

# Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica

Russel D. Andrews · Robert L. Pitman · Lisa T. Ballance

Received: 27 March 2008 / Revised: 17 June 2008 / Accepted: 17 June 2008 / Published online: 30 July 2008  
© Springer-Verlag 2008

**Abstract** During January/February 2006, we satellite-tracked two different ecotypes of killer whales (*Orcinus orca*) in McMurdo Sound, Ross Sea, Antarctica, using surface-mounted tags attached with sub-dermal darts. A single Type B whale (pinniped prey specialist), tracked for 27 days, traveled an average net distance of  $56.8 \pm 32.8$  km day<sup>-1</sup>, a maximum of 114 km day<sup>-1</sup>, and covered an estimated area of 49,351 km<sup>2</sup>. It spent several days near two large emperor penguin (*Aptenodytes forsteri*) colonies, a potential prey item for this form. By contrast, four Type C killer whales (fish prey specialists) tracked for 7–65 days, traveled an average net distance of  $20 \pm 8.3$  km day<sup>-1</sup>, a maximum of 56 net km day<sup>-1</sup>, and covered an estimated area of only 5,223 km<sup>2</sup>. These movement patterns are consistent with those of killer whale ecotypes in the eastern North Pacific where mammal-eating ‘transients’ travel widely and are less predictable in their movements, and fish-eating ‘residents’ have a more localized distribution and more predictable occurrence, at least during the summer months.

**Keywords** Antarctica · Killer whale · Ecotype · Ross Sea · Satellite tracking

## Introduction

Long-term research on killer whales (*Orcinus orca*) in the Northeast Pacific and Antarctica has revealed that they can comprise populations of up to three sympatric, largely non-interbreeding ecotypes that specialize on different prey types (Ford et al. 1998; Baird 2000; Pitman and Ensor 2003). Furthermore, specific prey preferences among these ecotypes appear to be linked to different foraging habitats and movement patterns (Ford et al. 2000). In the eastern North Pacific, for example, the relationship between feeding and movement patterns has led to three ecotypes being referred to as ‘transients’, a marine mammal-eating form; ‘residents’, a fish-eating form that specializes on salmonids, and ‘offshores’, a less well-known form that spends little time in coastal areas and whose food habits are largely unknown but do include fish (Bigg 1982; Ford et al. 2000; Baird 2000; Jones 2006). All three North Pacific killer whale ecotypes have overlapping geographic ranges (at least during summer), but residents occupy smaller ranges and are more predictably located than either transients or offshores.

Recently, three different killer whale ecotypes were described from Antarctica based on field observations of color pattern differences, apparent prey specialization, habitat and herd size differences (Pitman and Ensor 2003), as well as differences in body length for at least two of the forms (Pitman et al. 2007). The three ecotypes were designated Types A, B and C, and it was suggested that they might represent different species. Type A, apparently the nominate form, lives in open water and preys mainly on Antarctic minke whales (*Balaenoptera bonaerensis*); Type B lives in loose pack ice where it preys mainly on seals (see also Visser et al. 2008), and Type C forages deep in the pack ice and among leads in the fast ice, and fish is its only known prey (see also Krahn et al. 2008).

---

R. D. Andrews (✉)  
University of Alaska Fairbanks School of Fisheries and Ocean Sciences, and the Alaska SeaLife Center, P.O. Box 1329,  
Seward, AK 99664, USA  
e-mail: RussA@alaskasealife.org

R. L. Pitman · L. T. Ballance  
NOAA Fisheries, Southwest Fisheries Science Center,  
8604 La Jolla Shores Dr., La Jolla, CA 92037, USA

Little is known about either local or seasonal movement patterns of Antarctic killer whales. Current evidence suggests that Type A is probably migratory, moving to Antarctica during the southern summer to prey upon Antarctic minke whales, which also migrate there for the summer, then moving back to lower latitudes during the southern winter (Kasamatsu and Joyce 1995; Mikhalev et al. 1981). Less is known about the movements of the ice-inhabiting types (B and C). Both have been photographed once in New Zealand waters, for example, suggesting they could be migratory (Visser 1999; Pitman and Ensor 2003). Both forms normally forage in the ice, however, so either might be able to live in Antarctic waters year round, and in fact both have been documented there during the winter (Pitman and Ensor 2003).

Types A and B killer whales are circumpolar in Antarctic waters, but Type C has only been reported from eastern Antarctica (Pitman and Ensor 2003). The Type C killer whale appears to be a summer resident in McMurdo Sound in the southern Ross Sea where it is by far the most common form in and around the icebreaker channel (see below). For example, one of us (RLP) saw one or more groups of Type C whales during 17 of 18 helicopter flights out of McMurdo during the 2004–2005 and 2005–2006 seasons. Type B killer whales have been identified in the icebreaker channel only once, but they are sometimes seen in nearshore areas by penguin researchers based on Ross Island (Ballard and Ainley 2005; Ainley personal communication).

During December–February each year, one or two icebreakers are present in McMurdo Sound to break a channel through the fast ice so supply ships can access McMurdo Station. Depending on the amount of ice cover in a given year, the distance through the fast ice between McMurdo Station and open water can range from 20 to over 150 km. Since at least the early 1970s, killer whales have been recorded annually in McMurdo Sound shortly after the ice-breaking has begun. The whales have apparently learned to take advantage of foraging habitat made available when the icebreaker(s) opens up the channel, which allows whales to forage deeper into the fast ice than they could otherwise (Pitman and Ensor 2003).

The occurrence of killer whales in the icebreaker channel and associated leads provides an unparalleled opportunity to approach within a few meters of free-swimming individuals and attach satellite transmitters. Until recently, the only killer whales that have been satellite tracked were individuals that were captured and instrumented on board a ship (Similä et al. 2001). During January–February 2006, we used an air-gun or crossbow to attach satellite tags to the dorsal fin of Type C and Type B killer whales in McMurdo Sound. Here we present our tracking results and describe the movement patterns of Type B and Type C killer whales in the southern Ross Sea, and compare both to analogous transient and resident ecotypes in the eastern North Pacific.

## Materials and methods

Our operations were based out of McMurdo Station, on Ross Island, in the southern Ross Sea, Antarctica (Fig. 1a) from 14 January to 2 February 2006. We located killer whales by flying in a helicopter along the icebreaker channel and leads opened by the icebreaker. When a group was located, we traveled approximately 3–5 km ahead in their direction of travel, landed the helicopter where the lead or channel narrowed, or near an area of open water in the channel, and waited for the whales to swim past us (Fig. 2).

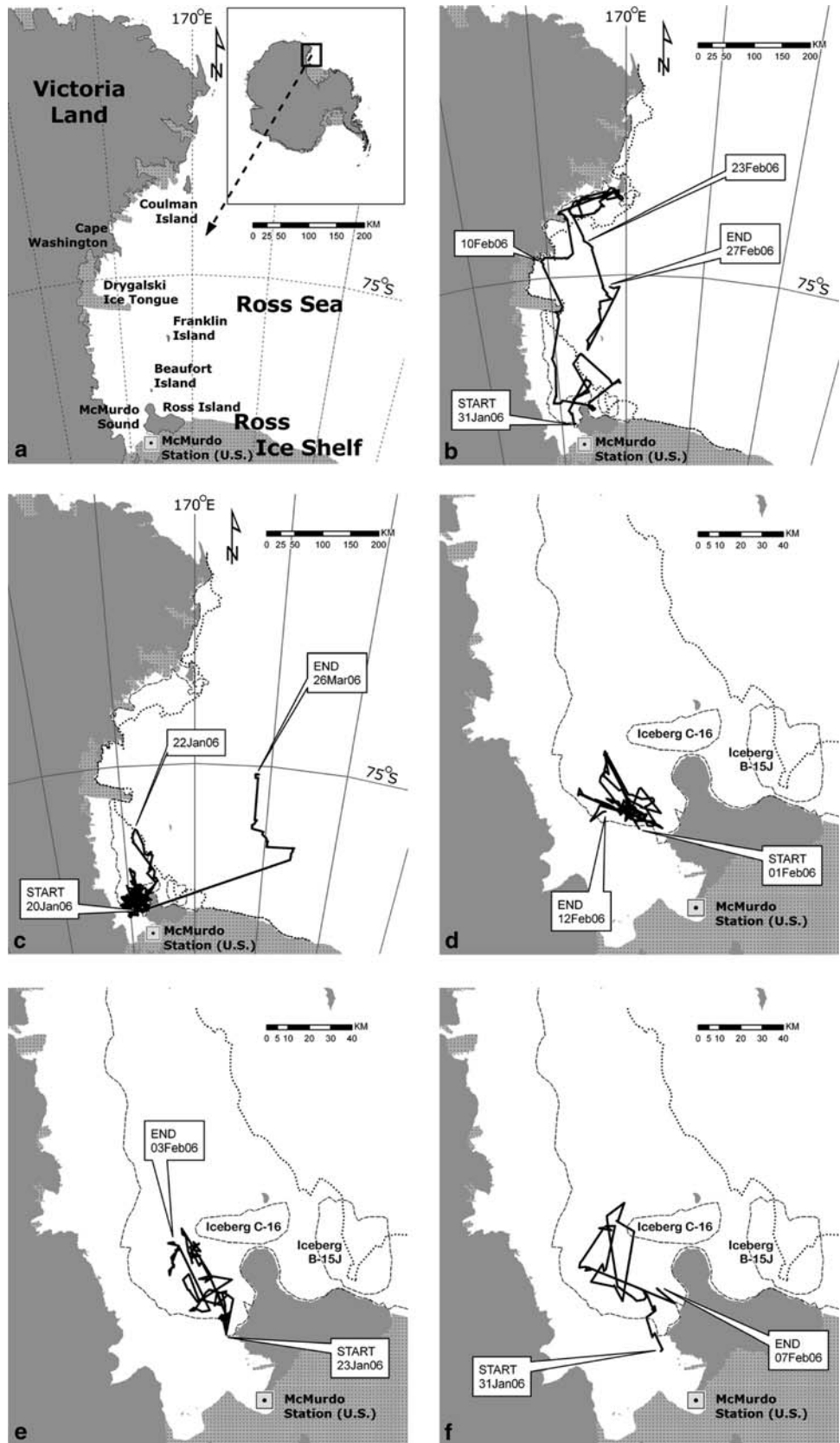
The satellite transmitters were surface-mounted with sub-dermal attachments (Andrews et al. 2005) and were based on the SPOT5 location-only Argos transmitter (Wildlife Computers, Redmond, WA). The transmitter electronics were cast in epoxy (Scotchcast 5, 3 M, Austin, TX) in three different designs that we refer to based upon their shape and whether they were attached with one or two darts: (1) single-dart (tag dimensions: 4.8 cm × 4.8 cm by 1.5 cm tall, 48 g); (2) low profile double-dart (9.0 cm × 3.2 cm by 1.5 cm tall, 56 g); (3) compact double-dart (6.0 cm × 3.5 cm by 2.5 cm tall, 41 g; Fig. 3). All transmitters had an 18.0-cm antenna mounted on the side opposite from the attachment darts. The stainless steel barbed darts were designed to penetrate up to 6.5 cm into the dorsal fin tissue (Fig. 3).

The single-dart and compact double-dart transmitters were remotely attached to the dorsal fin using an adjustable pressure, modified air-gun (Model JP.SP-25, Dan-Inject, Børkop, Denmark). The low profile double-dart transmitter was delivered with a crossbow equipped with a 68.0 kg (150 lb) draw limb, with a 25.4 cm (10 in.) power stroke. The tag antenna was inserted into a hollow aluminum shaft or crossbow bolt. On contact with the dorsal fin, the bolt or shaft fell away and was retrieved by a tether line, leaving the transmitter attached to the dorsal fin. All transmitters were remotely attached by standing on the ice edge and launching the tag as a whale swam by within 1–5 m (Fig. 2).

To conserve power, tag transmissions were limited by a submersion sensor to times when the whales were at the surface, but no more frequently than once per 30 s. The transmitters were also limited to only 200 transmissions per day and only during 00:00 hour–10:00 hours GMT. Transmissions were scheduled to occur daily during January and February, every fifth day in March, April, and May, and every tenth day thereafter. With this duty-cycle the batteries should have provided enough power for 7–12 months of transmissions.

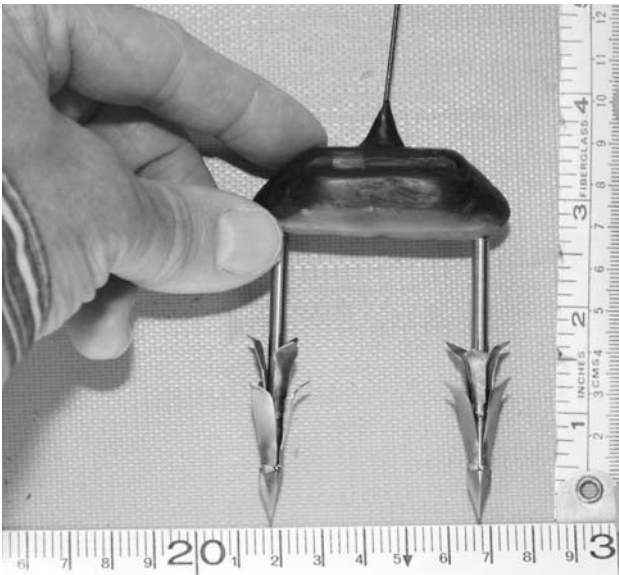
Geographic locations of transmitters were determined by Service Argos (=CLS America) using the Doppler shift created by the satellite passing overhead. We determined the plausibility of each location using the Douglas Argos filter

**Fig. 1** **a** The study area in the western Ross Sea, Antarctica, and satellite tracks of: **b** Type B killer whale # 57558; **c** Type C whale # 57557; **d** Type C, whale # 57556; **e** Type C whale # 47725; **f** Type C whale # 57548, plotted with the margin of the land-fast ice edge on January 20 (dotted line) and February 15 (dashed line). Note that maps **d–f** are zoomed to a larger scale than the others





**Fig. 2** Attaching a satellite tag to a Type B killer whale in a fast ice lead in McMurdo Sound, southern Ross Sea, Antarctica in February 2006



**Fig. 3** The compact double-dart satellite transmitter design that resulted in the longest attachment durations

v.7.03 (Douglas 2007). This filter consists of a systematic algorithm that considers location class (LC), proximity to previous and subsequent locations, rate of movement, and the acuteness of the angle formed by the previous and consecutive locations. We considered locations to be plausible and retained them for analyses if the LC index was 3 or 2 or if the distance to the previous or subsequent location was  $<3$  km. All other locations were removed if the rate of movement between consecutive locations exceeded  $25 \text{ km h}^{-1}$  or the angle formed by the previous and subsequent locations indicated extreme return-movements that we considered characteristic of typical Argos error and not representative of plausible behavior of killer whales (i.e., the farther an individual moves, the less likely

it is to immediately return back to the same vicinity with no intervening location fixes on the outward or return path). Killer whales can travel at over  $30 \text{ km h}^{-1}$  for short periods of up to 15 min (C. Matkin, personal communication), with an estimated maximum sustainable swimming speed of  $20 \text{ km h}^{-1}$  (Guinet et al. 2007); therefore we chose  $25 \text{ km h}^{-1}$  as the upper limit for our purposes.

We calculated the 90% minimum convex polygon (MCP) area that was used or traversed by the whales using the Animal Movement Analysis ArcView Extension (Hooge and Eichenlaub 2000). This was done not to estimate a proper home range, but rather to provide a rough comparison of movement rates, area coverage and habitat use for the different ecotypes. For the Type C whale tagged on 20 January 2006 [whale #57557] we used only the location points from the time of tagging until 06 March 2006, which was when that whale began a directed migration out of McMurdo Sound as the southern Ross Sea began to freeze up (Fig. 1c). Mean and maximum net daily travel distances were calculated for each whale using one location per day, the location with the best Argos location class for that day. The position of the ice edge (Fig. 1b–f) was determined from Ross Sea MODIS images courtesy of the MODIS Rapid Response Project at NASA/Goddard Space Flight Center.

## Results

We tagged three killer whales with compact double-dart transmitters (two Type C whales and one Type B), one Type C whale with a single-dart transmitter, and one Type C with a low-profile double-dart transmitter (Table 1). We observed no visible response to the tag attachment in four of the five tagged whales. The whale tagged with the single-dart tag responded by accelerating slightly in a startle response. We resighted only one of the tagged whales during our study: whale #57556, a Type C, tagged with a compact double-dart transmitter and photographed 9 days after tagging. We examined a high-resolution photograph of the tag taken at a distance of 3 m: after 9 days it appeared that the transmitter had pulled approximately 0.5 cm away from the surface of the fin. No abnormalities of the fin were seen at the attachment site.

The five killer whales we tracked remained within the Ross Sea and transmitted for 7–65 days (Table 1; Fig. 1b–f). All five transmitters performed well, providing on average four good-quality locations (Argos LC1 or better) each day, even though we limited the tags to only 200 transmissions per day.

The two ecotypes had distinctly different movement patterns. Among the Type Cs, whale #57557, tagged on January 20 and tracked for 65 days, traveled north, out of

**Table 1** Deployment and tracking details for killer whales satellite-tagged in McMurdo Sound, Antarctica, January/February 2006

Whale number	Transmitter type <sup>a</sup>	Date deployed 2006	Deployment location	Ecotype (see text)	Age/sex	Number of days tracked	Mean daily travel distance <sup>b</sup>	Maximum km day <sup>-1</sup> traveled
57557	C-dd	20 January	77° 27' S 165° 57' E	C	Ad. male	65	29.6 ± 13.2	55.9
57556	C-dd	23 January	77° 33' S 166° 58' E	C	Ad. male	11	15.5 ± 9.0	30.9
57558	C-dd	31 January	77° 29' S 166° 04' E	B	Ad. female	28	56.8 ± 31.8	114.3
57548	LP-dd	31 January	77° 37' S 166° 00' E	C	Ad. female	7	24.1 ± 9.7	33.7
47725	sd	1 February	77° 29' S 165° 36' E	C	Ad. female	11	11.1 ± 9.7	32.7

<sup>a</sup> *C-dd* compact double-dart, *LP-dd* low profile double-dart, *sd* single-dart

<sup>b</sup> Mean distances are km day<sup>-1</sup> ± SD

the icebreaker channel and then moved approximately 100 km northwestward along the pack ice edge before returning to the tagging site 4.5 days later (Fig. 1c). Subsequently, it and the other three Type C whales remained within a relatively small area in McMurdo Sound. For the last week of January, the Type C whales spent nearly all of their time in the icebreaker channel and adjacent leads and polynyas, but as the ice edge retreated into the southern end of McMurdo Sound they began spending more time near the ice edge. The minimum convex polygon area that included 90% of the location points (MCP 90) for all of the Type C whales from 20 January 2006 to 06 March 2006 was 5,223 km<sup>2</sup>. Sometime between March 6 and 11 (when the transmitter's duty cycle was 1 day on/4 days off), whale #57557 moved out of McMurdo Sound, on an east-northeast heading, then turned and headed north into the central Ross Sea. It ceased transmitting on March 26 at a point 337 km northeast of the McMurdo Sound tagging site. Ice images taken on this last day of transmission show that the whale was within 6 km of the advancing ice edge as the Ross Sea was beginning to freeze over.

In contrast to the relatively localized movements of the Type C whales, the Type B whale moved extensively (Table 1; Fig. 1b) and covered an MCP90 area of 49,351 km<sup>2</sup>. After being tagged on January 31, it moved out of the icebreaker channel and headed northwest of Ross Island, traveling out and around Beaufort Island, before returning to the fast ice edge in McMurdo Sound 1 week later. It then moved north along the land-fast ice edge of the Victoria Land coast towards the Drygalski Ice Tongue. Farther north, it spent about 30 hours around the ice edge just south of Cape Washington. It then spent 10 days crossing back and forth in the waters between Cape Sibbald and Coulman Island, spending considerable time on the southwest side of Coulman Island. On February 13, near Coulman Island, it reached a maximum of 430 km from the tagging site. On February 22, it headed back south again, reaching Franklin Island on February 26, when it turned around and headed back along its path and was 100 km north of Franklin Island in open water when the transmissions ended on February 27.

## Discussion

Reports on reductions in sea ice extent in both the Arctic and Antarctica (Curran et al. 2003) have focused attention on the effect of sea ice changes on the animals that make the ice their home (e.g. Jenouvrier et al. 2006). The recent recognition that two distinctly different forms, possibly even species (LeDuc et al. 2008), of killer whales inhabit the pack ice in Antarctica means that they may be especially vulnerable to changes in sea ice coverage. The extent of that vulnerability will depend on how dependent they are on sea ice for foraging and possibly whether the ice provides protection from predation by the larger offshore Type A ecotype (Shevchenko 1975; Pitman et al. 2007). Tracking local and seasonal movements of these different ecotypes will provide important information on their ability to cope with projected changes in their environment.

Until recently, the only way to monitor the movements of killer whales was through costly and difficult live captures to attach instruments or attempts to follow them in a boat. Such methods would be extremely challenging in the pack ice of Antarctica, so almost nothing has been known about the movements of Antarctic killer whales. With the new attachment methods, reductions in the size of satellite transmitters and easy access to killer whales in the McMurdo icebreaker channel, it is now possible to study the Antarctic pack-ice killer whales in much greater detail.

We propose that these new remotely attached satellite tags are effective tools for studying killer whale behavior, but it was difficult for us to assess the effects of tagging on individual whales during our brief time on the ice. We were able to resight just one of our whales, and only for a few minutes. However, in four out of five whales we did not observe any immediate response to tagging, and the fifth whale showed only a mild startle. There was also no evidence of tagging-site avoidance, or anomalously slow movements post-tagging that might indicate an adverse effect of tagging (Geertsen et al. 2004). Although we agree with assertions that researchers should be wary of the effects of the tag and tagging process on the behavior and movements of cetaceans (Geertsen et al. 2004; Elwen et al.

2006), our observations suggest that the remote attachment method and small surface-mounted transmitters had little effect on the killer whales we tagged.

Despite the limited sample size and tracking durations in this study (maximum of 65 days), we did observe intriguing differences in movements of Types B and C killer whales in the southern Ross Sea during the austral summer. The Type C whales, with the exception of one moderate-length excursion out along the ice edge by one individual, spent late January through February in a relatively small area in McMurdo Sound, moving on average only 20 net km day<sup>-1</sup> compared with the Type B whale, whose mean daily net travel distance was 57 km day<sup>-1</sup> (Table 1; Fig. 1b–f). The MCP90 value for the Type B killer whale was 49,351 km<sup>2</sup>, nearly ten times larger than the area (5,223 km<sup>2</sup>) covered by all four Type C whales combined.

These differences in movement patterns may relate to differences in foraging strategies and/or preferred prey. In McMurdo Sound, Type C killer whales have been observed with Antarctic toothfish (*Dissostichus mawsoni*) in their mouths (Pitman and Ensor 2003). Stomach content descriptions from presumed Type C specimens collected by Russian whalers during the 1970s did not identify fish to species (Berzin and Vladimirov 1983), so Type C killer whales may consume other fish prey. Among potential prey species is the Antarctic silverfish (*Pleuragramma antarcticum*), which constitutes more than 90% of the abundance and biomass of mid-water fish in the Ross Sea shelf area (La Mesa et al. 2004). Krahn et al. (2008) have suggested that Antarctic toothfish are not a major diet item and that a lower-trophic level fish prey such as silverfish or other nototheniids is more consistent with nitrogen-15 stable isotope levels in Type C killer whales. The presence of an abundant prey source such as silverfish in the Ross Sea could explain why Type C whales did not range extensively during late January and February.

In contrast, the Type B killer whale apparently had to range over a much greater area in order to successfully forage. Type B killer whales have been observed attacking Weddell (*Leptonychotes weddellii*), leopard (*Hydrurga leptonyx*), crabeater (*Lobodon carcinophagus*) and southern elephant (*Mirounga leonina*) seals, and possibly minke and humpback (*Megaptera novaeangliae*) whales (Pitman and Ensor 2003). Some Type B whales have even been observed creating waves to wash hauled-out seals off of ice floes (Smith et al. 1981; Visser et al. 2008). There are many Weddell seal rookeries between McMurdo Sound and Coulman Island along the western coast of the Ross Sea, in the area where the Type B whale spent the first half of February. While mature seals can be found in the near-shore fast ice and the pack ice (Stewart et al. 2003), weaned Weddell seal pups can be found all along the loose pack ice of the western Ross Sea during February (Burns et al. 1999;

Stewart et al. 2000), making them vulnerable to killer whale predation.

It may be significant that the tracked Type B whale spent time in the vicinity of Cape Washington and Coulman Island (Fig. 1a, b), sites of the two largest emperor penguin (*Aptenodytes forsteri*) colonies in the world (Barber-Meyer et al. 2008). It is not clear whether killer whales are important predators of penguins, but there have been a number of published reports of killer whales feeding on penguins (Condy et al. 1978; Guinet 1992; Guinet and Bouvier 1995). Type B killer whales have been videotaped on at least two occasions in the Peninsula area of Antarctica chasing gentoo penguins (RLP personal observation), although it is difficult to discern in these cases if they were actually foraging or just harassing the penguins (Ballard and Ainley 2005). More recently, Type B killer whales in Terra Nova Bay, in the western Ross Sea, were observed chasing Adélie penguins (*Pygoscelis adeliae*; Lauriano et al. 2007). Although prey remains were not observed in this case, an adult male surfaced with a penguin in its mouth, which it apparently passed off to an adult female underwater, and the penguin was not seen again after the killer whales dove. Satellite tracking has shown that most adult and juvenile emperor penguins leave the Ross Sea in early summer (Kooyman et al. 1996, 2000), although at least some remain in the area (Lauriano et al. 2007; we also saw some during our operations), and are potential prey items for Type B killer whales.

The difference in movement patterns, travel rates and range sizes we observed between the mammal-eating Type B and the fish-eating Type C killer whales in this study are similar to the differences described for the mammal-eating transients and fish-eating residents of the eastern North Pacific (ENP). Transients travel less predictable routes and cover larger ranges than the sympatric residents (Morton 1990; Baird 2000; Ford et al. 2000). The divergence of these different ecotypes likely evolved independently in Antarctica and the ENP, as genetic sequence data from the mitochondrial control region shows that the Type B mammal-eating whales are more closely related to Type C whales and the fish-eating ENP residents than they are to the mammal-eating ENP transients (LeDuc et al. 2008).

In both hemispheres, it is likely that mammal-eating killer whales have learned to not spend too much time hunting in any one area because their feeding success could decline as their prey adopts more effective anti-predator strategies when faced with frequent predator encounters. Harbor seals can distinguish between the underwater calls of resident and transient killer whales, and they respond strongly to transient calls by leaving the area (Deecke et al. 2002). Therefore, mammal-eating transients are much quieter, making fewer echolocation clicks (Barrett-Lennard et al. 1996) and pulsed calls (Deecke et al. 2005) than fish-eating

residents. Although fish have been shown to respond to the simulated echolocation sounds of their killer whale predators (Wilson and Dill 2002), fish responses are more subtle and their hearing abilities are much less acute than those of marine mammals. Given that the Type B killer whale we tracked in the Ross Sea traveled more widely than the Type C whales, and visual observations confirm that Type B whales rarely spend much time in one area, it appears that the sensitive hearing and anti-predator strategies of marine mammal prey may have shaped the behavior of marine mammal-eating killer whales in both the ENP and Antarctica.

One important difference, however, between the mammal-eating forms is that the Type B whales often take their prey off of ice floes while ENP transients typically attack marine mammals while they are swimming. Killer whale vocalizations made underwater will not travel very far in air, so acoustic stealth might not be so critical for Type B killer whales. To further understand the evolution of the different hunting strategies in killer whale ecotypes we will need more research on Type B whales, including acoustic recordings and an estimate of the proportion of prey that is taken in the water versus off the ice. In any event, it appears that a diet of marine mammal and possibly penguin prey has caused the Type B killer whales to converge on a movement and foraging strategy that is more similar to that of ENP transients than to the partially sympatric Type C whales.

**Acknowledgments** Our research was supported by grants from National Science Foundation (OPP-0338428), National Geographic Society, and US Marine Mammal Commission, was approved by the Alaska SeaLife Center Institutional Animal Care and Use Committee (03-006), and was conducted under NOAA Fisheries Office of Protected Resources permit #782–1719 and Antarctic Conservation Act permit 2004-009 M#2. We thank TJ Moore at SWFSC for GIS support and all those at NSF, Raytheon, and McMurdo Station that made this work possible, especially J Walker and the helicopter pilots and crews of Petroleum Helicopters International. Development of satellite transmitters was funded by grants from NOAA and the US Fish & Wildlife Service to the Alaska SeaLife Center and was dependent upon help from R Hill, T Rupley and others at Wildlife Computers, as well as C Matkin, B Hanson, S Norberg, B Barrie, and V Aderholt. D Ainley provided observations in McMurdo Sound.

## References

- Andrews RD, Mazzuca L, Matkin CO (2005) Satellite tracking of killer whales. In: Loughlin TR, Calkins DG, Atkinson S (eds) Synopsis of Research on Steller Sea Lions: 2001–2005. Alaska SeaLife Center, Seward, pp 238–248
- Baird RW (2000) The killer whale: foraging specializations and group hunting. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies. University of Chicago Press, Chicago, pp 127–153
- Ballard G, Ainley D (2005) Killer whale harassment of Adélie penguins at Ross Island. *Antarct Sci* 17:385–386
- Barber-Meyer SM, Kooyman GL, Ponganis PJ (2008) Trends in western Ross Sea emperor penguin chick abundances and their relationships to climate. *Antarct Sci* 20:3–11
- Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim Behav* 51:553–565
- Berzin AA, Vladimirov VL (1983) A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters [in Russian]. *Zool Zhurnal* 62(2):287–295
- Bigg MA (1982) An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep Int Whal Comm* 32:655–666
- Burns JM, Castellini MA, Testa JW (1999) Movements and diving behaviour of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biol* 21:23–36
- Condy PR, Van Aarde RJ, Bester MN (1978) The seasonal occurrence and behavior of killer whales *Orcinus orca*, at Marion Island. *J Zool Lond* 184:449–464
- Curran MAJ, van Ommen TD, Morgan VI, Phillips KL, Palmer AS (2003) Ice core evidence for Antarctic sea ice decline since the 1950 s. *Science* 302:1203–1206
- Deecke VB, Slater PJ, Ford JKB (2002) Selective habituation shapes acoustic predator recognition in harbour seals. *Nature* 420:171–173
- Deecke VB, Ford JKB, Slater PJB (2005) The vocal behavior of mammal-eating killer whales: communicating with costly calls. *Anim Behav* 69:395–405
- Douglas D (2007) The Douglas Argos-Filter. Accessed 1 October 2007. <http://alaska.usgs.gov/science/biology/spatial/manual.html>
- Elwen S, Meyer MA, Best PB, Kotze PGH, Thornton M, Swanson S (2006) Range and movements of female Heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry. *J Mammal* 87:866–877
- Ford JKB, Ellis GM, Barrett-Lennard L, Morton AB, Palm R, Balcomb KC (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can J Zool* 76:1456–1471
- Ford JKB, Ellis GM, Balcomb KC (2000) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington State. UBC Press, Vancouver
- Geertsen BM, Teilmann RA, Kastelein HNJ, Vlemmix HNJ, Miller LA (2004) Behaviour and physiological effects of transmitter attachments on a captive harbour porpoise (*Phocoena phocoena*). *J Cetacean Res Manag* 6:139–146
- Guinet C (1992) Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. *Can J Zool* 70:1656–1667
- Guinet C, Bouvier J (1995) Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Can J Zool* 73:27–33
- Guinet C, Domenici P, de Stephanis R, Barrett-Lennard L, Ford JKB, Verborgh P (2007) Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. *Mar Ecol Prog Ser* 347:111–119
- Hooge PN, Eichenlaub B (2000) Animal movement extension to Arcview. ver. 2.0. Alaska Science Center, Biological Science Office, US Geological Survey, Anchorage
- Jenouvrier S, Barbraud C, Weimerskirch H (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. *Polar Biol* 29:413–423
- Jones IM (2006) A northeast Pacific offshore killer whale (*Orcinus orca*) feeding on a Pacific halibut (*Hippoglossus stenolepis*). *Mar Mamm Sci* 22:198–200
- Kasamatsu F, Joyce GG (1995) Current status of odontocetes in the Antarctic. *Antarct Sci* 7(4):365–379
- Kooyman GL, Kooyman TG, Horning M, Kooyman CA (1996) Penguin dispersal after fledging. *Nature* 383:397

- Kooyman GL, Hunke EC, Ackley SF, van Dam RP, Robertson G (2000) Moulting of the emperor penguin: travel, location, and habitat selection. *Mar Ecol Prog Ser* 204:269–277
- Krahn MM, Pitman RL, Burrows DG, Herman DP, Pearce RW (2008) Use of chemical tracers to assess diet and persistent organic pollutants in Antarctic Type C killer whales. *Mar Mamm Sci* 24(3):643–663
- La Mesa M, Eastman JT, Vacchi M (2004) The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biol* 27:321–338
- Lauriano G, Fortuna CM, Vacchi M (2007) Observation of killer whale (*Orcinus orca*) possibly eating penguins in Terra Nova Bay, Antarctica. *Antarct Sci* 19:95–96
- LeDuc RG, Robertson KM, Pitman RL (2008) Mitochondrial sequence divergence among Antarctic killer whale ecotypes is consistent with multiple species. *Biol Lett* 4:426–429
- Mikhalev YAM, Ivashin V, Savusin VP, Zelenaya FE (1981) The distribution and biology of killer whales in the Southern Hemisphere. *Rep Int Whal Comm* 31:551–566
- Morton AB (1990) A quantitative comparison of the behaviour of resident and transient forms of the killer whale off the central British Columbia coast. *Rep Int Whal Comm (Spec Issue)* 12:245–248
- Pitman RL, Ensor P (2003) Three forms of killer whales in Antarctic waters. *J Cetacean Res Manag* 5:131–139
- Pitman RL, Perryman WL, LeRoi D, Eilers E (2007) A dwarf form of killer whale in Antarctica. *J Mammal* 88:43–48
- Shevchenko VI (1975) Karakter vzaimootnoshenii kasatok i drugikh kitoobraznykh. *Morsk Mlekopitayushchie Chast' 2*:173–175 [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]
- Similä T, Holst JC, Øien N, Hanson B (2001) Satellite and radiotracking study of movements of killer whales in the wintering grounds of herring in Norway. European Cetacean Society, annual meeting, Rome 5–10.5.2001
- Smith TG, Siniff DB, Reichle R, Stone S (1981) Coordinated behaviour of killer whales, *Orcinus orca*, hunting a crabeater seal, *Lobodon carcinophagus*. *Can J Zool* 59:1185–1189
- Stewart BS, Yochem PK, Gelatt TS, Siniff DB (2000) First-year movements of Weddell seal pups in the western Ross Sea, Antarctica. In: Davison W, Howard-Williams C (eds) Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, pp 71–76
- Stewart BS, Yochem PK, Gelatt TS, Siniff DB (2003) The pack ice niche of Weddell seals in the Ross Sea. In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, Van Der Vies SM, Wolff WJ (eds) Antarctic biology in a global context. Backhuys Publishers, Leiden, pp 224–228
- Visser IN (1999) Antarctic orca in New Zealand waters? *N Z J Mar Freshwater Res* 33:515–520
- Visser IN, Smith TG, Bullock ID, Green GD, Carlsson OGL, Imberti S (2008) Antarctic Peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Mar Mamm Sci* 24:225–234
- Wilson B, Dill LM (2002) Pacific herring respond to simulated odontocete echolocation sounds. *Can J Fish Aquat Sci* 59:542–553