floe at high speed. They turned abruptly in front of the floe sending a large wave over it that swept the seal into the water. The seal was not seen again and was presumably taken by the whales.

O. Carlsson (pers. comm.) reported that a group of Type B killer whales in the Peninsula area charged an ice floe five times with a Weddell seal (*Leptonychotes weddellii*) on it, washing the seal off with a wave each time. The whales swam off without harming the seal and Carlsson thought it might have been a training session for the two calves that were present. W. Fraser (pers. comm.) observed a different foraging tactic near Palmer Station, Anvers Island (the type of killer whale was not specified but was presumably Type B). The whales approached a leopard seal (*Hydrurga leptonyx*) on an ice floe and an adult male whale tilted up one side of the floe with his head and spilled the seal into the water where the rest of the group were waiting.

Type B may also prey upon whales but clear evidence is lacking (Table 1). RLP observed a pod chasing a group of minke whales, possibly attacking them. Another Type B group closely followed three humpbacks whales (*Megaptera novaeangliae*), including a calf, for 30min, and another group harassed, and probably attacked, a group of four humpbacks. Type B has also been reported attacking Gentoo penguins (*Pygocelis papua*; Table 1), but it is not known to what extent any of these forms feed on penguins in Antarctica.

Type C apparently feeds mainly on fish (Berzin and Vladimirov, 1983) and has been photographed carrying large Antarctic toothfish (*Dissostichus mawsoni*) on at least two occasions (Thomas *et al.*, 1981; Wu, 2002). There are unconfirmed reports that suggest that they may feed on other prey also. Various personnel at McMurdo Station, Ross Sea, have reported that they have seen killer whales attacking both penguins and seals just off the base there on several occasions. Although it is not known which type of killer whales were involved (or even if these were really attacks), Type C is by far the most common form in the McMurdo area and would be the most likely candidate. S. Lundgren (pers. comm.) reported that a killer whale near the Cape Lazarev Ice Shelf lunged out of a lead and pinned him against the ice briefly before sliding back into the water. His photo shows that the whale was a Type C and its behaviour suggests that this form may also take prey (i.e. penguins or seals) off the ice.

DISCUSSION

Based on field observations and a review of available photographs, three distinct forms of killer whales were identified in Antarctic waters (Types A, B and C). Available evidence on colour patterning, group size, body size, habitat, geographical distribution and food habits, suggests that Type A is referable to *O. orca*. Type B has apparently not been specifically noted previously and, to our knowledge, has no taxonomic standing. (Although, based on what is currently known about the distribution of Type B and the collection/sighting localities of '*Orcinus nanus*' [Mikhalev *et al.*, 1981], there is some limited circumstantial evidence to suggest that they might be the same.) Based on the preliminary distribution information, Type C is the most common pagophilic form in the Indian Ocean sector where most of the Soviet Antarctic whaling was conducted during the 1979-80 season, it has a larger average group size than the other two mammal-eating forms, it is known to eat fish and is therefore probably the type that Berzin and Vladimirov (1983) described as *O. glacialis*. Since types B and C are both pack-ice-inhabiting forms that are often coloured yellow, it is possible that specimens of both types were combined in the descriptions of either Mikhalev *et al.* (1981) or Berzin and Vladimirov (1983); this is especially true if (as seems likely) both are confirmed as 'dwarf' forms. These issues will not be resolved until specimens become available, and perhaps not even then.

The three different types of killer whales all appear to have distinct habitat and diet preferences, colour patterning and average group sizes. Clear geographic and habitat segregation was identified with an offshore, circumpolar form (Type A), and two nearshore, pagophilic forms that also appear to have distinct habitat preferences: Type B ranges around the continent in the loose pack-ice but is particularly common in the Antarctic Peninsula area; Type C occurs most of the way around the continent along the edges of the fast ice and in dense pack-ice, but is as yet unrecorded from the Peninsula area.

There is also strong evidence for dietary specialisation among the three types: Type A takes mainly Antarctic minke whales; Type B regularly takes pinnipeds, but perhaps whales and penguins also; Type C appears to prey mainly on fish. Berzin and Vladimirov (1983) reported the stomach contents of 785 killer whales taken by the Soviet fleet in 1979/80, a sample that included 156 'white' (= *O. orca*; Type A) and 629 'yellow' (= *O. glacialis*; Type C?) individuals. The main prey items they found (in frequency of occurrence) were: *O. orca* - 3.2% fish, 89.7% marine mammals, 7.1% squid; *O. glacialis* – 98.5% fish, 0.4% marine mammals, 1.1% squid. Mikhalev *et al.* (1981) also reported relatively infrequent mixing of prey types in Antarctic killer whale stomachs. (Here again, the possible presence of an unrecognised third type of killer whale in either of the two Soviet studies and the fact that the pack-ice forms (B and C) are not always coloured yellow, make the results of those studies difficult to interpret.) A potential implication of dietary specialisation (and perhaps size disparity) among the three forms is an incidence of 'cannibalism' in southern killer whales reported by Shevchenko (1975) that may have been a case of a larger, mammal-eating form (A or B) preying upon a smaller form (B or C).

Most interesting is the apparent evolutionary parallel between the killer whale community of Antarctica and that of the northeastern Pacific. The North Pacific community is also substructured by dietary specialisation, with a nearshore, mammal-eating form (often referred to as 'transients') living in close proximity to a nearshore, fish-eating form ('residents') (Bigg *et al.*, 1987; Baird, 2000). The larger group size of Type C killer whales relative to A and B types is also consistent with the pattern of herd size versus prey preferences found in the Northeast Pacific, where the mammal-eating form typically ranges from 1-7 individuals per herd and the fish-eating form ranges from 5-50 individuals (Bigg *et al.*, 1987). Possible causal links between diet and herd size are discussed by Baird and Whitehead (2000). A third form of killer whale in the North Pacific ('offshores') is rarely encountered in nearshore waters and has unknown prey preferences.

Despite the similarities between these two communities, the different forms of Antarctic killer whales appear to be more divergent from one another than the Northeast Pacific

forms. For example, the Antarctic forms are more distinct morphologically with respect to colour patterning, length and probably other anatomical features, as well as in parameters relating to reproduction (size and age of first reproduction, seasonality, testis size, etc.) (Mikhalev *et al.*, 1981; Berzin and Vladimirov, 1983; this study). We suspect that the presence and differential use of sea ice in Antarctica could have been a major factor in spurring this divergence, by promoting specialised foraging adaptations and contributing to more complete habitat segregation. By contrast, in the Northeast Pacific at least the two nearshore killer whale trophotypes share much of the same habitat (Baird, 2000). As further evidence of reproductive isolation among the Antarctic forms, no mixing of types within herds was found (nor by Berzin and Vladimirov, 1983), nor were any photographs found that clearly showed eyepatches of individual whales that were not unambiguously assignable to type (i.e. no apparent intergrades).

A recent investigation of killer whale genetics found relatively little diversity among killer whales worldwide (Hoelzel *et al.*, 2002), but the only Antarctica sample available for that study was from a single Type A animal (Olavarría, pers. comm.). This study found that there are three morphologically distinct types of killer whales in Antarctica that do not appear to mingle in schools or hybridise, although they have overlapping geographic ranges. This suggests that isolating mechanisms are already in effect and, under a Biological Species Concept (Mayr, 1969), they may each warrant separate species status. Evidence from molecular genetic analyses and additional morphological studies will be important in verifying this interpretation.

Killer whales are common top predators in Antarctica; in order to understand their role in the Antarctic ecosystem it will be necessary to clarify the taxonomic relationships, further identify the ecological traits, and determine the relative abundance of the three forms described here.

ACKNOWLEDGMENTS

The International Whaling Commission and the Institute of Cetacean Research, Tokyo, allowed the authors to use unpublished sightings data from whale survey cruises in Antarctic waters; we thank them for their cooperation. The National Science Foundation (US) allowed the senior author to conduct an important part of this research onboard the US Coast Guard Icebreaker *Polar Star* in Antarctica; Captain Dave MacKenzie (USCG) was especially supportive of our onboard activities. The Abercrombie and Kent Foundation allowed the senior author to conduct research while onboard the cruise ship MS *Explorer*; we thank V. Underwood, T. Dennis and K. Crosbie for use of ship time for this project. This study would not have been possible without the cooperation of many of our colleagues and we are indebted to the following people for providing us with their unpublished photographs and data on Antarctic killer whales: J. Bannister, P. Best, O. Carlsson, J. Cato, J. Cotton, T. Dennis, W. Fraser, D. Hembree, R. Hucke-Gaete, S. Imberti, M. Jorgensen, G. Joyce, D. Larsen, S. Leatherwood, S. Lundgren, F. Marques, J. Mastro, K. Matsuoka, C. Olavarría, P. Olson, M. Pope, T. Pusser, S. Rankin, R. Reeves, K. Robertson, R. Rowlett, K. Sekiguchi, D. Thiele, F. Todd, S. Todd, F. Ugarte, I. Visser, M. Webber, R. Williams, N. Wu and the British Antarctic Survey. R. Baird, R. Brownell, J. Heyning, R. LeDuc and W. Perrin improved this paper with their comments. B. Ballenger, K. Clement and J. Wilson assisted with fieldwork; J. Fluty drafted Fig. 2.

REFERENCES

Awbrey, F.T., Thomas, J.A., Evans, W.E. and Leatherwood, S. 1982. Ross Sea killer whale vocalizations: preliminary description and comparison with those of some Northern Hemisphere killer whales. *Rep. int. Whal. Commn* 32:667-70.

Baird, R.W. 2000. The killer whale: Foraging specializations and group hunting. pp. 127-53. *In:* J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (eds.) *Cetacean Societies*. University of Chicago Press, Chicago. 433pp.

Baird, R.W. and Whitehead, H. 2000. Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* 78(12):2096-105.

Baker, A.N. 1983. *Whales and Dolphins of New Zealand and Australia. An Identification Guide*. Victoria University Press, Wellington, NZ. 133pp.

Berzin, A.A. and Vladimirov, V.L. 1982. Novyi vid kosatok iz Antarktiki. *Priroda* 6:31-32. [Translated in 1983 as "A new species of killer whale from the Antarctic" by S. Pearson, National Marine Mammal Laboratory, Seattle, WA].

Berzin, A.A. and Vladimirov, V.L. 1983. Novyi vid kosatki (Cetacea, Delphinidae) iz vod Antarktiki. *Zool. Zh.* 62(2):287-95. [Translated in 1984 as "A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters" by S. Pearson, National Marine Mammal Laboratory, Seattle, WA 98115, USA].

Bigg, M.A., Ellis, G.M., Ford, J.K.B. and Balcomb, K.C. 1987. *Killer Whales: A Study of Their Identification, Geneaology and Natural History in British Columbia and Washington State*. Phantom Press, Nanaimo, British Columbia. 79pp.

Bonner, N. 1998. *Whales of the World*. Blandford Press, London. 192pp.

Budylenko, G.A. 1981. Distribution and some aspects of the biology of killer whales in the South Atlantic. *Rep. int. Whal. Commn* 31:523-5.

Carwardine, M., Hoyt, E., Fordyce, R.E. and Gill, P. 1998. *Whales, Dolphins and Porpoises*. Readers Digest Books, Surrey Hills, NSW, Australia. 288pp.

Dahlheim, M.E. and Heyning, J.E. 1999. Killer whale *Orcinus orca* (Linnaeus, 1758). pp. 281-322. *In:* S.H. Ridgway and R.J. Harrison (eds.) Vol. 6. *Handbook of Marine Mammals*. Academic Press, London. v-xix+486pp.

Evans, W.E., Yablokov, A.V. and Bowles, A.E. 1982. Geographic variation in the color pattern of killer whales (*Orcinus orca*). *Rep. int. Whal. Commn* 32:687-94.

Gill, P.C. and Thiele, D. 1997. A winter sighting of killer whales (*Orcinus orca*) in Antarctic sea ice. *Polar Biol.* 17(5):401-4.

Heimlich-Boran, S.L. and Heimlich-Boran, J.R. 1994. *Killer Whales*. Voyageur Press, Stillwater, Minnesota. 72pp.

Hoelzel, A.R., Natoli, A., Dahlheim, M.E., Olavarría, C., Baird, R.W. and Black, N.A. 2002. Low worldwide genetic diversity in the killer whale (*Orcinus orca*): implications for demographic history. *Proc. R. Soc. Lond. Ser. B.* 269:1467-73.

International Whaling Commission. 1982. Report of the Workshop on the Identity, Structure and Vital Rates of Killer Whale Populations, Cambridge, England, June 23-25 1981. *Rep. int. Whal. Commn* 32:617-31.

Ivashin, M.V. 1981. USSR. Progress report on cetacean research June 1979-May 1980. *Rep. int. Whal. Commn* 31:221-6.

Jehl, J.R., Jr., Evans, W.E., Awbrey, F.T. and Drieschmann, W.S. 1980. Distribution and geographic variation in the killer whale (*Orcinus orca*) populations of the Antarctic and adjacent waters. *Antarct. J. US.* 15:161-3.

Kasamatsu, F. and Joyce, G.G. 1995. Current status of odontocetes in the Antarctic. *Antarct. Sci.* 7(4):365-79.

Lanting, F., Rowell, G. and Doubilet, D. 1999. *Living Planet*. Crown Publishers, New York. 256pp.

Lundgren, S. and Carlsson, O. 2001. *Antarctica*. Ice is Nice Publishing House, Malmö, Sweden. 95pp.

Martin, A.R. (ed.). 1990. *Whales and Dolphins*. Salamander Books, London, New York. 192pp.

Mayr, E. 1969. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts. 811pp.

McGonigal, D. and Woodworth, L. 2001. *The Complete Story: Antarctica*. Five Mile Press, Victoria, Australia. 608pp.

Mikhalev, Y.A., Ivashin, M.V., Savusin, V.P. and Zelenaya, F.E. 1981. The distribution and biology of killer whales in the Southern Hemisphere. *Rep. int. Whal. Commn* 31:551-66.
Miyashita, T., Kato, H. and Kasuya, T. (eds.). 1995. *Worldwide Map of Cetacean Distribution Based on Japanese Sighting Data*. National Research Institute of Far Seas Fisheries, Shimizu, Japan. 140pp.
Miyazaki, N. 1992. Sightings of killer whales in the Southern Hemisphere. *IBI Reports* 3:47-59.
Monteath, C. 1996. *Antarctica: Beyond the Southern Ocean*. Harper Collins, Sydney, Australia. 160pp.
Nykbakken, J.W. 2001. *Marine Biology*. Benjamin Cummings, San Francisco, California. 496pp.
Payne, A. and Crawford, R. (eds.). 1989. *Oceans of Life (off South Africa)*. Vlaeberg Publishers, Cape Town. xii+380pp.
Perrin, W.F. 1972. Color patterns of Spinner porpoises *Stenella cf. S. longirostris* of the Eastern Pacific and Hawaii with comments on delphinid pigmentation. *Fish. Bull.* 70(3):983-1003.
Porter, E. 1978. *Antarctica*. E.P. Dutton, New York. 168pp.
Rice, D.W. 1998. *Marine Mammals of the World. Systematics and Distribution.* Special Publication No. 4. The Society for Marine Mammology, Lawrence, Kansas. 231pp.
Rowell, G. 1995. *Poles Apart*. University of California Press, Berkeley, California. 183pp.
Shevchenko, V.I. 1975. Karakter vzaimootnoshenii kasatok i drugikh kitoobraznykh. *Morsk Mlekopitayushchie Chast'* 2:173-5. [Translated in 1976 as "The nature of interrelationships between killer whales and other cetaceans" by the Translation Bureau (WRI), St. Anne de Bellevue, Multilingual Services Division, Department of the Secretary of the State of Canada, Translation Series 3839].
Shiriahi, H. 2002. *A Complete Guide to Antarctic Wildlife*. Alula Press, Degerby, Finland. 510pp.
Smith, T.G., Siniff, D.B., Reichle, R. and Stone, S. 1981. Co-ordinated behaviour of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Can. J. Zool.* 59:1185-9.
Stone, G. 2001. Exploring Antarctica's islands of ice. *Natl. Geogr. Mag.* 200:36-51.
Taylor, R.J.F. 1957. An unusual record of three species of whale being restricted to pools in Antarctica sea-ice. *Proc. Zool. Soc. Lond.* 129:325-31.
Thomas, J.A., Leatherwood, S., Evans, W.E., Jehl, J.R., Jr. and Awbrey, F.T. 1981. Ross Sea killer whale distribution, behavior, color pattern and vocalizations. *Antarct. J. US.* 1981 Review:157-58.
Todd, F. 1993. *Antarctic Splendor*. Hancock House Publishers Ltd, British Columbia, Canada. 177pp.
Visser, I.N. 1999. Antarctic orca in New Zealand waters? *NZ J. Mar. Freshwater Res.* 33:515-20.
Visser, I.N. and Mäkeläinen, P. 2000. Variation in eye-patch shape of killer whales (*Orcinus orca*) in New Zealand waters. *Mar. Mammal Sci.* 16:459-69.
Wu, N. 2002. The ice-plungers. *BBC Wildl.* 20:49-57.
Yukhov, V.L., Vinogradova, E.K. and Medvedev, L.P. 1975. Obe'kt pitaniya kosatok (*Orcinus orca* L.) v Antarktike i sopredel'nykh vodakh. *Morsk Mlekopitayushchie Chast'* 2:183-255. [Translated in 1976 as "The diet of killer whales (*Orcinus orca* L.) in Antarctic and adjacent waters" by the Translation Bureau (WRI), St. Anne de Bellevue, Multilingual Services Division, Department of the Secretary of the State of Canada, Translation Series 3844].

Date received: December 2002.
Date accepted: July 2003.